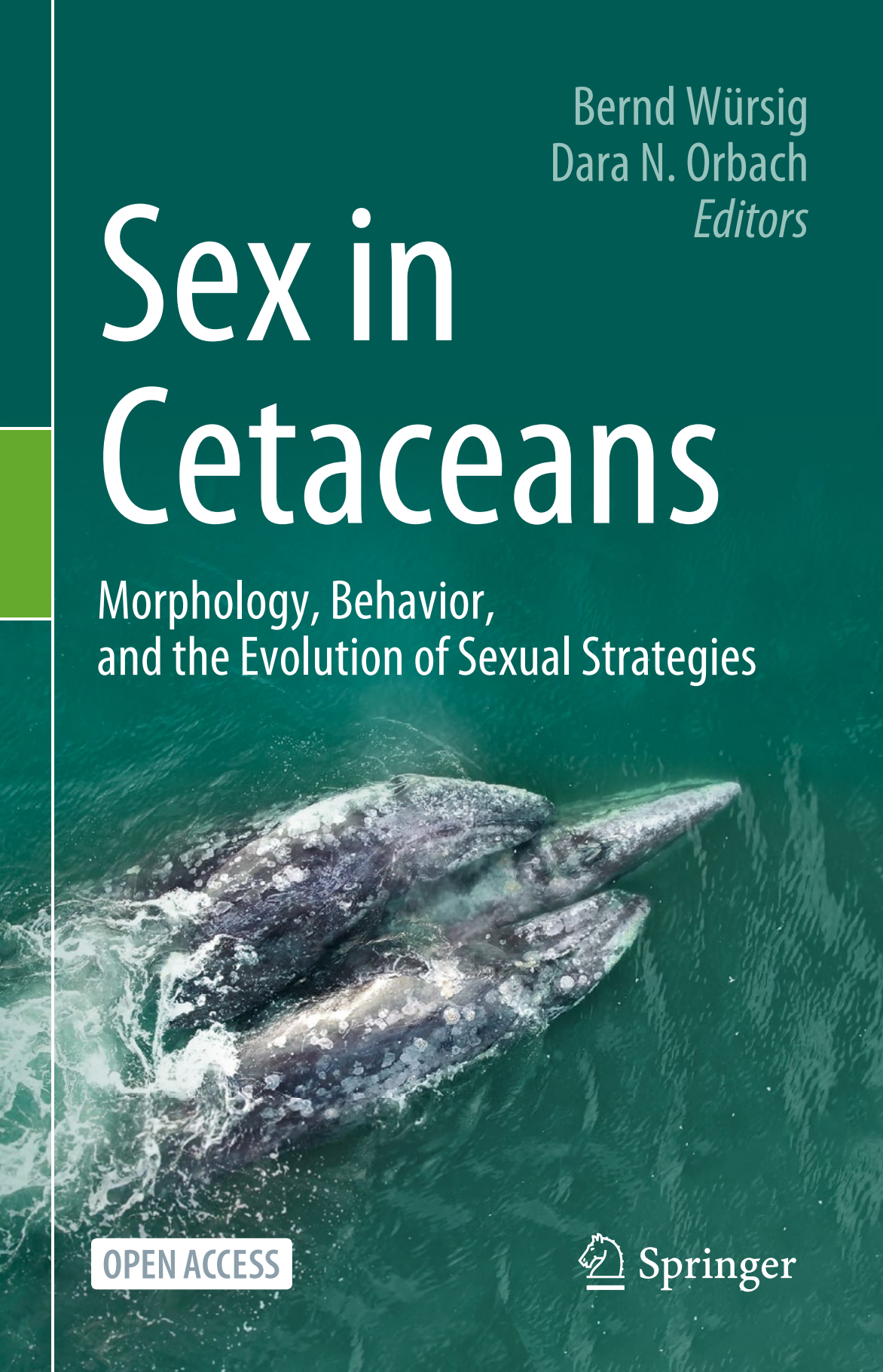Bernd Würsig
Dara N. Orbach

Editors

Sex in Cetaceans

Morphology, Behavior, and the Evolution of Sexual Strategies

Springer

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Cover image: Several species of cetaceans engage in male-male scramble competition for access to a
single female. In gray, bowhead, and right whales, there is often much white water at the surface while
males attempt to position themselves to mate with the female. Accumulating data support female
mate choice and that females make it difficult for all or some males to mate. This image from an
unoccupied aerial vehicle shows two sexually active gray whales "hug" the female in the center. Image
by Fabian Missael Rodríguez-González, with permission.

Preface

When we editors first envisioned this book on cetacean sexual strategies and tactics, we worried that there was not enough known on the subject to produce an in-depth specialty book that spanned the vast cetacean populations and species. After all, mating often occurs beneath the surface of the water out of sight of human observers, with copulation not having been witnessed (or at least not published) for most cetacean species. When we surveyed colleagues, we received back the resounding supportive response: "Do it—It is time!". Sex in Cetaceans: Morphology, Behavior, and the Evolution of Sexual Strategies has demonstrated that there is a wealth of knowledge within the discipline and much work ahead for aspiring cetologists. We hope that this compilation will serve as a foundational tool for academics and non-academics in identifying the knowns and unknowns and shape where the discipline could progress. We point out that sex can be fun or function in learning; thus, not all sexual acts are procreative in nature. Some examples are homosexual mating and copulation among sexually immature animals.

Historically and regardless of species, much research into sexual selection has used a male-centric perspective, with males believed to have active roles and females generally believed to have passive roles in conception. Because cetacean pregnancy is at least 11 and up to 17 months in duration, the minimum interbirth interval is one year and generally much more, the duration of lactation can span 7 years in some species, and paternal care is unconfirmed, females are heavily invested temporally and energetically in their offspring's survival. Selection of "the best" mate who will increase offspring viability via heritable traits is critical and it is unlikely that females mate "promiscuously" without discerning among prospective mates. Yet, it is unclear which traits are "the sexiest" among cetaceans, as the fluid three-dimensional oceanic habitat poses unique constraints and liberties that differ from terrestrial and arboreal environments. Whereas sexual size dimorphism is generally advantageous on land to monopolize a female, adroitness and agility may be favored in the ocean. The ability to survive—perhaps evident from many battle scars indicative of physical combats, attainment of a large body size, or "ornaments" that pose handicaps—may also contribute to a male's "sexiness". As underwater sound travels

faster and with less attenuation than in air, acoustics produced by males may provide females with cues about prospective suitors. A large relative testes-to-body-size ratio—higher in cetaceans compared to terrestrial counterparts likely due to relief of gravitational constraints—and penis length may augment fertilization success during and post-copulation through sperm competition and cryptic female choice. This book explores these ideas, including the post-copulatory aspects of reproduction related to rearing of offspring.

Chapter 1 lays the groundwork of sex and sexual strategies, in general, in mammals, and especially in marine mammals, while Chap. 2 provides a foundation in genetic tool use to explore the consequences of sex. Chapters 3–6 investigate broad evolutionary aspects of sex in cetaceans, including morphologies such as dentition (Chap. 3), hindlimbs (Chap. 4), female reproductive anatomy (Chap. 5), gonads (Chap. 6), and sexual dimorphism (Chap. 6). Chapters 7–11 explore sexual behaviors in nature and captivity (Chap. 9), including non-conceptive mating (Chaps. 7 and 8), infanticide (Chap. 10), and the application of promising drone technology as a novel vantage point for observations (Chap. 11). Chapters 12–19 delve into species-specific morphologies, genetics, and behaviors in toothed whales, including bottlenose dolphins (Chap. 12), Risso's dolphins (Chap. 13), dusky and spinner dolphins (Chap. 14), pilot whales (Chap. 15), killer whales (Chap. 16), beaked whales (Chap. 17), porpoises (Chap. 18), and sperm whales (Chap. 19), with our apology that not all species could be represented. Chapters 20–23 focus on sex in baleen whales, including humpback whales (Chap. 20), right whales (Chaps. 20 and 23), gray whales (Chap. 21), and bowhead whales (Chap. 22). Chapter 24 discusses aspects of sex and sexual strategies that provide important considerations in the health and welfare of individuals, populations, and species of cetaceans. We gave authors much leeway, so the "voice" among chapters may be quite different (e.g., "managed care" vs "captivity"). We did not make moral ("human") judgments when editing the chapters of this compendium, and we believe that the authors did not do so either.

We thank the authors for making this book an up-to-date compendium of concepts in sex and procreation within cetaceans. We thank the >50 reviewers, some anonymous and some acknowledged, who reviewed and provided insightful edits to the 24 chapters. We especially thank Thomas A. Jefferson, who served as guest editor of several chapters of which we editors were co-authors, and who shepherded those manuscripts through the thorough peer-review processes. We thank Éva Lörinczi and Bibhuti Sharma of Springer Nature for selflessly giving good advice and moral encouragement. We also thank our universities, Texas A&M University at Galveston and Texas A&M University-Corpus Christi for generously providing funds to make this compendium open access, with digital versions of all chapters free to all readers.

Submitted with respect, Bernd Würsig and Dara N. Orbach

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Contents

Chapter 1
Sex and Behavior

Bernd Würsig, Jacquline Rich, and Dara N. Orbach

Abstract We provide a conceptual primer for sexual selection and conflict, mating systems, and socio-sexual behaviors and patterns among animals, largely with mammalian and cetacean examples. The important roles of mate choice are discussed (including female choice) and the occasional fluidity of sexual roles. An overview of topics pertinent to sex and behavior is described, including evolutionary drivers (the concept of "why sex after all?") followed by general mammalian and cetacean mating strategies and tactics. We describe mating systems (monogamy, polygyny, polyandry, polygynandry) with the present understanding that most cetaceans do not have monogamous or polyandrous mating systems. The primer includes brief introductions to historical knowledge and highlights emerging areas of research within the field of sex in cetaceans, with context for other chapters of this book. As part of overall sexual behavior, alloparental care, female reproductive senescence, and non-procreative behaviors including homosexual and necrocoital mating are also introduced.

Keywords Female choice · Homosexuality · Mating strategies · Mating systems · Mating tactics · Polygynandry · Polygyny · Reproductive senescence · Sex · Sexual dimorphism · Sexual selection

1.1 Why Sex After All?

Sexual reproduction, as proposed by Darwin (1871), has remained somewhat enigmatic due to several resounding disadvantages to sexual intercourse. In the most common case of a stationary gamete (an egg) and a mobile gamete (a sperm), one-half of female and male genetic materials are united to form a new living progeny. Passing on only one-half of ones' genome is inherently disadvantageous

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if parthenogenesis (one form of asexual reproduction, without sperm) and complete replication of the genome are alternative possibilities (Williams and Mitton 1973). Compared to basal invertebrates and plants, which often have both sexual and asexual reproduction capabilities, it remains unclear why more derived vertebrates generally lack asexual means of reproduction. One hypothesis for this observed pattern is that sexual reproduction has been evolutionarily locked into place for most birds and mammals (Williams 1971). Through sexual reproduction in vertebrates, the possibility exists of passing on at least some autosomal genes that are disadvantageous for the progeny. Additionally, it takes inordinate temporal and energetic investments to find a suitable and reproductively active partner. Once found, there is no assurance that either or both partners are fertile or have compatible gametes. The transmission of diseases from a parent to offspring also looms as a potential detriment of breeding. Thus, why engage in sexual reproduction in spite of all the potential disastrous outcomes?

Sexual reproduction persists due to a number of practical advantages, the most obvious being the production of offspring derived from a female and male that survived to reproduce (Darwin 1871). If the parents survived long enough to breed, then the progeny have inherited genetic materials providing a reasonable chance to also survive to reproduce, given a similar environment, habitat, and ecosystem. Genes may be inherited by offspring that are not immediately needed for survival in the present ecology, but may be useful later on in a different set of habitats or if exposed to particular diseases (Van Valen 1973; Hamilton et al. 1990). Parental genetic material may also provide progeny with an advantage over coevolving species, providing the ability to evolutionarily "outrun" competitors (Van Valen 1973); this hypothesis was expanded by Hamilton (1980) to recognize the advantage sexual reproduction provides to individuals who remain in constant flux with their parasites. Recent evidence on New Zealand snails, *Potamopyrgus antipodarum*, and the crustacean *Daphnia dentifera* illustrate relationships between modes of reproduction and parasite load within two host species and their respective parasites (Gibson et al. 2017, 2018; Gowler et al. 2021).

Due to anisogamy (males produce smaller and less energetically costly gametes than females) and variation in parental investment, the sexes are not reproductively symmetric (Trivers 1972; Maynard Smith 1978; Andersson 1994). In most cases, female reproductive success is limited by resources to invest in parental effort, causing females to distribute themselves relative to resources (Trivers 1972; Emlen and Oring 1977). Unfavorable mate selections have higher fitness costs in females than males; females' gametic energetic input is much higher than males, and in mammals, females have limited opportunities to produce offspring due to the lengths of gestation and lactation. Accordingly, females generally become the "choosy" sex because they cannot increase their fitness potential through excess matings as males can. Excess matings may have a negative impact on female fitness (Maklakov et al. 2005). Increased progeny numbers may reduce maternal investment per offspring and result in a net decrease in offspring survival to sexual maturity. Therefore, females benefit by selecting a high-quality mate.

The operational sex ratio (instantaneous ratio of sexually active males to sexually receptive females; Emlen and Oring 1977) is often male-biased because sperm are energetically "cheap" to produce and more males are available to mate than females. Males can increase their fitness by mating (potentially indiscriminately) with many fertile females. Strong sexual selection driven by intrasexual variation in the reproductive success of males persists in multiple species. Thus, males generally distribute themselves relative to females and invest heavily in mating effort, especially in species where paternity is uncertain (Daly and Wilson 1983). Males may further increase their fitness through their ability to successfully monopolize a female. Depending on female group size, range, and seasonality of breeding, males vary in their abilities to monopolize females, which influences the mating system (Ralls and Mesnick 2019a).

Evidence that males distribute themselves relative to females can be gleaned by comparing social patterns between the sexes. For an example in cetaceans, dolphins generally live in fission-fusion societies, where groups break apart and join together, often on an hourly basis (an early record provided for dusky dolphins, *Lagenorhynchus obscurus*; Würsig and Würsig 1980) or on an inter-day basis (an early record provided for Hawaiian spinner dolphins, *Stenella longirostris*; Norris and Dohl 1980). Females often occur alone, with their calves, or in short-term associations with females in a similar reproductive state (Gibson and Mann 2008; Elliser and Herzing 2013), whereas males may occur in small groups with stable alliances (Connor and Krützen 2015; Brightwell and Gibson 2023, this book). It has been hypothesized that individuals decrease their group size because of strong competition for resources (i.e., Hoare et al. 2004). Accordingly, male and female association patterns are predicted to be similar if resource competition and predation pressure are the only driving forces (Maynard Smith 1978). However, as natural selection and fitness pressures act on cetaceans, males distribute themselves relative to mating opportunities. When females are clustered in space and time, males may exhibit direct female defense. Whereas when females are dispersed, males may monopolize females through leks or by roving (Ralls and Mesnick 2019a).

1.2 Mating Systems

Mating system designations reflect the predominant relationship among individuals in the population. Such relationships can vary seasonally or last throughout an individual's lifetime and can refer to either social or genetic relationships. Mating systems can be broadly defined as monogamous or polygamous. In a monogamous system, one female and one male mate exclusively within at least one estrous cycle, whereas in a polygamous system, individuals mate with more than one partner. Polygamy can be further divided into polygyny (one male mates with multiple females), polyandry (one female mates with multiple males), and polygynandry (multi-mate; females and males mate with multiple partners). The term

"promiscuity" is discouraged as it suggests a randomness to mate selection and no overt mate choice.

Certain biological and social indicators, such as sexual dimorphism, testes size, and sociality, may be used to predict mating systems among cetaceans where matings cannot be easily observed (Ralls and Mesnick 2019a). However, actual mating success can be best-deduced by studying genetically determined offspring (Gerber and Krützen 2023, this book). Sexual dimorphism of skull structures and teeth in ancestral and present-day cetaceans is discussed by Loch et al. (2023, this book), and testes sizes are reviewed by Chivers and Danil (2023, this book), all with implications regarding sexual strategies. In general, characteristics with few differences between sexes tend to broadly indicate either monogamous or multi-mate (polygynandrous) mating systems (Mesnick and Ralls 2018). Many cetaceans are monomorphic (i.e., the sexes do not have greatly disparate body size or shape differences beyond teeth and genitals), and it can be quite difficult to determine the sex of a toothed or baleen whale by external morphology (Jefferson et al. 2015). Figure 1.1 presents images of overt sexually dimorphic external morphologies of males and females for select odontocete species and includes several monomorphic odontocetes as well as one mysicete example (humpback whale, *Megaptera novaeangliae*). In general, adult female baleen whales tend to be larger than similarly aged males, probably because females must be large to effectively produce and nurse large precocial offspring (Mesnick and Ralls 2018).

One obvious potentiality resulting from the general trend of monomorphism among cetaceans is that sight and smell are less important sensory modalities compared to most terrestrial mammals (Tyack 2019). External morphology may not be as important a conveyor of sex and sexual tactics in cetaceans as in many other mammals, although it may be of similar importance especially in dimorphic species. Communication and echolocation (the latter for odontocetes) and other acoustic signals may be of similar importance to cetacean sexual relationships as sight and smell are for most terrestrial mammals (Tyack 2019, for odontocetes). In mysticetes, sexual tactics largely rely on sound (Clark and Garland 2022), although female/male physical adroitness may also be of great importance (Brown and Sironi 2023, this book; Koski et al. 2023, this book; Swartz et al. 2023, this book). The elaborate breeding songs of humpback whales are one such example (Dunlop 2022; Eichenberger et al. 2023, this book).

1.2.1 Monogamy

In monogamous mating systems, one female and one male share a reproductive bond. Females and males tend to be physically monomorphic, and both sexes invest heavily in offspring care until offspring can survive independently. In species with biparental care, social and ecological constraints may preclude males from extra-pair mating. However, extra-pair copulations are common among monogamous pairings (i.e., European pied flycatcher, *Ficedula hypoleuca*; Grinkov et al. 2022), supporting
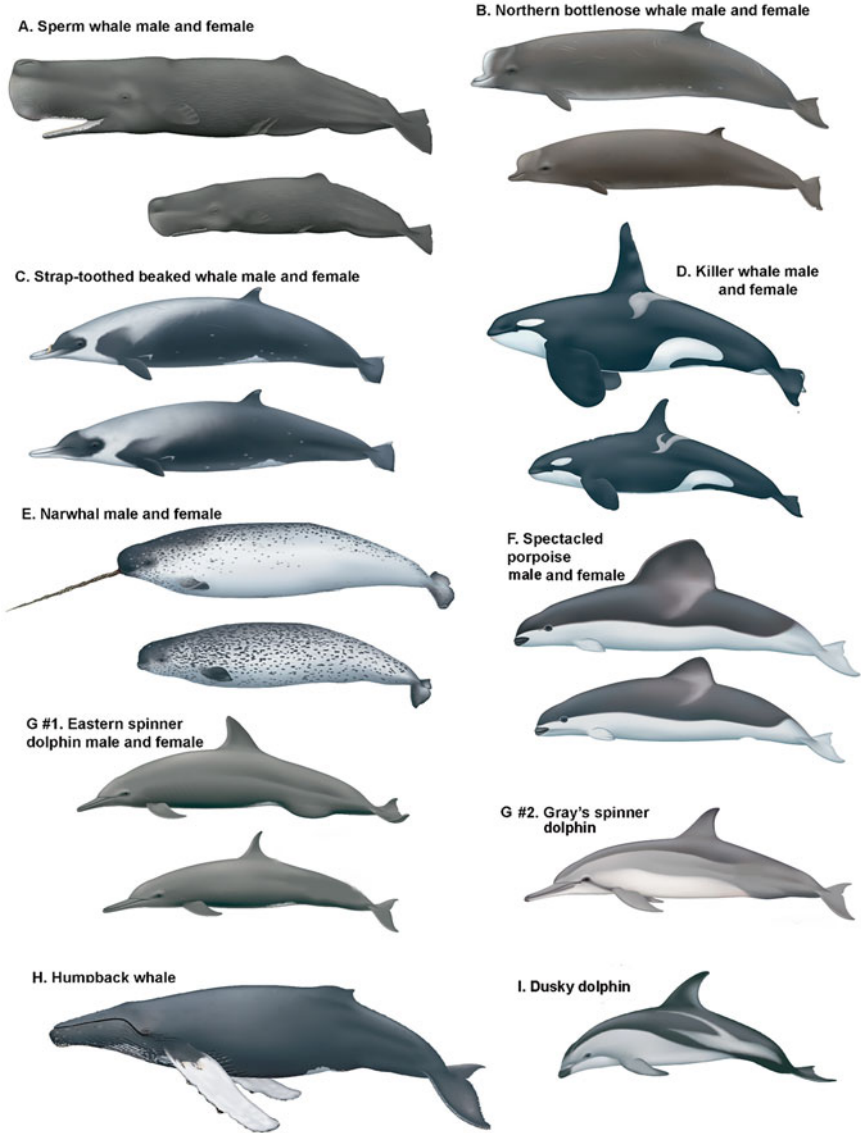
Fig. 1.1 Several cetaceans with variable dimorphologic features between females and males. (**A**, **B**, **D**, **E**, **F**, and **G**#1) show strong differences in body configurations and size. Drawings are to scale between the sexes, but not to scale across species. (**C**) of the strap-toothed beaked whale indicates the externally visible large tooth of males, common in beaked whales. (**G**#2, **H**, and **I**) show animals with very muted sexual dimorphism, so only one figure representing both sexes is shown. (**G**#1) of the eastern spinner dolphin shows strong sexual dimorphism, while most other spinner dolphins of the species *longirostris* are of the "gray-type," with little difference males vs. females (**G**#2). (**H**) of the humpback whale indicates that females and males have similar external morphologies, while females are slightly larger on average than males. (**I**) of the dusky dolphin also shows only muted sexual dimorphism. Species are (**A**) sperm whale (*Physeter macrocephalus*), (**B**) northern bottlenose whale (*Hyperoodon ampullatus*), (**C**) strap-toothed

sexual selection's fundamental tenet that conflicts exist between the sexes concerning maximizing lifetime reproductive success (Kokko and Jennions 2014).

Among non-mammalian (non-lactating) species with primarily monogamous mating systems, hungry offspring may be fed by either parent. For example, monogamous mating systems are common among birds (although not necessarily mutually exclusive with other mating systems). Biparental care ensures one parent is available to sit on the nest, keep the eggs warm, and protect the offspring, while the other parent forages. If the male does not invest in paternal care, his progeny have a reduced likelihood of survival. Thus, the male has a higher probability of his genes perpetuating if he aids with offspring rearing over abandoning his progeny to inseminate additional mates. In species where males offer parental care, such as in many externally fertilizing fishes, male care of the nest can attract more potential mates, further increasing the male's fitness (Lindström et al. 2006). Monogamy is uncommon among mammals, in which the female gestates the fetus in her body and nurses the offspring with milk, curtailing a male's role in parental care (Lukas and Clutton-Brock 2013). It has been suggested that one species of odontocete, the franciscana (*Pontoporia blainvillei*), may have a monogamous mating system due to their reverse sexual size dimorphism, lack of evidence to support male-male aggression or sperm competition, and prevalence of unrelated male-female pairs caught as bycatch in the same nets (Wells et al. 2013). More research on this and other cetacean species is needed relative to the possibility of monogamy.

1.2.2   Polygyny

In polygynous mating systems, males mate with multiple females, and females generally invest extensively in offspring care. In contrast, males invest little if any effort in parental care as paternity is uncertain. Males compete to varying degrees for access to receptive females and then mate with as many females as possible, often resulting in extensive sexual dimorphism. Males may have elaborate morphological features or "displays" that deter rival males, attract females in estrus by demonstrating males' ability to survive despite the handicap induced by their displays (Zahavi and Zahavi 1997), or attract females with desirable traits that may be inherited by their offspring. Male body size and fighting ability are often critical to establish dominant positions associated with access to mates (Andersson 1994).

In highly polygynous societies such as elephant seals (*Mirounga* spp.), only a few males sire the majority of offspring in a colony (Leboeuf 1972; Le Boeuf and Laws

Fig. 1.1 (continued) beaked whale (*Mesoplodon layardii*), (**D**) killer whale (*Orcinus orca*), (**E**) narwhal (*Monodon monoceros*), (**F**) spectacled porpoise (*Phocoena dioptrica*), (**G#**1 and **G#**2) eastern and gray's spinner dolphin (*Stenella longirostris orientalis* and *S. l. longirostris*, respectively), (**H**) humpback whale (*Megaptera novaeangliae*), and (**I**) dusky dolphin (*Lagenorhynchus obscurus*) (figure by Uko Gorter, with permission)

1994). Infanticide (the killing of non-offspring young) occurs in some terrestrial species, potentially to rapidly induce estrus in the mother and gain another opportunity to inseminate her (Hrdy 1977; Clutton-Brock 2016). Among odontocetes, evidence of infanticide is accruing in several species (Barnett et al. 2009; McEntee et al. 2023, this book). Males may also engage in forced copulations (a term preferred over "rape" when referring to animals/wildlife) with sexually mature females, sexually immature individuals of either sex, heterospecifics, dead conspecifics, and inanimate objects (pinnipeds (Rohner et al. 2020) and sea otters, *Enhydra lutris* (Harris et al. 2010)). Recent examples of interspecific necrocoitus between common bottlenose dolphins (*Tursiops truncatus*) and short-beaked common dolphins (*Delphinus delphis*; Methion and Díaz López 2021), intraspecific necrocoitus in common bottlenose dolphins (Kincaid et al. 2022), and masturbatory and homosexual behaviors in captive Yangtze finless porpoises (*Neophocaena asiaeorientalis*; Zhang et al. 2015; see also da Silva and Spinelli 2023, this book; Ham et al. 2023, this book) have been reported.

1.2.3 Polyandry

In polyandrous mating systems, one female mates with multiple males, and males generally take care of the young. There are numerous polyandrous species of fishes and birds (e.g., pheasant-tailed jacana, *Hydrophasianus chirurgus*; Fresneau et al. 2021); however, polyandry seems scarce in habitats with ample resources. Polyandrous females can have more striking external markings than their counterpart males. Males in polyandrous species generally have large testes sizes relative to their body size as sperm competition among males is hypothesized to play an important role in paternity determination (Gomendio and Roldan 1993). The uncertain nature of paternity in polyandrous systems decreases the risk of infanticide by male conspecifics, such as in some new world monkeys (e.g., marmosets and tamarins, family Callitrichidae; Pradhan and van Schaik 2008). Polyandrous females have increased fitness within inbred populations, as shown with red flour beetles (*Tribolium castaneum*; Michalczyk et al. 2011).

The challenging nature of studying mating in aquatic mammals makes it difficult to identify polyandry while ruling out polygynandry with certainty in cetaceans. However, several examples of polyandry exist, including the well-studied population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. In this population, multiple males form stable and ongoing alliances and then isolate and consort with a single female. Although paternity is not divisible and males in alliances are not necessarily kin, each male has a higher likelihood of inseminating a female if cooperating within an alliance than attempting to mate with a female on his own (Connor et al. 2000b). Similar to humans and chimpanzees (*Pan troglodytes*), these male alliances among bottlenose dolphins are formed among non-related males with strong social bonds commencing at adolescence (Gerber et al. 2021). Populations of common bottlenose dolphins around Florida and other

areas (Ermak et al. 2017; Brightwell and Gibson 2023, this book) and perhaps Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas (Elliser and Herzing 2013) also exhibit cooperative male alliances. Further long-term studies of cetacean populations may reveal increased prevalence of the alliance formation phenomenon. Little is currently known about post-copulatory mechanisms that female cetaceans may induce to control paternity in polyandrous systems. Further research is needed to determine the degree of female choice and potential additional benefits conferred to females in polyandrous species.

1.2.4   Polygynandry

Polygynandry, which incorporates aspects of both polyandry and polygyny, involves both sexes mating with multiple partners during one reproductive period. Polygynandrous females and males tend to be monomorphic in coloration and size, so there can be confusion between monogamy and polygynandry from body structure alone. Females have much at stake if inseminated by a poor choice of sexual partner. By remating subsequently with a different partner, females have the possibility to increase offspring fitness and the genetic diversity of their progeny (Davies et al. 2012). Similar to polygynous mating systems, males in polygynandrous mating systems tend to not invest in parental care; however, male mating tactics in these systems may vary over a male's lifetime (Silk et al. 2020). Male mating tactics to control paternity and increase fitness are well understood in polygynandrous mating systems and include mate-guarding, male-male competition, and sperm competition, as seen in polygynandrous passerines (Briskie 1993). However, mechanisms of cryptic female choice to control paternity are less well understood. Overall, polygynandry can lead to increased care of young and decreased infanticide by males, as their own genetic progeny might be present.

Polygynandry is likely the most common mating system among cetaceans (Tables 1.1 and 1.2). As direct observations of mating are uncommon, large relative testes size is often used to infer a polygynandrous mating system due to the correlation with increased sperm competition (Kelley et al. 2014). Right whales (*Eubalaena* spp.) are presumed to be polygynandrous due to their very large testes size, weighing one metric ton (Brownell Jr and Ralls 1986; Burnell 2001). Other mysticetes such as gray whales (*Eschrichtius robustus*) and bowhead whales (*Balaena mysticetus*) are also hypothesized to have polygynandrous mating systems due to their large relative testes sizes and low aggressive behavior among males (Brownell Jr and Ralls 1986). However, it is difficult to determine whether these mysticete species are polygynandrous or polyandrous due to limited data on female mating patterns (Ralls and Mesnick 2019a). Among odontocetes, polygynandry has been proposed particularly among the Delphinidae family (oceanic dolphins; Caspar and Begall 2022). For example, dusky dolphins, killer whales, long-finned pilot whales (*Globicephala melas*), and harbor porpoises (*Phocoena phocoena*) all have proposed polygynandrous mating systems due to their large relative testes sizes

Table 1.1 Mating tactics of male odontocetes and potential fitness costs to both sexes (table from Orbach (2019), with permission)

Male mating tactic	Potential costs for males	Potential costs for females	Examples	Species	References
Display competition	• Increased conspicuousness to predators • Time/energy not spent foraging or detecting predators	• Time/energy evaluating males • "Dishonest" signals • Lower offspring survival if inexperienced in evaluating males	Object carrying and posturing	Humpback dolphins (*Sousa sahulensis*)	Allen et al. (2017)
Contest competition	• High risk of injury • Increased conspicuousness to predators • Time/energy not spent foraging or detecting predators	• Not directly choosing mate • Risk of injury if male aggressive to female	Weaponry—"battle teeth"	Some beaked whale (family: Ziphiidae)	McCann (1974), Heyning (1984), Pitman (2018)
Endurance competition	• Extensive temporal investment • Lost mating opportunities with other females • Reduced paternity in alliance	• Prevented from mating with preferred mate • Reduced socializing opportunity • Risk of injury if coerced	Mate-guarding/consortships	Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)	Connor et al. (1996)
Scramble competition	• Extensive energetic expenditure on challenging chases • Conditional on competitive sperm	• Time/energy actively evaluating male and avoiding rejected males	Maneuverability during mating chases	Dusky dolphins (*Lagenorhynchus obscurus*)	Markowitz et al. (2010), Orbach et al. (2014)
Sperm competition	• Tissue costly to maintain • Conditional on male copulation success	• Limited choice of copulation partners	Strong seasonal testes mass and cellular activity patterns	Short-beaked common dolphins (*Delphinus delphis*)	Murphy et al. (2005)

Table 1.2 Mating tactics of female odontocetes (table from Orbach (2019), with permission)

Female mating tactic	Example/evidence	Species	References
Signal discrimination	Extended mating chases led by females that may be used to evaluate male maneuverability	Dusky dolphin (*Lagenorhynchus obscurus*)	Markowitz et al. (2010)
Mate choice copying	Suggested by patterns of paternal relatedness within matrilineal groups	Sperm whale (*Physeter macrocephalus*)	Richard et al. (1996)
Evasive behaviors	Females fled from pursuant males, moved to shallow waters where males could not fit beneath them, rolled ventrum-up, and raised flukes in the air so their genital groove was inaccessible	Dusky dolphin (*Lagenorhynchus obscurus*)	Orbach et al. (2015)
Polyestry/ multiple matings	Hypothesized mechanism to improve fertility, reduce sexual harassment costs, and obscure paternity	Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	Connor et al. (1996)
Modified genitalia	Complex vaginal folds that occlude penetration of the penis	Harbor porpoise (*Phocoena phocoena*)	Orbach et al. (2017)

(Ralls and Mesnick 2019a). Dusky dolphins have a multi-mate system in which males compete and chase females to successfully copulate, a classic example of scramble competition (Orbach et al. 2015). For many cetacean species, particularly among odontocetes, behavioral and anatomical indicators support a polygynandrous mating system.

1.2.5 Mating Systems as a Continuum

Although polygamous mating systems are often described as discrete categories (polygynous, polyandrous, or polygynandrous), they are best viewed as a gradient with animals within a population falling along the continuum. Spinner dolphins can be used as a model cetacean species to highlight how mating systems are not defined by phylogenies, but vary according to ecological and social constraints. Although the spinner dolphin is closely related to many polygynandrous species, some populations of spinner dolphins have been hypothesized to have more polygynous than polygynandrous mating systems. Anatomical evidence in support of divergent mating systems includes differences in testes weights. Testes weights are higher among males in the whitebelly spinner dolphin population (an intermediate physical form between eastern and Gray's spinner dolphin (*Stenella longirostris orientalis* and *S. l. longirostris*, respectively, Fig. 1.1g#1 and g#2) than in the eastern spinner dolphin population, indicating a polygynandrous mating system in the whitebelly

spinner dolphin (Perrin and Mesnick 2003). Recent work that examined the genetics of mating system variation among spinner dolphins found single nucleotide polymorphisms in genes which appear to be associated with social behavior, providing further evidence for selection among spinner dolphin ecotypes for different mating systems (Andrews et al. 2021). The costs and benefits of group living vary with ecological conditions and have led to the evolution of different mating strategies and social structures among cetacean species and populations (Acevedo-Gutiérrez 2018). Many species hedge their bets and blur among mating system categories by utilizing a combination of tactics.

Mating systems in cetaceans pose a unique challenge to researchers due to limited opportunistic observations. Consequently, mating systems have not yet been described for many cetacean species, but most cetacean mating systems are hypothesized to be polygynandrous or polygynous (Wells et al. 1999). As resources in the ocean are constantly moving, territoriality is unlikely in cetaceans; thus, females are widely distributed and can seldomly be monopolized by a single male. Additionally, female cetaceans have long interbirth intervals compared to many terrestrial mammals (Whitehead and Mann 2000; Lukas and Clutton-Brock 2012). Gestation is typically 11 months and is timed such that offspring are born during seasons of warm water when thermoregulation demands are reduced. Some cetacean species have even longer gestation periods, such as sperm whales (16 months; Ohsumi 1965) and killer whales (17 months; Duffield et al. 1995). Lactation is brief among baleen whales and often consists of 6 months of nourishing the offspring with very fat-rich milk (up to 40% fat) to facilitate rapid offspring growth, with weaning timed to correspond with seasonal migrations to foraging grounds (Lockyer 1984). In contrast, lactation is prolonged and of comparatively lower fat content among toothed whales, lasting on average 1.5 years and up to 7 years (Reynolds III and Rommel 1999). The lengthy lactation period among odontocetes allows for extensive social bonding between mother and calf and the development of advanced foraging tactics to capture prey and ensures social learning to support offspring survival (Brodie 1969; Tyack 1986). Interbirth intervals in cetaceans range from 1 year, such as in the harbor porpoise, to over 6 years in the short-finned pilot whale (*Globicephala macrorhynchus*; Taylor et al. 2007). Thus, female cetaceans are under strong selection pressures to invest in calf rearing, including ensuring safety and obtaining food. Female cetaceans generally minimize their temporal and energetic expenditures in seeking out mates. Male cetaceans, in contrast, do not incur limitations imposed by parental care and can invest time and energy in searching for receptive mates. However, males face constraints in their abilities to locate, guard, and compete for females, which have led over evolutionary time to many diverse mating strategies and tactics within and among cetaceans.

1.3   Sexual Selection

Sexual selection theory has traditionally posited that the evolution of diverse mating strategies at the species and population levels is driven by the selective forces of mate competition (intrasexual competition) and mate selection (epigamic selection; Darwin 1871). A recent proliferation of theoretical and empirical research has expanded the sexual selection framework to recognize an additional significant evolutionary force, sexual conflict, in which the increasing fitness of one sex produces a fitness cost for the other sex (Arnqvist and Rowe 2005). The sexual selective forces of mate competition, mate choice, and sexual conflict are each driven by direct or indirect mechanisms, which are not mutually exclusive.

Direct mechanisms increase or decrease the fitness (survival and reproductive success) of the choosy sex through direct material advantages or disadvantages. Direct benefits may include nuptial gifts, territories, food, defense (i.e., against predators or ardent males), or parental investment. For example, female hangingflies (*Hylobittacus apicalis*) mated for longer with males that provided large insects for her to eat during copulation than those who did not; she is hypothesized to convert this food into nutrients for her offspring (Thornhill 1976). Direct costs involved in sexual selection may include increased risk of predation, expenditure of energy and time, exposure to parasites, sexually transmitted diseases, injury, or death (Jennions and Petrie 2000).

In contrast to direct benefits, indirect mechanisms increase or decrease the genetic fitness of the offspring without providing the choosy sex with material gains or losses. The benefits provided by indirect mechanisms are hypothesized to evolve by two models: (1) Fisher's (1958) "runaway" selection/"sexy sons" model and (2) Zahavi's (1975) "handicap"/"good genes" model. Fisher's (1958) "runaway" model proposes that courters possess genetically based traits and choosers possess covarying genetically based preferences for these traits that result in a positive feedback loop. Choosers continue selecting courters with exaggerated traits to produce "sexy sons" capable of attracting mates (through their inheritable exaggerated phenotype) to pass their genes on to future generations. In contrast, Zahavi's model (1975) proposes that choosers prefer courters with "good genes" that increase the bearer's fitness and increase their offspring's survival and reproduction. The elaborate courter traits are "handicaps" to their bearer, and the bearer's ability to survive despite the costly trait provides honest evidence of their overall genetic quality. The "sexy sons" hypothesis differs from the "good genes" hypothesis in that "sexy sons" inherit genes purely for attracting mates, whereas "good gene" offspring inherit genes for utilitarian aspects of survival and reproduction.

Two other mechanisms have been hypothesized to drive sexual competition: antagonistic coevolution and sensory bias models. In the antagonistic coevolution or "chase away" model, courters and choosers coevolve traits in an evolutionary "arms race" to maintain control of paternity (Holland and Rice 1998). Thus, choosers may not evolve a preference for a courter's traits, but rather evolve resistance to less elaborate courter traits (e.g., cetacean genitalia; Orbach et al.

2023, this book). In the sensory bias model, courters capitalize on a chooser's preferences through sensory exploitation, sometimes even before the preferred trait has evolved. The choosy sex typically acquires the trait in a non-mating context, and the chooser has a pre-existing bias before the courter exploits it to increase reproductive success. The courter's signal falls within the chooser's sensory sensitivity such that signals evoke a response and are selected for by reducing costs to the courter (i.e., searching for a mate; Basolo 1990).

Sexual conflict theory highlights conflicting dynamics between the sexes in reproductive encounters in addition to coevolving adaptations and counter-adaptations hypothesized to reduce costs. Sexual conflict can consist of distinct or manifest behavioral, physiological, or anatomical mechanisms that have been hypothesized to increase the fitness of one sex at a fitness cost to the opposite sex (Tregenza et al. 2006). Most research on sexual conflict theory uses insect models (e.g., Eberhard 1985). Theoretical principles and predictions from these models may be limited in their applicability to large-brained, highly social mammals, which experience different ecological constraints and may invest more in parental care than insects (Stumpf et al. 2011). Cetacean genitalia provide a clear example of sexual conflict. Female cetaceans are unique in possessing vaginal folds, protrusions of the vaginal wall into the vaginal lumen. Vaginal folds appear to physically occlude the penis during copulation (Orbach et al. 2017) and may provide females with a mechanism to control paternity by angling her body during copulation to prevent deep penetration of the penis and ejaculation near her ovaries (Orbach et al. 2020). Among harbor porpoises, male sexual behavior has coevolved with the reproductive anatomy of both sexes, and males only approach females on her left-hand side, which appears to bypass the vaginal fold labyrinth (Keener et al. 2018; Orbach et al. 2020; Webber et al. 2023, this book). The evolutionary steps of genital morphology and mating behavior adaptations remain unclear, although the evidence is clear for an evolutionary "arms race" and a possible mating tactic to control paternity during or post-copulation (Tregenza et al. 2006).

1.4 Mating Strategies and Tactics

Mating strategies are fixed, conditional, or mixed genetically based mechanisms that are hypothesized to increase reproductive success under certain social and ecological conditions. Mating strategies are essential to find mates and engage in copulations and can include pre-, during-, and post-copulatory mechanisms. Mating strategy evolution is influenced by multiple factors including the distribution of resources, predation pressures, and costs and benefits of group living (Ralls and Mesnick 2019a). Unlike for mammals in many terrestrial ecosystems (Clutton-Brock 2016), territories are not defended by cetaceans in the ocean (Ballance 2018), and males employ mating strategies that are hypothesized to monopolize fertilizations despite potential costs to females. Most male odontocetes use similar strategies to search for receptive females and spend little time with them other than to mate (Connor et al.

2000a; Boness et al. 2002), although there are exceptions (e.g., mate-guarding tactic, Tables 1.1 and 1.2). Intraspecific sexual selection forces are generally strong among cetaceans (Ralls and Mesnick 2019a) and have resulted in the evolution of sexually selected traits among some cetacean species (Loch et al. 2023, this book). Much previous research on cetacean mating strategies has presented males as the actively competing sex and females as the passive choosing sex (Connor et al. 2000b). However, females may have a much more active role than previously considered (e.g., Orbach et al. 2015).

The mechanism underlying female sexual motivation is an understudied area that warrants further research, including the concept that both sexes have a "libido" (sexual drive). Much of the current knowledge of female sexual motivation comes from studies on rats (*Rattus* spp.), which have shown that female sexual motivation is impacted by experience, mate preference, and hormonal control (Guarraci and Frohardt 2019). Research into female sexual motivation in mammals has been limited to small mammals and humans. Current research on sexual motivation in large non-human mammals, such as cetaceans, remains primarily focused on males. The lack of female perspectives on sexual motivation research can be attributed in part to the historical gender bias within reproductive research (Ogden 2021). In recent years, an increasing number of investigators have broadened the field of reproductive research to include a stronger focus on females' roles in reproduction, and their work has illuminated previously unknown female roles in sexual selection (Orbach 2022). However, further expansion of female perspectives within the field is needed to fully understand the underlying evolutionary and coevolutionary mechanisms of sexual reproduction of both sexes.

While mating strategies have an underlying genetic framework, mating tactics are the phenotypic or behavioral manifestation of the strategy. As sexual maturity and social maturity are not ubiquitous, it can take some males prolonged periods to obtain mating opportunities, resulting in an adoption of alternative mating tactics. Non-mutually exclusive female and male mating tactics have recently been reviewed among cetaceans (Tables 1.1 and 1.2; Orbach 2019). Additional mating tactics observed among marine mammals but not documented among cetaceans include site-guarding, group-guarding, and leks. Site-guarding can occur when females range more widely than the males' capabilities of sequestering them. A site, or territory, is established by a male through which females roam in search of food and safety. Males do not attempt to herd particular females into that established territory, but instead attempt copulations as females pass through. Sea otters exhibit resource defense polygyny through site-guarding territories and engaging in aggressive copulations with females who enter the territories (Pearson and Davis 2021). Group- or "harem"-guarding occurs when males defend an area occupied by a collection of females for short (seasonal) or long (interseasonal) times. Males actively herd females who attempt to leave the area. Group-guarding is common among some seals and has been described particularly well for northern elephant seals (*Mirounga angustirostris*; Le Boeuf and Reiter 1988). Leks occur when males display and females observe, mating with the male that appears most attractive to them. Leks appear to occur in several pinnipeds such as the New Zealand sea lion

(*Phocarctos hookeri*), California sea lion (*Zalophus californianus*), and some populations of harbor seals (*Phoca vitulina*; Campagna 2018). A type of "floating lek" has also been proposed for Amazon river dolphins or boto (*Inia geoffrensis*; Martin et al. 2008) and humpback whales (Clapham 1996).

The mating tactics of cetaceans are in some cases inherently different from other species, regardless of mating system, because of the constraints of living in the ocean. Females distribute themselves relative to resources essential for foraging opportunities and protection from predators. Resources can be thin and spread over thousands of kilometers in the open ocean, leading to wide female distributions. Subsequently, males are unable to monopolize multiple females simultaneously. Unlike the terrestrial environment, there are few hiding places in the ocean for cetaceans to evade predators or ardent male suitors. Yet cetaceans live in a three-dimensional landscape where costs of locomotion are low, and they can dive to depth or move to shallow waters as a potential escape mechanism. For example, when exposed to killer whale vocalizations, humpback whales exhibit behavioral changes including increased dive times and moving away from the "predator" sound (Curé et al. 2015). While elaborate vocalizations occur on the mating grounds of large baleen whales (Clark and Garland 2022), mating-related sounds/songs are dangerous for small cetaceans in many habitats as they could attract their main predator, killer whales. Because of natural selection pressures associated with aquatic living, cetaceans are also constrained in their development of secondary sexual characters to attract a mate. For example, the sleek body design of cetaceans reduces hydrodynamic drag forces, and their low surface-area-to-volume ratio is critical in thermoregulation (Ralls and Mesnick 2019b). Protrusive secondary sexual characteristics, like the elaborate tail feathers of male peafowl (genus *Pavo* and *Afropavo*), would prevent streamlined swimming. Nevertheless, the exaggerated large dorsal fin and pectoral flippers in male killer whales (Wright et al. 2023, this book), large dorsal fin of male spectacled porpoises (*Phocoena dioptrica*, Fig. 1.1), and erupted large tooth of male narwhals (*Monodon monoceros*, Fig. 1.1) indicate that there is female choice of males relative to their (apparently disadvantageous) body morphology (Zahavi 1975, 1993).

1.5   Alloparental Care

Alloparental care is a form of cooperation that occurs when an individual performs a behavior that (1) benefits a calf of which it is not the parent, (2) benefits the calf and its mother, and (3) would not be performed if the calf were not present and is therefore costly to the actor (Riedman 1982; Mann and Smuts 1998). The highly social behaviors comprising alloparental care have been reported in a variety of odontocetes, terrestrial mammals (e.g., primates (*Cebus olivaceus*, O'Brien and Robinson 1991; *Cebus nigritus*, Baldovino and Di Bitetti 2008), buffalo (*Bubalus bubalis*, Murphey et al. 1995), guanacos (*Lama guanicoe*, Zapata et al. 2010), bats (*Pipistrellus pipistrellus*, de Fanis and Jones 1996; *Pteropus rodricensis*, Kunz et al.

1994), fishes (Wisenden 1999), and birds (Riedman 1982)). Alloparental care appears to have evolved convergently across several mammalian taxa, potentially as an adaptation to counter predation pressure or high energetic demands on mothers while rearing offspring.

In some terrestrial birds and mammals, young males (and at times females) may help females partnered with other males to rear neonates, which may seem purely altruistic, but has functions (Trivers 1985). If cooperative neonate rearing occurs in systems where the male helpers have reasonably assured mating opportunities outside their own immediate group, they may stay and help due to being related in some degree to the young they assist. Such kin-selected altruism functions to support the prevalence of ones' genes in the population. Additionally, by staying within the safety of their group, male helpers may survive to perhaps mate within or outside of the group as they further mature. There is limited evidence for males helping to rear young among cetacean species. Resident killer whales of both sexes do not disperse from their natal groups (Baird 2000), and the genetic strategy to treat all young as relatives could increase inclusive fitness in a closed population (e.g., Wright et al. 2023, this book). Male humpback whales "escort" females, both with and without calves. Male humpback whales likely do not offer parental care, and the "escorting" behavior probably serves as mate-guarding of females with whom they have recently mated or with whom they are attempting to mate. While this "escorting" behavior has clear benefits for the males, female humpback whales may benefit from the presence of male "escorts" through reduced risk of predation or harassment from other males (Ransome et al. 2021).

Females may also aid in the care of offspring that are not their own. For example, a sperm whale may guard a calf that is not her offspring from predators, while its mother is foraging on a deep dive (Whitehead 1996; Eguiguren et al. 2023, this book). The kin selection hypothesis for the evolution of social allomaternal care particularly applies to cetaceans that live with relatives in closed matrilineal social groups (Konrad et al. 2019). Allomaternal care is widespread among odontocetes in captivity and in the wild and has been reported in beluga whales (Aubin et al. 2022), bottlenose dolphins, sperm whales, spinner dolphins, killer whales, harbor porpoises, pilot whales, and bottlenose whales (*Hyperoodon ampullatus*; reviewed in Whitehead and Mann 2000). Additional evidence of a female Indian Ocean humpback dolphin (*Sousa plumbea*) providing alloparental care for an Indo-Pacific bottlenose dolphin calf and a common dolphin calf indicates that allomaternal care can be interspecific (Conry et al. 2022).

One form of allomaternal care is allonursing, in which an individual lactates to feed a non-offspring. Although allonursing poses potential costs such as disease transfer and high maternal energetic output (reviewed by Mota-Rojas et al. 2021), allonursing has evolved across multiple taxa in situations where such associated costs are low (reviewed by MacLeod and Lukas 2014). Allonursing has been reported in free-ranging sperm whales (Gordon 1987), captive beluga whales (Leung et al. 2010), and captive bottlenose dolphins (Dudzinski et al. 2022). Evidence of allonursing in sperm whales comes from direct observations of two non-twin calves nursing simultaneously from one female (Gordon 1987), one calf

suckling from different adults (Gordon 1987), and more lactating females than calves found in groups (Best et al. 1984). Older females typically perform the allonursing, and corresponding energetic demands appear to decrease with age (Ekvall 1998). Allonursing can increase nutrient transfer to offspring or alleviate parental care responsibilities such that kin can allocate resources to future offspring. Oblique cultural transmission of communication and navigation skills could potentially be taught to calves during allonursing and sustained interactions (Best et al. 1984). Allomaternal care has been hypothesized as a critical parameter that led to the evolution of sex- and age-class segregation and polygynous mating systems in sperm whales (Gero et al. 2013). Variation in diving capabilities of mothers and calves, combined with high predation pressure on calves, selected for allomaternal care social systems to protect calves while mothers foraged. This biased the operational sex ratio and led to segregations in social schooling by age and sex such that large roving males have an unequal share of matings in a polygynous mating system. While allonursing has not been reported in mysticetes, allonursing has been reported in African elephants (*Loxodonta* spp.; Lee 1989), which share several life history parameters with sperm whales (Weilgart et al. 1996), in African lions (*Panthera leo*), and in other terrestrial species (Karniski 2019).

1.6 Reproductive Senescence

Reproductive senescence, when a female continues to live for a prolonged period after she is capable of conceiving and delivering, occurs in mammals, birds, fishes, and invertebrates. However, this phenomenon remains rare. In cetaceans, reproductive senescence has been reported in resident killer whales and short-finned pilot whales (Marsh and Kasuya 1986, overall review by Croft et al. 2015). Lengthy post-reproductive lifespans in beluga whales (*Delphinapterus leucas*) and narwhals suggest that reproductive senescence has evolved independently in multiple odontocete species (Ellis et al. 2018). It is hypothesized that reproductive senescence in cetaceans, particularly those with matrilineal societies, could facilitate cross-generation learning and culture (Whitehead 2015). For example, killer whales exist in matrilineal societies within which the reproductively inactive females (mothers and grandmothers) play an important role in cultural transmission of ecological knowledge that may promote the survival and fitness of their offspring (Brent et al. 2015). Recently, reproductive senescence has been subcategorized as fertility senescence (reproductive physiology aging) and maternal-effect senescence (declining capabilities with age to provision and rear offspring), and Karniski et al. (2018) showed both effects in their long-term study of Indo-Pacific bottlenose dolphins.

1.7   Homosexuality

There is much evidence of animal homosexual (same-sex) behavioral interactions. Homosexual pairings may help the young better survive than with heterosexual pairings, as with male black swans (*Cygnus atratus*; Braithwaite 1981), as aggressive males are adept at keeping large territories around their communal nest. Homosexuality also often grades into bisexuality with some same-sex and some opposite-sex behaviors, including tight social unions related at times to age/development of one or both partners. In contrast, several species of sheep (*Ovis* spp.) have a high prevalence of pure homosexuality with the same greeting and courting actions as in heterosexual sheep (Poiani 2010). Apparent homosexual behavior in the form of beak to genital nudging was described for spinner dolphins (Norris and Dohl 1980) and common bottlenose dolphins (Wells et al. 1987). Male common bottlenose dolphins were observed mounting male Atlantic spotted dolphins; however, male spotted dolphins were not observed mounting male common bottlenose dolphins in mixed-species groups (Herzing and Elliser 2013). Additional field studies of homosexual behavior among Indo-Pacific bottlenose dolphins have noted higher levels and longer duration of socio-sexual behavior among male-male pairs of dolphins than among male-female and female-female pairs (Mann 2006). Homosexual behaviors have also been reported among sexually mature bowhead whales (Würsig and Clark 1993) and among sexually mature and immature southern right whales (*Eubalaena australis*; Sironi 2004). More examples of homosexual behaviors among cetaceans are reviewed by Ham et al. (2023, this book).

   Homosexual behavior can have variable functions in animals, with interpretations often clouded by human sentiment. Common themes of the function of homosexual mating are to relieve boredom, practice sex, achieve social dominance, play, promote social bonding, and increase the availability of sexual partners (Bagemihl 1999). What has not been adequately explored is that sex may be pleasurable in animals. It was recently shown that the clitoris of female common bottlenose dolphins is highly innervated, suggesting sexual experiences are pleasurable for female dolphins (Brennan et al. 2022). Such information is likely to lead to more advanced understanding of hetero-, homo-, and bisexuality across the animal kingdom.

1.8   Summary and Future Directions

This chapter provides a basic review of the evolutionary costs and benefits of sexual reproduction, mating systems, sexual selection, mating strategies and tactics, and several socio-sexual behaviors. Within cetaceans, most species whose mating systems are known are polygynous or polygynandrous. The majority of cetaceans do not have strong sexual dimorphism (pronounced differences in female and male external morphology), although there are exceptions (Ralls and Mesnick 2019a, b).

Mating tactics and strategies can vary within species and among populations according to social and ecological drivers. The evolution of reproductive systems and behaviors in cetaceans is likely driven by traditional models of sexual selection and emerging theories including sexual conflict. Several socio-sexual behaviors have been well-described across cetacean species, including alloparental care, allonursing, and homosexuality. Additional physical sexual associations not explored in detail here include autoeroticism (masturbation), oral and anal sex, potential sex stimulation in odontocetes by sound, interspecies sex (which can be procreative), sex with non-reproductive infants and juveniles, and necrocoitus. Intriguing reports such as sexual stimulation by bubbles need to be further investigated as they indicate potential cooperation in eroticism between females and males and potentially among members of the same sex (Jones et al. 2022). A general review of some of the above behaviors is provided by Balcombe (2006) and Bowyer (2022). Our chapter does not investigate steroid sex hormonal functions, such as the roles of testosterones, estrogens, and androgens (Sapolsky 1997; Ketterson and Nolan Jr 1999). Areas of future research include alternative approaches to explore mating strategies, particularly in deep-diving or pelagic cetacean species, investigation of potential mechanisms of cryptic female choice, and long-term studies of specific cetacean populations to explore the relationship between sexual and social behaviors. Exploration of these areas will further current understanding of sexual reproduction in cetaceans and open potential avenues for comparisons across taxa.

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Chapter 2
Genetic Tools to Investigate the Consequences of Sex

Livia Gerber and Michael Krützen

Abstract The primary purpose of sex is reproduction. However, because not all mating events result in fertilization and only a small number of species provide biparental care to their young, successfully reproducing individuals can rarely be identified from behavioral observations alone. Genetic tools permit reliable identification of an individual's parents and thus of successfully reproducing individuals, because each parent passes on half of their genetic material to their offspring. In cetaceans, genetic tools are required to identify a female's already weaned offspring and to detect successfully reproducing males due to the absence of paternal care. To date, relatively few studies have investigated variables linked to reproductive success in this taxon, owed to the difficulty of sampling entire cetacean populations. We summarize currently known factors that are linked to successful reproduction in whales, porpoises, and dolphins, as well as in terrestrial mammals with comparable life histories that give birth to single young.

2.1 Introduction

Sex cannot adequately be studied without considering its consequences. At first glance, it seems obvious that sex may lead to the production of offspring. However, in most species, more mating events take place than fertilizations, raising the question of which matings are actually successful. This question is of particular importance in species where individuals mate with more than a single partner

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(polygamy), as it is the case in most mammal species (Clutton-Brock 1989; Würsig et al. 2023, this book). The identification of successfully reproducing individuals is of evolutionary significance because only mating events that result in the production of offspring contribute to the next generation's gene pool and thus to an individual's evolutionary fitness.

Behavioral observations provide insights into "who mates with whom?", while genetic tools shed light on "who sires whose offspring?". Although the answer to these two questions can be the same, research across mammals has shown that in most species, only a subset of individuals that are ready to mate successfully sire offspring (Lukas and Clutton-Brock 2014). Since the 1990s, when genetic tools became readily available to ecologists, multiple studies have explored parentage in natural populations (Flanagan and Jones 2019), while only a limited number of studies involving genetic tools have investigated reproductive success in cetaceans. Marine mammals are generally more difficult to study than terrestrial ones. As well, marine mammals have slow life histories, requiring populations to be studied over long periods of time. In addition, some cetacean species, particularly whales, have a wide distribution with migration routes spanning half the globe (Stern and Friedlaender 2018), increasing the difficulty in sampling populations. In this chapter, we introduce the genetic tools used to investigate reproductive success and provide an overview of what is known to influence reproductive success in terrestrial mammals with high cognitive abilities, slow life histories, and giving birth to single offspring and thus are expected to face similar constraints as cetaceans. We then summarize the studies carried out in cetaceans before drawing comparisons between cetaceans and terrestrial mammals.

2.1.1   The Need for Genetic Tools to Understand Reproductive Success

During the first days (3–5 days in the hooded seal (*Cystophora cristata*) or years (1.5–3+ years in the sperm whale, *Physeter macrocephalus*) of their lives, mammals depend on their mothers for milk. Successfully reproducing female mammals can therefore be reliably recognized via behavioral observations of them with dependent offspring. The identification of successfully reproducing males, in contrast, requires genetic tools. The reasons for this necessity are that even in closely monitored populations not all matings are recorded. Furthermore, there is a considerable number of extra-pair matings in monogamous species, extra-group copulations in polygynous populations (one-male multi-female groups), matings with multiple partners in polygamous species such as cetaceans (Würsig et al. 2023, this book), and the lack of paternal care in most mammal species (Kleinman 1977). In cetaceans, the challenge of identifying successfully reproducing males based on behavioral data alone is further exacerbated by copulations occurring below the surface, while behavioral data are mostly collected via boat-based surveys. Furthermore, in

long-lived animals, genetic tools can aid in assigning individuals to their mothers once mature, which can prove useful to increase our knowledge on populations where long-term behavioral records are unavailable.

2.2 Genetic Tools for Parentage Analysis

2.2.1 Genetic Sampling

Genetic analyses are based on DNA, the hereditary material of almost all organisms. Most cells of an individual mammal contain two almost identical copies of its full genome. Thus, genetic analyses can be carried out from any source containing an individual's cells, such as the skin, muscle, or whole blood. To date, most genetic analyses in cetaceans are based on skin samples obtained via biopsy dart (Baker et al. 2018). The biopsy darts, designed to retain the skin's top layers as well as some of the underlying blubber, are fired from a modified rifle or a crossbow (Fig. 2.1; Lambertsen 1987; Krützen et al. 2002). Wound healing usually progresses well after sampling, with no evidence of infection at the biopsy site (Krützen et al. 2002). Furthermore, there are no known long-term behavioral consequences of collecting biopsies, as individuals resume their activities often within minutes after having been sampled (Barrett-Lennard et al. 1996; Krützen et al. 2002).

Alternative, less invasive sampling methods have been proposed for cetaceans such as DNA sampling from blow (Frère et al. 2010c), skin swabs (Harlin et al. 1999), or feces (Parsons et al. 2003a). All of these alternatives require close contact to cetaceans for material collection, are more time-consuming compared to biopsy sampling, and do not present a feasible alternative for most studies (Parsons et al. 2003a; Frère et al. 2010c). However, these alternative approaches can yield valuable insights as their collection can supplement genetic information with hormone analyses to measure stress or reproductive status. Over the past years, researchers began

Fig. 2.1 A skin sample is collected from a bottlenose dolphin in Shark Bay using a modified rifle (left panel). The biopsy dart penetrates the skin and then bounces free of the animal while retaining a skin sample (middle panel). The dart consists of a steel tip holding the skin sample and a floating polycarbonate body that permits easy sample recovery at sea (right panel). Image credit: Shark Bay Dolphin Project, Svenja Marfurt (left panel), Samuel Wittwer (middle and right panel)

to analyze DNA fragments present in aquatic environments as a result of metabolic waste, such as shed dead skin cells (Ruppert et al. 2019). The DNA fragments collected non-invasively from the environment are referred to as environmental DNA (eDNA). A major advantage of eDNA sampling is that no or very few permits are needed for sampling and that sample collection can also occur unmonitored by leaving a passive filtration system in the water (Bessey et al. 2021). To date, eDNA is mainly used to identify the presence of species. However, emerging techniques might soon permit individual-level analysis such as paternity and maternity analyses (Adams et al. 2019).

2.2.2 Parentage Analysis

Using genetic parentage analysis, an individual's offspring can be identified because it inherits one half of each parent's genome. Accordingly, parent-offspring relationships can be resolved using genetic techniques. To date, most genetic parentage analyses in natural animal populations have been conducted by analyzing 10 to 20 highly variable microsatellites (Flanagan and Jones 2019). Microsatellites are fragments in the genome consisting of repeated sequence motifs of one to six DNA base pairs (e.g., GA or TAC as a repeat of a two or three base pair motif, respectively). Individual microsatellite markers have multiple alleles differing in repeat number and thus fragment length. Owed to the elevated mutation rate of microsatellites compared to nuclear DNA (Lynch 2007), they are highly variable, resulting in differing microsatellite "fingerprints" between individuals. Because each parent contributes one half to the genome of their offspring, the genetic microsatellite fingerprint of a descendant matches half their mother's and half their father's (Fig. 2.2).

There are three main approaches to parentage analysis: exclusion, likelihood-based parentage assignment, and Bayesian parentage analysis (Jones et al. 2010). Exclusion is an approach assuming that an individual can be excluded as a parent when none of its alleles matches the offspring under consideration. Although this approach appears compelling, it is rarely used nowadays because it has multiple pitfalls, such as scoring errors that can lead to the true parent being excluded. The currently most used technique is likelihood-based parentage assignment—a method based on likelihood ratios between the two competing hypotheses that two individuals either represent a parent-offspring dyad or are unrelated (Marshall et al. 1998). The widely used software CERVUS permits likelihood-based parentage assignment employed in a user-friendly graphical user interface (GUI, Kalinowski et al. 2007). Bayesian parentage analysis permits the inclusion of information that is thought to influence reproductive success, such as age or dominance rank. This information is then taken into account when calculating the probability that an individual is another's parent. The incorporation of such information requires profound knowledge of the population and the species under consideration (Flanagan and Jones 2019). Possibly because such information is often unavailable for natural
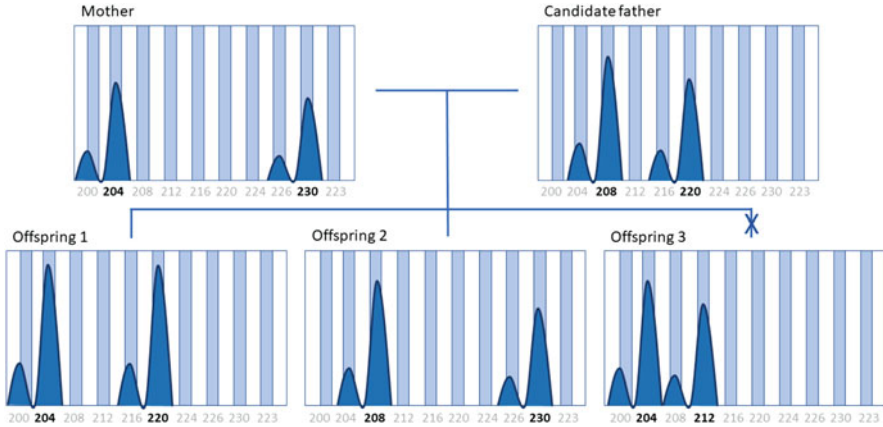
Fig. 2.2 Microsatellite "fingerprints" of a hypothetical mother, her three offspring, and a candidate father. Each offspring shares half of each parents' alleles. Hence, offspring 1 obtained allele 204 from the mother, while allele 220 must stem from the father. Similarly, offspring 2's copy of allele 208 must be present in the father because offspring 2 received allele 230 from the mother. Offspring 3 inherited the mother's copy of allele 204. Because allele 212 is not present in the candidate father, offspring 3 was most likely sired by another male in the population than the candidate father

populations, this approach is rarely used. Independent of which method is chosen, parentage analysis is more powerful in cases where mothers are known and genotyped, as it can be inferred which of the offspring's alleles are derived from the mother and thus which alleles must stem from the father (Huisman 2017).

Sex information of the genotyped individuals can further facilitate parentage analysis as it permits the separation of the genotyped individuals into candidate mothers and fathers. This is valuable in species with low levels of sexual dimorphism as is the case for most delphinids (Mesnick and Ralls 2018a). Genetic sexing has been employed in many studies as a fast and reliable means for sex determination. It is carried out by testing for the presence/absence of sex-chromosomal markers. In mammals, where females are the homogametic sex (XX), only X-chromosomal markers are detected. In contrast, males are the heterogametic sex (XY) and test positive for both X- and Y-chromosomal markers (Fig. 2.3). Sexing in cetaceans is often done by a joint analysis of the X-linked and Y-linked exons of the ZFX and ZFY genes (Bérubé and Palsbøll 1996).

2.2.3 Genetic Marker Systems for Parentage Analysis

Due to their hypervariable nature, microsatellites have long been the most-used genetic marker for parentage analysis (Flanagan and Jones 2019). Across species, microsatellites were the genetic markers of choice to investigate many parameters

Fig. 2.3 Electrophoresis gel showing PCR products of a reaction amplifying X- and Y-chromosomal markers. Males (samples 993, 995, 999, 1001) have two bands, because they are carriers of both sex chromosomes (XY), while females (samples 994, 996, 997, 998, 1000) can be identified as individuals with single bands (XX) (image credit: Manuela Bizzozzero)
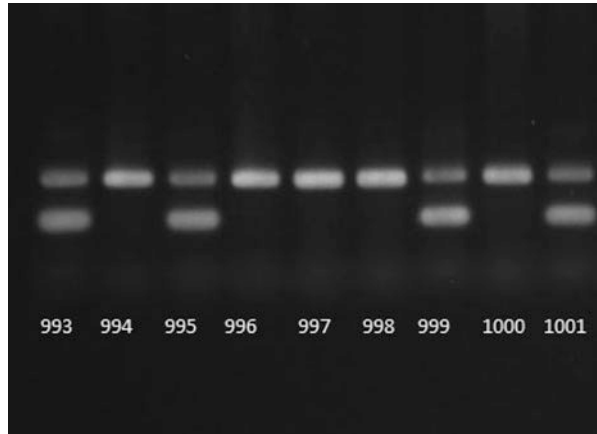
important in evolution and ecology such as dispersal patterns, migration rates, population size, and kinship (Hodel et al. 2016). However, population geneticists now widely use next-generation sequencing (NGS) approaches. Compared to traditional sequencing approaches, including microsatellite genotyping where only few loci are considered, NGS approaches permit the parallel genotyping of millions of single nucleotide polymorphisms (SNPs). Because these high-resolution SNP data are better suited to address ecological and evolutionary questions, there has been a dramatic decrease of studies using microsatellites over the past decade.

SNPs typically have two different alleles per locus, while microsatellites often have multiple alleles. Compared to a single microsatellite locus, single SNPs are therefore less informative. Reliable parentage assignment can be achieved by analyzing as few as ten highly polymorphic microsatellite markers but requires 100 SNPs (Weng et al. 2021). However, because NGS permits the simultaneous sequencing of millions of SNPs, this requirement is commonly met without difficulty. Like microsatellites, the SNPs used for parentage analysis are inherited in a Mendelian fashion, meaning that the offspring receives one copy from each parent. Thus, the same suite of analytical software can be used. Furthermore, compared to microsatellite data, a large number of SNPs derived from an NGS approach are much better suited to estimate pairwise relatedness, thereby permitting to assign dyads to other relationship categories than parent-offspring.

2.3 Paternity Success in Male Mammals

2.3.1 Variables Influencing Reproductive Success in Terrestrial Male Mammals

In most mammal species, more males are ready to reproduce than females because paternal care is absent in 95%–97% of species (Kleinman 1977) and the production of offspring requires a considerable time and energy investment from females, caused by gestation and lactation. This difference in parental investment causes a conflict between the sexes, where males often compete which each other over access to females. Because some males are better competitors than others, or successfully employ alternative non-competitive strategies (e.g., sneaking fertilizations without the knowledge of other males), the reproductive success among males is highly variable. For example, the variance of male lifetime reproductive success in rhesus macaques (*Macaca mulatta*) is five times larger compared to females (Dubuc et al. 2014).

Given that reproduction for males mainly consists of mating, male reproductive success is influenced by access to fertile females. Depending on the distribution of females, males employ different strategies (van Schaik and van Hooff 1994). If females are highly dispersed, males are likely to have less control over access to females compared to females aggregated in groups with high site fidelity. Where females can be monopolized, males frequently engage in contest competition, involving aggressive behavior, but also in sperm competition, attempting to outcompete other males that mate with the same female by ejaculating larger sperm quantities. In contrast, in populations where females are more dispersed, males are more likely to employ a roaming strategy (scramble competition), aiming to find and mate with females before others do. Furthermore, females might be more willing to mate with certain males (mate choice competition), potentially such with persuasive courtship behavior. These male mating tactics are not mutually exclusive, requiring males to compete on multiple levels, further complicating a male's pursuit for a mate.

In most mammals, females remain in their natal area (Greenwood 1980) and as a result cluster with their female relatives. To avoid inbreeding, males often leave their natal area once mature. To reproduce, males join new groups, where they compete with other males over reproductive opportunities. These opportunities can arise by replacing the breeding male of a polygynous (single-male, multi-female) group. In polygynandrous (multi-male, multi-female) groups, males frequently compete with other males to attain a high rank because dominant males sire more offspring in many species (Moore et al. 1995; Clutton-Brock and Isvaran 2006; Majolo et al. 2012). Male dominance is often established by agonistic interactions. Hence, body size and strength are good predictors of male status and thus reproductive success. Nevertheless, it is rare that a dominant male exclusively sires all offspring in a group (Clutton-Brock and Isvaran 2006). Genetic tests found that over 80% of all offspring can be sired by males other than the alpha male in rhesus macaques, with females

adjusting their willingness to mate with subordinates depending on whether other group members were present or not (Overduin-de Vries et al. 2012). Subordinate males therefore appeared to use a different mating tactic, engaging in sneaky copulations which the dominant male does not notice. A male's ability to monopolize offspring is thus also influenced by his capability to closely guard females (Clutton-Brock and Isvaran 2006). This is also true for single-male, multi-female mating systems. Although the resident male sires, on average, a larger proportion of offspring in this mating system compared to one where multiple adult males are present, genetic tests revealed that a low percentage of paternities are frequently obtained by another male than the group's single resident adult male (Clutton-Brock and Isvaran 2006).

Body size and strength are not only important in stable single or multi-male-female groups but also in species forming all-female groups. African elephants (*Loxodonta africana*), for example, form highly mobile groups consisting of a lead female (the matriarch), her offspring, and sometimes the matriarch's sisters and their offspring (Archie et al. 2006). Female offspring remain in the group, but males leave the group once mature. Female elephants are fertile for a short window of 3 to 6 days every 3 to 9 years (Moss and Poole 1983; Poole and Moss 1989). As a result, male elephants face the challenge of locating an incredibly limited and highly mobile resource while preventing access from other males (Poole 1989; Poole and Moss 1989). Males are expected to be better competitors with increasing size. As a result, male elephants might have been selected to grow throughout their lives (Lee and Moss 1995). Paternity analyses in elephants confirmed that older and hence larger elephants sired more offspring than younger males (Hollister-Smith et al. 2007; Rasmussen et al. 2007). This effect was even more pronounced when males were in largely testosterone-driven musth, a condition where males are more aggressive and sexually active.

In some species, males cooperate to gain access to females or attain a higher rank (Smith 2014), which increases their chances to mate. Such male cooperation mostly occurs in the form of temporary coalitions in which multiple males collaborate to compete against a single or multiple others. Due to the indivisibility of fertilizations, male cooperation poses an evolutionary paradox: although all males get to mate, only a single male succeeds in siring offspring. However, kin selection can resolve this paradox in cases where coalitions or alliances consist of relatives. Genetic studies confirmed that kin selection underlies cooperation in male cheetahs (*Acinonyx jubatus*, Caro 1990; Caro and Kelly 2019) and some, but not all, coalitions in lions (*Panthera leo*, Packer et al. 1991; Chakrabarti et al. 2020) and chimpanzees (*Pan troglodytes*, Mitani et al. 2000; Langergraber et al. 2007).

In cases where alliances and coalitions were not found to be kin-biased, cooperation often occurred among males with close social bonds (Berghänel et al. 2011; Feldblum et al. 2021; Gerber et al. 2022). Social bonds can be defined as affiliative and persisting relationships and are sometimes referred to as "friendships" (Silk 2002; Cords and Thompson 2017; Massen 2017). A study in chimpanzees revealed that males with vast social networks and strong social bonds to others sired more offspring compared to males with few or weak social bonds (Feldblum et al. 2021).

In Barbary macaques (*Macaca sylvanus*), males affiliating in the non-mating season formed coalitions during the mating season (Berghänel et al. 2011); the strong social bonds facilitating coalition formation in this species correlated with future social status and thereby paternity success (Schülke et al. 2010). Although kinship facilitated social bond formation, the majority of social bonds were formed among non-kin (De Moor et al. 2020). Coalition formation thus can increase a male's direct and indirect fitness.

2.3.2 Variables Contributing to Reproductive Success in Male Cetaceans

Female cetaceans are highly mobile, often dispersed, and have three dimensions to escape mating attempts by males. Thus, cetacean females cannot easily be monopolized, resulting in males having little control over access to females. Because of this, most male cetaceans have to search for receptive females to mate with while outcompeting other males, either by mate guarding, physical fights, or display competition like songs (Mesnick and Ralls 2018a, b).

Genetic paternity tests in multiple cetacean species found that paternity skew was low, thereby confirming that males lack control over access to females and thus are likely to employ a roaming approach to find females. In humpback whales (*Megaptera novaeangliae*), 62 calves were assigned to 51 fathers, indicating that most males who successfully sired an offspring did so only once; no male was identified as the father of more than three calves (Cerchio et al. 2005). Similarly, in Atlantic spotted dolphins (*Stenella frontalis*), seven males sired ten offspring (Green et al. 2011), all of whom were 18 years or older despite males reaching sexual maturity between 12 and 15 years old, suggesting that older males have higher chances of siring offspring compared to younger ones. In North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*), genetic analyses found reproductive success to be skewed toward older males (Frasier et al. 2007; Ford et al. 2011). In killer whales, aggressive encounters between males have rarely been observed, implying that the greater reproductive success of older males compared to younger males is because they are preferred by females or due to them having an advantage in sperm competition. In North Atlantic right whales, a single female and 2 to 40 males form mating groups referred to as surface active groups (SAGs), within which males aggressively compete for positions closest to the female (Kraus and Hatch 2001; Parks et al. 2007). Over the course of an average SAG, lasting 1 hour, the female copulates approximately 60 times with multiple males, implying intense sperm competition (Kraus and Hatch 2001). Considering that testes may not yet be fully developed in young adult males engaging in SAGs, older males may indeed have an advantage (Frasier et al. 2007).

Bottlenose dolphins (*Tursiops* spp.) have a wide distribution with distinct morphological and behavioral differences among populations. In some populations

where sexual size dimorphism is low, males form cooperative alliances to mate with females (Möller et al. 2001; Parsons et al. 2003b; Whitehead and Connor 2005). Compared to acting alone, multiple cooperating males are believed to be better at preventing females from escaping coerced matings. Additionally, multiple males can outcompete single males. In Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, for example, non-allied males sired no or very few offspring (Krützen et al. 2004; Gerber et al. 2022). A study on the same species but in a different location (Port Stephens, Australia) found that alliance size correlated with reproductive success, suggesting that larger alliances have higher chances of siring offspring compared to smaller ones (Wiszniewski et al. 2012). However, cooperating with others to gain mating opportunities might be costly because only one male will be able to sire a female's single offspring per pregnancy.

Multiple studies investigated whether kin selection can explain alliance formation in bottlenose dolphins. In a *Tursiops* cf. *australis* population in South Australia and a *Tursiops truncatus* population in the Bahamas, allied males appeared to be more closely related than expected by chance (Parsons et al. 2003b; Diaz-Aguirre et al. 2018). However, this was not the case for the *Tursiops aduncus* populations in Shark Bay and Port Stephens, both in Australia (Möller et al. 2001; Gerber et al. 2021). Paternity success in Shark Bay was predicted by social integration; male dolphins with strong social bonds to their alliance partners sired more offspring compared to those with weaker bonds (Gerber et al. 2022). Thus, the differences between these populations might disappear if conducted with more comparable datasets and methods. Bottlenose dolphins are the only cetacean taxon where male reproductive success has been studied in multiple populations over a wide geographic scale. The differing results suggest that males employ different mating tactics, potentially dependent on their ecological and social environments that can differ within a species. Whether this is also the case in other cetacean taxa remains to be investigated.

2.4   Reproductive Success of Female Mammals

2.4.1   *Variables Influencing Reproductive Success in Females*

The reproductive success of females is influenced by their access to resources and their reproductive timespan as a result of the energetic and temporal demands of gestation and lactation (Clutton-Brock 1989). Young mammals are dependent on their mothers for nutrition and are therefore found in association with their mothers during the first period of their lives. For that reason, genetic tests are rarely required to identify a female's offspring, at least not in well-monitored long-term study populations. However, genetic tools can be useful to identify whether females embedded in a vast kin network have higher lifetime reproductive success compared to such with few relatives.

Philopatry, defined as an individual's tendency to remain in the area where it was born (Mayr 2013), increases the chances to have access to kin. In most mammals, females are philopatric, possibly because females gain more benefits from remaining in their natal area than males (Greenwood 1980). Benefits include the avoidance of the energetic demands of dispersal and the maintenance of a familiar diet in a familiar habitat with familiar individuals (Clutton-Brock and Lukas 2012). In group-living individuals, female philopatry results in females being in the same social groups as their relatives (Clutton-Brock and Lukas 2012; van Noordwijk et al. 2012), while in solitary species, female relatives frequently have adjoining habitats, as, for example, observed in Bornean orangutans (*Pongo pygmaeus*) (van Noordwijk et al. 2012). Using genetic tools, it was found that although related and unrelated female orangutans had similar home-range overlaps, related females spent more time in association and permitted their offspring to play, which was not the case for the offspring of unrelated females (van Noordwijk et al. 2012). Similarly, a study in African elephants found that group fusions were more likely to occur when the matriarchs of the groups were related than unrelated (Archie et al. 2006). Moreover, fissions within a group were influenced by genetic relatedness; female elephants remained in the same group as their relatives (Archie et al. 2006).

Yellow baboons (*Papio cynocephalus*) live in multi-male with multi-female groups. Females are philopatric. Unlike males, where social status depends on the outcome of aggressive interactions, females inherit the social status of their mothers (Samuels et al. 1987). Compared to low-ranking females, high-ranking females benefit from better access to resources and thus often have large-for-age offspring (Altmann and Alberts 2005). Yet, the influence of dominance rank on female reproductive success is generally low (Altmann and Alberts 2003; Cheney et al. 2004). However, the offspring of females with close social bonds to other females had higher rates of offspring survival and lived longer compared to females with weaker social bonds (Silk et al. 2009). Most social bonds were formed among related females. Nevertheless, females without relatives formed social bonds to non-kin conveying the same fitness benefits (Silk et al. 2009). Thus, social bonds to relatives and non-relatives contribute to female reproductive success. Overall, studies on terrestrial mammals suggest that solitary as well as group-living females benefit from affiliating with their female relatives.

2.4.2 The Influence of Female Relatives on Reproductive Success in Cetaceans

Cetaceans are long-lived mammals with slow life histories; after a gestational period of 9–17 months, females give birth to a single calf (Drinkwater and Branch 2022). Calves are dependent on their mothers for the first period of their lives, leading to long inter-birth intervals ranging from 1 to 7 years (Mesnick and Ralls 2018b). In all cetacean species, calves are born precocial, meaning they can move independently,

come to the surface for air, and maintain proximity with their mothers from birth (Whitehead and Mann 2000). However, females benefit from being in association with other females through cooperative hunting, increased vigilance, joint defense of their calves and themselves, and potentially allomaternal care (i.e., temporal care of a calf by a non-mother; Würsig et al. 2023, this book). In sperm whales (*Physeter macrocephalus*), for example, young individuals are accompanied at the surface by different group members, while other group members, including mothers, forage at depth (Whitehead 1996; Gero et al. 2009).

Female group composition is often influenced by kinship. Killer and sperm whales, for example, form stable matrilineal units consisting of a female and her male and female offspring (Ford 2018). A kinship analysis in sperm whales found that females preferably affiliated with close kin within social units (Konrad et al. 2018). However, maternal relatives also maintain stronger bonds in dynamic fission-fusion societies consisting of multiple matrilines, such as bottlenose dolphins (Frère et al. 2010b).

In the well-studied Indo-Pacific bottlenose dolphins in Shark Bay, Australia, females form loose kin-biased social networks (Frère et al. 2010b). Female dolphins inherit the social network of their mother (Frère et al. 2010a), which affects their reproductive success because calving success (Frère et al. 2010b) and the survival of male offspring (Stanton and Mann 2012) are influenced by a female's social bonds to others. A potential influence of social bonds on reproductive success was also found in female humpback whales; female pairs that were observed together over multiple years sired the most offspring (Ramp et al. 2010). It is unclear whether these associations were kin-biased or not. However, research on different individuals in the same location found maternally related females more likely to associate than expected by chance (Weinrich et al. 2006), implying that associations in this species might contribute to direct and indirect fitness.

In at least some killer whale populations, females form "pods" consisting of a matriarch and her sons and daughters. The calves of older matriarchs suffer from higher mortality rates compared to their daughter's offspring in the same group (Croft et al. 2017). Furthermore, the presence of a post-reproductive mother increased survival of her older sons (Foster et al. 2012). With increasing age, the indirect fitness benefits gained from helping offspring might therefore outweigh the direct fitness benefits gained from reproducing. This might have contributed toward the evolution of reproductive senescence (menopause) in this species. The evolutionary fitness of female cetaceans can thereafter not simply be understood as a by-product of resource availability but depends on a species' social structure and the availability of kin therein.

2.5 Comparison Between Terrestrial and Marine Mammals

The transition from terrestrial into marine habitats by the predecessor of marine mammals was facilitated by morphological, physiological, and behavioral adaptations. However, despite large morphological differences, marine and terrestrial mammals with slow life histories and singleton births face similar constraints resulting in analogies. Cetaceans and long-lived terrestrial species, such as primates and elephants, thus bear striking behavioral similarities; all three possess high cognitive skills and have the ability for social learning (Lee and Moss 1999; Whiten and van de Waal 2017; Whitehead and Rendell 2021). Primates, cetaceans, and elephants belong to different taxonomic orders (primates, Primata; elephants, Proboscidea; cetaceans, Artiodactyla or Cetartiodactyla). Thus, these shared traits are the result of convergent evolution (i.e., they have evolved independently). Genetic studies in marine and terrestrial mammals established that analogies among marine and terrestrial mammals can also be observed as regards their reproduction; the monopolization potential of females affects male reproductive success, while females benefit from being in association with relatives. However, there are also differences among the species inhabiting land and sea.

Like most mammals, cetaceans are either polygynous or polygynandrous. However, reproductive skew in marine mammals is much lower compared to terrestrial mammals (Frasier et al. 2007), possibly because males have less control over access to females in aquatic species where females can move in three dimensions or because paternity data are still scarce even in the most-studied populations. If multiple males cooperate, females are less likely to outmaneuver males, which might have contributed to the evolution of male alliances in species that are able to move in three dimensions such as chimpanzees with remarkable climbing skills (Watts 1998), some birds (e.g., long-tailed manakins (*Chiroxiphia linearis*), McDonald and Potts 1994), and bottlenose dolphins (Connor and Krützen 2015).

Social status has a profound effect on male reproductive success in a multitude of mammalian species. Yet, little is known of the existence of dominance hierarchies in cetaceans (Tyack 2018). Although the lack of supporting evidence for dominance hierarchies in cetaceans does not mean that they are non-existent, it is likely that dominance hierarchies do not govern inter-individual interactions to the same extent as in terrestrial species. Compared to females in terrestrial mammal species, female cetaceans can move in three dimensions and thus might have increased abilities to avoid matings with undesired males. Furthermore, marine food sources such as fish and krill are widely distributed and cannot easily be monopolized by social groups, resulting in vast overlapping home ranges or migratory lifestyles. Lack of controlled access to females and of clustered resources may have contributed to the (apparent) lack of social hierarchies.

The lack of social hierarchies, however, does not mean that social interactions are of less importance in marine compared to terrestrial mammals. The presently most complex social system known outside of humans is in male bottlenose dolphins in Shark Bay, Australia, that cooperate in multi-level alliances over access to females

(Connor and Krützen 2015). Similar to humans (Snyder-Mackler et al. 2020) and chimpanzees (Feldblum et al. 2021), same-sex social bonds positively contributed to the evolutionary fitness of male and female bottlenose dolphins in Shark Bay (Frère et al. 2010b; Gerber et al. 2022). In females but not males, social bonds are often biased toward relatives (Frère et al. 2010b; Gerber et al. 2021).

In African elephants, a matriarch's ability to assess threats from predators increases with age (McComb et al. 2011). In killer whales, old females lead their matrilines to alternative feeding grounds when prey abundance at their current site is low, thereby ensuring the survival and health of their relatives, in particular of their adult sons (Brent et al. 2015). The indirect fitness benefits gained from assisting relatives, combined with the increased mortality rates of their own offspring with age, might have contributed to the evolution of reproductive senescence in killer whales. This is similar to humans, where grandmothers increase their inclusive fitness by caring and providing for their daughter's children (Shanley et al. 2007). Mothers can also positively influence the reproductive success of their sons. In bonobos (*Pan paniscus*), males that live in the same groups as their mothers sire more offspring compared to males without their mothers (Surbeck et al. 2019). The influence of maternal presence on male reproductive success in cetaceans is largely unexplored. However, a female killer whale cooperated with her adult son in killing an unrelated female's calf (Towers et al. 2018), potentially to increase his own reproduction. In order to aid their sons, females may hinder other males from mating or bring their sons in proximity to estrus females as observed in bonobos (Surbeck et al. 2011). In cetaceans, mothers could positively influence the fitness of their sons where both sexes remain in their natal area and sexual dimorphism is low, such as for some bottlenose dolphin populations or other delphinids (Mesnick and Ralls 2018a).

2.6   Conclusions and Future Directions

Genetic advances over the past two to four decades have confirmed what scientists, dating back to the theories of Darwin, already suspected: factors improving a male's access to females increase male reproductive success while female reproductive success is positively affected by variables influencing their own and their offspring's survival. The large diversity in reproductive strategies and tactics across mammals exemplifies that there are often multiple ways that reproductive success can be maximized. Similarities occur between terrestrial and marine species, while in each realm there is large diversity; this implies that reproductive strategies are often the result of convergent evolution and that somewhat similar selective pressures are experienced on land and in the sea.

Due to the slow life histories of cetaceans, paternity studies require that populations are monitored over a long time, and such studies are rare. Nevertheless, the results from long-term investments provide unique insights into mating strategies and tactics, and are invaluable to increase our understanding of how individuals maximize individual (and as a by-product, evolutionary) fitness. Novel molecular

techniques might decrease the large amount of time dedicated to sampling and monitoring populations required for parentage analyses; passive eDNA collection might permit the collection of population-wide samples within a few weeks. Furthermore, epigenetic clocks produce reliable age estimates for cetaceans including bottlenose dolphins (Peters et al. 2023), beluga whales (*Delphinapterus leucas*, Bors et al. 2021), and humpback whales (Horvath et al. 2022). Using epigenetic clocks in populations where individual ages are unknown will greatly facilitate parentage analyses because the direction of a parent-offspring relationship will be known (i.e., the older individual will be assigned as parent of the younger one and not vice versa). In the next decade, advances in molecular biology will permit the ability to fill some of the numerous gaps of knowledge on cetacean reproductive success, thereby learning more about what variables contribute to direct fitness in the marine realm.

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Chapter 3
Skulls, Teeth, and Sex

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Abstract Males and females of a species may differ in external appearance or other features. Sexual dimorphism often relates to mating behavior, via male-male competition for access to females (through direct fighting and/or indirect display), female choice of mates, or sexual conflict. In many mammals, skulls and teeth often display sexual dimorphism. Cetaceans show extraordinary variation in their dentition, and because teeth are often preserved, the evolutionary origins of these morphological novelties can be tracked in the fossil record. Sexual dimorphism has been proposed in several fossil cetaceans (i.e., pakicetids, protocetids, fossil beaked whales) and some odontocetes (notably *Odobenocetops*), and mainly inferred from differences in tooth size, skull dimensions, and thickening of skull bones. Within modern taxa, unusual differences in the dentition between the sexes have been observed in deep-diving beaked whales and arctic narwhals, the unicorns of the sea. Mandibular tusks in beaked whales are unusual because they erupt only in males, erupt only at sexual maturity, and protrude outside the mouth rather than projecting into the oral cavity. In beaked whales, the tusk-like dentition seems to have a minimal role in feeding, and functions as weapons or displays for intrasexual (e.g., male-male combat) and intersexual (e.g., female mate choice) competition, and possibly for female harassment by males seeking to mate. In narwhals, the long and spiralled left tusk commonly only erupts in males and is presumed to play a prominent role in male-male fighting or displays for female mate choice. Except for narwhals and beaked whales, sexual dimorphism in skull and dental structures is not prominent in cetaceans. However, we still do not know whether functional aspects such as enamel

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structure and thickness, mechanical properties, and chemical composition of dental tissues may vary between males and females.

3.1   Sexual Dimorphism in Mammals

Sexual dimorphism is defined as the two sexes of a species differing in external appearances or other features. Sexual dimorphism generally involves different body sizes, forms, proportions, other external features on the body (e.g., crests, combs, wattles protruding from the head), or different integumentary coverings (e.g., hair, scales, feathers) between males and females (Clutton-Brock 2007; Roughgarden 2015). Such differences normally relate to three aspects of mating that might involve agonistic behaviors: (1) male-male competition for access to females via direct fighting or indirect display, (2) female choice of mate(s), and (3) sexual conflict (Arnqvist and Rowe 2005; Hosken and House 2011; Parker and Pizzari 2015; Würsig et al. 2023, this book).

Although sexual dimorphism can relate to differences in body size, coloration, or other external body features, this chapter focuses on cranial characteristics. In many mammals, skulls and teeth are commonly sexual dimorphic (Martin et al. 1994; Gittleman and Valkenburgh 1997) and serve as both indicators of and tools for sexual selection (Radinsky 1981). Skulls of males often exhibit larger overall size and allometrically larger dimensions than females, even when corrected for body size, notably for zygomatic width and condylobasal length (Biknevicius and Van Valkenburgh 2019). The increased size of skulls of males may function in male-male combat, displays to attract females or threaten potential rival males, or potentially for combat with females during sexual coercion. Large cranial or braincase bones, usually in males, may serve to anchor displays such as enlarged antlers and horns, or as protection from head-butting or other forms of physical combat experienced during agonistic behavior (Andersson 2019; Lopez and Stankowich 2023).

Sexual differences in mammalian skulls can also reflect differences in jaw adductor musculature and consequent bite forces (Gittleman and Valkenburgh 1997). Such cranial differences might relate to sexual dimorphism in the mammalian dentition, with males often possessing larger teeth than females (Leutenegger and Cheverud 1985; Dayan et al. 1992; Martin et al. 1994). This occurs in several marine mammals including some pinnipeds (Mccann 1981). As with skull bones, the larger teeth of males compared to females might serve several distinct functions including displays to woo females or threaten rival males, or physical combat with rival males. Alternately, the larger teeth of males might reflect size/shape differences in skulls, differences in diet, or differences in foraging ecology and feeding methods. Male mammals typically exhibit greater heterodonty—shape and size differences among teeth—relative to females, with canines often significantly larger (Harvey et al.

1978). The trend toward larger teeth and greater dental diversity in males compared to females is also apparent in cetaceans.

### 3.1.1 Fossil Evidence for Sexual Dimorphism in Cetaceans

For fossil and modern cetaceans, determining sexual dimorphism relies on understanding the amount of variation in a morphological feature present in a single species (O'leary et al. 2000; Marx et al. 2016). This is difficult to determine in fossils because the rare and fragmentary nature of specimens hampers our understanding of intraspecific variation.

Raoellids—in particular the genus *Indohyus*—are small artiodactyls from the middle Eocene of the Indian subcontinent that are considered a sister group to cetaceans. Studies on dental material revealed no evidence of sexual dimorphism in the teeth of *Indohyus* (Thewissen et al. 2020). Analysis of several deciduous and permanent teeth of the early Eocene *Pakicetus inachus* showed the lower canines varied in size and may have been sexually dimorphic (Gingerich and Russell 1990; Marx et al. 2016). Sexual dimorphism was also inferred in protocetids, middle Eocene amphibious archaeocetes. Two skeletons of *Maiacetus inuus* from the Habib Rahi Formation of Pakistan, one of which was smaller and carried the skull and partial skeleton of a near-term fetus, suggest males were about 10% larger in skeletal linear dimensions and had canines 20% larger than females (Gingerich et al. 2009). Sexual dimorphism, although considered moderate, suggests limited male-male competition during reproduction in protocetids (Gingerich et al. 2009).

Sexual dimorphism has also been implied in several late Miocene beaked whales including *Messapicetus* sp. from Peru. A large sample of *Messapicetus* sp. from the same locality and geological age suggests intraspecific variation in the size and shape of the tusks, accompanied by thickened premaxillae dorsally closing the mesorostral groove in the rostrum of *Messapicetus* (Lambert et al. 2010). In modern beaked whales (family: ZiphiidaeZiphiidae), similar features may be used in intraspecific fights between adult males, with the rostrum strengthened to avoid fractures. The holotype (the type of specimen used to describe a species) of the fossil ziphiid *Dagonodum mojnum* from the upper Miocene of Denmark and sister taxon of *Messapicetus* was inferred as being male due to its enlarged tusks (Ramassamy 2016).

Odobenocetops, a Pliocene South American odontocete remarkable for apparently striking evolutionary convergence with walruses (*Odobenus*), had a pair of posteroventrally oriented long tusks, with the right tusk five times longer than the left (De Muizon 1993; De Muizon and Domning 2002). A skull of *O. peruvianus* with two small tusks of similar size has been attributed to a female (De Muizon et al. 1999), implying that *Odobenocetops* was also sexually dimorphic. While the tusk of male narwhals typically erupts from the left maxilla, in *Odobenocetops* the larger tusk erupts from the right premaxilla (De Muizon and Domning 2002). Tusks in *Odobenocetops* have been interpreted to aid in benthic feeding as observed in
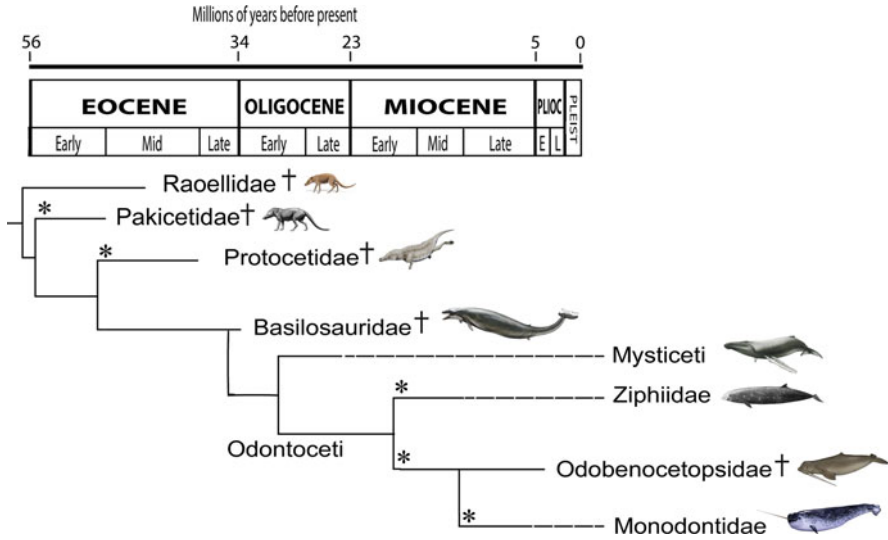
Fig. 3.1 Simplified cetacean phylogeny over time, including Raoellidae as sister group. Families in which sexual dimorphism has been inferred and discussed in this chapter are marked with an asterisk (key: asterisk = sexual dimorphism in skull/teeth; cross = extinct; dashed lines = living lineages)

walruses, but also might have had social functions such as displays (Marx et al. 2016). Figure 3.1 shows a simplified cetacean phylogeny over time, including Raoellidae as sister group, and families in which sexual dimorphism has been inferred and discussed in this chapter.

3.1.2 Sexual Dimorphism in Modern Cetaceans

As in numerous other mammals, skull size and shape differ between males and females of some odontocete species. This difference is especially pronounced in sperm whales, Physeteridae, and beaked whales, Ziphiidae (Nakamura et al. 2013; Gol'din 2014). Overall head size and shape are also sexually dimorphic in many odontocetes, with males often having a longer rostrum and more prominent melon than females (Mesnick and Ralls 2018). These structural differences are likely related to differing behaviors between the sexes. For example, males engage in more head-butting and aggressive behaviors than females, as seen in bottlenose whales *Hyperoodon*, in which the enlarged and densely ossified heads of males are used for ramming each other during fights (Gowans and Rendell 1999; Macleod 2018; Mesnick and Ralls 2018). Another example is the difference in sound production frequencies and magnitude between the sexes, especially in sperm whales (Cranford 1999; Mesnick and Ralls 2018). Some studies have suggested sexual dimorphism in

linear measurements and tooth counts in odontocete skulls, with greatest parietal width and tooth count in males (striped dolphin, *Stenella coeruleoalba* (Carlini et al. 2013); common bottlenose dolphin, *Tursiops truncatus* (Hersh et al. 1990)).

In most odontocetes, teeth are the most pronounced sexually dimorphic feature in the cranial region (Silverman and Dunbar 1980; Heyning 1984; Dines et al. 2015; Fordyce 2018). The dentition is crucially important for feeding in some but not all odontocetes; in some species, teeth are a poor descriptive character if technically an apt diagnostic one (Werth 2000). Although some odontocetes exhibit the highest tooth counts of all eutherian mammals (i.e., longirostrine oceanic and riverine dolphins, some of which average up to 240 teeth), numerous odontocete species have few if any erupted teeth as adults or as juveniles (Uhen 2018; Werth et al. 2019). For example, Risso's dolphins, *Grampus griseus*, and sperm whales, *Physeter macrocephalus*, have erupted teeth only in the lower jaw. Sperm whales occasionally exhibit a congenital defect in which the mandible develops in a spiralled curve that cannot fit the upper jaw (Nasu 1958; Spaul 1964); they also sometimes exhibit broken mandibles that re-heal at an improper angle and prevent normal occlusion (Heezen 1957). Sperm whales with abnormal jaws and no functional dentition appear to be healthy (Nakamura 1968); their stomach contents indicate they feed on prey of the same type and size as sperm whales with normal jaws and dentition (Clarke et al. 1988; Werth 2000). This means that cetacean teeth do not always function in feeding (Uhen 2018). Many cetacean taxa with few teeth (e.g., monodontids, beaked whales, sperm whales) are powerful suction feeders, a major adaptation that facilitates life in the water. This indirectly allows teeth to be released from constraints associated with feeding and to be exapted for other purposes such as weaponry and sexual displays (Werth 2000).

## 3.2 Teeth and Sex in Cetaceans: The Case of Beaked Whales and Narwhals

Most beaked whales except for Shepherd's beaked whales, *Tasmacetus shepherdi*, have one or two pairs of erupted teeth. These mandibular (lower or dentary) teeth typically exist as robust and heavy tusk-like structures; they may also have unusual shapes, such as the flattened plates that encircle the upper jaw and restrict gape in male strap-toothed whales, *Mesoplodon layardii* (Fig. 3.2). This pair of lower teeth in beaked whales are unusual because they: (1) erupt only in males (except for the genus *Berardius*, in which teeth erupt in both sexes), (2) erupt only at the onset of sexual maturity, (3) protrude outside the mouth rather than projecting into the oral cavity, and (4) are frequently covered with barnacles or other epizoic organisms. It is difficult to claim that beaked whales use such dentition to capture, ingest, or process prey because stomach contents indicate that female beaked whales ingest the same type and size of prey with no discernible differences in foraging methods or feeding mechanisms (Werth 2000).

Fig. 3.2 The strap-toothed
whale *Mesoplodon layardii*
in frontal view. The lower
tusks grow as flattened
plates that encircle the upper
jaw and restrict mouth gape

Beaked whales are exceptional divers (Tyack et al. 2006). Evidence from tag, stomach content, and morphological data indicate that beaked whales rely largely if not exclusively on suction feeding to capture, ingest, and transport individual prey (Werth 2000). The large hemicylindrical tongue of beaked whales is rapidly withdrawn from the oral cavity in piston-like fashion via hyolingual retraction and depression (Heyning and Mead 1996). This draws water and prey into the mouth unidirectionally with ingested water then purged. A bilateral pair of external throat grooves aids beaked whales in accommodating the volume of water ingested via suction feeding, as in gray whales, *Eschrichtius robustus* (Werth 2007). A lack of bite marks on stomach contents confirms that beaked whale teeth are generally neither used nor needed for feeding and plausibly explains the absence of erupted teeth in females (Werth 2000). This also explains the reduced gape in the strap-toothed whale, due to dental encirclement of the rostrum, which seems to hinder feeding.

Why, then, do male ziphiids possess a pair of large, erupted, tusk-like teeth? These appear to have two functions: weapons or displays for intrasexual (male-male combat) and intersexual competition (female mate choice (Berglund et al. 1996), Fig. 3.3). Heyning (1984) and MacLeod (1998) described patterns of
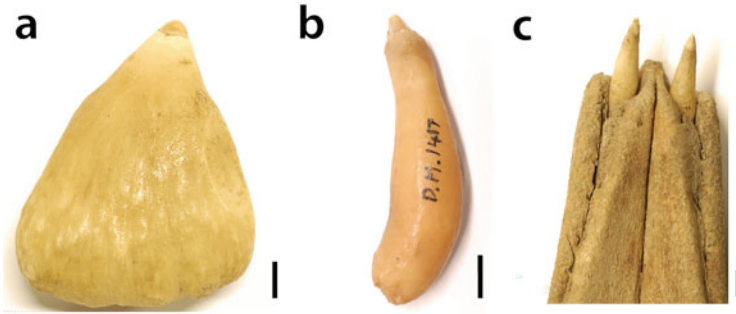
Fig. 3.3 Lower tusks in beaked whales. Scale bar = 1 cm. (**a**) Arnoux's beaked whale (*Berardius arnuxii*), (**b**) Southern bottlenose whale (*Hyperoodon planifrons*), and (**c**) Cuvier's beaked whale (*Ziphius cavirostris*)

Fig. 3.4 A beached Cuvier's beaked whale in Newfoundland. Note the body scarring and rake marks presumably inflicted by tusks of other individuals (photo by Silver Leapers, Wikimedia Commons)

conspicuous, prominent, linear scarring in beaked whales caused by fighting with tusks. There were numerous deep scratches, scrapes, and gouges along the head, trunk, and tail stock of males, some of which closely resembled parallel rake marks generated by biting or dental scraping on the body surface of dolphins (Heyning 1984; Fig. 3.4). That such scars seldomly occur in female beaked whales indicates that erupted male teeth are used to compete for females (Macleod 1998). In addition to direct male-male battles, the displayed scars may act as "honest signals" to indicate the fitness of potential mates (Andersson 2019; Würsig et al. 2023, this book). The use of dentition to subdue females has not been observed, although behavioral interactions have only rarely been observed among beaked whales.

Female beaked whales exhibit significantly less body scarring than males (Heyning 1984; Macleod 1998); It is possible that scars on females are intentionally or incidentally inflicted when males harass females to mate, as noted for parallel rake marks also inflicted by teeth on bodies of female bottlenose dolphins, *Tursiops truncatus* (Connor et al. 2005; Marley et al. 2013). Due to their elusive behavior and deep-diving capabilities, beaked whales are the poorest known cetaceans; the few ecological studies on beaked whales focused on diving and acoustic behaviors (Baird 2019; Alves et al. 2023, this book).

Heyning (1984) hypothesized that during the evolution of mesoplodont beaked whales (*Mesoplodon*, the largest beaked whale genus), teeth migrated caudally along the mandibles and became more elevated above the rostrum in males compared to females. At the same time, the mesorostral canal became more densely ossified— another dimorphic feature also of mature ziphiids—reinforcing the male rostrum for more effective dental combat. Compared to females, male mesoplodont teeth are: (1) larger and more robust in size, (2) more triangular in shape (often with a sharp, pointed main cusp, perhaps to aid in fighting or scarring opponents), (3) located more caudally, and (4) positioned higher (more dorsally) in the mandible, along a bony arch that curves with a convex dorsal side, likely to aid in the tooth's use as a weapon or display (Macleod 1998; Macleod 2000). These structural differences are paralleled by different behaviors between the sexes, with at least some male beaked whales documented as significantly more aggressive than females (Heyning 1984; Gowans and Rendell 1999).

Another cetacean with extreme dental dimorphism between the sexes is the monodontid narwhal, *Monodon monoceros* (literally, "one tooth, one tusk"). The narwhal is known for its long spiralled tusk (Nweeia et al. 2012), which presumably gave rise to unicorn legends (Bruemmer 1993). Narwhal tusks are exceptionally enlarged left upper teeth in the general position of mammalian canines, with a left-handed spiral; they can grow to 3 m in length and weigh around 10 kg (Hay and Mansfield 1989; Fig. 3.5). The tusks normally erupt only in males. In females, both the left and right upper canines—the only two functional teeth of narwhals—are normally unerupted. However, on rare occasions a female narwhal has an erupted tusk (Uhen 2018; Fig. 3.6). Even more rare are males with two tusks, from both left and right upper canines (Uhen 2018; Garde and Heide-Jørgensen 2022).

As with beaked whales, there are no appreciable dietary or foraging differences between male and female narwhals. Isotopic analysis indicates that the slight differences in prey type and size of male and female narwhals are not statistically significant, with males slightly larger in body size and at times foraging at greater depth than females (Watt and Ferguson 2015). It is possible that males are better able to stir up benthic prey with their tusks; however, tusks may also hinder capture of benthic prey by male narwhals (Watt et al. 2013). Narwhals frequently travel in sex-segregated groups, which might also explain slight dietary differences along with regional and seasonal changes in diet (Marcoux et al. 2009).

There has been continued speculation that male narwhals possibly swing their tusks to tap or strike at small- and medium-sized fish to disable or stun prey prior to ingestion (Bruemmer 1993). Although this idea has received attention in popular

Fig. 3.5 Tusk of a male narwhal on exhibit at the Naturmuseum Senckenberg, Frankfurt, Germany
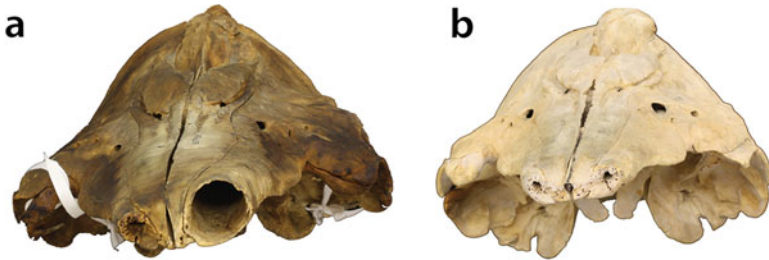
Fig. 3.6 Frontal view of the narwhal skull. Note the enlarged left canine alveolus in males. (**a**) male and (**b**) female

press based on subjective analysis of videorecordings from aerial drones (WWF Canada 2017), it has not been verified by peer-reviewed publications. Given that female narwhals have longer lifespans than males (Hay and Mansfield 1989), tusks do not seem to confer selective advantages in prey acquisition.

Narwhals are known to exhibit sexually driven dominance hierarchies (Bruemmer 1993). Given the lack of appreciable differences in diet or dental function between males and females in narwhals and beaked whales, their erupted teeth likely serve as dimorphic characters playing prominent roles in male-male fighting (Best 1981) or displays for female mate choice (Kelley et al. 2015; Graham et al. 2020). Just as dental differences in beaked whales relate to sexual dimorphism, the same is likely true of narwhal tusks, which have prompted much speculation as to potential function(s), including roles in spearing or disabling prey (Best 1981), serving as "swords" for direct male competition (e.g., horns of butting rams; Graham et al. 2020), or serving as sensory structures to sense changes in water temperature or chemistry (Nweeia et al. 2012; Fig. 3.7).

The only other monodontid species besides the narwhal is the beluga whale (white whale), *Delphinapterus leucas*. Beluga whales are thought to ingest prey primarily via intraorally generated suction produced by rapid retraction and

Fig. 3.7 Narwhal males surfacing. Note the spiralled tusk protruding out of the water (photo by NOAA/Climate.gov, Wikimedia Commons)

depression of the large tongue (Werth 2007). The dentition of the beluga whale exhibits some dimorphism, with males often bearing larger teeth even when corrected for body size; males may also exhibit slightly more dental wear and body scarring (Ham et al. 2021).

3.3   Future Directions

Although our understanding of morphological differences between the sexes is increasing, our knowledge of sexual dimorphism in cetaceans is still incomplete, especially for elusive and poorly known species. Except for narwhals and beaked whales, sexual dimorphism in skull and dental structures seems minimal in cetaceans. For most modern odontocetes, the shape, size, and number of teeth are similar among males and females. However, we still do not know whether functional aspects such as enamel structure and thickness, mechanical properties, and chemical composition of dental tissues vary between males and females (e.g., Loch et al. 2013a, b, 2014), and future studies should investigate this.

In addition to their role in mating systems, sexual dimorphism may also foster resource partitioning between the sexes (Andersson 2019). A crucial caveat is that not all dimorphism is necessarily adaptive or functionally/ecologically significant. Differential phenotypes may be the inadvertent by-product of sex-specific physiology or development (e.g., levels of testosterone or other morphogenetic hormones).

Although such sexual differences are valid dimorphisms, they might not reflect different functions or other roles in male and female behavior, physiology, or performance.

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Chapter 4
Cetacean Evolution: Copulatory and Birthing Consequences of Pelvic and Hindlimb Reduction

Lisa Noelle Cooper, Robert Suydam, and J. G. M. Thewissen

Abstract The earliest fossil cetaceans (archaeocetes) dramatically shifted the shape and articulation of the pelvis and hindlimbs during the land-to-sea transition. Archaeocetes were mostly semi-aquatic "walking whales" that used powerful hindlimbs to walk on land and swim to reach new aquatic sources of food. However, skeletons of the latest diverging lineages of archaeocetes, the basilosaurids, showed that the pelvis initially lost articulation with the sacrum, and hindlimbs were reduced and encased within the body wall. Consequently, basilosaurids were no longer able to bear their weight on land and probably had a different mating strategy compared to the other archaeocetes. Basilosaurid mating behaviors were probably consistent with those of modern cetaceans, including lateral- and ventral-facing copulation. Moreover, a pelvic girdle that was no longer constrained by vertebral and limb attachments likely freed fetal development from size constraints at birth, allowing for the birth of large fetuses. This study reports new data showing growth of the pelvis with age in modern bowhead whales (*Balaena mysticetus*) and their implications for left-right asymmetry and sex difference in pelvic dimensions among modern cetaceans. Reproductive structures present in modern cetaceans and artiodactyls were probably present in archaeocetes, including pelvic attachment of muscles associated with erection and mobility of the penis, the ischiocavernosus, in males and the clitoris of females. Within females, transverse folds along the vaginal canal are present in some terrestrial artiodactyls, modern cetaceans, and probably archaeocetes. Vaginal folds were probably exapted to assist in successful aquatic copulation in all fossil and modern cetaceans as they may protect some sperm from the lethal effects of sea water. Taken together, shifts in the pelvic girdle of cetaceans occurred over 40 million years ago and probably required changes in mating behaviors that were consistent with those seen in modern cetaceans.

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4.1 Introduction

Cetaceans (whales, dolphins, and porpoises) are derived from even toed ungulates (artiodactyls) and have a rich fossil history beginning about 50 million years ago. Early archaeocetes were quadrupedal, and within about 12 million years, the bodies of these whales became streamlined, pelves detached from the vertebral column, hindlimbs were reduced and encased within the body wall, and propulsion was provided by a novel appendage, the tail fluke (Thewissen and McLellan 2009). These changes in the post-cranial skeleton committed whales to life in the water as they were no longer able to bear their weight on land. This chapter reviews evolutionary changes in the pelvic girdle of archaeocetes, speculates on their potential consequences for muscle evolution and mating behaviors, and presents new ontogenetic data on dimensions of the pelves of modern bowhead whales. Taken together, these data create an evolutionary framework that allows readers to understand the morphological diversity and functional shifts that led to the mating systems of modern cetaceans.

4.2 Robust Pelves and Hindlimbs in Some Archaeocetes

4.2.1 Pakicetids, Ambulocetids, Remingtonocetids, and Protocetids

The earliest recovered fossil archaeocetes were collected in rocks of Pakistan and India that are about 48 million years old. These whales, called pakicetids and ambulocetids (Fig. 4.1b), were amphibious, and their robust hindlimb and tail may have aided in aquatic locomotion (Thewissen et al. 1994, 1996, 2001). The pelvis was fused to the sacrum and displayed a robust obturator foramen (Fig. 4.2) and a well-developed acetabulum for articulation with the femur. The femur and tibia were also thick and dense with mineral, a characteristic that likely allowed pakicetids and ambulocetids to achieve neutral buoyancy in water (Madar 1998; Thewissen et al. 2007). The feet of pakicetids and ambulocetids were broad and probably displayed soft tissue webbing between the digits (Madar 2007) that supported locomotion on soft substrates and increased the surface area of the foot during pelvic and hindlimb undulations during swimming. Mating could have occurred either on land or in water, and it is unclear what mating strategies could have been employed, other than an artiodactyl-like mating approach that included males mounting the females caudally.
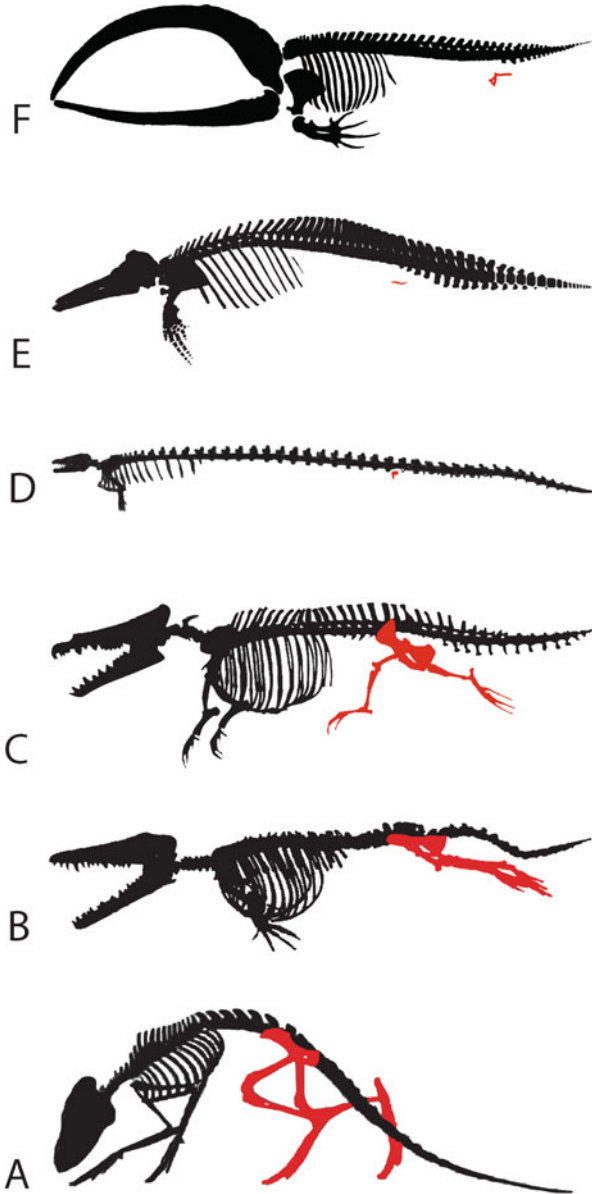
Fig. 4.1 Skeletal evolution along the land-to-sea transition in archaeocetes (**a**–**d**) and morphology of the skeleton in the modern bottlenose dolphin (*Tursiops*) and bowhead whale (*Balaena*). Elements of the pelvic girdle, pelvis, and hindlimbs are shown in red. Other skeletal elements are shown in black. The fossil raoellid *Indohyus* (**a**, Thewissen et al. 2007) had a pelvic girdle typical of artiodactyls. This morphology was retained in archaeocetes, the earliest fossil whales, including *Ambulocetus* (**b**, Thewissen et al. 1996) and the protocetid *Maiacetus* (**c**, Gingerich et al. 2009). Basilosaurid archaeocetes showed a dramatic shift as the pelvis no longer had a bony connection with the vertebral column, and the hindlimbs were reduced to tiny vestiges, as seen in *Basilosaurus* (**d**, Gingerich et al. 1990). Modern cetaceans retain a reduced pelvis, and sometimes hindlimbs, immersed within the body cavity. The pelvis of the bottlenose dolphin (*Tursiops truncatus*, **e**) has a

Fossils of remingtonocetids were recovered from similar aged rocks from present-day India and Pakistan (Gingerich et al. 1997; Thewissen and Bajpai 2001). These archaeocetes were also amphibious but displayed a greater number of bones within their vertebral column, a more gracile skeleton, and a pelvis that was like that of pakicetids (Thewissen and Bajpai 2001). The limbs, although not as robust as those of pakicetids or ambulocetids, were sufficient to support terrestrial locomotion (Bajpai and Thewissen 2000). However, bones of the manus (hand) and pes (foot) are unknown. The pelvic and hindlimb morphologies suggest remingtonocetids probably mated like pakicetids and ambulocetids.

As in pakicetids, ambulocetids, and remingtonocetids, the pelves and hindlimb of protocetids, from 48–33 million years ago, retain a robust pelvic girdle that shared a bony attachment with the sacrum and functioned to support both terrestrial and aquatic locomotion (Fig. 4.1c). Protocetids differ from earlier families of archaeocetes in that they were cosmopolitan with skeletons documented throughout most of the globe. The protocetid whale, *Maiacetus* (Fig. 4.1c), is known from two skeletons that are about 12% different in size, leading to the conclusion of sexual dimorphism in total body size, with the males being larger than females (Gingerich et al. 2009). *Peregocetus*, a quadrupedal protocetid found in Peru from sediments dating to the middle Eocene, showed the sacrum was attached to the pelvis, the hindlimb was functional in both terrestrial and aquatic locomotion, and the digits were capped with small hooves (Lambert et al. 2019). Morphology of the vertebral column suggested aquatic locomotion was supported by a powerful tail that likely functioned in concert with the hindlimbs during aquatic locomotion, similar to modern otters (Geisler 2019).

In contrast, the pelvis of the protocetid *Georgiacetus*, recovered from late middle Eocene sediments dated to about 40 million years ago in North America, showed a pelvis that may have lacked a bony connection to the vertebral column and robust hindlimbs (Hulbert 1998). The concavity that supports pelvic articulation with the femur, the acetabulum, is well developed, suggesting that hindlimb locomotion was supported. Because *Georgiacetus* is unlike other protocetids in potentially lacking articulation between the pelvis and sacrum, it is reasonable to imagine that there were multiple lineages of protocetids swimming in the Eocene oceans and that some of these may have undergone an evolutionary shift toward a lack of function of the pelvis (Hulbert 1998).

Protocetids probably utilized caudal mounting as in other early archaeocetes. Curiously, the presence of a small skeleton partially within the body cavity of the adult protocetid *Maiacetus* has been interpreted as evidence of a head-first birth on land (Gingerich et al. 2009). This hypothesis has since come into question as the

Fig. 4.1 (continued) tiny pelvis that floats within the abdominal cavity and lacks hindlimbs (Cozzi et al. 2017). In contrast, some bowhead whales (*Balaena mysticetus*, **f**) retain a pelvis and reduced hindlimbs within the body cavity (Thewissen et al. 2009). All images are not to scale and are shown with equal body lengths to illustrate the relative size of the pelvis and hindlimb elements
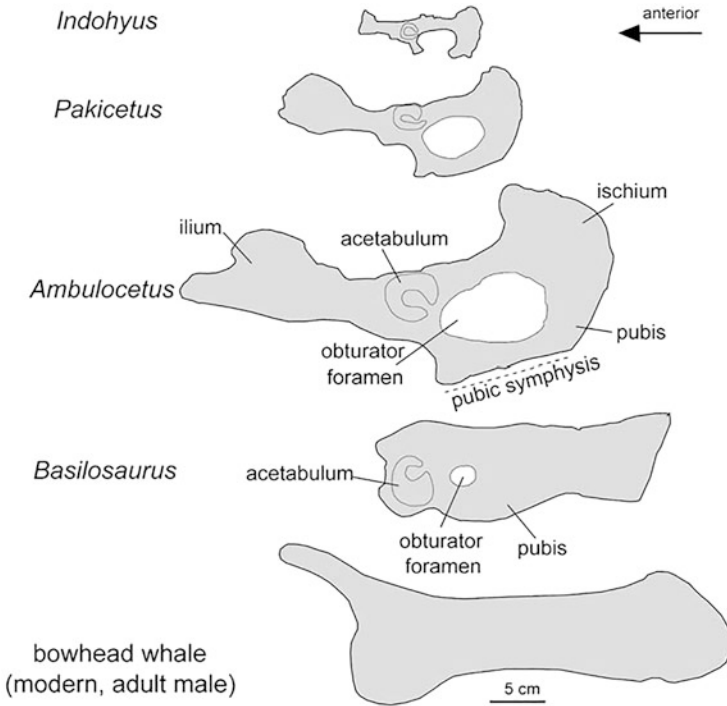
Fig. 4.2 Outlines of the pelves illustrating pelvic evolution in archaeocetes and the bowhead whale (Thewissen et al. 2009). Like what is found in terrestrial mammals, the earliest cetaceans (e.g., *Pakicetus* (composite of H-GSP 30395, 30213), *Ambulocetus* (H-GSP 18507)) and their relatives, including the raoellid *Indohyus* (Ranga Rao 256), had robust pelves that had a bony attachment to the vertebral column as seen in most terrestrial mammals. This attachment was lost at least in basilosaurids, as evidenced by the reduced pelvis of *Basilosaurus* (US National Museum 12,261). Basilosaurid archaeocetes were no longer able to bear their body weight on land and were obligatorily aquatic. In modern bowhead whales (pictured here is the pelvis of an adult male, *Balaena mysticetus*, NSB-98B5), the acetabulum and obturator foramen are lost, and the ilium is reduced. In modern cetaceans, and probably basilosaurid archaeocetes, the reduced pelvis is a site of muscular attachment for muscles associated with the genitals of both sexes

proposed fetus could also have been ingested by the whale during feeding or been a displaced fetus (Thewissen et al. 2009).

4.2.2 Basilosaurid Archaeocetes, Pelvic Detachment, and Hindlimb Reduction

Basilosaurids were the latest diverging lineage of archaeocetes from the late Eocene epoch (38–34 million years ago) and showed an altogether different trajectory in hindlimb and pelvic evolution. In these large-bodied whales (Fig. 4.1d), the pelvis

(Fig. 4.2) was no longer in contact with the sacrum, and the hindlimbs were encased within the body wall (Uhen 1998). These were the first cetaceans to have lost their ability to walk and mate on land and were therefore obligatorily aquatic. Rather than using their limbs for propulsion, these archaeocetes used a tail fluke, and *Basilosaurus* may have employed whole body undulations while swimming (Gingerich 2003).

Basilosaurus isis was 16 meters long, but the pelvis (Figs. 4.1d and 4.2) was shorter than the lumbar vertebrae. The left and right sides of the pelvis articulated with another via a pubic symphysis, as in terrestrial mammals. The tiny hindlimbs, which contained representative elements of most of the limb, were thought to be encased within the soft tissues of the body wall; if they did protrude from the body wall, they might have been involved as a potential aid in positioning their elongated bodies (i.e., copulatory guides, Gingerich et al. 1990). The hindlimbs of all *Basilosaurus* and *Dorudon* (5 meters long) were too reduced to support body weight on land (Uhen 2004).

All basilosaurid archaeocetes lacked articulation between the pelvis and spine, resulting in necessary changes for copulation and birth. Copulation was no longer feasible on land, and these archaeocetes were uniquely released from the constraints of life on land. By losing bony connections between the pelvis and vertebral column and reducing the size of hindlimbs, the size of the fetus was no longer constrained by having to fit through the aperture of the bony pelvic girdle to be born big, thereby setting the stage for the novel evolution of extreme brain size (Smaers et al. 2021; Waugh and Thewissen 2021) and gigantism (Goldbogen and Madsen 2018) in later diverging cetaceans. Beyond setting the stage for larger fetuses and adults, the loss of the bony constraints on the size of the birth canal allowed for larger calves. In modern cetaceans, larger-bodied calves can survive colder water through heat conservation, thus enabling births in colder marine environments (Galatius 2005; Keener et al. 2018). Mating behaviors in these archaeocetes may have been like modern cetaceans in which mating pairs position themselves in the water with (a) touching ventral surfaces, (b) side by side in which the male arches his penis to fertilize the adjacent female (Slijper 1962), and/or (c) a male's ventrum contacts the female's flank, so the pair is positioned cross-wise during very rapid, energetic copulation (Keener et al. 2018; Webber et al. 2023, this book).

4.2.3 Even-Toed Ungulates: Artiodactyls

Cetaceans evolved from terrestrial even-toed ungulates (Mammalia: Artiodactyla) that were hoofed and quadrupedal. Their closest living relative is the large-bodied and amphibious *Hippopotamus* (Lihoreau et al. 2015), but their ancient artiodactyl relatives, including raoellids (Figs. 4.1a and 4.2) and dichobunids, had a more gracile body plan with fully functional pelves and hindlimbs. The sacrum in all artiodactyls remains fused to the vertebral column. Because evidence from the fossil record is limited to skeletal remains, assignment of sex of these fossils is difficult.

However, fossil evidence shows that pelves of two lineages of Eocene artiodactyls with small body sizes compared to archaeocetes, raoellids (Figs. 4.1a and 4.2) (Cooper et al. 2011) and dichobunids (Thewissen and Hussain 1990), may have displayed two sizes, and the inference is that the female pelvis is smaller than that of males (Kaufmann et al. 2013) as in modern *Hippopotamus* (Shannon et al. 2021). Beyond differences in body size between the sexes, the large pelvis of males may offer a greater anchor for attachment of the muscles associated with penile erection (ischiocavernosus), and retention of the site of attachment may have driven retention of the bony pelvis of cetaceans even while undergoing hindlimb loss.

Unlike most other mammals, morphology of the vaginal wall of some female artiodactyls displays transverse folds that protrude into the lumen of the vagina, which are described as successive funnels (Slijper 1962; Nickel et al. 2004; Orbach et al. 2017b). These structures create undulating relief that may act as an impedance, impose selection on sperm, keep sea water out of the vagina, or enable females to control the depth of penile penetration and prospective paternity (Orbach et al. 2020). Vaginal folds have been found in *Hippopotamus* (Laws and Clough 1965), the closest modern relatives to cetaceans. Like cetaceans, *Hippopotamus* also mate in water (Dixson 2021). Other artiodactyls and cetaceans display these transverse folds (Slijper 1962; Kleinenberg et al. 1969; Orbach et al. 2017b; Tarpley et al. 2021), but they are not present in most non-cetacean marine mammals (e.g., seals, sea lions, manatees, and sea otters) (Orbach et al. 2021). Included in the epithelium of the folds are mucous cells that contribute to thick mucus lining the lumen of some of the folds, which lodged spermatozoa in the bowhead whale (*Balaena mysticetus*) (Tarpley et al. 2021). It could be that these folds originated in terrestrial artiodactyls and were exapted to also impede the passage of water into the vaginal canal (Orbach et al. 2020). Sea water is known to be fatal to the sperm of bottlenose dolphins (*Tursiops truncatus*) (Schroeder and Keller 1989). Among many other adaptations, it could be that the presence of these folds facilitated the ability of archaeocetes to successfully copulate in a saltwater habitat, thereby partially allowing for a completely aquatic lifestyle to have evolved in the Eocene epoch (Orbach et al. 2023, this book).

Hippopotamus are known to copulate in water, and intromission may last minutes, whereas intromission of the more terrestrial pygmy hippopotamus (*Choeropsis liberiensis*) lasts only seconds (Dixson 2021). The latter strategy includes a single copulatory thrust, and intromission that lasts for seconds is the more common copulatory strategy among some artiodactyls and modern cetaceans (e.g., boto (*Inia*), harbor porpoise (*Phocoena*), dusky dolphin (*Lagenorhynchus*), and killer whale (*Orcinus orca*)) (Brennan and Orbach 2020; Dixson 2021).

4.2.4 Modern Cetaceans: Pelves, Hindlimbs, and Genitals

Cetacea includes two suborders, baleen whales (mysticetes) and toothed whales (odontocetes). In all modern cetaceans, the pelvis is reduced and floating within
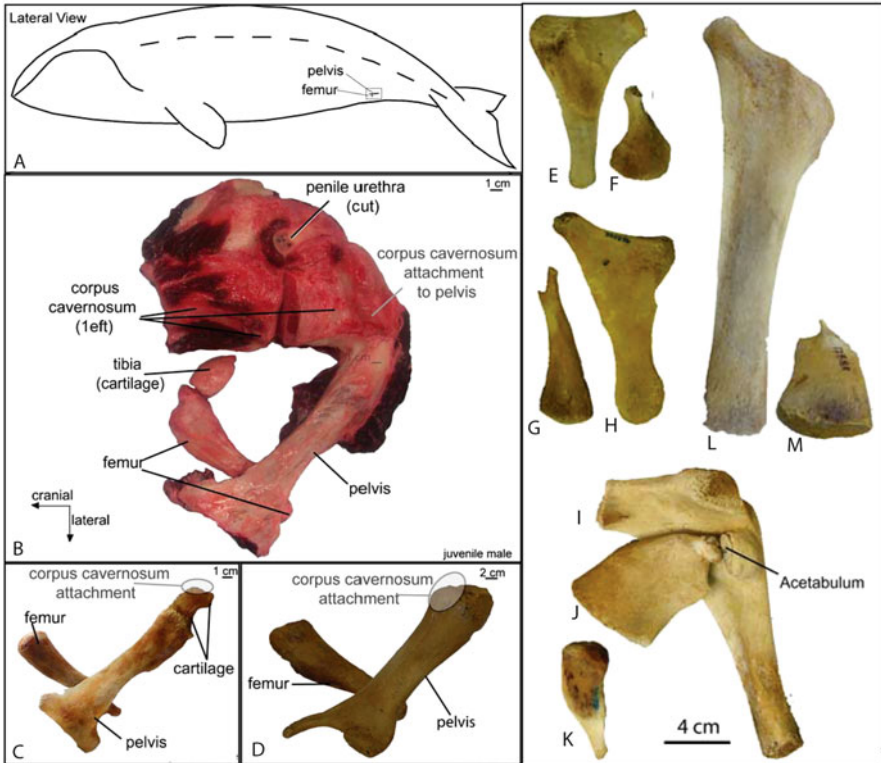
Fig. 4.3 Pelves of male bowhead whales (*Balaena mysticetus*) and soft tissue attachments (modified from Thewissen et al. 2009, 2021). Pelves are found near the genital slits and are associated with a triangle-shaped femur and more rarely a tibia (**b**) and metatarsal (not shown). In males, the ischiocavernosus muscle and corpus cavernosum share an insertion on the anterior surface of the pelvis. (**a**) Schematic of a male bowhead in lateral view. (**b**) Results of a dissection of a juvenile male (NSB-06B4) showing the pelvis attaches to the femur with a synovial joint and the presence of a tibia. (**c**) The pelvis and femur of the juvenile pictured in b. (**d**) The pelvis and femur from NSB-98B5, an ~60-year-old male, for comparison. The pelvis (**e**) and femur (**f**) of a yearling female (NSB-1992B17). The pelvis (**h**) and femur (**g**) of an ~4-year-old female (NSB-1992B20). The pelvis (**i**), femur (**j**), and tibia (**k**) of a ~ 7-year-old male (NSB-1992B2). The pelvis (**l**) and femur (**m**) of an ~13-year-old male (NSB-2017B18). Only (**d**) is sexually mature

soft tissues of the body cavity (Figs. 4.1e, f, 4.2, and 4.3). Pelves are ossified, except for *Kogia*, which may display cartilaginous pelves (Benham 1901), but this animal was young and with potentially incomplete ossification. This pelvis bone is typically dash, or comma-shaped, and has lost most morphological similarities with the pelves of the earliest archaeocetes (Figs. 4.1 and 4.2). Instead, this thin bone may only be 1–3% of the body length in embryos and adults (Hosokawa 1951). The pelvis of males is typically larger than that of females, and it retains an anterior surface that acts as an anchor for the muscle that supports penile erection (Dines et al. 2014). Among odontocetes, the pelvic bones can sometimes be palpated by a human
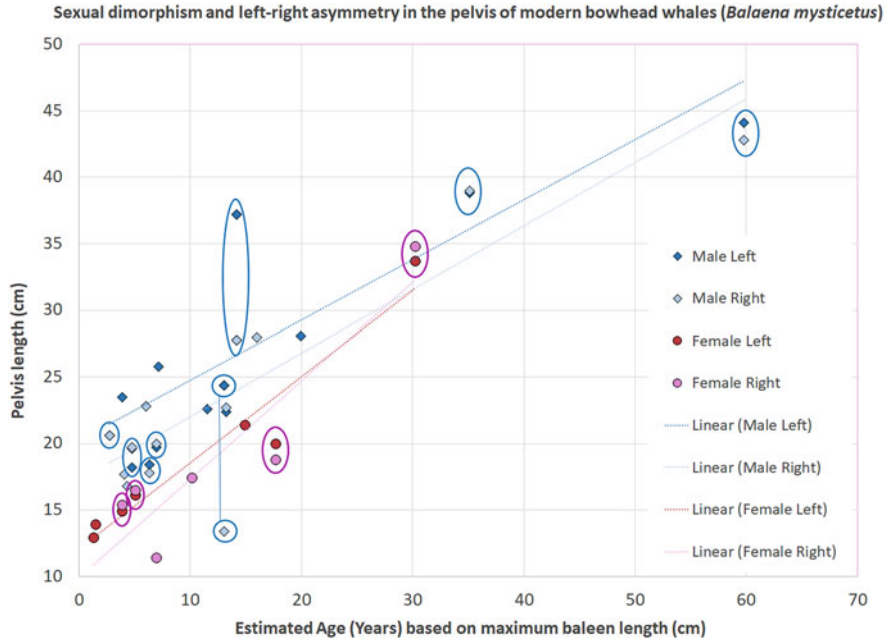
Fig. 4.4 Modern bowhead whales (*Balaena mysticetus*) have pelves that increase in length with age. Pelves of males (diamonds) are generally larger than those of age-matched females (circles). As in other cetaceans, pelves show inconsistent asymmetry between left and right pelves within a single whale (ellipses). Y-axis is the pelvis length in centimeters. X-axis is the age of whales based on maximum baleen length and sex (Lubetkin et al. 2012). Data for males are shown in blue diamonds with the left pelvis shown in dark blue and the right pelvis shown in light blue. Data for females are shown in red circles with the left pelvis shown in dark red and the right shown in pink. Pelves were collected by Robert Suydam and J.G.M. Thewissen. Linear male left: $y = 0.452x + 20.22$, $R^2 = 0.6516$. Linear male right: $y = 0.4776x + 17.222$, $R^2 = 0.785$. Linear female left: $y = 0.6475x + 12.082$; $R^2 = 0.9423$. Linear female right: $y = 0.7384x + 9.9463$, $R^2 = 0.8418$

researcher beside the genital slits in some beluga whales (*Delphinapterus leucas*). Male beluga whales display a pelvis that is greater in length compared to females. In females, pelves are connected to muscles of the vagina and may ensure tight closure of the vagina (Kleinenberg et al. 1969).

Within baleen whales, some bowhead whales (*Balaena mysticetus*) have an exceptional lifespan over 200 years (George et al. 1999, 2021; Wetzel et al. 2017; Vazquez et al. 2022). This study reports an ontogenetic assessment of growth of the pelvic bones of both sexes in bowheads, based on the length of the pelvic bones recovered from deceased whales. In all measured pelves, length increased with age (Fig. 4.4, Table 4.1). As in other cetaceans (Struthers 1881), male bowheads display longer pelves compared to females perhaps as a structural anchor for the mechanical strains associated with contraction of the ischiocavernosus muscles. Results show pelves of some members of both sexes may display left-right asymmetry, but which

Table 4.1 Length measurements of the pelvis and hindlimb elements (femur, tibia) of whales with ages estimated in years based on the longest baleen length (Lubetkin et al. 2008). Data are illustrated in Fig. 4.3. NSB = North Slope Borough, Division of Wildlife Management

Bowhead ID	Sex	Body length (m)	Longest baleen (cm)	Age estimate (years)	Left pelvis length (cm)	Right pelvis length (cm)	Left femur length (cm)	Right femur length (cm)	Left tibia length (cm)
NSB-18B9	Male	8.6	119	2.747	20.6	20.6	5	5.2	
NSB-92B18	Male	8.8	140	3.878	23.5				
NSB-13B17	Male	9.2	143	4.079		17.7		6.2	
NSB-18B22	Male	8.6	146	4.294		16.8		11.2	
NSB-13B15	Male	9.7	152	4.776	18.2	19.6	13.2	14.4	
NSB-93B1	Male	9.88	152	4.776		19.7			
NSB-18B4	Male	9.9	164	6.043		22.8		6.8	
NSB-13B14	Male	9.2	166	6.316	18.4	17.8	14.8	14.4	
NSB-92B21	Male	9.55	170	6.945	19.7	20	9.4	7.4	7.5
NSB-17B9	Male	9.4	171	7.125	25.8		7.2		
NSB-17B13	Male	10.1	189	11.563	22.6		8.2		
NSB-17B18	Male	10.3	196	13.04	24.4	13.4	6.4	6.4	
NSB-16B16	Male	9.3	196	13.04	24.4		14.6		

NSB-12B16	Male	10.31	197	13.258	22.4		11.4	
NSB-12B24	Male	10.13	197	13.258		22.7		6.5
NSB-17B14	Male	10.1	201	14.148	37.2	27.8	10.4	10.4
NSB-17B14	Male	10.1	201	14.148	37.2	27.8	10.4	10.4
NSB-13B11	Male	11.3	209	16.024		28		18.8
NSB-92B15	Male	11.7	224	19.946	28.1		12.1	14.2
NSB-93B3	Male	13.34	265	35.144	38.8	39		
NSB-98B5	Male	15.14	297	59.819	44.1	42.8	23.9	26.5
NSB-13B19	Male	8				14.6		6.4
NSB-92B17	Female	7.5	79	1.323	12.9		6.2	
NSB-12B23	Female	8.48	86	1.529	13.9		11.3	
NSB-92B20	Female	8.5	140	3.878	14.9	15.4	10.6	
NSB-12B18	Female	9.4	155	5.048	16.1	16.5	13.1	
NSB-18B10	Female	8.9	170	6.945		11.4		
NSB-17B17	Female	9.3	182	10.167		17.4		

(continued)

Table 4.1 (continued)

Bowhead ID	Sex	Body length (m)	Longest baleen (cm)	Age estimate (years)	Left pelvis length (cm)	Right pelvis length (cm)	Left femur length (cm)	Right femur length (cm)	Left tibia length (cm)
NSB-13B16	Female	10.7	205	14.923	21.4		5.4		
NSB-12B17	Female	10.82	217	17.67	20	18.8	7.9		
NSB-12B21	Female	13.34	262	30.261	33.7	34.8	8.2		
NSB-92B19	Female	10.5			23.2	23.2	13.2		

side is larger varies (Fig. 4.4, Table 4.1). Unlike odontocetes, the hindlimbs of bowhead whales are ossified vestiges encased within the body wall and include a triangular-shaped femur with an occasional tibia (Fig. 4.3) that may or may not be ossified (Thewissen et al. 2021). At least the femur displays left-right asymmetry in bowheads, and this asymmetry does not always match that of the pelvis (Table 4.1). Rarely, a metatarsal is present. Occasionally, in at least juvenile bowheads, anomalous hindlimb buds may appear just caudal to the nipples, far lateral and caudal to the genital slit (Thewissen et al. 2021). Taken together, results show that left-right asymmetry in bowheads probably lacks a specific sidedness in which either the left or the right pelvis is typically larger than the other.

The penis can be meters in length in some species of whales (Slijper 1962). The penis of cetaceans consists of erectile tissue filled with collagen and elastic fibers, which differs from the spongy tissues in the penis of most mammals (Orbach et al. 2017a). The ischiocavernosus muscles in cetaceans are anchored by the pelvis (Fig. 4.2b) in males and attach near the distal end of the penis. This muscle aids in fluid retention within the paired corpus cavernosa during erection and may allow for the cetacean penis to move side to side as well as up and down (Dines et al. 2014). The pelvis is under selective pressure associated with larger penis size as males that practice polygynandry display greater-sized testes, ischiocavernosus muscles, greater-sized penises, and pelves (Dines et al. 2014). Potentially, because of the mechanical stresses associated with erection and directional movements of the penis, the pelves of males are generally larger than those of females. Males with greater-sized and more dexterous penises than other males are potentially able to overcome female resistance and deposit sperm deeper than others in the vaginal canal. Females of species that have larger male pelves also display larger pelves, potentially due to shared patterns of outgrowth and ossification of the pelves (Dines et al. 2014). Within females, the ischiocavernosus muscles attach to the clitoris and pelvis. In beluga whales, the ischiocavernosus muscles partially attach to the wall of the vagina and the pelvis (Kleinenberg et al. 1969).

Mating behaviors in modern cetaceans vary but are broadly associated with brief copulation (seconds to minutes) and with minimal or no pelvic thrusts (Slijper 1962; Orbach et al. 2014; Brennan and Orbach 2020; Dixson 2021). Mates may position themselves by (a) touching ventral surfaces in which the male can easily eject seminal fluid into the vagina; (b) aligning side by side in which males extend their long, curved penis and quickly eject seminal fluid into the vagina of an adjacent female (Slijper 1962); and (c) assuming a crisscrossed pattern in which the male's ventrum comes in contact with the female's flank and rapidly penetrates and ejaculates into her vagina (Keener et al. 2018; Webber et al. 2023, this book). At least some of these behaviors were probably used by basilosaurid archaeocetes, as they were the first cetaceans to copulate exclusively in water, and caudal mounting was impossible without hindlimbs. Short intromissions and fewer pelvic thrusts in basilosaurids may have prevented sea water from entering the vagina.

4.3 Embryonic Evidence of Pelvic Girdle Evolution

In vertebrates, limb buds protrude from the body wall, and as outgrowth proceeds, a greater number of skeletal elements are added until a full limb is formed. In embryonic dolphins, hindlimb buds form initially but are absorbed by the body before birth (Thewissen et al. 2006). Hindlimb buds of dolphins are present for a shorter amount of developmental time compared to those of bowhead whales (Gavazzi et al. 2023). As a result, the pelvic girdle of most dolphins includes just a pelvis, but in baleen whales such as bowheads, the pelvis can usually be associated with one to two additional elements near the middle of the pelvis, and these are presumed to be the femur and tibia (Fig. 4.5) (Eschricht and Reinhardt 1866; Hosokawa 1951; Thewissen and McLellan 2009). In dolphins, the truncated
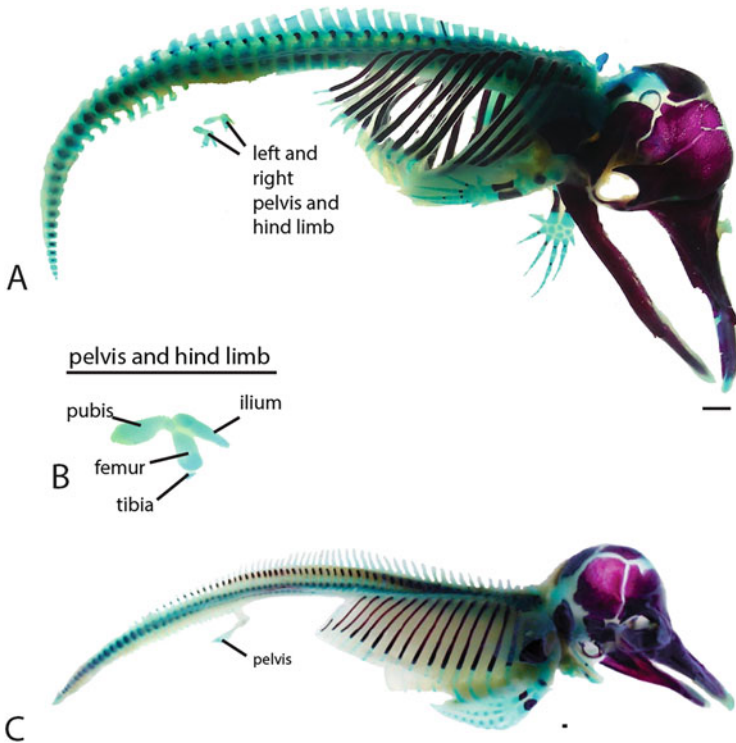
Fig. 4.5 Modern cetaceans retain a small pelvis and sometimes parts of a reduced hindlimb immersed within their bodies. Within the bowhead whale (*Balaena mysticetus*, NSB-2000B3F), fetal specimens (**a**) show a cartilaginous pelvis that connects to some bones of the hindlimb (**b**, femur, tibia) but lacks a bony connection with the vertebral column. Within pantropical spotted dolphins (*Stenella attenuata*, LACM 94285), fetal specimens (**c**) show a cartilaginous pelvis that lacks an associated hindlimb and lacks articulation with the vertebral column. Images show fetal specimens with most soft tissues removed and connective tissues are stained such that bone is red and cartilage is blue. Scale bars are 1 cm in length

hindlimb buds stop synthesizing SHH, a protein that is essential for outgrowth and patterning of developing limbs, thereby shutting down limb outgrowth earlier compared to terrestrial mammals (Thewissen et al. 2006). In contrast, the hindlimb buds of embryonic bowhead whales probably undergo a greater duration of SHH signaling compared to dolphins and therefore develop an ossified femur and tibia. In all adult cetaceans, these hindlimbs are encased within the body wall and lack a role in locomotion. Functional hindlimbs were lost in archaeocetes about 40 million years ago in basilosaurids, and this could be due to truncated SHH expression (Thewissen et al. 2006).

Left-right asymmetry in the pelvis of some cetaceans is a characteristic of stickleback fish and manatees (Nganvongpanit et al. 2020) with modified *PITX-1* expression (Shapiro et al. 2006; Chan et al. 2010). It could be that *PITX-1*, or a similar gene(s), could be associated with the impressive left-right asymmetry found in the pelves of many cetaceans. Female cetaceans also display left-right asymmetry, suggesting that this is perhaps a consequence of asymmetrical growth, from an outgrowth pattern that is no longer under selection, and the functional consequence of this is unknown. It also could be that left-right asymmetry of the pelvic bone of male cetaceans may be associated with curvature of the penis (Orbach et al. 2020), although this hypothesis has yet to be tested with quantitative evidence linking curvature of the penis of adults with sidedness of the pelvic bones.

4.4 Conclusion

During the first 12 million years of cetacean evolution, archaeocetes underwent an exceptional land-to-sea transition, and the pelvic girdle radically transformed from an organ of locomotion and reproduction to an organ solely supporting muscles associated with genitalia. Small pelves and associated hindlimbs, if any, were relocated within the body wall, and as a consequence, basilosaurid archaeocetes were no longer able to mate on land. Mating via caudal mounting, like in terrestrial artiodactyls, was no longer possible. Based on evidence taken from the modern relatives of archaeocetes, including terrestrial artiodactyls and cetaceans, this study speculates on the copulation behaviors of ancient whales. Males may have had dexterous penises capable of depositing sperm in females that were oriented ventrally or along their flanks. Duration of intromission and pelvic thrusts were probably minimized, partially to protect the vaginal canal and sperm from intrusion of sea water. Transverse folds within the vaginal canal of these archaeocetes may have been exapted to also offer protection from the intrusion of sea water into the vaginal canal.

Consequences of the size reduction and relocation of the pelvic girdle probably released constraints on the fetus. By losing bony connections between the pelvis and vertebral column and reducing the size of hindlimbs, head or body size of the fetus of basilosaurid archaeocetes was no longer constrained by having to fit through the pelvic girdle (aperture). A larger body size could have provided a thermodynamic

advantage as larger calves of modern cetaceans are known to fare better in colder water. Moreover, this expansion of the birth canal may have laid the stage for the eventual expansion in brain size in modern odontocetes (e.g., dolphins, beluga whales) and gigantic body sizes, including blue whales, the largest mammals ever.

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Chapter 5
Sexual Anatomy of Female Cetaceans: Art and Science Contribute Insights into Functionality

Dara N. Orbach, Uko Gorter, and Sarah Mesnick

Abstract The relationship between sexual selection and the diversity and rapid evolution of male genitalia has been well-documented across many animal taxa, while the morphological variability of female genitalia has received comparatively little attention. Female whales, dolphins, and porpoises possess unusual flaps, folds, and blind sacs in their vaginas, which vary among taxa and may serve several functions. We review the relationship between form and function of these unusual vaginal structures in cetaceans and discuss evidence that supports or refutes various functional hypotheses. A compilation of three-dimensional vaginal endocast models, contemporary high-resolution photographs of dissected reproductive tracts, and detailed anatomical illustrations ranging over 175 years are used to highlight the diversity of forms and fill in gaps in taxonomic knowledge. We discuss the complementary nature of anatomical illustrations and modern analytical and visual tools and how they can help us better understand the evolution of such unusual morphological structures. We identify opportunities for future studies in cetacean genital evolution and discuss the insights they may provide into mating strategies of cetaceans.

Keywords Anatomical illustrations · Cetacean · Female · Functional anatomy · Morphology · Sexual selection · Vagina · Vaginal fold

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5.1 Introduction

Across vertebrates, there is a paucity of research on female genital morphology compared to male reproductive organs (Hosken and Stockley 2004; Sloan and Simmons 2019). Male intromittent organs are varied and are described as the most rapidly diverging anatomical structure among species with internal fertilization (Eberhard 1985; Arnqvist 1998). Among insects, male reproductive structures are often used to determine species designation (Tuxen 1970; Eberhard 1985). Female genital morphology, in contrast, has been relatively understudied and undervalued. Compared to external and rigid male intromittent organs, female genitals were thought to be invariable (Eberhard 1996; Eberhard and Ramirez 2004) and more challenging to manipulate as they are soft and located internally within the body (Eberhard 1985; Córdoba-Aguilar 2010; Simmons 2014). Additionally, males were hypothesized to have the more dominant role in mating compared to females (Darwin 1871), and the field of genital evolution was biased with predominantly male researchers (Ah-King et al. 2014). While empirical evidence has refuted the validity of these reasons for preferential investigation of male reproductive morphology over female reproductive morphology, the field of genital evolution continues to explore male reproductive structures more frequently than female genital organs from the 1980s through the present day (Ah-King et al. 2014; Orbach 2022).

Part of the challenge in comparing morphological structures across taxa and exploring diversity and functionality is that ubiquitous defined landmarks are usually essential. A geometric morphometric approach is often used to characterize the shape of an anatomical structure, in which consistent morphological landmarks are present in all samples (Adams et al. 2004). Yet when assessing soft tissues such as female genitalia, morphological landmarks can be difficult to definitively identify. Alternative approaches can be used instead, sometimes supported by three-dimensional visualization. For example, the complexity of the vaginas of cetaceans (whales, dolphins, and porpoises) was explored using linear measurements (Orbach et al. 2017b), two-dimensional geometric morphometrics (Orbach et al. 2018), and alpha shape complexity scores of three-dimensional models (Orbach et al. 2021), which all relied on high-quality images.

Another major challenge in comparing anatomy within and across clades is that inconsistent terminology may be used to characterize unusual features. For example, the unique vaginal structures occurring among cetaceans have been identified for over 230 years (Hunter 1787). These vaginal structures have been termed circular folds (Ommanney 1932; Green 1977; Tarpley and Hillmann 1999), pseudo-cervices (Pycraft 1932; Schroeder 1990), rings of transverse folds (Chen et al. 1984), spermathecal folds (Meek 1918), transverse rugae (Jackson 1845), vaginal folds (Morejohn and Baltz 1972; Clarke et al. 1994; Orbach et al. 2016), and vulvular folds (Murie 1873). From the diversity of these terms, it is unclear if all authors refer to the same anatomical structures. Inclusion of supporting illustrations and images that complement anatomical descriptions can reduce ambiguity and incongruence. In this chapter, we explore the diversity of female cetacean reproductive morphology

and emphasize the value of integrating art (e.g., illustrations, three-dimensional graphics) with science.

5.2 Unusual Genital Morphology of Cetaceans

Unlike most mammals (excluding sirenians), cetaceans are fully aquatic with no time spent on land. Over evolutionary time, natural selection pressures have driven many anatomical adaptations that facilitate high-energy-efficient lives in marine environments. In addition to sexual selection pressures that may drive sexually dimorphic traits (i.e., beaked whale dentition, Alves et al. 2023, this book; sperm whale (*Physeter macrocephalus*) body size, Eguiguren et al. 2023, this book; killer whale (*Orcinus orca*) dorsal fins, Wright et al. 2023, this book), natural selection pressures can enable and/or constrain mating. For example, female dusky dolphins (*Lagenorhynchus obscurus*) use their three-dimensional environment to evade males by diving within the water column (Markowitz et al. 2023, this book). Yet male cetaceans generally do not have large ornamental displays that would increase hydrodynamic drag, as found in many terrestrial mammals (Würsig et al. 2023, reviewed in this book). Phylogenetic history can also constrain anatomy. Male cetaceans have a fibroelastic penis, like all closely related even-toed ungulates, yet unlike most mammals that have a vascular penis (Slijper 1966). The fibroelastic penis possesses erectile tissue filled with elastin fibers and collagen that can further engorge with blood during arousal (Slijper 1966). As the penis of cetaceans is in a semi-turgid state, it is held within the body cavity, likely to reduce drag while swimming. However, the penis is everted prior to intromission and sometimes while swimming rapidly (dusky dolphins, Orbach et al. 2015), suggesting it is built to withstand drag forces without damage.

Female cetaceans also have unusual genital features, such as a comparatively small uterus, since the fetus develops in a uterine horn instead (Slijper 1966). The ovaries of cetaceans retain *corpora luteum* scars after ovulation, which are instrumental in many life history studies of cetaceans such as counting ovulation events (Dabin et al. 2008; Chivers and Danil 2023, this book). Perhaps most intriguing is the presence of diverse vaginal folds across cetacean species (Orbach et al. 2017b, 2018). Although these vaginal folds are a shared characteristic with even-toed ungulates (Pabst et al. 1998), we have not found any literature on artiodactyls describing comparable structures. Pigs (*Sus domesticus*) have several ring-like structures within their cervices (Dyce et al. 2010), yet the tissues of the vaginal folds in cetaceans have been histologically confirmed as non-cervical and of similar structural composition to other vaginal tissues (Orbach et al. 2016). The vaginal folds of cetaceans represent an unparalleled level of diversity in reproductive structures among vertebrates (Fig. 5.1; Orbach et al. 2017b).

Fig. 5.1 Comparison of female cetacean genital morphology. The excised reproductive tracts are positioned ventral up with an incision down the midline. The uterine horns are at the top of each specimen, and the vaginal opening is at the bottom. The species are (1) *Balaenoptera acutorostrata*, (2) *Delphinapterus leucas*, (3) *Delphinus capensis*, (4) *Delphinus delphis*, (5) *Eschrichtius robustus*, (6) *Globicephala macrorhynchus*, (7) *Globicephala melas*, (8) *Kogia breviceps*, (9) *Kogia sima*, (10) *Lagenorhynchus acutus*, (11) *Lagenorhynchus albirostris*, (12) *Lagenorhynchus obliquidens*, (13) *Lagenorhynchus obscurus*, (14) *Megaptera novaeangliae*, (15) *Mesoplodon bidens*, (16) *Mesoplodon europaeus*, (17) *Mesoplodon peruvianus*, (18) *Mesoplodon stejnegeri*, (19) *Orcinus orca*, (20) *Phocoena phocoena*, (21) *Phocoena sinus*, (22) *Physeter macrocephalus*, (23) *Sousa plumbea*, (24) *Stenella attenuata*, (25) *Stenella coeruleoalba*, (26) *Stenella frontalis*, (27) *Tursiops aduncus*, and (28) *Tursiops truncatus* (figure modified from Orbach et al. (2018). Additional details about the specimens are provided in Supplemental Table 5.1)

5.2.1 Functions of Vaginal Folds

Several alternative and non-mutually exclusive hypotheses have been proposed for the function(s) of vaginal folds in cetaceans (Table 5.1; Clarke et al. 1994; Orbach et al. 2016).

5.2.1.1 Natural Selection Functions of Vaginal Folds

Among the hypotheses supporting natural selection factors, vaginal folds may provide a physical barrier to prevent birth of the underdeveloped fetus during pressure changes while diving (Kellogg 1938). It has also been proposed that vaginal folds could aid in parturition as they funnel caudally and could thus provide a passageway for the fetus (Meek 1918; Slijper 1962). The extensive diversity in the number, shape, size, and positioning of vaginal folds across species does not support

Table 5.1 Proposed hypotheses for the functions of vaginal folds in cetaceans. Hypotheses are categorized based on natural or sexual selection pressures, conflict or cooperation between the sexes to control paternity, and when the function would occur relative to intromission

Selection pressure	Conflict or cooperation between the sexes	During or post-copulation	Function	Citation
Natural		During	Prevent seawater entry into the upper reproductive tract during intromission	Slijper (1962); Green (1972, 1977); Chen et al. (1984); Schroeder (1990); Robeck et al. (1994)
Natural		Post	Prevent miscarriages during diving	Kellogg (1938)
Natural		Post	Aid in parturition	Meek (1918); Slijper (1962)
Sexual	Cooperation	During	Stimulate ejaculation	Meek (1918); Harrison (1969)
Sexual	Cooperation	Post	Plug to retain semen	Meek (1918); Harrison (1969)
Sexual	Cooperation	Post	Pathway for semen	Orbach et al. (2016)
Sexual	Cooperation	Post	Pump to uptake semen	Bonner (1980)
Sexual	Conflict	During	Reduce the forces of intromission	Orbach et al. (2019a)
Sexual	Conflict	During	Constrain penis penetration depth during intromission	Orbach et al. (2017a)
Sexual	Conflict	During	Create vaginal labyrinth for the penis	Orbach et al. (2020)
Sexual	Conflict	Post	Expel sperm from undesirable males	Orbach et al. (2016)

either of these hypotheses as convergence in vaginal fold form and location are expected if they function to interact with the fetus (Orbach et al. 2017b, 2018, 2021).

Vaginal folds could function like a "squeegee" during copulation that wipes off seawater from the distal end of the penis and prevents the incursion of saltwater into the upper reproductive tract (Slijper 1962; Green 1972, 1977; Chen et al. 1984; Schroeder 1990; Robeck et al. 1994) as saltwater may be lethal to at least common bottlenose dolphin (*Tursiops truncatus*) sperm (Schroeder and Keller 1989) and beluga whale sperm (O'Brien et al. 2008). The orientation of the vaginal folds toward the caudal vaginal opening support the "squeegee" hypothesis, as do the often ring or funnel shapes of the vaginal folds (Orbach et al. 2016, 2017b). However, if vaginal folds were to "squeegee" the penis, the caudal fold that first contacts the external environment should be largest and the cranial fold the smallest, yet the opposite pattern occurs (Orbach et al. 2017b). Vaginal folds are also present in a freshwater river dolphin (baiji, *Lipotes vexillifer*, Chen et al. 1984). Seawater effects on dolphin sperm are not ubiquitous, with mortality rates varying depending on osmolality and exposure duration (unpublished data).

5.2.1.2 Sexual Selection Functions of Vaginal Folds

Most hypotheses related to the function(s) of vaginal folds in cetaceans suggest that sexual selection likely plays an important role, both during and after copulation (Table 5.1). Older hypotheses tended to focus on ways vaginal folds could aid or assist sperm in reaching the ova ("cooperation"), while more recent hypotheses focus on the possibility that the folds exert control over access to the ova and "conflict" between the sexes over which sperm reach the ova (Table 5.1). Vaginal folds were found to have a higher stiffness than other reproductive tract tissues in female common bottlenose dolphins, potentially indicating that the folds function to dampen the forces and damage to the vagina and cervix during rapid intromission (Orbach et al. 2019a).

Computed tomography (CT) scans revealed that the depth of penile penetration during copulation appears to be curtailed by large vaginal folds that present a physical barrier to the penis (Orbach et al. 2017a). The pattern is particularly obvious in harbor porpoises (*Phocoena phocoena*; Orbach et al. 2017a, 2020). Harbor porpoises have comparatively complex vaginal fold patterns among cetaceans, with one caudal vaginal fold that is especially prominent, thick, deep, and asymmetrically positioned (Orbach et al. 2017a, 2020, 2021). Male harbor porpoises exclusively sexually approach a mate on her left side (Keener et al. 2018; Webber et al. 2023, this book), which appears to be the only orientation in which the penis can bypass the vaginal fold labyrinth (Orbach et al. 2020). Thus, vaginal fold complexity and asymmetry appear to have coevolved with laterality of male (and possibly female) sexual behaviors in an evolutionary arms race of adaptations and counter-adaptations to control paternity (Arnqvist and Rowe 1995; Orbach et al. 2019b, 2020).

During copulation, physical contact from the vaginal folds could stimulate the penis and induce ejaculation (Meek 1918; Harrison 1969). The clitoris of the common bottlenose dolphin is more innervated than any other animal known to experience pleasure during copulation (Brennan et al. 2022). As the penis is homologous to the clitoris (Brennan 2016), and the bottlenose dolphin penis is also highly innervated (unpublished data), physical contact is likely important in inducing ejaculation. The extensive coevolution in shape between female and male reproductive morphologies among cetaceans (Orbach et al. 2017a) supports the ejaculation stimulation hypothesis. Future studies that explore contact points of the penis with vaginal folds during intromission will be valuable in discerning potential stimulatory functions.

Vaginal folds could assist with sperm storage and transport after copulation. Seminal vesicles and bulbourethral glands (i.e., Cowper's gland, present in most mammals but absent in marine mammals) aid in semen coagulation (Williams-Ashman 1984). As male cetaceans lack both these anatomical features, the aperture of the vaginal folds with a tight seal would help prevent the loss of semen (Meek 1918; Slijper 1966; Harrison 1969). Vaginal folds may provide a pathway for semen to travel toward the ovaries (Orbach et al. 2017b). The vaginal folds of bottlenose dolphins are composed of fine longitudinal bands (Orbach et al. 2016). Longitudinal bands on the cervical mucosa of bovines and goats aid in sperm transport (Mattner 1968; Mullins and Saacke 1989). Vaginal folds may produce a pump-like action to uptake semen (Bonner 1980). Alternatively, vaginal folds may act antagonistically in sperm transport. Although some species can shunt sperm within their reproductive tracts away from sperm storage organs or ova (arctiid moths, *Utetheisa ornatrix*, Curril and LaMunyon 2006; domestic fowl, *Gallus gallus domesticus*, Pizzari and Birkhead 2000), the vaginal folds of cetaceans are composed of smooth muscle and are not under somatic control, suggesting females cannot selectively expel sperm from particular mates (Orbach et al. 2016). Further research is needed to explore innervation patterns and mechanisms of vaginal peristalsis.

The interspecific diversity in vaginal folding suggests that female genitalia are under strong selective forces. While research on vaginal fold functionality has expanded substantially in the past decade, there are still many unknowns that preclude a definitive role of vaginal folds. Studies are needed that further investigate the interactions of vaginal folds and surrounding tissues with penises, semen, and seawater to test functional hypotheses. Research using in vivo animals will be particularly valuable and may provide insights not evident using ex vivo samples. Molecular and biochemical studies will be essential to explore physiological mechanisms related to vaginal fold functionality. Characterization of differences between species, age classes, and individuals will also assist (Orbach et al. 2017b). Such quantitative characterizations of anatomical structures are aided when augmented by detailed visuals including illustrations, three-dimensional models, and photographs.

5.3   Art Augments Science

We compiled female reproductive tract images to illustrate the diversity in genital form within cetaceans. We include contemporary photographs from dissections and three-dimensional visualization, as well as historic and current illustrations to demonstrate how different tools can complement each other and provide perspectives that aid in the understanding of functionality and evolution of anatomical structures.

5.3.1   *Dissection, Three-Dimensional Models, and Photographs*

Excised reproductive tracts of female cetaceans were collected opportunistically by marine mammal stranding networks across the USA and occasionally in other countries. The specimens were provided to authors DNO or SLM under the National Oceanic and Atmospheric Administration National Marine Fisheries Services parts authorization letters or permits from the Convention on International Trade in Endangered Species of Wild Fauna and Flora. We requested whole reproductive tracts from cetaceans of any age class (calf, immature, mature) or reproductive state (resting, pregnant, lactating) that were less than 48 hours postmortem. The specimens were immediately frozen ($-20°C$) upon removal from the postmortem animals. When possible, the excised reproductive tracts included the intact genital opening, vagina, cervix, uterine horns, and ovaries. Specimens were shipped and stored frozen ($-20°C$) until thawed for making endocasts and/or dissection.

For select females, we made silicone molds of the vaginal lumen and caudal os (opening) cervix. The reproductive tracts were suspended with the vaginal openings facing up. The vaginal lumen was filled with Mold Star® 16 FAST or Elite HDTM light body dental silicone (Orbach et al. 2021). Once solidified, the silicone endocasts were carefully extracted to prevent tearing the reproductive tract tissues. The endocasts were digitized with a Canon EOS Rebel T5i camera with 100 mm lens. A photogrammetric technique was applied; overlapping photographs of the endocasts were used to build three-dimensional models that were reconstructed and scaled in 3DF Zephyr lite (3Dflow SRL) photogrammetry software (Supplemental Video 5.1; Orbach et al. 2021).

The genitals were cleaned to remove excess ligament and muscle tissues not part of the reproductive tract. The specimens were oriented in a dorsal recumbency on a dissecting table. To open the reproductive tracts for visualization and measurements, a single incision was made down the ventral midline from the bifurcation in the uterine horns to just cranial to the clitoris (Orbach et al. 2016). Care was taken not to cut through the clitoris so that its functionality could be subsequently investigated (Brennan et al. 2022). The uterine horns were opened by incisions down the midline on the ventral plane to search for fetuses. Mucus was gently scraped out of the reproductive tracts. High-resolution digital photographs were collected from a
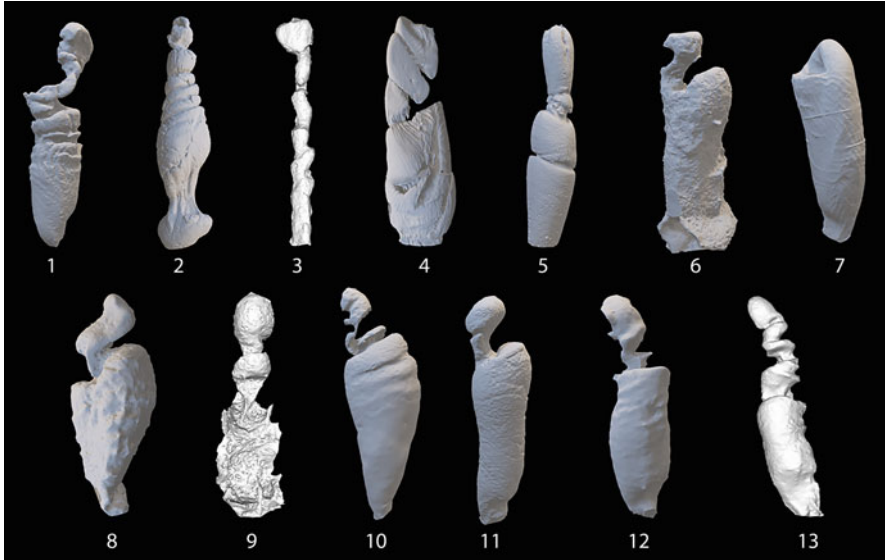
Fig. 5.2 Three-dimensional reconstruction of silicone endocasts of the vaginal lumen and cervix of 13 cetacean species. The cervix is at the top of each model, and vaginal opening is at the bottom. The invaginations in the models are regions where vaginal folds protrude into the vaginal lumen. The species are (1) *Eschrichtius robustus*, (2) *Megaptera novaeangliae*, (3) *Mesoplodon densirostris*, (4) *Kogia breviceps*, (5) *Stenella attenuata*, (6) *Stenella coeruleoalba*, (7) *Delphinus delphis*, (8) *Lagenorhynchus albirostris*, (9) *Lagenorhynchus obscurus*, (10) *Lagenorhynchus obliquidens*, (11) *Orcinus orca*, (12) *Tursiops truncatus*, and (13) *Phocoena phocoena* (figure modified from Orbach et al. (2021). Additional details about the specimens are provided in Supplemental Table 5.2)

bird's-eye view using different models of Nikon and Canon cameras concurrently with linear measurements (Orbach et al. 2016). A single representative photograph of each species was selected to display diversity. When possible, the representative photograph was from a sexually mature animal in early stages of decomposition, with the photograph in clear focus and depicting the entire genital organ. Photographs were edited in Adobe Photoshop 2023 to delete excess tissues.

As depicted in Figs. 5.1 and 5.2, there is extensive interspecific variation in vaginal shapes among cetacean species. Shape complexity of the vagina is driven by the diversity of vaginal folds (Orbach et al. 2021). Patterns were similar when using alpha shape complexity scores of three-dimensional vaginal endocasts (Fig. 5.2), linear measurements of dissected organs, or geometric morphometric analysis of two-dimensional photographs from dissections (Fig. 5.1). There does not seem to be a strong phylogenetic signal; female genital shape evolves rapidly even among closely related taxa (Orbach et al. 2017b, 2018, 2021). Factors associated with sexual selection including relative testes size, and with natural selection including relative neonate size, do not explain the extensive genital shape variation and complexity among female cetaceans (Orbach et al. 2018, 2021). The question of
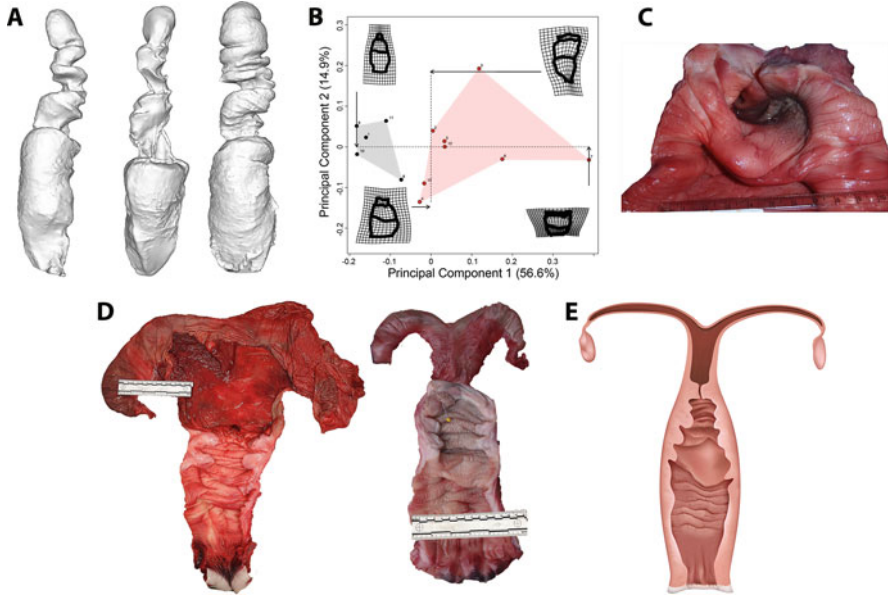
Fig. 5.3 Visual tools used to explore intraspecific reproductive tract variation in female harbor porpoises (*Phocoena phocoena*). (**a**) Three-dimensional reconstruction of silicone vaginal endocasts of three animals. The cervix is at the top of each model, and vaginal opening is at the bottom (modified from Orbach et al. 2021). (**b**) Principal component analysis showing the morphospace of reproductive tract images subjected to two-dimensional geometric morphometric analysis. The gray-shaded area denotes sexually immature females, and the red-shaded area identifies sexually mature females (modified from Orbach et al. 2018). (**c**) Image of partially dissected vagina in cross-sectional view. The prominent vaginal fold forms a tongue-like thick flap that spirals into cranial vaginal folds. (**d**) Images of two dissected reproductive tracts of sexually mature females. The animals are positioned in a dorsal recumbency with the uterine horns at the top. An incision was made down the midline to highlight the vaginal folds. (**e**) Modern illustration of the opened reproductive tract of a sexually mature female positioned in a dorsal recumbency. The illustration emphasizes the asymmetric vaginal folds and their relative size

what drives vaginal fold diversity in cetaceans remains unanswered. Perhaps statistical patterns are not yet apparent as the available data of cetacean reproductive tracts is missing representative specimens from many of the about 96 extant species.

There is also extensive intraspecific variation in vaginal shapes among cetaceans, which was only partly explained by allometry and ontogeny (Fig. 5.3; Orbach et al. 2018, 2020, 2021). Visual aids help highlight the breadth of gross morphological variation among female reproductive organs. We use the harbor porpoise to further demonstrate how art can augment science. In the assessment of vaginal endocast complexity and shape, substantial differences were found between individual harbor porpoises (Fig. 5.3a; Orbach et al. 2021). Similarly, individual variation accounted for 52.6% of total reproductive tract shape variation using a two-dimensional geometric morphometric approach (Orbach et al. 2020). Sexually mature harbor porpoises had wider overall reproductive tracts with prominent cranial vaginas

compared to sexually immature individuals (Fig. 5.3b; Orbach et al. 2018). Overall variation in the reproductive tract shape of harbor porpoises was mostly driven by the relative size of the caudal vagina followed by a bias in the right or left curvature of the reproductive tract (Orbach et al. 2020). The vaginal folds formed a spiral pattern in harbor porpoises (Fig. 5.3c; Supplemental Video 5.1). The chirality ("handedness") of the largest vaginal fold (Fig. 5.3c), which is captured with the endocasts (Fig. 5.3a), is visually absent when the reproductive tract is fully opened (Fig. 5.3d). Scientific illustrations (e.g., Figure 5.3e) can help fill in gaps and provide insights into the evolutionary drivers of cetacean vaginal diversity. Illustrations are particularly helpful in showing these structures intact through cutaways and cross-sections.

5.3.2 Historical Illustrations of Female Cetacean Reproductive Tracts

Historical illustrations, created in an era before digital or high-resolution digital photography, provide a snapshot of current knowledge at that time. Historical illustrations can highlight key aspects of anatomical structures, eliminating unnecessary elements that are often byproducts of dissections. Illustrations can emphasize specific anatomical structures by using dark shading or muting to remove surrounding tissues, unlike photographs. Illustration can also conceptually and visually communicate through cutaways, sections, and transparencies. The illustrations were created by working directly with the anatomist(s) performing the dissections or, in some cases, by the scientists.

Figures 5.4 and 5.5 include historical illustrations of cetacean genitalia from ten species dating from 1848 (Fig. 5.4c) through 1949 (Fig. 5.5d). The cranial vaginas of the three species of baleen whales (blue whale, Fig. 5.4a; fin whale, Fig. 5.4b; sei whale, Fig. 5.4c) illustrated between 1848 and 1882 fill data gaps; our dissections of female baleen whale genitalia have been limited to minke whales (Fig. 1.1) and humpback whales (Fig. 1.14). The blue whale is the largest animal to have ever lived and has a proportionately large reproductive tract. Logistical constraints of shipping and storing such sizable frozen specimens limit access to baleen whale reproductive tracts, particularly of sexually mature animals. Some frozen excised specimens we dissected were in early stages of tissue atrophy, which may yield spurious characterizations.

The historical illustrations further complement the dissection images by detailing features of functional importance. For example, Fig. 5.5c and g portray a harbor porpoise and white-beaked dolphin female reproductive tract, respectively. These two illustrations emphasize longitudinal pleats in the cranial vagina and vaginal folds that may function as channels for semen; these pleats are less overt in dissection photographs (Figs. 1.20 and 1.11, respectively). Figure 5.4c captures the fine leaflike vaginal folds of the sei whale, an attribute we confirmed in the
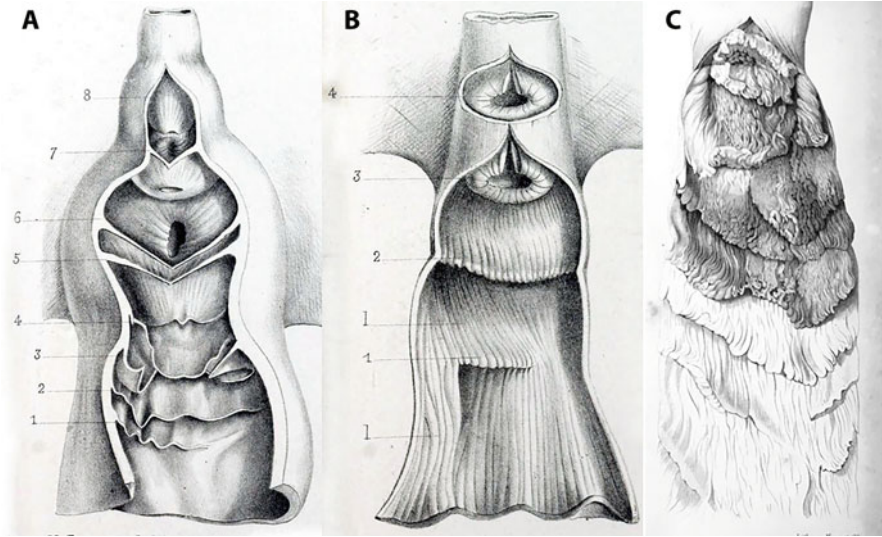
Fig. 5.4 Compilation of historical illustrations of female baleen whale (mysticete) reproductive tracts. The species are (**a**) *Balaenoptera musculus* (Beauregard and Boulart 1882), (**b**) *Balaenoptera physalus* (Beauregard and Boulart 1882), and (**c**) *Balaenoptera borealis* (Vrolik 1848). The illustrations highlight the cervix (top) and cranial vagina (bottom)

beluga whale yet did not adequately capture with a photograph (Fig. 1.2). In contrast, Fig. 5.5c depicts the thick rounded vaginal folds of the harbor porpoise; the largest vaginal fold can be over 5 cm in depth and 16 mm in thickness, which is conveyed in the three-dimensional endocast (Fig. 5.3a) and cross-sectional photograph (Fig. 5.3c), but not in the bird's-eye view photograph (Fig. 5.3d). Revisiting historical illustrations has been enlightening and crucial to our current understanding of cetacean genital morphology.

5.4 Conclusions and Future Directions

The field of female genital evolution remains a rich and vastly underexplored area of basic anatomical research across all taxa (Ah-King et al. 2014; Orbach 2022). Female cetaceans have the most diverse vaginal morphologies within a vertebrate clade due to the presence of vaginal folds that vary in number, shape, size, and positioning across species (Orbach et al. 2017b). Several functional hypotheses for vaginal folds related to sexual and natural selection pressures have been proposed. Further research is needed to empirically test hypotheses. Experiments exploring the genitals of live animals will be of particular utility in ascertaining if there is "cooperation" or "conflict" between the sexes to control paternity (e.g., Arnqvist and Rowe 2005). For example, experiments could track the movement of
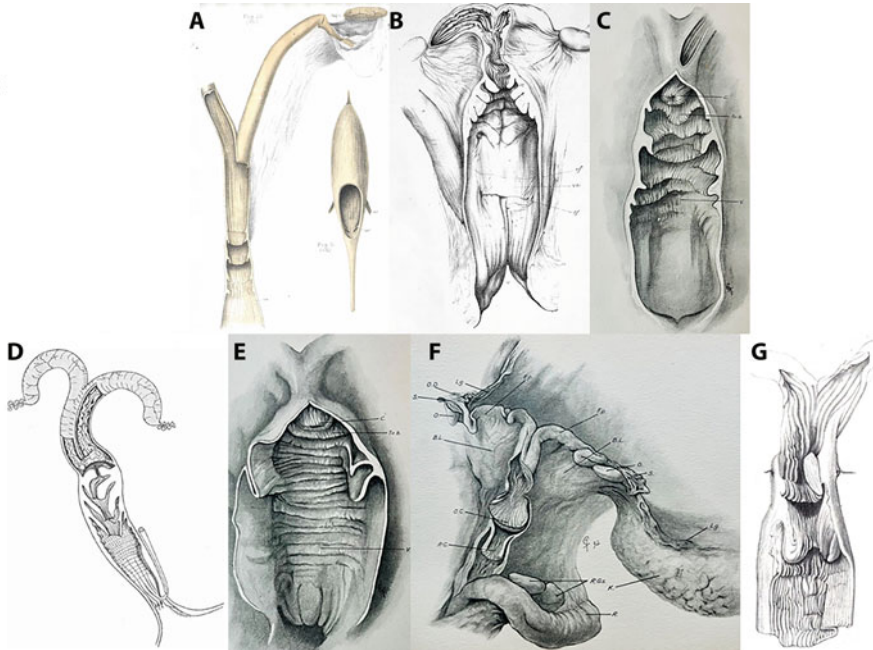
Fig. 5.5 Compilation of historical illustrations of female toothed whale (odontocete) reproductive tracts. The species are (**a**) *Ziphius* sp. (Scott and Parker 1889), (**b**) *Platanista gangetica* (Anderson 1878), (**c**) *Phocoena phocoena* (Pycraft 1932), (**d**) *Globicephala melas* (Harrison 1969), (**e**) *Tursiops truncatus* (Pycraft 1932), (**f**) *Delphinus delphis* (Pycraft 1932), and (**g**) *Lagenorhynchus albirostris* (Van Beneden 1861)

fluorescently labeled sperm that are artificially inseminated into the vagina of a live female to assess if vaginal folds assist with sperm uptake, retention, or rejection. Research is needed to validate the hypothesis that seawater is lethal to cetacean sperm (Schroeder and Keller 1989; O'Brien et al. 2008), as the duration of exposure and salinity levels may vary results. The benign or hostile nature of the vagina can be explored by testing the concentration of leukocytes or the community composition of the microbiome. The potential role of cervical mucus as a semen plug warrants investigation. Further research is needed to understand if the longitudinal bands within the vagina provide protected channels for sperm transport and how these channels may vary with estrous state.

As copulation is a direct mechanical interaction between females and males, sexual selection likely acts concurrently on the genitalia of both sexes (Brennan 2016). Although this chapter focuses on the genital morphology of female cetaceans, studies on intromittent organs are needed, especially those that integrate gross morphology, microanatomy, and varied visual tools to underscore diversity and functionality. Comparative studies of cetacean male genitalia have been limited to the relative testes sizes and penis lengths of baleen whales (Brownell and Ralls 1986). There are historic illustrations that depict broad interspecific variations in

cetacean penis morphology and showcase extraordinary examples of unusual reproductive structures. For example, the Indus river dolphin (*Platanista minor*) lacks the pelvic bones that anchor the muscle that erect the penis in other cetacean species (Pilleri 1976; Dines et al. 2014). The Indus river dolphin also has erectile side lobes and a fibrous septum between the corpora cavernosa, which are anomalous traits among cetacean genitalia (Pilleri 1976). Future research on cetacean reproductive tracts, particularly when complemented with graphical imagery, will facilitate improved understanding of sexual and mating systems.

Knowledge of sexual anatomy can inform our understanding of cetacean mating systems and provide clues into the mating strategies of the sexes. For example, testes mass (relative to body size) is positively correlated with the intensity of sperm competition across many taxa, including cetaceans, and provides insights into the relative strength of pre- or post-copulatory sexual selection (Kenagy and Trombulak 1986; Dines et al. 2015). Similarly, many of the hypotheses related to the functions of vaginal folds in cetaceans support a role in sexual selection. The number, size, and complexity of vaginal folds vary widely across cetacean species. While the mechanism remains unknown, the diversity likely reflects opportunities for cryptic female choice or other forms of post-copulatory sexual selection. The harbor porpoise stands out as a species with extravagant genitalia in both sexes. Females have thick, complex, and spiralized vaginal folding (Fig. 5.3, Orbach et al. 2020). Males have some of the largest testes relative to body size of any mammal (Kenagy and Trombulak 1986). The vaginal folds and deep recesses may curtail the depth or direction of penile penetration and/or semen movement (Orbach et al. 2017a, 2020). While the order of development of complex vaginal labyrinths, large relative testes sizes, long penises, and lateralized mating behavior remain unknown, it is clear that the genitalia of both sexes of harbor porpoises have coevolved (Orbach et al. 2020). Further exploration of the reproductive anatomy, mechanics of copulation, and mating behavior of both sexes are warranted.

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Chapter 6
Interspecific Comparison of Reproductive Strategies

Susan J. Chivers and Kerri Danil

Abstract Knowledge of cetacean life history, morphology, and social behavior provides clues to the niche-specific adaptations that have evolved to maximize reproductive fitness. An essential component of a species' life history is mating, particularly the sex-specific mating strategies that have evolved. Mating strategies vary within and among species reflecting phylogenetic constraints and the interplay of selective forces molding each species' adaptations. The suite of cetacean mating strategies that have evolved ultimately determines how a species' mating system operates. Thus, mating systems provide a unifying framework to compare and contrast cetacean strategies for reproduction and mating. Theory predicts that the degree of sexual size dimorphism (SSD) and the relative testes size of mammalian species will be good indicators of their mating system. However, interspecific and intraspecific variability in SSD and relative testes size reveal unique tradeoffs made in response to evolutionary pressures and ecological processes that result in exceptions to the theoretical predictions. In this chapter, we review current knowledge of cetacean reproductive biology and how that information furthers our understanding of their mating systems.

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6.1   Introduction

Mammalian mating systems have long interested scientists seeking to understand how species maximize reproductive fitness, and those of cetaceans are no exception. Mating systems describe the mating dynamics between the sexes, often in terms of the number of mates. Operationally, a suite of mating strategies has evolved to control the number of mates while maximizing an individual's reproductive fitness. The evolutionary constraint of internal gestation and subsequent lactation among mammals means that the parental investment by females is greater than that of males. This inherent disparity in contributing to the production of offspring means that the evolutionary pressures on females and males differ, with females maximizing reproductive fitness by ensuring survival of offspring, while males seek multiple mates. Thus, all mammals are predisposed to polygamous mating systems (Trivers 1972; Clutton-Brock et al. 1989; Clutton-Brock and Parker 1992).

Cetacean mating systems, like those of other mammals, are expected to be polygamous with multiple partners among reproductive individuals. The two cetacean suborders, the baleen (mysticetes) and toothed whales (odontocetes), are predicted to be predominantly polygynous, a form of polygamy in which individual males mate with multiple females. Additionally, the polygamous systems of polyandry in which individual females mate with multiple males, and of polygynandry (multi-male multi-female) in which both females and males have multiple mates, are predicted to play a role. Observations consistent with these predictions suggest that all three mating systems occur in cetaceans (Mesnick and Ralls 2018a; Gerber and Krützen 2023, this book; Würsig et al. 2023, this book).

Mating systems provide a framework for discussing sex-specific mating strategies, because they represent the synthesis of evolutionary pressures on a species' life history characteristics, including attributes of their reproduction (e.g., interbirth interval, age at attainment of sexual maturity (ASM) and longevity), morphology (e.g., body size and shape), and behavior (e.g., group dynamics, mating) that maximize reproductive fitness (Fig. 6.1). Most of what we know about cetacean reproduction and morphology has come from cross-sectional studies using biological material collected from dead animals sampled from direct or indirect takes or found stranded on beaches (e.g., Lockyer 1984; Perrin and Reilly 1984). However, longitudinal studies have provided unique and valuable insights about the sociobiology of species, including the life history and social strategies associated with mating and reproduction (Mann and Karniski 2017; Trillmich and Cantor 2018). The multi-decadal longitudinal studies of the bottlenose dolphin (*Tursiops* spp.; Connor et al. 2000b; Wells 2019), humpback whale (*Megaptera novaeangliae*) (Cartwright et al. 2019), killer whale (*Orcinus orca*) (Baird 2000; Ford 2019), and sperm whale (*Physeter macrocephalus*; Whitehead and Weilgart 2000; Cantor et al. 2019) together with the longer, but not multi-decade, studies of the dusky dolphin (*Lagenorhynchus obscurus*; Würsig and Würsig 2010) and Hawaiian (or gray's) spinner dolphin (*Stenella longirostris longirostris*; Norris et al. 1994; Lammers 2019) have contributed greatly to understanding the complexities of cetacean social
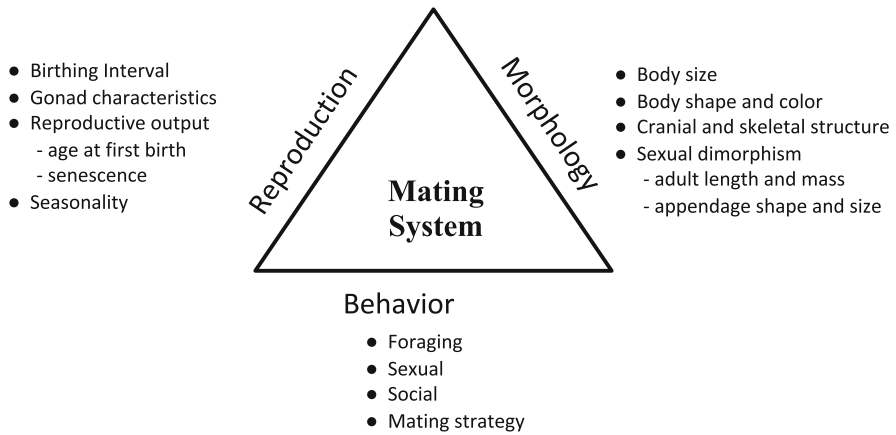
Fig. 6.1 Comparing and contrasting attributes of cetacean reproduction, morphology, and behavior provide insight about their mating systems and the role of sexual selection in the evolutionary process forming species-specific adaptations

systems and the variability in lifetime reproductive output among individuals. This is knowledge that cannot be obtained from cross-sectional studies and is particularly valuable to interpreting life history characteristics, especially parameter estimates, that differ between cross-sectional and longitudinal studies (Mann and Karniski 2017).

In this chapter, we present an overview of cetacean life history characteristics focusing on the reproductive and morphological characters associated with mating. We use the term mating strategies to refer to mate selection within a mating system, which is defined by the number of mates per individual. This terminology is consistent with the published literature, which also uses the term "reproductive strategies" in this context (e.g., Connor et al. 2000a; Whitehead and Mann 2000; Boness et al. 2002). We consider the term mating strategies to be a general term that encompasses the tactics, or operational mechanisms of mating, about which we know little for most cetacean species. We focus on providing as broad a comparison of species as possible to complement the other chapters in this book presenting updated information about the sexual strategies of bottlenose dolphin, Risso's dolphin (*Grampus griseus*), killer whale, sperm whale, gray whale (*Eschrichtius robustus*), bowhead whale (*Balaena mysticetus*), and right whale (*Eubalaena* spp.). As our knowledge of cetacean mating strategies improves, so too will our understanding of their mating systems. The inherent difficulties of studying most cetacean species means that reviewing what we know about mating will facilitate revising proxies to infer the mating strategies of the least known and most difficult-to-study species and identifying the knowledge gaps limiting our understanding of their mating systems and the evolutionary forces molding them.

6.2   Reproduction

All cetaceans are large and long-lived mammals. Females produce few offspring during their reproductive years and bear the energetic costs of gestation and lactation to rear calves with little or no contribution from males. Studies of cetacean reproductive biology have primarily focused on females to facilitate the development of conservation and management plans, because females are the limiting sex and define the inherently low population growth rates of all species. Consequently, less is known about male life history strategies. However, biological studies of male reproduction have contributed to understanding some of the variability in cetacean mating systems.

6.2.1   Females

The morphology and histology of cetacean ovaries and reproductive tracts have been quite well studied for a number of toothed and baleen whale species. Much early research focused on understanding the female reproductive system, which contributed to later studies of cetacean life history strategies (e.g., Harrison et al. 1969, 1972; Slijper 1979; Lockyer 1984; Perrin and Reilly 1984). The maturation and ovulation processes of female cetaceans, including delayed sexual maturity, are similar to those of other large, long-lived mammals. In cross-sectional studies, sexually mature female cetaceans are typically identified by the presence of a fetus or milk in the mammary glands or by detecting evidence of an ovulation. The latter is indicated by the presence of a corpus luteum (CL) or corpus albicans (CA) on the ovary (Fig. 6.2). The CL is an endocrine gland that forms to produce the hormones necessary to maintain pregnancy and degenerates to a CA after an infertile ovulation

Fig. 6.2 Stages of delphinid ovary development from immature (left) to mature (center) and to mature and pregnant (right). The mature ovary (center) shows multiple corpora albicantia, which are the scars of regressed corpora lutea that remain after ovulation and pregnancy. The mature and pregnant ovary (right) shows the corpus luteum (smooth round structure on top of the ovary) that forms when ovulation occurs and remains throughout pregnancy (Credit: M. Lynn, NOAA, NMFS, Southwest Fisheries Science Center, La Jolla, CA)
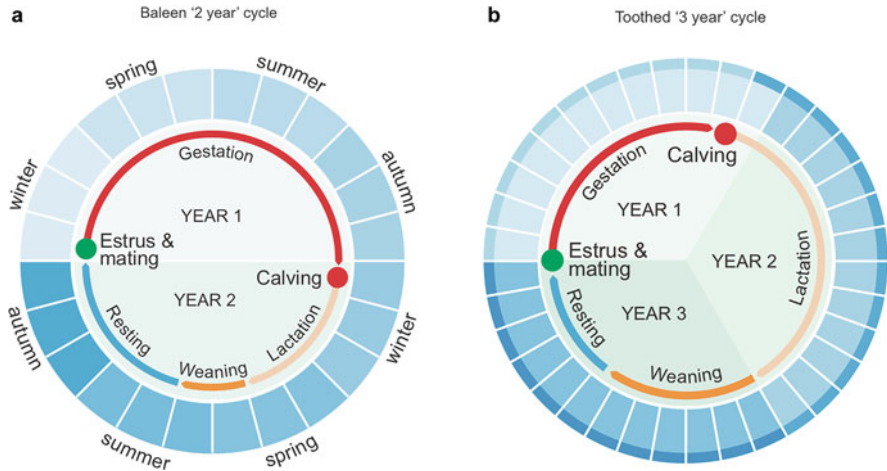
Fig. 6.3 The reproductive cycle of (**a**) baleen whales is typically 2 years and is correlated with their annual migration between winter breeding and summer feeding grounds, while that of (**b**) toothed whales is a minimum of 3 years in most species with the lactation period lasting 2 or more years in some species (Credit: Reproduced from Berta (2015) with permission from Ivy Press, UK)

or following birth if pregnancy occurs. CAs are thought to persist indefinitely in cetaceans and provide a record of past ovulations (Perrin and Donovan 1984), but there is some evidence that they do not persist and that CAs resulting from ovulation and pregnancy have different characteristics (Takahashi et al. 2006; Dabin et al. 2008). Age-specific CA accumulation rates differ within species. The hypotheses for this pattern include underlying differences in pregnancy rates reflecting variability in the health of adult females, mating success, resource availability, or anthropogenic stressors (Perrin and Henderson 1984; Perrin and Mesnick 2003; Ferreira et al. 2014).

Cetaceans give birth to single, large and precocial young after a gestation period of approximately 1 year. The lengthy gestation in part balances the cost of producing a large neonate capable of swimming and diving with its mother when born. The reproductive cycle is typically 2 years in baleen whales and 3 years in many toothed whale species (Fig. 6.3). Baleen whale breeding and calving are more synchronous and less variable than those of toothed whales. Among toothed whales, the small delphinids tend to have fairly diffuse calving peaks that may include spring and fall peaks, while nearly all species have extended (i.e., >1 year) lactation periods (Perrin and Reilly 1984; Connor et al. 2000b; Whitehead and Mann 2000; Chivers et al. 2016; Chivers 2018).

Reproductive success varies throughout the life of large and long-lived mammals. The lower reproductive success associated with older age at attainment of sexual maturity is thought to be due in part to the physiological tradeoffs between reproduction and growth that occurs as individuals continue to grow to physical maturity after becoming sexually mature (Stearns 1977; Clutton-Brock 1984; Segura et al.

2021). Like other mammals, adult female cetaceans exhibit stage-specific changes in reproductive rates with evidence of lower reproductive success among newly mature females equated to fewer successfully weaned calves. This pattern has been documented in the well-studied common bottlenose dolphin (*Tursiops truncatus*) (Wells and Scott 1990) and in several baleen whales, including the fin whale (*Balaenoptera physalus*) (Lockyer 1987), North Atlantic right whale (*E. glacialis*), and southern right whale (*E. australis*) (Browning et al. 2010; Miller et al. 2011). Lower reproductive rates among older adult female common bottlenose dolphin have also been documented as longer interbirth intervals with an extended (i.e., 3- to 8-year) lactation period (Wells and Scott 1990). Similarly, ovulation rates, and thus presumably reproductive rates, have been found to be lower for older individuals in other delphinid species. These include the pantropical spotted dolphins (*Stenella attenuata attenuata*) and spinner (*S. longirostris*) dolphins, false killer whale (*Pseudorca crassidens*), and long- and short-finned pilot whales (*Globicephala melas* and *G. macrorhynchus*, respectively), in which post-reproductive females have been identified by atrophic ovaries (Perrin et al. 1976, 1977; Marsh and Kasuya 1984; Perrin and Reilly 1984; Martin and Rothery 1993; Photopoulou et al. 2017). Post-reproductive females have also been identified in Baird's beaked whale (*Berardius bairdii*), beluga whale (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), northern right whale dolphin (*Lissodelphis borealis*), and sperm whale, which suggests this trait has evolved independently several times within the toothed whales (Ellis et al. 2018). The percentage of post-reproductive, or senescent, females differs markedly among toothed whale species, but to date, there is no evidence of post-reproductive females in baleen whales. The adaptive significance of this life history characteristic is not yet understood. However, the hypothesis that post-reproductive females may increase the reproductive success of related individuals is supported by evidence that species with the greatest proportion of post-reproductive females are those with fairly complex and often matrilineal social structures. For example, post-reproductive females care for young that are not their own but may be those of related individuals in sperm whale, short-finned pilot whale, and killer whale populations (Christal et al. 1998; Whitehead 1998; Ottensmeyer and Whitehead 2003; Ward et al. 2009).

Annual variability in reproduction in cetaceans may be linked to resource availability influencing the body condition of females. Cross-sectional studies have provided data to link body condition and fertility (e.g., fin whales; Lockyer 1986), while longitudinal studies have provided valuable insight into how reproductive output varies among individuals and is influenced by environmental conditions. For example, annual monitoring of gray whale calf production since 1994 revealed a positive correlation between seasonal access to Arctic feeding grounds and calf production; more forage for pregnant adult females results in higher calf production. This linkage contributes to interpreting how Arctic ecosystem changes impact gray whales (Perryman et al. 2020; Moore et al. 2022). The influence of the environment on reproductive output is as important to understand for the conservation and management of cetacean species as are the selection pressures molding their life histories to maximize lifetime reproductive fitness.

6.2.2 Males

The life history characteristics of males are less well known than those of females. This largely reflects that knowledge of males is less critical to understanding cetacean population dynamics than that of females. However, male life history characteristics provide a more complete picture of a species' reproductive potential and insights about mating strategies.

Male reproductive tracts were also well studied early on in cetacean biology (e.g., Harrison et al. 1972; Slijper 1979) and found to be similar to those of other mammals. One obvious difference between terrestrial and aquatic mammals is that the reproductive organs of aquatic mammals are inside the abdominal cavity. This adaptation evolved with other traits associated with streamlining cetaceans for aquatic life. For example, the internalization of the male reproductive tract was accompanied by the evolution of a countercurrent heat exchanger to thermoregulate the testes to ensure spermatogenesis (Rommel et al. 1992, 2007).

Histological examination of the testis tissue has documented the sexual maturation process of cetaceans, which is typically mammalian (Perrin and Reilly 1984; Plön and Bernard 2007). Identifying sexually mature males from histological sections (Fig. 6.4) provides the ability to describe sexually mature males from proxies, including testis weight, total body length (TL), and age (e.g., Chivers et al. 1997). TL is often the most readily available information for cetaceans and correlates well with body mass and testes weight to provide a valuable proxy for identifying sexually mature individuals (for baleen whales, see Lockyer 1976; for toothed whales, see Perrin et al. 2005; for monodontids, see Kelley et al. 2014b). The ability to use proxies of male sexual maturity facilitates estimating age and TL at attainment of sexual maturity from larger data sets than might otherwise be available for cross-sectional life history studies (Lockyer 1984; Perrin and Reilly 1984).

6.3 Sexual Dimorphism

Sexual dimorphism refers to differences in external and internal features (e.g., TL, color patterns, cranial morphology) between the sexes. Sexually dimorphic traits are the result of evolutionary pressures acting differently on the sexes, with sexual selection playing a key role. For example, growth patterns differ between the sexes in most cetacean species, resulting in some degree of sexual dimorphism (Boness et al. 2002). Both sexes have high growth rates from birth through weaning that then become progressively slower until reaching full adult size. However, the sex that grows to be the largest typically sustains higher growth rates after weaning. In cetaceans, this is generally the male (Ralls and Mesnick 2009; Mesnick and Ralls 2018b).

Differential growth patterns result in males having an older ASM than females. The largest difference in ASM is in species with the greatest degree of male-biased

(a)

(b)

(c)
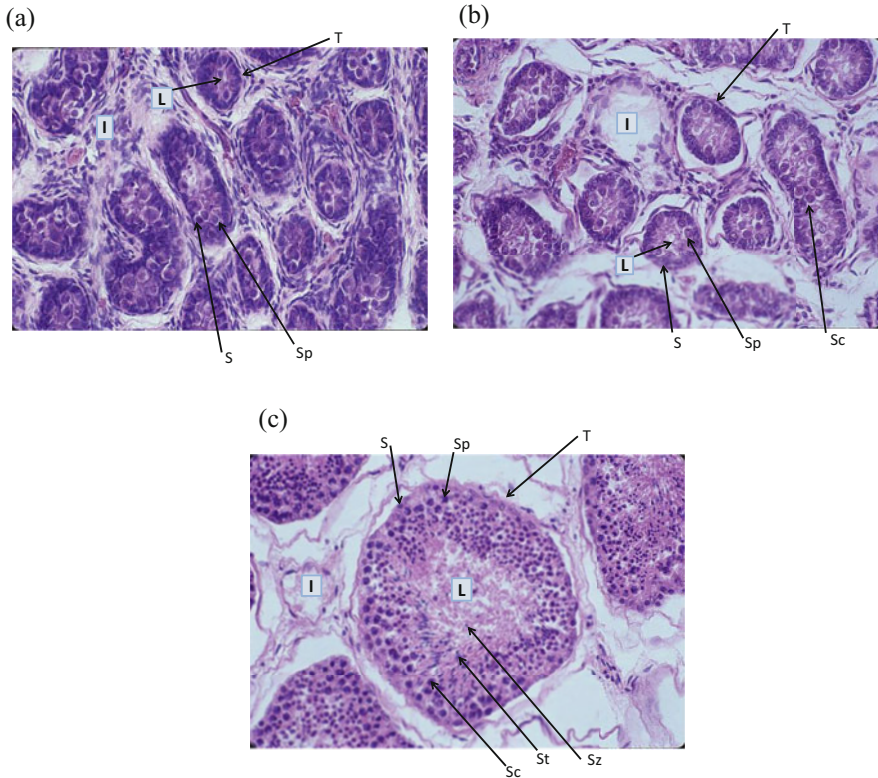
Fig. 6.4 Histological sections of (a) immature, (b) maturing (or pubertal), and (c) mature testes collected from pantropical spotted dolphin (*Stenella attenuata attenuata*) specimens provide an example of testes maturation in male cetaceans. Components of the testes visible at 40x magnification for each stage are labeled: T = seminiferous tubule, I = interstitial tissue, L = lumen, S = Sertoli cells, Sp = spermatogonia, Sc = spermatocytes, St = spermatids, and Sz = spermatozoa. The maturity stages can be identified by increasing seminiferous tubule diameter (T), decreasing interstitial tissue (I), and evidence of active spermatogenesis as males mature (Credit: S. Chivers, NOAA, NMFS, Southwest Fisheries Science Center, La Jolla, CA)

sexual size dimorphism (SSD). For example, adult male sperm whales are more than 60% bigger than females and reach sexual maturity at approximately 20 years of age compared to 9 years in females (Whitehead 2018). The difference is similar in killer whales and the long- and short-finned pilot whales, reflecting the additional time required to grow to about 85% of their asymptotic length, which is the approximate size at which all mammals become sexually mature (Laws 1956). On the other hand, the small delphinids with little SSD reach sexual maturity at more similar ages. For example, male common bottlenose dolphins and pantropical spotted dolphins reach sexual maturity only about 3 years later than females (Perrin and Reilly 1984).

SSD in cetaceans is typically expressed as the ratio of male-to-female adult TL. Among baleen whales, females are generally 5% larger than males. This

female-biased SSD provides females more blubber storage capacity to meet energetic demands of migration and reproduction, especially lactation. Similarly, female-biased SSDs occur among the smallest toothed whales, which are the porpoises and river dolphins, and these females are as small as they can be to produce a precocial calf that is large enough to survive (Ralls 1976). Among the other toothed whales, SSD is male-biased and, while variable, is relatively moderate (i.e., ~5–10%) in most species (Mesnick and Ralls 2018b; Cantor et al. 2019).

Within the toothed whales, males of many of the delphinids (family Delphinidae) are more robust (e.g., heavier) than females but differ little in TL. Additionally, differences in the external morphology of the sexes are evident in comparisons of the size and shape of the head, dorsal fin and peduncle (e.g., anal hump), dentition, and uro-genital color patterns. Notable examples include the head shape of sperm whales, the dorsal fins of killer whales and members of the Globicephalinae family, the dorsal fin and post-anal hump of eastern spinner dolphins (*S. l. orientalis*), the uro-genital color patterns of Dall's porpoise (*Phocoenoides dalli*), the tusk of narwhals, and the dentition of beaked whales. If sexual selection is an evolutionary driver of sexually dimorphic traits, then such traits can allow for inferences about mating systems (Mesnick and Ralls 2018b).

6.4 Mating Systems

Mating strategies maximize an individual's reproductive success. Thus, cetacean males may spend time searching for receptive females to sire as many offspring as possible, while females may invest heavily in rearing calves. Interspecific variability and intraspecific variability in mating strategies revealed by longitudinal studies suggest that a population's social behavior and ecological niche influence the evolution of mating tactics and strategies. Thus, mating tactics operating within a given strategy are expected to reflect the tradeoffs made by individuals to maximize their reproductive success (Mesnick and Ralls 2018a; Boness et al. 2002). However, the mating strategies of most cetacean species have been inferred from SSD and relative testes size, which is the ratio of testes size to body size, and actual mating tactics remain poorly known.

6.4.1 Female Mating Strategies

Like other large long-lived mammals, adult female cetaceans invest heavily in each calf reared. Females need to meet demands of gestation and lactation and to protect their young from predators; their fitness is enhanced by choosing a mate that can provide valuable resources or good genes (Trivers 1972; Stearns 1977; Clutton-Brock 1989; Clutton-Brock et al. 1989).

Cetacean female mating strategies remain poorly understood (Orbach 2019). The inherent difficulties studying cetaceans that live in oceanic habitats contribute to this and further exacerbate conducting studies to evaluate the role of sexual selection in molding mating strategies. The role of female choice has been considered less important than the largely more obvious behaviors of males competing with each other for mates or resource guarding. However, there is mounting evidence that female choice shapes behavioral and physiological adaptations that ultimately define mammalian mating systems (Birkhead and Møller 1993; Gomendio and Roldan 1993a, b; Gomendio et al. 1998). Among cetaceans, evidence of female choice has been revealed by long-term studies of humpback whales, right whales, common bottlenose dolphins, and dusky dolphins documenting that females avoid or repel males attempting to mate (Brownell and Ralls 1986; Palsbøll et al. 1992; Clapham 1996, 2000; Connor et al. 2000b; Whitehead and Mann 2000; Boness et al. 2002; Orbach et al. 2015).

Two categories of female choice tactics have been proposed from observations made in longitudinal studies of the dusky dolphin, Indo-Pacific bottlenose dolphin, and sperm whale. The tactics are either behavioral (signal discrimination, mate choice copying, and evasive behaviors) or physiological (polyestry/multiple matings and modified genitalia) (Orbach et al. 2023, this book). The behavioral tactics focus on mate choice by evaluating cues from male secondary sexual characters (discussed in the next section) or copying the choices of other females and avoiding mating with undesirable males. In contrast, the physiological tactics focus on avoiding conceptions from poor quality males by repeated estrus cycling or mating or excluding sperm from the uteri. Cross-sectional studies of vaginal morphology contribute to the sperm exclusion hypothesis, which is also referred to as the physiological "modified genitalia" tactic of mate choice. While vaginal length correlates with cetacean TL and not vaginal fold diversity (Orbach et al. 2017), intraspecific comparisons of vaginal fold diversity may provide some clues to the selective pressures that formed them (Orbach et al. 2021). Three species with complex vaginal morphology—long vaginal length and cumulative vaginal fold length—also have evidence of heavy investment in sperm competition by males. These are the pygmy and dwarf sperm whales (*Kogia breviceps* and *K. sima*, respectively) and harbor porpoise (*Phocoena phocoena*). The similarity in life history traits supporting relatively high reproductive output in these species (Read and Hohn 1995; Plön 2004) may provide future insights about the functionality of this morphology (Dines et al. 2014, 2015; Orbach et al. 2017, 2021). However, the role of female choice will likely remain unknown for most species.

6.4.2   Male Mating Strategies

Cetacean mating systems are predominantly classified as variations of multimale mammalian systems with male mating strategies inferred from traits shaped by sexual selection: behavior, phenotype, especially secondary sexual characteristics,

SSD, and relative testes size. To sire as many offspring as possible, cetacean males are expected to compete with each other for access to mates directly using combat or display methods to exclude rivals or attract females (pre-copulatory behavior) or indirectly through sperm competition (post-copulatory behavior; Dines et al. 2015; Mesnick and Ralls 2018a; Orbach 2019). Aggressive intermale competition for mates is inferred from external scars on males of species with relatively small testes and marked secondary morphological characters (e.g., narwhal tusks and beaked whale teeth) (McCann 1974; Silverman and Dunbar 1980; MacLeod 1998; Dines et al. 2015; Loch et al. 2023, this book). Many morphological and physiological traits are likely the result of sexual selection producing variation ultimately associated with mating strategies as evolutionary pressures mold species to their environment. The resulting adaptations reflect access to resources: prey, predators, and mates influencing a species' distribution, range, group size, and social structure.

A minority (~30%) of toothed whales exhibit pre-copulatory mating behaviors with about half participating in aggressive combat and half displaying to attract mates, while the majority (~70%) exhibit post-copulatory traits associated with sperm competition (Dines et al. 2015). The tactics of sperm competition remain unknown, and the associated traits (e.g., penis length, penis shape, sperm quantity, and sperm morphology) are expected to vary among species as has been observed in other mammals (Gomendio and Roldan 1993b; Gomendio et al. 1998; Tourmente et al. 2011). Additional variability in mating strategies is also expected to be associated with mating behavior as has been observed in bottlenose dolphins (Connor et al. 2000b) and inferred for spinner dolphins (Perrin and Mesnick 2003). We will discuss these examples further below, because they suggest that mating tactics may contribute to operational variability in mating strategies within species.

The potential for sperm competition in some baleen whales is considered high because females have multiple mates per estrus (Brownell and Ralls 1986). However, longitudinal studies have revealed variability in male mating strategies for several species. For example, humpback whales exhibit intermale competition during the winter breeding season, which includes setting up three-dimensional leks in areas selected by females for calving and singing to attract mates (Clapham 2000; Connor et al. 2000a). Intermale competitions have also been observed in right whales with callosity-induced skin scarring resulting from aggressive encounters (Connor et al. 2000a; Kraus and Hatch 2001). Because establishing how intermale competitions control access to females has proven difficult, sperm competition is suggested as the primary mating strategy of right whales as it is for bowhead and gray whales. Little is known about blue (*Balaenoptera musculus*), Bryde's (*B. edeni*), fin (*B. physalus*), and minke (*B. acutorostrata*) whales' mating strategies, but songs recorded for these species may play a role in finding, attracting, or guarding potential mates (Brownell and Ralls 1986; Boness et al. 2002; Eichenberger et al. 2023, this book).

The mating strategies of toothed whales are somewhat better known than those of baleen whales largely due to the longitudinal studies of bottlenose dolphins, sperm whales, and killer whales. Male alliances have been observed in both the Shark Bay

(Australia) population of Indo-Pacific bottlenose dolphins (*T. aduncus*) and the Sarasota Bay (Florida, USA) population of common bottlenose dolphins. The alliances are temporary formations consisting of two or three males accompanying reproductively active females to control mating access to them, with intermale aggression also observed in the Shark Bay population. However, there is no evidence of male alliances being formed, or of any other types of male defense of females, to control reproductive access to females in two other common bottlenose populations: Moray Firth, Scotland, and Doubtful Sound, New Zealand (Connor et al. 2000b; Lusseau 2007). While male alliances are presumed to be a type of pre-copulatory behavior, paternity studies have revealed that alliance membership does not ensure mating or reproductive success (Duffield and Wells 1991; Wells et al. 1999; Krützen et al. 2004).

Studies of sperm whales have revealed that intermale aggression and sound occasionally play a pre-copulatory role but that males primarily rove among groups of females in search of mates (Whitehead and Weilgart 2000). Similarly, resident killer whales rove among pods brought together by summer prey aggregations to mate with receptive females not in their natal group. This behavior likely ensures outbreeding (Baird 2000). Long-finned pilot whales have a social structure similar to killer whales, and molecular genetics has confirmed that roving males ensure outbreeding by mating outside their natal groups (Amos et al. 1993).

SSD and relative testes size as proxies—Assembling comparative data sets to infer mating strategies from SSD and relative testes size is challenging because of differences in reported metrics among studies. For example, adult TL may be expressed as a mean, maximum, or an estimated asymptote, and characteristics of adults may differ depending on whether TL, appendage morphology, or reproductive organ data are used to identify them. Similarly, relative testes size may be calculated as the ratio of combined or singular testis weight with or without epididymis to body size: TL or weight. However, TL is used more frequently than body weight, because TL data are more readily available for most species, and correlates well with body weight (Brownell and Ralls 1986; Connor et al. 2000a). Consequently, the data compiled for mating strategy studies will differ, including which species were represented and which metrics were selected (Table 6.1). Even so, the overall conclusions of studies have been similar, because the focus has been on interspecific patterns, which are largely robust to the data metrics chosen.

Toothed whales adhere to Rensch's rule of allometry, which predicts that SSD scales with body size in mammalian lineages with male-biased SSD, with two notable exceptions (Casper and Begall 2022). The exceptions are the species that do not have male-biased SSD: the beaked whales (family Ziphiidae) and the Amazon river dolphin (*Inia geoffrensis*). The large size of beaked whales predicts that SSD will be male-biased, but instead the species have a predominantly female-biased SSD or are monomorphic. Male beaked whales also have relatively small testes and distinct dentition, which is a secondary morphological character, used in intermale combat and display behavior suggesting a significant investment in pre-copulatory mating behaviors in this family (Heyning 1984; Dines et al. 2015; Pitman 2018). On the other hand, a female-biased SSD is predicted for the Amazon river dolphin, but

Table 6.1 The number of baleen and toothed whale species included in studies using sexual size dimorphism (SSD) and testes size relative to male total body length as proxies to infer cetacean mating systems

Study	Adult total body length			Testes size			Analyses
	Baleen whale species	Toothed whale species	Metric	Baleen whale species	Toothed whale species	Metric	
Connor et al. (2000a)	4	25	Mean of sexually and physically mature and estimated asymptotic length	0	10	Maximum combined weight without epididymis	Allometry of SSD for cetaceans and relative testis size for toothed whales; one species per genus to mitigate phylogenetic bias
Plön and Bernard (2007)	3	15	Categorized as monomorphic, female-biased, or male-biased from literature	3	15	Combined testes weight as percent of total body weight	Proposed mating strategies using SSD, relative testes size, group size, and behavior
Dines et al. (2015)	11	47	Maximum	11	47	Maximum combined weight with and without epididymis	Multivariate approach to evaluating pre- and post-copulatory behavior
Casper and Begall (2022)	0	57	Mean; most extreme difference between sexes observed	0	0	None	Phylogenetic test of Rensch's rule for allometric scaling of SSD

their SSD is male-biased, and males have been observed with scars and injuries consistent with aggressive intermale competition for mates (Martin and Da Silva 2006). These examples demonstrate the unique evolutionary pressures molding cetacean species and the importance of considering the pre-copulatory role of mating behavior and secondary morphological characters in mating strategies.

The relative importance of pre- and post-copulatory behaviors in male cetacean mating strategies was furthered by Dines et al. (2015), who combined patterns in SSD and relative testes size with other traits likely molded by sexual selection, including secondary morphological characteristics and mating behaviors. Species with investment in pre-copulatory behaviors tend to have relatively small testes and distinct secondary sexual traits (e.g., dentition in most of the beaked whales and song in some baleen whales), which allow them to control access to females by engaging in combat or in ritualized displays to attract females. Examples of aggressive intermale combat include narwhals using their tusks in aggressive intermale interactions (Silverman and Dunbar 1980; Kelley et al. 2014b) and some beaked whales, especially *Mesoplodon* sp., using their teeth in combat (Pitman 2018). However, most (~70%) cetacean species (n = 58) in the Dines et al. (2015) study exhibited investment in predominantly post-copulatory traits. Among these species, most had limited male-biased SSD coupled with moderate to large relative testes size suggesting sexual selection favors sperm competition as the predominant post-copulatory investment. This negative correlation between SSD and relative testes size in toothed whales is consistent with that observed in all mammals and is one that correlates with mating systems (Kenagy and Trombulak 1986; Kelley et al. 2014a).

6.4.2.1 Intraspecific Comparisons

Relatively few studies have characterized the male mating strategies of subspecies, or populations, within cetacean species. However, geographic variation in the external morphology and molecular genetics has revealed evidence for long-term isolation of populations within species. The accumulation of differences in traits in isolated populations has been sufficient to support the recognition of discrete populations within species and interspecific and intraspecific taxonomic revisions (Perrin 2018). This geographic variation may be associated with variability in the mating tactics that have evolved within species.

Geographic variation in the external morphology of Eastern Tropical Pacific (ETP) spotted dolphins, spinner dolphins, and common dolphins resulted in the recognition of several populations and subspecies among them (Perrin et al. 1985; Dizon et al. 1994). Examining the mating strategy proxies for the ETP dolphin subspecies currently recognized to those published for small delphinids provides some context for assessing the variability in these proxies and identifying those that may have unique adaptations associated with their mating strategies (Fig. 6.5). For example, the study that compared male reproductive characteristics of the eastern spinner dolphin subspecies to those of the whitebelly (a hybrid of *S. l. orientalis* and *S. l. longirostris*) spinner dolphin revealed evidence to support the idea that different
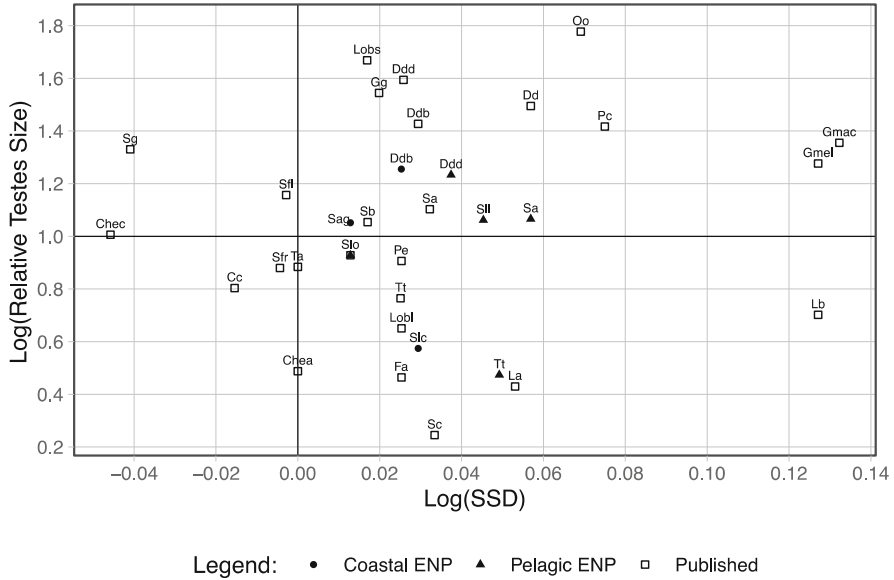
Fig. 6.5 Sexual size dimorphism (SSD) and relative testes size for subspecies of eastern North Pacific Ocean (ENP) spotted dolphins, spinner dolphins, and common dolphins using data collected from fisheries bycatch specimens are plotted together with published values for 35 delphinid species from Connor et al. (2000a) and Dines et al. (2015). The data point labels reflect the taxonomic name for each species and subspecies represented. For the ENP: pantropical spotted dolphin (Sa), coastal spotted dolphin (Sag), eastern spinner dolphin (Slo), whitebelly spinner dolphin (Sll), Central American spinner dolphin (Slc), short-beaked common dolphin (Ddd), long-beaked common dolphin (Ddb), and common bottlenose dolphin (Tt). For the published data, ordered by SSD: Hector's dolphin (Chec), Guiana dolphin (Sg), Commerson's dolphin (Cc), Atlantic spotted dolphin (Sfr), tucuxi (Sfl), Heaviside's dolphin (Chea), Indo-Pacific bottlenose dolphin (Ta), eastern spinner dolphin (Slo), dusky dolphin (Lobs), rough-toothed dolphin (Sb), Risso's dolphin (Gg), common bottlenose dolphin (Tt), melon-headed whale (Pe), Pacific white-sided dolphin (Lobl), pygmy killer whale (Fa), short-beaked common dolphin (Ddd), long-beaked common dolphin (Ddb), pantropical spotted dolphin (Sa), striped dolphin (Sc), Atlantic white-sided dolphin (La), common dolphin (Dd), killer whale (Oo), false killer whale (Pc), Northern right whale dolphin (Lb), long-finned pilot whale (Gmel), and short-finned pilot whale (Gmac)

polygamous mating systems were operating. Specifically, socially and sexually dominant male eastern spinner dolphins were identified as those with high sperm production, distinct secondary sexual characteristics (i.e., a post-anal hump, forward-canted dorsal fin), and a relative testes size about half that of whitebelly spinner dolphins. These observations are consistent with a more polygynous mating system in eastern spinner dolphins and a multi-male multi-female mating system in whitebelly spinner dolphins (Perrin and Mesnick 2003).

Selective pressures may be influencing the mating strategies of other toothed whale species that exhibit geographic variation in their external morphology (e.g., SSD and secondary sexual characters) and relative testes size. These species include the false killer whale, narwhal, beluga whale, common dolphin, and pantropical

Table 6.2 Sexual size dimorphism (SSD) calculated using the mean and maximum adult total body length (cm; TL) data for female and male common dolphins (*Delphinus delphis*) and pantropical spotted dolphins (*Stenella attenuata*) sampled from incidental bycatch and stranded specimens in the eastern North Pacific are presented along with relative testes size calculated from combined testes with epididymis weights (g) and maximum male adult TL. For the common dolphin, the subspecies and Eastern Tropical Pacific (ETP) populations recognized are presented: *D. d. bairdii* (eastern North Pacific long-beaked common dolphin, LBCO), *D. d. delphis* (short-beaked common dolphin, SBCO) from the northern (N), central (C), and southern (S) populations. For ETP pantropical spotted dolphins, the coastal subspecies (*S. a. graffmani*) and populations of *S. a. attenuata* (northeastern (NE), western (W) and southern (S)) are presented (Perrin et al. 1985). For reference, the data used in the analyses by Dines et al. (2015) are included

Subsp./stock	N Female TL	N Male TL, Testes weight	SSD (TL mean)	SSD (TL max)	Relative testes size
Common dolphin					
LBCO	56	141, 6	1.040	1.057	12.22
SBCO—N	90	147, 6	1.041	1.097	8.82
SBCO—C	843	947, 613	1.020	1.113	10.89
SBCO—S	17	13, 11	0.989	1.106	18.53
LBCO—Dines				1.070	26.72
SBCO—Dines				1.140	31.26
Pantropical spotted dolphin					
Coastal	159	106, 48	1.028	1.025	11.26
NE	5754	4378, 1201	1.011	1.136	11.64
W	1777	1315 445	1.010	1.064	10.39
S	2092	1713, 504	1.016	1.059	10.27
Sa—Dines				1.070	11.27

spotted dolphin. As observed in the ETP spinner dolphins, the relative testes size of false killer whales off South Africa is about half that of those off Japan (7.7 versus 14.1), but unlike the ETP spinner dolphins, the SSDs of these populations are the same (Ferreira et al. 2014). These data suggest differences in their mating strategies may be revealed when more data are available. Similarly, comparisons of mating strategy proxies for Canadian Arctic populations of narwhal and beluga whales reveal interspecific and intraspecific differences. The larger relative testes size of beluga whales, which range from 2.01 to 3.63 among populations, suggests they are more polygynandrousthan narwhals, which have relative testes sizes ranging from 1.8 to 2.7. In contrast, the negative correlation of narwhal tusk length with testes size suggests tusks may play a role in display soliciting female choice and intermale aggression (Silverman and Dunbar 1980; Kelley et al. 2014b). In the ETP, populations of common dolphin (*Delphinus delphis*) and pantropical spotted dolphin exhibit relatively low SSDs (i.e., <15%) and relative testes size ranging from 8.8 to 12.2, which are characteristics consistent with sperm competition being the

dominant mating strategy. However, the variability observed in these proxies among populations suggests other traits may have evolved to influence male mating success within this strategy (Table 6.2).

Additional studies quantifying sexual dimorphism in other biological and morphological characteristics contribute to inferring species' mating strategies when combined with SSD, relative testes size, and group size. For example, Plön et al. (2012) compared the sexual dimorphism in relative organ size for three small delphinid species off South Africa and found that the results were consistent with the overall differences in their body size, relative testes size, distribution and range, and group size and structure. In concert, the authors suggested the primary mating strategies differed with the Indo-Pacific humpback dolphin (*Sousa chinensis*) having a harem-like strategy, the Indo-Pacific bottlenose dolphin engaging in frequent copulations, and the long-beaked common dolphin sperm competition. Similarly, Yahn et al. (2022) characterized variability in the degree of dorsal fin sexual dimorphism in four species of toothed whales belonging to the subfamily Globicephalinae sampled off Hawaii: the false killer whale, short-finned pilot whale, melon-headed whale (*Peponocephala electra*), and pygmy killer whale (*Feresa attenuata*). Variability ranged from fairly extreme in short-finned pilot whales to more limited in false killer whales. The authors proposed that this evidence supported pre-copulatory mating behavior as likely in all of these species. This hypothesis differs from that of Dines et al. (2015), which listed pre-copulatory selection for short-finned pilot whales only. These examples illustrate some of the complexities associated with inferring mating strategies from proxies and the value of including multiple sexually dimorphic traits, especially those likely to be under sexual selection, along with group size and social behaviors to reveal how species likely implement their mating strategy.

6.5 Social Behavior

Mating is one aspect of cetacean life histories that contributes to group formation and the only one we will consider here. The size, dynamics, and behavior of individuals within groups reflect the spatiotemporal patchiness of resources in the environment and the benefit to individuals coming together to breed, forage, or avoid predators (Acevedo-Gutierrez 2018; Trillmich and Cantor 2018). Mating behaviors are a key component of mating strategies and remain poorly understood for most cetaceans. Our understanding of cetacean mating strategies is limited to the six species that have been the focus of longitudinal studies and includes the multi-decadal studies of sperm whales, killer whales, and bottlenose dolphins (McHugh 2019).

Baleen whales are largely solitary, and the aggregations that occur on summer feeding and winter breeding grounds are predominantly structured around the availability of resources: prey and mates. Similarly, aggregations of toothed whales are structured around the availability of these resources as well as the need to protect calves from predators during the extended lactation period of most species.

Successfully protecting calves contributes to an individual's lifetime reproductive fitness, which can be further enhanced by communal living and cooperating with kin (Rendell et al. 2019). Toothed whales are largely social with many of the smaller species living in groups characterized by fission-fusion dynamics with group size and membership frequently changing, while several of the larger species form matrilines (e.g., killer whales, pilot whales, and sperm whales) that are more stable (Christal et al. 1998; Ottensmeyer and Whitehead 2003; Gowans et al. 2008; Cantor et al. 2019; Gowans 2019). Long-term studies have contributed insights about the social behaviors associated with mating, including the formation of male alliances controlling access to reproductive females in bottlenose dolphins (Wells et al. 1999; Connor et al. 2000b), and how roving males find mates to ensure outbreeding in sperm whales (Whitehead and Weilgart 2000; Eguiguren et al. 2023, this book). Studies detailing social behaviors are essential to understanding mating strategies and tactics, and the data collected from longitudinal studies will aid in identifying the proxies most informative for inferring mating strategies of difficult-to-study species.

6.6   Conclusions and Future Directions

The apparent diversity among cetacean mating systems reflects the variability in their reproductive strategies, which differ markedly between baleen and toothed whales (Mesnick and Ralls 2018a). To date, cetacean mating systems are considered partially predictable from SSD and relative testes size as they are for other mammals (Kenagy and Trombulak 1986). These metrics, together with the role of secondary sexual characteristics and behavior, reveal the contribution of pre- and post-copulatory traits in mating strategies. Evidence of intermale competition through combat or display controlling access to females suggests that pre-copulatory traits play a significant role in mating in a minority of species (~30%). On the other hand, the investment in relatively large testes evident for the majority (~70%) of species suggests that post-copulatory traits, especially sperm competition, dominate cetacean mating strategies (Dines et al. 2015). One noteworthy exception among odontocetes is the franciscana (*Pontoporia blainvillei*). To date, the franciscana is the only cetacean to exhibit long-term patterns of social interaction consistent with a single male, or monogamous, mating system, which is rare among mammals (Connor et al. 2000a; Wells et al. 2013).

Mating systems for most cetaceans will likely continue to be predicted from proxies. The ability to identify additional proxies of traits molded by sexual selection will improve our understanding of mating strategies. Comparative interspecific and intraspecific studies using cross-sectional data combined with data obtained from techniques developed to study the reproductive biology of wild populations in situ will contribute to quantifying and evaluating potential proxies to infer mating strategies of the lesser-known species. The use of remote technologies such as application of existing molecular genetic techniques to reveal male reproductive success through paternity (e.g., Krützen et al. 2004) will play a greater role in these

studies, particularly as the collection of biological samples for cross-sectional studies continues to decline. While the highly mobile, wide-ranging, largely pelagic nature of cetaceans will continue to limit our knowledge of most species, our understanding of the complexities of their reproductive and mating strategies will be expanded by on-going multi-decadal longitudinal studies.

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Chapter 7
Non-conceptive Sexual Behavior in Cetaceans: Comparison of Form and Function

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Abstract Non-conceptive sexual behavior (NCSB) is phylogenetically widespread, having been documented in 35 of the 87 extant cetacean species, but function and form of NCSB have not been studied in comparative manner. Many cetacean species engage in NCSB across a wide variety of settings and contexts (e.g., play, sexual, affiliative). NCSB includes both social and non-social sexual behaviors, such as non-social masturbation on the environment or social same-sex thrusting toward a conspecific, but importantly, none of the behavior described as NCSB affords reproduction. While these two general categories encompass all sexual actions, the behaviors are diverse depending on species, social structure, and sex of the individual being observed. Social sexual behavior presumably has individual or social benefits. This chapter organizes what is known about NCSB in cetaceans by summarizing NCSB repertoires from peer-reviewed literature and discussing proposed functions (e.g., practice for reproduction, attracting opposite-sex mates, reducing the reproductive opportunities of same-sex conspecifics, reinforcing dominance relationships, alliance formation, reconciliation, and social tension reduction). Further, the form or behavioral repertoire, the sex of the individuals engaging in NCSB, the environment observed in, and whether NCSB was present or absent in general are noted from each of the articles reviewed. Overall, NCSB behavior observed across species shares similar elements (e.g., thrusting, lateral presentations) in both Mysticeti and Odontoceti. NCSB tends to be more prevalent among sexually

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immature compared to sexually mature individuals. Additionally, NCSB is more prevalent between male conspecifics compared to females when animals engage in same-sex NCSB. Interspecific NCSB has also been reported for a number of species. While most reports come from toothed whales, the limited observations of baleen whales have also found that many species engage in NCSB, making it likely that NCSB is included in the behavioral repertoire of most cetacean species. NCSB likely aids in forming and maintaining social relations and/or in the development of sexual repertoires in cetaceans, not unlike what has been proposed for primates. We hope this chapter sparks interest in comparative studies of NCSB and sheds light on the similarities of NCSB across species.

7.1   Introduction

Non-conceptive sexual behavior (NCSB), or socio-sexual behavior, is sexual in form but does not facilitate direct reproduction and has been reported in more than 300 animal species from insects to primates (Bagemihl 1999; Bailey and Zuk 2009). NCSB often involves mounting interactions during which the participants employ stereotyped copulatory movements (including pelvic thrusting) in non-reproductive contexts. NCSB can occur between two sexually immature individuals (Gunst et al. 2013), sexually immature and sexually mature (Ogawa 2006), two same-sex sexually mature animals (Hohmann and Fruth 2000), two opposite-sex sexually mature animals (Gunst et al. 2020), or even between different species (Gunst et al. 2018). Socio-sexual behavior is a subset of NCSB that appears sexual in terms of its outward form but is thought to primarily be used to mediate adaptive goals that are not directly related to reproductive coitus (Wickler 1967). These adaptive goals are often employed to solve social problems the participants encounter.

Multiple functions have been proposed for NCSB, including practice for reproduction, attracting opposite-sex mates, reducing the reproductive opportunities of same-sex conspecifics, reinforcing dominance relationships, alliance formation, reconciliation, and social tension reduction (reviewed in Vasey 1995; Bagemihl 1999; Bailey and Zuk 2009). For example, female mountain gorillas (*Gorilla g. beringei*) may use NCSB to re-affirm dominance hierarchy (Grueter and Stoinski 2016). In Japanese macaques (*Macaca fuscata*), sexually mature females mount sexually mature males (often with pelvic thrusting), which prompts the male to mount the female (Gunst et al. 2020). Mutual genital contact, where one animal touches the genitals of the other and vice versa, between male yellow baboons (*Papio cynocephalus anubis*) appears to facilitate alliance formation (Smuts and Watanabe 1990), and ventro-dorsal mounting among female vervet monkeys (*Cercopithecus aethiops*) appears to achieve the same function (Fairbanks 2002).

Table 7.1 Hypotheses and predictions on the function of non-conceptive sexual behaviors

Hypothesis	Predictions
Dominance	• Social NCSB will be asymmetrical between partners (i.e., one animal directs significantly more NCSB toward another) • Associated with other agonistic behaviors • NCSB is directed toward subdominant animals
Bonding	• Social NCSB is reciprocal and symmetrical • Occurs between animals that associate frequently with one another
Greeting	• NCSB is employed when two animals (or two groups) reunite after being separated for an extended time
Learning	• Animals should engage in more NCSB and socio-sexual behavior when sexually immature compared to when they are sexually mature • If socially learned, those with access to mature animals should learn more quickly than those who do not have access
Practice	• Animals that engage in more NCSB should be more successful in reproduction (i.e., there would be a positive correlation between time spent engaged in NCSB and the number of offspring)
Pleasure	• If animals engage in NCSB because they find it pleasurable, the genitals of animals should make physical contact with animate or inanimate objects to stimulate themselves (i.e., not just sexual/courting presentations, which are likely not physically pleasurable) • For males, ejaculation may occur when they find the behavior pleasurable
Play	• NCSB that aligns with Burghardt's (2005) criteria of play behavior • Is more frequent in the sexually immature period of life
Multi-functional	• NCSB falls into more than one of the above categories (e.g., the NCSB is playful and is used to learn or practice sexual behaviors)

The topic of NCSB has been most studied in primates; however, non-primate exemplars do exist. For example, courtship behavior, mounting, and pair-bonding appear to facilitate alliance formation between male graylag geese (*Anser anser*; Kotrschal et al. 2006). Research on NCSB has also focused on smaller animals with little attention to large mammalian species, although, once again, exceptions exist (Hill et al. 2014). For example, evidence suggests that mounting between domestic cattle helps reinforce dominance relationships during periods of social uncertainty and stress (Klemm et al. 1983). For the most part, however, NCSB appears to be characterized by some mixture of both sexual and socio-sexual motivations (Vasey 1995; Bagemihl 1999). In bonobos (*Pan paniscus*), genito-genital rubbing is accompanied by vocalizations and facial expressions that are indicative of sexual reward, but it also appears to reduce social tension associated with food sharing (Hohmann and Fruth 2000).

Steadily increasing interest in cetaceans over the past 70 years has led to an explosion in the literature on various behavioral topics for these aquatic mammals. This growth in focus and the ability to study smaller cetacean species housed in managed care facilities have enabled a substantial increase in knowledge (e.g., behavior, physiology; see Chap. 10). This chapter reviews the literature on NCSB in cetaceans by outlining the distribution among species, general behavioral repertoire, and potential functions (Table 7.1).

7.2 Distribution of NCSB Across Mysticeti and Odontoceti

To illustrate the widespread distribution of NCSB across Cetacea, we created a cladogram using cladistic data from ten K tree project data (Arnold et al. 2010) and FigTree (Rambaut 2018). To date, 35 of the 87 extant species of Cetacea have been observed engaging in NCSB, in both managed care facilities and wild settings, with some species engaging in inter-species NCSB (Fig. 7.1). However, we suspect this is

Fig. 7.1 A cladogram of all known species of cetacean. The cladogram represents species that we know engage in non-conceptive sexual behavior (NCSB), the environment NCSB have been observed in, the sex of the animals that have been described engaging in NCSB, and if they engage in NCSB with species other than their own. Star symbols indicate the presence of interspecies sexual behavior. White squares indicate that NCSB has been observed in males, gray indicate NCSB has been observed in females, and black squares indicate both sexes have been observed engaging in NCSB. White triangles indicate NCSB has been observed in the wild, gray indicate NCSB has been observed in managed care, and black triangles indicate NCSB has been observed in both environments. Finally, white circles indicate that NCSB is absent or has not been reported, while black circles indicate NCSB has observed in that species

an underestimation as many cetaceans are under-studied (e.g., Ziphiidae, beaked whales). Evidence for this underestimation was found when comparing the research effort (i.e., the number of articles published on each species of Cetacea) as reported by Fox et al. (2017), compared to the presence or absence of NCSB. Employing a logistic regression (R Core Team 2020), we found that the number of articles previously published on a given species, as reported by Fox et al. 2017, predicted the presence or absence of NCSB in a given species that we report in this chapter ($\chi^2_{88} = 95.89$, $p < 0.001$). This finding suggests that as species are studied more, evidence for NCSB in additional species will be found; though, this is a crude measurement and should only be used to encourage the study of behavior in species that are rarely reported on. This might be true of the highly cryptic Ziphiidae, which are rarely observed despite the number of species (i.e., more than 19) within this family. However, this prediction may be inaccurate as gregarious species, and thus the ones most likely to engage in NCSB, are more frequently studied. With increased behavioral observation through the use of drones (reviewed by Whitt et al. 2020; Ramos et al. 2023, this book), we suspect more species will be observed engaging in NCSB and that this behavior will be understood in greater detail (e.g., Orbach et al. 2020); though other factors, such as social structure, are far more important in predicting if a species engages in NCSB.

7.3 Behavioral Repertoire and Physical Form of NCSB

While most prominent in toothed whales, many species of baleen whales have also been observed engaging in NCSB with the behavioral repertoire of NCSB described across species showing similarities. Typically, NCSB consists of a few behaviors (e.g., thrusting, intromission, genital presentation, genital contact or manipulation, penile erections, and contact of another's body with an individual's ventral area); however, bouts of NCSB can also consist of just one of the behaviors listed in Table 7.2. Many of these behaviors (e.g., penile erections and ventral contact) also occur during courtship (e.g., Hill et al. 2015; Lilley et al. 2022), so describing the partners involved is important when deciphering if the behavior being observed is non-conceptive or copulatory. Species-specific descriptions of behavior, as well as corresponding references, are available as Supplementary Material.

NCSB can be contactless (Fig. 7.2) or involve physical contact (Fig. 7.3). For example, beluga whales (white whales, *Delphinapterus leucas*) engage in s-posture sexual presentations and lateral sexual presentations frequently without contact (Lilley et al. 2022), with sexually mature males often doing so toward sexually immature individuals (Hill et al. 2015; Lilley et al. 2020) (Fig. 7.4). Bubbles also seem to be a part of the beluga NCSB repertoire and may be used to communicate, either as a visual signal or as a result of vocalization (Hill et al. 2015). However, insertion, intromission, genital rubbing, mouthing, thrusting, and petting involve contact, whether it be with a conspecific, heterospecific, or inanimate object. Both contactless and contact NCSB occur between same-sex partners (male-male and

Table 7.2 An ethogram of non-conceptive sexual behaviors

Behavior	Description	Families
Bubbles	Bubbles produced from blowhole, most commonly in a small stream	Monodontidae
Erection	Penis is extended externally from the genital slit; penile displays	Balaenidae, Balaenopteridae, Delphinidae, Iniidae, Lipotidae, Monodontidae, Phocoenidae
Insertion	Insertion of flukes, pectoral fins, or dorsal fin into the genital slit of another individual; or insertion of penis into the blowhole or anus of another individual	Delphinidae, Iniidae
Intromission	Animal inserts the penis into the genital slit of another individual	Balaenidae, Balaenopteridae, Delphinidae, Iniidae, Monodontidae, Phocoenidae
Genital rub	The actor moves its genital region along the receiver's body or object	Balaenopteridae, Delphinidae, Iniidae, Monodontidae
Lateral presentation swim	Animal positioned on its side, with pectoral fins perpendicular to the water surface and ventral side directed at the second animal	Balaenopteridae, Delphinidae, Monodontidae, Phocoenidae
S-posture	Animal positioned on its side, while its body is curved in an s-position, with pectoral fins perpendicular to the water surface and ventral side directed at the second animal	Balaenopteridae, Delphinidae, Monodontidae, Phocoenidae
Mouthing of genitals (goosing/nuzzling)	Rostrum positioned on the genitalia with contact/insertion	Balaenopteridae, Delphinidae, Monodontidae
Open mouth	Mouth is open in the context of a sexual interaction	Monodontidae
Thrust/ mounting	Animal is near the second animal and making body movements that move the genitals closer to the other individual (and usually the other individual's genitals)	Balaenopteridae, Delphinidae, Monodontidae, Phocoenidae
Petting	Flipper-to-genital contact; often in a stroking motion	Balaenidae, Balaenopteridae, Delphinidae, Iniidae

Note: See Supplementary Material for a full list of citations and species descriptions

female-female pairings) and mixed-sex partners, age-matched and non-age-matched partners, and between different species.

NCSB is most easily recognized when the partners are incapable of reproduction (i.e., two males or two females engaging in NSCB, two sexually immature animals engaging in NSCB, one sexually mature and one sexually immature animal engaging in NCSB, between two species that cannot produce hybrids) or with a dead conspecific (i.e., necrocoitus; Dudzinski et al. 2003; Kincaid et al. 2022). In addition, sexual behavior with an object or the environment (e.g., masturbation) is also a form of NCSB. When sexual behavior occurs between mixed-sex pairs and both animals

Fig. 7.2 A form of non-tactile sexual behavior exhibited by humpback whales. Known as penis extrusions, an immature and sexually mature male swims with penile erections (Illustration by Nichole Ham and inspired by Pack et al. (2002))
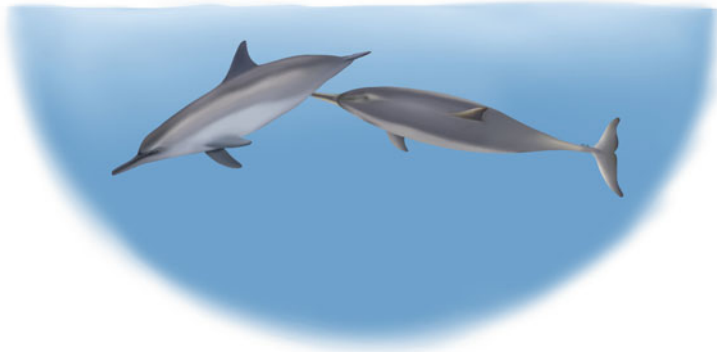
Fig. 7.3 Beak-to-genital contact made by spinner dolphins. In this case, a female inserts her beak into the genital slit of a male dolphin (Illustration by Nichole Ham and inspired by Norris and Dohl (1980) and Wells (1984))

are sexually mature, it is very difficult to determine if the behavior observed was NCSB in context or conceptive behavior, unless life history or hormonal information is available (e.g., age, sex, pregnancy status). For that reason, we describe behavior between same-sex partners, sexually mature-immature partners, or behavior between two species, with the caveat that NCSB likely also occurs between sexually mature mixed-sex partners. As well, in some species, NCSB may occur between multiple partners simultaneously (e.g., surface-active groups; Parks et al. 2007) (Fig. 7.5).
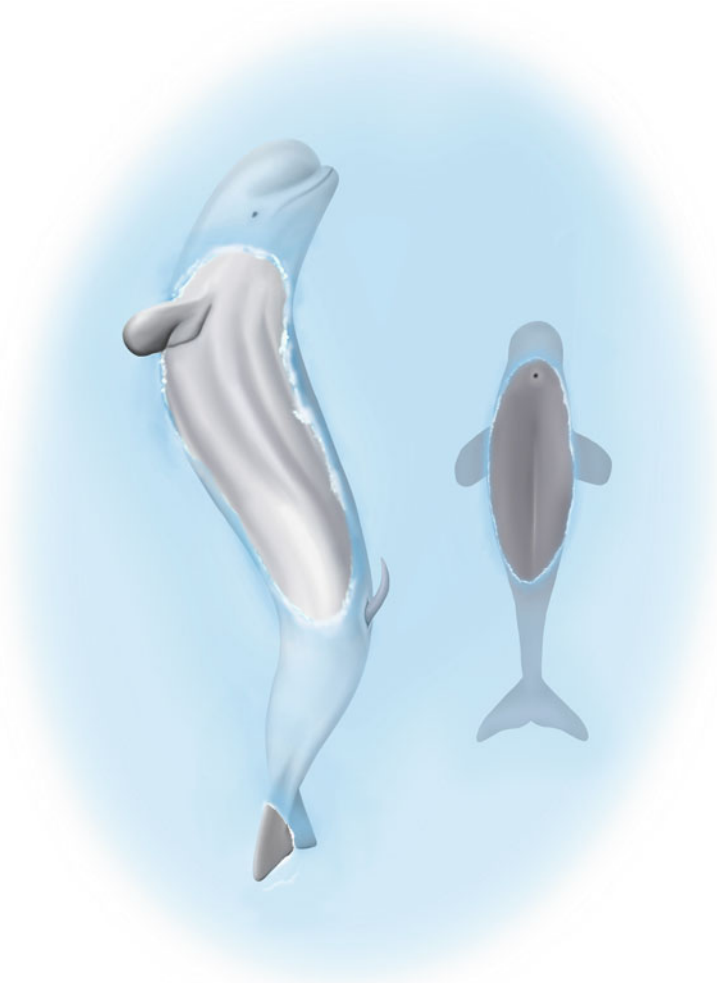
Fig. 7.4 A sexually mature male beluga exhibits an s-posture display, with a penile erection, toward a sexually immature whale. This, a non-tactile form of non-conceptive sexual behavior, is a sexual display used during courtship and in bouts socio-sexual behavior and sexual play (Hill et al. 2015; Lilley et al. 2020; Ham et al. 2022) (Illustration by Nichole Ham and inspired by Hill et al. (2015))

7.4 Possible Functions of NCSB

For some species, NCSB emerges within the first months of life, while for others it takes much longer. For example, thrusts and erections in sexually immature bottlenose dolphins (*Tursiops* spp.) and Yangtze finless porpoises (*Neophocaena*
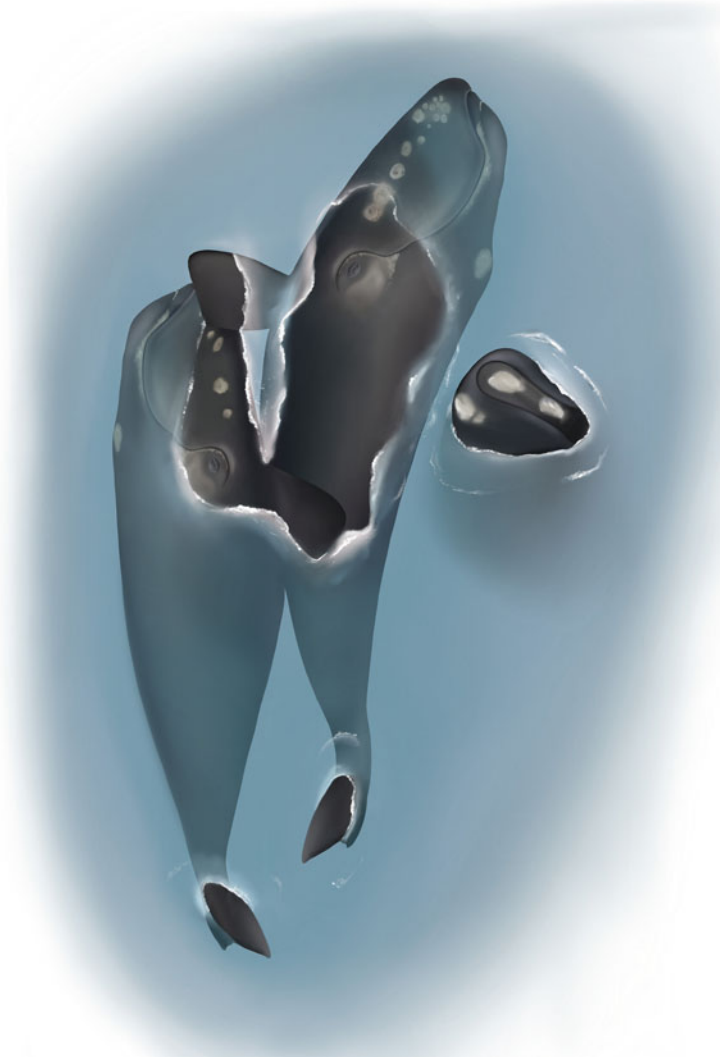
Fig. 7.5 Right whales engaging in tactile sexual activity. A male rubs his ventral region on a sexually immature while a third whale is present. Often characterized as a surface active group, this illustration is inspired by Donnelly (1967), Kraus and Hatch (2001), Parks et al. (2007), and Lonati et al. (2022) (Illustration by Nichole Ham)

phocaenoides asiaeorientalis) emerge in the early months of life (Mann 2006; Xian et al. 2010), whereas thrusts are only observed after the first few months and erections after the first year of life in beluga whales (Ham et al. 2022). This variation could be due to differences in developmental timelines, juvenile periods, or social structures, but understanding the emergence of a behavior ultimately provides clues

to the function of the behavior (e.g., practice, social bonding). Detailed studies of the development of NCSB can provide clues to the function, benefit, and adaptive value these behaviors might have on mating ecology, social relationship management, and the development of sexual behavior (Table 7.1).

7.4.1 Managing Social Relationships: Dominance, Greeting Behavior, and Bonding

While tooth raking is frequently associated with agonism and dominance relationships (Scott et al. 2005; Lee et al. 2019; Ham et al. 2021a; Grimes et al. 2022), NCSB has also been suggested to play a role in the formation of dominance relationships (Östman 1991; Mann 2006; Wu et al. 2010; Furuichi et al. 2014; Harvey et al. 2017; Serres et al. 2021) and may even occur at the same time. Dominance relationships among individuals may influence the success of copulatory behavior. One interesting question should be explored: are those that are more dominant more successful in copulatory behavior? Further, are these animals more successful because they are more dominant or because they engage in NCSB more frequently to maintain their dominance position or both? Studying the dominance position and number of offspring, in addition to the frequency of NCSB, for a given individual would begin to answer some of these questions.

In addition to dominance, same-sex NCSB can help manage social relationships or reduce social tension, especially for those species where social groups include unrelated individuals, as in some primates (reviewed by Vasey 1995; Furuichi et al. 2014). There is also evidence that dolphins employ NCSB in managing social relations (*Tursiops* spp.; Würsig and Würsig 1979; Connor and Mann 2006; Mann 2006; Harvey et al. 2017; *Stenella longirostris*, Norris and Dohl 1980; *Sousa* spp. Saayman and Tayler 1979; *Lagenorhynchus obscurus*, Würsig and Pearson 2014). This function may be especially true for those species that live in large pods and/or fission-fusion groups such as bottlenose dolphins, in which social relationships must be continuously negotiated, re-established, and re-affirmed. Long-term studies of Indian Ocean bottlenose dolphins (*T. aduncus*) have found that male dolphins develop long-lasting bonds or alliances with other males (Connor et al. 1992, 2001, 2006, 2022) characterized by recurrent NCSB and symmetrical relationships (Mann 2006).

For some species, including bottlenose dolphins in managed care facilities, sexual play occurs nearly every day (Brown and Norris 1956). Studies of wild cetaceans have reported frequent NCSB (Johnson and Norris 1994; Connor et al. 2000; Mann 2006). For example, male bottlenose dolphin calves engage in NCSB at a rate of 2.38 interactions per hour (Mann 2006), which is quite frequent considering the generally poor visibility conditions which obstruct the human observers. Additionally, despite displaying typical copulatory behavior with sexually mature females on a seasonal basis, sexually mature male beluga whales in managed care facilities display a high

frequency of NCSB throughout the year, except the month of peak conceptive behavior when male-male NCSB almost completely stops (Glabicky et al. 2010). With increasing age, the NCSB of beluga whales becomes seasonal, suggesting that maturity and fluctuation in hormone levels might be drivers (Ham et al. 2021b). The decrease in male-male pelvic thrusting during the months when beluga whales are mating suggests that pelvic thrusting serves both as a copulatory function (when directed toward females) and as a form of NCSB (when directed toward males). During the non-breeding months, the NCSB of same-sex thrusting seems to serve an adaptive social function such as social bonding or dominance hierarchy maintenance (Glabicky et al. 2010). Thus, for beluga whales, NCSB does not take the place of reproductive conceptive behavior but does seem to occupy a larger portion of a male beluga's social interactions. Furthermore, s-posturing in beluga whales occurs in both agonistic/aggressive displays and courting displays (e.g., Hill et al. 2015), but the s-postures have different topographies in each context. The overlap of behaviors in sexual and aggressive contexts could be a result of dominance relationships being displayed and reinforced through both sexual means and aggressive displays or could be the result of specific behaviors taking on different meanings in different contexts. NCSB in beluga whales is highly reciprocal (Lilley et al. 2020; Manitzas Hill et al. 2022), at least between sexually mature males and sexually immature males, so more information on the reciprocity of such behavior is needed to determine if dominance is a possible function for this species.

Not only does NCSB occur before sexual maturity in some cetacean species, NCSB also occurs among individuals who are post-reproductive. For example, female short-finned pilot whales (*Globicephala macrorhynchus*), which have a post-reproductive phase of their life (Acevedo-Gutiérrez 2018) and live in mixed sex and age, mid-sized pods (Fox et al. 2017), were found to have spermatozoa in their reproductive tract, postmortem (Kasuya et al. 1993). This suggests that although the females were no longer reproducing, they were still involved in sexual activity (Kasuya et al. 1993). The complex social groupings of short-finned pilot whales might explain the use of NCSB in non-reproductive females if they are employing NCSB to manage social relations.

In some killer whale (*Orcinus orca*) populations, differing matrilines/pods congregate seasonally when males of differing ages from different pods join, forming a temporary all-male group (Bagemihl 1999; Baird 2000). Once formed, the males engage in energetic NCSB. Around 90% of the observed male-male NCSB is reciprocal and includes turn-taking of genital rubbing (Bisther and Vongraven 1995; Bagemihl 1999). Despite the formation of all male pods of dissimilar ages, "adolescent" killer whales (12–25 years old) engage in these behaviors the most (Bagemihl 1999; Baird 2000). Individuals have partner preferences, interacting with the same conspecific year after year (Bagemihl 1999). More recently, an anecdotal report describes a mature and immature male engaging in genital-genital rubbing, with penile erections, in reciprocal manner (Sanvito and Galimberti 2022). In managed care facilities, reciprocation in killer whales is also observed, and it is seemingly used in managing social relations (Sánchez-Hernández et al. 2019). For killer whales, it seems that NCSB is being used as "social glue" (see Bailey and Zuk

2009) not only between members of the same pod but also among pods that coinhabit the same area.

It seems that NCSB is used by many cetacean species as a greeting behavior in brief meetings with other pods and even between different species (Saayman and Tayler 1979; Würsig and Würsig 1979, 1980; Heimlich-Boran 1988; Bisther and Vongraven 1995; Rendell and Whitehead 2001; Dudzinski 2010; Dudzinski et al. 2010; Nakamura and Sakai 2014; Würsig and Pearson 2014). NCSB-driven greeting rituals may be used as a way to evaluate the physical ability of the novel pod members as occurs in some primates and rodents (Pellis and Iwaniuk 1999; Smith et al. 1999). More observations of social group meetings and reunions are necessary to further investigate the role of NCSB as ritual greetings. Similarly, when animals living in managed care facilities are moved from one facility to another, researchers/ veterinarians/animal care staff should assess if NCSB is employed when animals are first introduced to one another, although this could also be a display of dominance.

To further understand the function of NCSB with respect to dominance, bonding, and other social functions of NCSB, more detailed analyses are needed, where observers note the partners involved and the results of behaviors. Given the high frequency of occurrence and prevalence across cetacean species (Fig. 7.1), NCSB is likely a very important aspect of cetacean social behavior.

7.4.2   Learning

NCSB might be used to practice general motor skills (D'Agostino et al. 2017), especially during sensitive periods of development (Byers 1998), and has also been suggested to be of potential importance for successful conceptive behavior later in life (Fairbanks 2002; Mann 2006), which may be more challenging in the three-dimensional aquatic environment. While empirical evidence of sexually immature animals engaging in NCSB to practice copulatory behavior is limited, this has been suggested for many species (beluga whales; Glabicky et al. 2010; Hill and Ramirez 2014; Hill et al. 2015; Lilley et al. 2020; Manitzas Hill et al. 2022; right whales (*Eubalaena* spp.); Thomas and Taber 1984; Kraus and Hatch 2001; Parks et al. 2007; D'Agostino et al. 2017; killer whales; Baird 2000; harbor porpoises (*Phocoena phocoena*); Keener et al. 2018; spinner dolphins; Estrade and Dulau 2017; bottlenose dolphins; Scott et al. 2005; Connor and Mann 2006; Kuczaj et al. 2006; Mann 2006; Kuczaj and Eskelinen 2014; Delfour et al. 2017; Harvey et al. 2017). The often-playful expression of NCSB may help fine-tune and enhance an individual's ability to copulate. It may be the case that engaging in NCSB play is essential to learning how to copulate. In flies (*Drosophila* spp.), the individuals that engaged in same-sex NCSB had a higher copulatory success rate (McRobert and Tompkins 1988) demonstrating the importance of NCSB. Turtles (*Chrysemys*, *Graptemys*, *Pseudemys*, and *Trachemys*) also engage in precocious NCSB, which supports that this form of "play" occurs across many taxa (reviewed by Burghardt 2005). Mann (2006) suggests that this "practice may be more important in dolphins

than terrestrial mammals because cetaceans are constantly in motion and females can easily turn belly-up or away from males during mating attempts" (p. 126).

To understand how important engaging in NCSB from a young age to learn and practice copulatory behavior requires further observational evidence. For example, comparing the frequency and form of NCSB as a sexually immature individual to how many offspring an individual has may provide some evidence on how important early NCSB experiences are. Immature male beluga whales with access to sexually mature males develop their sexual repertoire faster than those who did not have access to mature males (Ham et al. 2022). This variation in development does not confirm whether those beluga whales will be more successful in future copulatory behavior, but it suggests there is an element of learning involved. For populations where the life history of individuals is known (e.g., managed care facility beluga populations, bottlenose dolphins in Shark Bay), we suggest that the frequency of NCSB and the copulatory success rate be explored in tandem to determine if NCSB is learned and if the individuals who engage in more NCSB are more successful in copulatory behavior.

7.4.3 Pleasure

Another potential reason cetaceans engage in NCSB is that such behavior is pleasurable (Dudzinski et al. 2012). Whether it be masturbation on an inanimate surface or by rubbing on a conspecific, cetaceans likely experience a pleasurable sensation (Brennan et al. 2022). This does not exclude the possibility of adaptive functions. For example, the behavior might function to regulate dominance or manage social relations while also pleasurable and rewarding. However, the most obvious indication that this behavior may be pleasurable comes from observing cetaceans engaging in masturbation by themselves even though social partners are available.

Masturbation or genital rubbing has been described in toothed whales (McBride and Hebb 1948; McBride and Kritzler 1951; Spotte 1967; Caldwell and Caldwell 1977; Shane et al. 1986; Caldwell et al. 1989; Boede et al. 2018) and in baleen whales (Herman et al. 1980; Glockner-Ferrari and Ferrari 1985) and can even lead to ejaculation (Terry 1984). While most typically described in males—likely due to the obvious nature of the behavior, especially when the animal has a penile erection—females have also been observed masturbating (McBride and Kritzler 1951). A number of anecdotal reports describe female bottlenose dolphins engaging in a myriad of genital stimulation activities, including walls, objects, water, and each other (M. Sakai, personal communication, The Dolphin Company, Dolphin Quest). Bottlenose dolphin females possess a highly innervated and highly sensitive clitoris, suggesting that female masturbation and other NCSB are pleasurable (Brennan et al. 2022).

7.4.4 *Play*

If NCSB is performed in a playful context, it may be pleasurable and "fun" because it is cognitively stimulating (Kuczaj and Eskelinen 2014; Serres and Delfour 2017) and may even serve as a good indicator of positive welfare in both wild and managed care settings (Held and Špinka 2011; Ahloy-Dallaire et al. 2018). Many cetaceans engage in sexual play with others, also called "socio-sexual behavior" within the literature, although it should be classified as a type of play behavior (e.g., McBride and Hebb 1948; Brown and Norris 1956; Sauer 1963; Xian et al. 2010; Würsig 2018; Soriano Jimenez et al. 2021). These sexual play behaviors, most frequently reported in young animals (Thomas and Taber 1984; Mann 2006; Parks et al. 2007; Lilley et al. 2020; Manitzas Hill et al. 2022, this book), seem to be mostly exhibited in a social context where two or more animals incorporate aspects of their sexual repertoire (Table 7.2) into their rough-and-tumble play. It seems that cetaceans also incorporate sexual play in social or cooperative object play (Entiauspe-Neto et al. 2022). However, animals also engage in sexual play with objects in non-social contexts (Martin et al. 2008; Araújo and Wang 2012; Hill et al. 2015, da Silva and Spinelli 2023, this book).

Detailed studies of socio-sexual play in beluga whales (e.g., Hill et al. 2015; Lilley et al. 2020; Ham et al. 2022) and bottlenose dolphins (e.g., Mann 2006; Mackey et al. 2014) have revealed that the play of sexually immature animals influences social bonding and that there are sex differences in both the behaviors observed and the frequency in which males and females engage in sexual play. For beluga whales, sexual behaviors developed in a piece-meal fashion (Ham et al. 2022), with simpler behaviors (e.g., genital rubs) emerging before more complex behavior patterns (e.g., thrusting). Further, female and male immature beluga whales prefer to play with older males when engaging in NCSB, but prefer to play with same-age and -sex partners when engaging in non-sexual rough-and-tumble play (Ham et al. 2023). While sexually immature NCSB may be "fun," it the form of this sexual play suggests it might also be used in learning or practicing copulatory behaviors.

7.5 Why Sexualize a Social Behavior?

NCSB does not appear to serve just one function for any one cetacean species. The use of NCSB is widespread and can be used as communication (Gaskin 1982; Tyack 2000), self-pleasure (Dudzinski et al. 2012), dominance (Östman 1991; Mann 2006; Wu et al. 2010; Furuichi et al. 2014), or as a type of play (Dudzinski 1998; Mann 2006; Hill and Campbell 2014; D'Agostino et al. 2017). The combination of functions NCSB might serve for any given cetacean species depends on sociality and conceptive behavior strategy, among other factors such as age, sex, and species. Although the overall behavioral repertoire might look similar, the underlying mechanisms and functionality appear variable. This variability is likely greatly influenced

by the overall sociality of the cetacean species itself (Fox et al. 2017). For species that live in large pods, there is a greater opportunity for NCSB to occur, and NCSB may be less costly as there are multiple opportunities for reproduction. However, both conditions likely facilitate the increasingly diverse functions of the behavior. In contrast, relatively solitary whales, such as gray whales, may only engage in NCSB/NCSB during specific times of the year when they aggregate in social groups, such as during the mating season (Gilmore 1960; Swartz 1986). Species differences must be considered when trying to make sense of the functions of NCSB, if any.

One of the biggest questions that results from studying NCSB is, what value is added by sexualizing a social interaction? Why add a sexual component to social behaviors that could be otherwise devoid of sex? Despite there not being a concrete answer for cetaceans at this time, the following hypotheses can be formed: (1) NCSB allows for specific social bonding that other forms of contact do not, specifically in fission/fusion societies, where bonds have to be re-established quickly, it may be more effective than other social interactions that are devoid of sex; (2) NCSB is necessary for both learning and practicing in order to reproduce later; and (3) NCSB is associated with immediate sexual reward (i.e., pleasure). Bailey and Zuk (2009) provide a number of explanations for why same-sex NCSB has been adaptive for many diverse species; for example, flies engage in NSCB to practice sexual behavior, and American bison (*Bison bison*) use NCSB to manage intrasexual conflict. More recently, Monk et al. (2019) posited that same-sex NCSB is not the evolutionary paradox it was once thought to be. For cetaceans, NCSB, and specifically same-sex NCSB, is quite prevalent and could be due to a number of explanations. To Monk et al.'s (2019) point, this behavior seems characteristic of many species and a normal occurrence, even though it was not scientifically documented until relatively recently.

NCSB is an important part of many cetacean species' behavioral repertoire, comprising a substantial portion of their daily lives (e.g., Lilley et al. 2020). NCSB is important to study for exactly this reason. Although not directly used for reproduction, these behaviors can still be used to satisfy social demands. By understanding NCSB, we further our understanding of reproductive behavior and social relationships in non-human species (Vasey 1995; Bailey and Zuk 2009; Xian et al. 2010).

7.6   Conservation, Welfare, and Future Research

Beyond the basic science to better understand animal behavior, understanding NCSB can affect conservation and welfare in several ways. For example, there is evidence that for some species, individuals had better reproductive success if they participated in NCSB prior to sexual maturity (e.g., *Drosophila* spp., McRobert and Tompkins 1988). If practice is necessary for successful offspring production or practice makes an individual more reproductively successful, individuals with access to the appropriate setting for NCSB (e.g., social group composition) would have a

fitness advantage. Although paternity success as the result of NCSB prevalence has yet to be examined in many cetacean species, evidence in beluga whales points to the gradual development of the socio-sexual repertoire (Lilley et al. 2020; Ham et al. 2022). Specifically, behaviors non-essential for reproduction, such as genital rubs, were present early in life, but pelvic thrusts were not commonly part of the NCSB repertoire until beluga whales were sexually immature.

The exact social composition conducive to NCSB needs to be examined in further research and might vary by species. For example, young beluga whales were most likely to participate in NCSB when other young, and mostly male, conspecifics were present (Lilley et al. 2020), and sexually mature male beluga whales are most likely to engage in NCSB with other sexually mature males (Glabicky et al. 2010). If sexually mature males serve as role models for NCSB, even only occasionally, then social group composition might be very important for the continuation of endangered cetacean populations or species. Anecdotal observations have reported that sexually immature male bottlenose dolphins (*T. truncatus*) watch sexually mature males engage in a variety of attention-getting behavior in the presence of interested sexually mature females, supporting the hypothesis of mentoring in some species of odontocetes (personal communication, K. Dudzinski). For example, small populations of killer whales with seasonal breeding congregations may particularly benefit from NCSB if it indirectly enhances survival or reproductive potential.

Aside from conservation issues, the social welfare of some species may be enhanced by opportunities to engage in NCSB. In cetacean species that form long-term bonds with certain individuals (e.g., alliance formation in bottlenose dolphins), engaging in NCSB may facilitate those bonds, increase group cohesion, and provide social welfare benefits. NCSB may also help alliances form and therefore also increases reproductive fitness by contributing to the reproductive success of the male dolphins in alliances. At least for bottlenose dolphins, welfare appears to vary by access to and engagement with conspecifics (Clegg and Delfour 2018). This relationship could be tested in other species to determine the extent to which NCSB might impact social well-being.

7.7 Conclusions

Overall, there is much work to be done on the topic of NCSB in cetaceans. For many cetacean species, it is unknown if NCSB is exhibited at all, and for many of the species in which NCSB has been documented, there has yet to be a systematic study of ontogeny, repertoire, welfare benefits, or fitness benefits. The work thus far has provided evidence that NCSB is common and is also more important than simply an exaptation of reproductive behavior. Further, with the knowledge that many species engage in NCSB, researchers should aim to move beyond post hoc attribution of socio-sexual functions and work toward rigorous hypothesis testing to determine if NCSB is truly NCSB and has adaptive functions (Vasey 1995).

While we have attempted to provide discrete categories as to the function of NCSB to explain why cetaceans engage this behavior, our suggestions are likely over-simplified (Table 7.1). It is most plausible that for many species, NCSB is often playful—especially when sexually immature—but aids in social bond formation (with peers, their mother, and others) and social relation management. It is reinforced by the pleasurable nature of NCSB and, ultimately, improves reproductive outcomes, especially when the NCSB mirrors copulatory behavior patterns. With new observation techniques, such as drone recording and autonomous surface vehicles (reviewed by Whitt et al. 2020) and animals in managed care facilities, these studies are possible and should be explored, especially in those species that have been reported previously to engage in NCSB.

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Chapter 8
Play, Sexual Display, or Just Boredom Relief?

Vera M. F. da Silva and Lucas G. Spinelli

Abstract Cetaceans use objects and interact with conspecifics for play and social-
izing, often exhibiting complex behaviors that we do not understand. A few seconds
of activity on the water's surface rarely indicates intraspecific behaviors and inter-
actions. What has already been described chiefly for common bottlenose dolphins
(*Tursiops truncatus*) has been extrapolated to other species, with little information
on river dolphins despite their accessibility. In this chapter, we review what is known
about sexually related behaviors in different contexts, such as learning, play, sexual
display, aggression, and boredom (weariness and restlessness through a lack of
interest) among cetacean species, especially the Amazon river dolphin (*Inia
geoffrensis*).

Keywords Aggression · Boredom · Copulation · Distracted behavior · Homosexual
behavior · Object-carry · Play · Restlessness · Socio-sexual behavior

8.1 Introduction

Like many animals, cetaceans spend most of their time searching for food, moving
among locations, avoiding predators, socializing, and resting. However, cetacean
behavior is challenging to observe and interpret. Whales and dolphins spend most of

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their time submerged, often in turbid, low-light, or pelagic environments where observation is limited. The short time they spend at the surface often results in uncertainty and misinterpretation of their behavior by human observers. Some cetacean species are evasive or submerge when a boat or a diver approaches, making it difficult to record undisturbed behavior. New tools such as aerial drones offer unique opportunities for behavioral observations of cetaceans in the wild (Fettermann et al. 2022; Ramos et al. 2023, this book).

Many whale species are migratory and spend extended periods submerged. When near the coast, their large size makes them easier to observe. In contrast, dolphins are smaller, faster swimmers and often form social groups or pods. Regardless of size, most cetacean behavior occurs underwater (Würsig 2019, for odontocetes; Clark and Garland 2022, for mysticetes). Recording river dolphin behavior is also challenging because of water turbidity and discreet surface behaviors, even though they may live close to human settlements.

Knowledge of the size and structure of cetacean groups is essential for behavioral interpretation. Because social life demands different ecological and behavioral conditions, there are costs to group living, such as food and reproductive competition and interference, and fitness benefits, such as group vigilance and increased foraging success.

One difficulty in behavioral interpretation is discerning the difference between sexual (copulation, reproductive success) and socio-sexual behavior (Ham et al. 2023, this book). The latter includes behaviors not linked to reproduction but to a social context necessary for maintaining relationships among individuals, sometimes mistakenly interpreted as play. Here we review common behavioral categories for cetaceans, such as play, sexual and socio-sexual behavior, and the possibility of behaviors associated with boredom, defined here as disinterested or distracted behavior.

8.2 Play

Because of the accessibility of a few dolphin species in captivity and the wild, we know more about dolphin behavior than other cetaceans. Even for well-known species such as the bottlenose dolphins, the definition of play and its social role are still unclear. Burghardt (2005) proposed five criteria to define play: (1) play behaviors do not have a direct ecological function and therefore are not directly related to the individual's survival; (2) play is a behavior that brings pleasure or rewards to the individual, being spontaneous but intentional; (3) play is nothing more than a modification of an activity or behavior inherent in that individual; (4) play is often repeated, but it is not a rigid or stereotypical behavior; and (5) play does not co-occur with other activities such as foraging, reproduction, or defense.

According to Hill et al. (2017), play is a behavioral phenomenon commonly observed in calves and sub-adults of social and solitary species. Although play is

more common in young individuals, adults also engage in play, and it can be a solitary or group activity, especially in dolphins. Play behavior can occur throughout an individual's life and may be associated with learning and mechanical and sensory development (Hill et al. 2017). Play may prepare the individual for foraging, courtship, and mating. Cetacean calves play with their mother or conspecifics, which prepares them for complex social behavior (Mann and Smuts 1999; Nakamura and Sakai 2014). In adults, play takes on another role and varies in accordance with social context. It is not a common behavior in adult life; it seems to be a reflection of the behaviors and activities carried out by an immature animal in the adult phase, as these relate to the animal's immediate interest inself—a pleasure stimulus or in a context of interaction with other individuals (Mason 1968; Bekoff 1972; Cairns 1976). When adults play, they are often in a group with individuals of both sexes and various ages, which facilitates the transmission of information among individuals. Calves mimic adult behavior to learn foraging, courtship, and mating techniques (Galef and Laland 2005; Herzing 2005; Kuczaj and Yeater 2006).

Paulos et al. (2010) describe several play categories and list species participating in social play. These authors distinguish two types of play, social and parallel. Social play involves some form of cooperation, while parallel play occurs when individuals play in the same area but do not interact. Individuals may display different types of play behavior while swimming and using objects. Southern right whales (*Eubalaena australis*) perform several locomotory maneuvers considered as play, ranging from beating their caudal and pectoral flippers against the water to jumping and desynchronized swimming (Paulos et al. 2010). Killer whales (*Orcinus orca*) in coastal areas of Argentina display play-like behavior while teaching younger pod members to beach and return to deep water. However, this behavior in adults is also associated with capturing young sea lions on the shore (Rendell and Whitehead 2001). Captive common bottlenose dolphins (*Tursiops truncatus*) and beluga whales (*Delphinapterus leucas*) show similar adult-juvenile interactions with adults teaching their young to beach at the edge of pools; but it may be a stereotypic behavior (Hill 2009; Paulos et al. 2010; Hill and Ramirez 2014; Guarino et al. 2016).

In addition to swimming-related behaviors, play involves using abiotic and biotic objects. For example, bottlenose dolphins use puffer fish (*Tetraodon* sp.) as a recreational object, and spinner dolphins (*Stenella longirostris*) use seaweed (Fig. 8.1). In captivity, it is common for some species of dolphins to interact with plastic toys because of the artificial environment they are in and the activities they are subjected to (DelFour et al. 2017), but in the wild, this behavior is also observed on account of human garbage dumped in rivers and oceans. Species such as rough-toothed dolphins (*Steno bredanensis*) (Kuczaj and Yeater 2007), bottlenose dolphins (Sakai et al. 2006), and spinner dolphins (Norris 1991) have been recorded displaying cooperative play by throwing plastic objects and carrying plastic bags on their dorsal fin, flippers, tail, and rostrum.

Seaweed is often abundant near shore, and many cetaceans use it for play, passing it between their melon, pectoral flippers, flukes, and group members. Owen et al. (2012) reviewed the use of seaweed by different cetaceans, including humpback whales (*Megaptera novaeangliae*). They concluded that humpback whales' use of

Fig. 8.1 Spinner dolphin (*Stenella longirostris*) from the Brazilian Fernando de Noronha Archipelago, Brazil, exhibiting object play, carrying seaweed with its pectoral fin

seaweed is self-rewarding and not a form of social display, but instead, they use it as an object for play. Payne (1972) described the same behavior for southern right whales . Bowhead whales (*Balaena mysticetus*) were observed playing with logs up to 20 m long. This behavior included nudging or pushing the log with their head or body, lifting the log onto their back or tail stock, and while supine and keeping it between their pectoral flippers (Würsig et al. 1989). However, this activity also may be used to facilitate skin sloughing (Fortune et al. 2017).

The Amazon river dolphin or boto (*Inia geoffrensis*) is an inquisitive animal that approaches boats, the landing stages of riverside houses, and people swimming or fishing. There are accounts of botos pushing canoes, holding the paddles or keels of wooden canoes, and generally interacting with canoes with women and children. Interactions with people have generated many legends and are part of the folklore of indigenous Amazonians. This dolphin has been the source of local people's fascination, and most stories involving humans and botos have a sexual connotation (da Silva et al. 2017; Box 8.1).

> **Box 8.1 Sexual Accounts of Botos and Humans**
> In the Brazilian Amazon, no animal has held such fascination by humans as the boto. This is demonstrated by its importance in indigenous cosmology and by the number of existing legends and myths (da Silva et al. 2017). However, the most prevalent element associated with botos is the male's purported sexual power as flirter and seducer. A popular legend is about its ability to transform into a handsome white man and seduce young women during

(continued)

Box 8.1 (continued)

parties, usually during the full moon. Unwanted pregnancy, infant mortality, and miscarriages are also attributed to the boto; the shape of the aborted fetus can be compared to a "little boto," and perhaps this is why the idea of this supernatural paternity evolved (Lima 2012). Similarly, the female boto can also transform into a beautiful woman, usually white, naked, and with long hair, and she seduces fishermen in their canoes and takes them to the "enchanted city" (*encantados*) at the bottom of the river (Cravalho 1999; Amoroso 2013). Female boto can apparently excite the sexual interest of fishermen, and intercourse with them can supposedly lead to exhaustion, mental derangement, or even death (Smith 1981). Informal conversations with fishermen in the Brazilian Amazon several decades ago (by VMFS) revealed accounts of the sexual use of boto females caught accidentally in nets, sometimes leaving the animal tied with a rope to a tree by the caudal peduncle for several days.

The Cocama Indigenous people in the Peruvian Amazon call the boto "pira-wira" (pira = fish; wira = penis) "penis-fish" in reference to their sexual seduction power (Ruiz 2011). Among these abilities, they also attribute to the boto the detection and strong attraction to menstruating women (Slater 1994). Anatomical parts of this dolphin such as the eye, vagina, and penis are also considered magical charms. The eye was considered a powerful amulet of incredible love effectiveness capable of attracting the desired person when observed through the dry eye of the boto, previously prepared by a shaman or equivalent entity (Câmara-Cascudo 1954; da Silva et al. 2017). In a similar way, it is also believed that alcohol or perfume, with small pieces of the boto's genitalia, when spread over the body, exert great attraction on the loved one, "holding" the sexual partner (Smith 1981; Slater 1994). Beliefs involving botos and enchanted places below water served and perhaps still serve an important ecological role for the protection of habitats and animals in the region.

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Box 8.1 (continued)

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In the wild, botos play with aquatic plants and interact with snakes, stingrays, turtles, electric eels, large fishes, and other animals. These interspecific associations are sometimes playful behavior but may become harassment or predation. Botos sometimes carry debris in their mouths, such as discarded human clothes (Fig. 8.2), plastic bottles, and other objects. Adult male botos also interact with the calves of Amazonian manatees (*Trichechus inunguis*) and of conspecifics. The latter interactions are not well understood but may be attempted infanticide (Bowler et al. 2018), rough play, or agonistic behavior without the intention of killing the calf (da Silva et al. 2021, 2022; Projeto Boto unpubl. data). Intriguingly, there are no records of such behavior toward the sympatric tucuxi (*Sotalia fluviatilis*). The tucuxi is a highly social dolphin, occurring in groups of 2 to 6 and sometimes up to 15 individuals (Martin et al. 2004; Coimbra et al. 2016).

8.3   Sexual and Socio-Sexual Behavior

In contrast to sexual behavior, socio-sexual behavior is defined as sexual activity between individuals of different ages and sexes, which does not necessarily relate to reproduction. In some mammals, this behavior may be independent of hormonal influence (Lilley 2019). Instead, it may reinforce the relationships among individuals (alliance, dominance) or the development of courtship behaviors (Connor et al. 2000a, b). Socio-sexual behavior occurs in many species and mating systems (MacFarlane et al. 2007; Bailey and Zuk 2009).

By definition, in this context animals are engaged in genital contact between individuals of the same or opposite sex. These are tactile interactions in which one

Fig. 8.2 Amazon river dolphin (*Inia geoffrensis*) in the Central Amazon, Brazil, performing object play with different objects. (a) Playing with a large seed, throwing it in the air and catching it several times as a ball. (b) Using seaweed as object play and carrying it on its melon; at times using their rostrum. (c) Carrying a piece of human clothing and shaking it at the surface. (d) Playing with a stingray. It is possible that they also eat this cartilaginous fish and sometimes are stung by stingray spine

dolphin (initiator) touches the other (recipient) in the genital area with the tip of a flipper, with its fluke, rostrum, melon, with its genital (mounting), and perhaps the male also having an erection, with or without penetration of the other's genital slit, regardless of whether male-male or male-female (Serres et al. 2022).

The socio-sexual behavior in terrestrial animals, especially nonhuman primates, has been well described (Campbell 2007; Furuichi et al. 2014; Nakamura and Sakai 2014). In cetaceans, most descriptions of socio-sexual behavior are based primarily on bottlenose dolphins and, more generally, about males engaging in sexual behavior with conspecific males, perhaps as part of establishment of bonds (Connor and Krützen 2015). Sexual behavior in cetaceans is challenging to observe in the wild but has been described in the Indo-Pacific bottlenose dolphin (*T. aduncus*) (Mann 2006; Nakamura and Sakai 2014). The socio-sexual behavior in this species was observed in calves (Fig. 8.3) and continued into adulthood. These behaviors include pelvic thrusting, genital stimulation, so-called rooster struts, aerial displays, mouthing, S-postures, lateral presentation, and pursuit in pairs or large groups of sexually interactive individuals (Mann 2006; Nakamura and Sakai 2014; Hill et al. 2015).

In bottlenose dolphins, socio-sexual behavior among males occurs more often in calves and juveniles than in adults and even among female-female and male-male interactions. Play may be necessary for building alliances and strengthening ties among individuals of the same population. These relationships may last throughout

Fig. 8.3 Mother and calf Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from Mikura Island, Japan, engaged in social-sexual behavior. Mother was rubbing the genital area of her calf with the tip of her fin

life because males form alliances to prevent males from other groups from mating (Mann 2006; Connor 2007).

All age-sex classes participate in socio-sexual behavior or sexual play in the Indo-Pacific bottlenose dolphins described by Mann (2006) and Connor (2007). Several authors describe socio-sexual behavior as a form of social learning and for maintaining dominance hierarchies (Östman 1991; Harvey et al. 2017), forming alliances (Mann 2006; Bailey and Zuk 2009), and practicing reproductive behavior. However, Serres et al. (2022) consider these interpretations to be unvalidated. Working with different species of dolphins in captivity such as Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*), East Asian finless porpoises (*Neophocaena asiaeorientalis sunameri*), and bottlenose dolphins, they concluded that socio-sexual interactions may play a different role depending on the species and may be necessary for social interactions. For example, finless porpoises do not appear to engage in other social interactions except those enabling the establishment of bonds.

Unlike other dolphin species, the Amazon river dolphin exhibits different socio-sexual behavior (Martin et al. 2008). The first observations were made in the Mamirauá Reserve (AM, Brazil), a region of floodplains (*várzeas*), in which male dolphins carry branches, floating vegetation, or lumps of hard clay, which they display, apparently to impress females (Martin et al. 2008) (Fig. 8.4). When first observed, this behavior was interpreted as play, but accumulated evidence from many encounters later demonstrated that it is in fact socio-sexual behavior. Systematic observations revealed that the social structure of groups during this activity was mainly adults and, less frequently, juveniles (Martin et al. 2008). Because

Fig. 8.4 Social-sexual behavior performed by male Amazon river dolphin (*Inia geoffrensis*) in the Central Amazon, Brazil, using different types of objects. (a and b) Carrying a lump of clay. (c) Carrying and thrashing floating vegetation. (d) Carrying a stick

individuals in groups were reliably recognizable by observers, it was shown that in 75% of the observations of known individuals, the carrier was an adult male surrounded by other adult males and females. During this display, the carrier exposed its head at the surface while holding the object in its mouth, tossing it, or turning its body on its axis, almost like a dance, apparently to attract the attention of females. Other males exhibited aggressive interactions and excitement, but only one boto in the group was the carrier. This behavior occurs year-round but with higher frequency during the high water season, coincident with estrus (Martin and da Silva 2018), which indicates an association with seasonal mating (Martin et al. 2008). Araujo and Wang (2012) and Entiauspe-Neto et al. (2022) described similar behavior in botos from other geographical areas, such as the Araguaia River (Pará, Brazil) and the Tijamuchi River (Bolivia), confirming its common occurrence. The use of objects or adornment as a socio-sexual display is uncommon in nonhuman species and is rare in cetaceans. Allen et al. (2017) reported the behavior of male Australian humpback dolphins (*Sousa sahulensis*) carrying sponges in their mouths while producing specific vocalizations and performing body postures to attract females.

An encounter between two adult male botos and a Beni anaconda snake (*Eunectes beniensis*) was described by Entiauspe-Neto et al. (2022), who reported that two sexually mature male dolphins became sexually aroused during this interaction with erect and exposed penises, suggesting that this was socio-sexual behavior. This behavior could be predation or teaching juveniles how to kill a snake. However, this anaconda species is small, reaching a maximum length of 2 m, and therefore not a threat to adult male river dolphins.

Fig. 8.5 Four-year-old subadult male Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) from Mikura Island, Japan, engaged in social-sexual behavior; one was inserting his penis in another member of its pod

Male-male homosexual activity is a prevalent behavior among dolphins, with many observations for individuals in captivity (Andersen and Dziedzic 1964; Amundin and Amundin 1971; Sylvestre 1985; Östman 1991; Zhang et al. 2015) and some opportunistic observations in the wild (Mann 2006; Connor and Krützen 2015; Harvey et al. 2017). Mann (2006) described the homosexual behavior of Indo-Pacific bottlenose dolphins of Shark Bay, Western Australia, in which homosexual interaction among male calves is more frequent (~50%) than heterosexual interactions. Socio-sexual homosexual behavior may benefit males by providing opportunities to practice mating, which is essential for male reproductive success.

In spinner dolphins at the Brazilian Fernando de Noronha archipelago, SW Atlantic, pre-mating behavior was recorded with the male touching a female's flipper or body with his flippers or rubbing, nudging, or gently biting the genital slit with his beak. This behavior was observed among males and juveniles, and intromission occurred during mating-like behavior and the rubbing of genitals against each other (Silva et al. 2005).

Mating behavior was never observed in a study of Indo-Pacific bottlenose dolphins near Mikura Island, Japan, despite hundreds of hours of underwater observation and filming (Mai Sakai, personal communication). However, socio-sexual behavior was often observed, consisting of females mating with their male progeny and mating behavior among sub-adult males (Fig. 8.5), usually with 2 to 14 participants exchanging the roles of performer and recipient, sometimes in mixed groups (Furuichi et al. 2014; Nakamura and Sakai 2014).

Fig. 8.6 Homosexual behavior by Amazon river dolphin (*Inia geoffrensis*). (a) One male (initiator) swims belly up under the other male (recipient) with his penis erect and penetrates his genital slit. (b) The botos rotate their body. and the initiator introduced his penis completely into the recipient's genital slit. (c) They stopped rotating their bodies, copulating with their heads in opposite directions. (d) A second attempt to copulate. All activity was performed in a calm and gentle manner

In captivity, homosexual interactions among bottlenose dolphins were first reported by McBride and Hebb (1948) and later by Caldwell and Caldwell (1972). More recently, Serres et al. (2022) analyzed the socio-sexual interactions in three groups of small cetaceans (Yangtze finless porpoise, East-Asian finless porpoise, and bottlenose dolphins) and suggested this behavior among captive males may be associated with dominance hierarchies as described by Serres et al. (2019).

Because of turbid water, underwater observations in the Amazon river are challenging. As a result, tucuxi and boto mating behavior has not been reported despite many hours of monitoring (Projeto Boto unpubl. data). However, opportunistic underwater video recordings in a reservoir with clear water were made of homosexual behavior between two male botos with other individuals swimming nearby but not interfering (recorded by R. Romero/AMPA) (Fig. 8.6). Sylvestre (1985) reported homosexual behavior in captive male botos at the Duisburg Zoo, Germany, and Boede et al. (2018) at the Valencia Aquarium, Venezuela.

Male-female interactions during the mating season and the tooth-rake scars caused by male-male agonistic interactions were observed during the capture and handling of botos by Projeto Boto in the Central Amazon (Martin and da Silva 2006). Botos are sexually dimorphic, with males larger than females, and tooth-rake scars over much of their bodies, especially in adult males (Martin and da Silva 2006). Some larger individuals have areas of modified skin (cobblestones) on the shoulders and the caudal peduncle, which could be used as a shield or weapon during male-male aggression, suggesting competition for mating opportunities (Martin and da Silva 2006). Adult females with tooth-rake scars, although on a smaller scale when
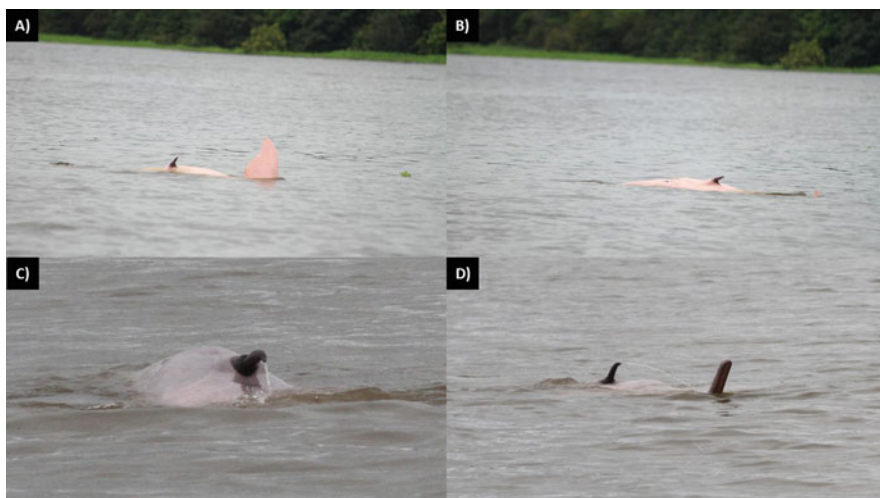
Fig. 8.7 Social-sexual behavior in an individual context. (a and b) Amazon river dolphin (*Inia geoffrensis*) displaying its erect penis above the water. (c and d) Amazon river dolphin displaying its erect penis above the water and urinating at the same time. (d) The urine stream is directed toward its own open mouth

compared to males, suggest agonistic interactions with males during mating (Projeto Boto, unpubl. data).

Cetacean sexual behaviors may provide individual pleasure in a social context. In several cetacean species, such as Hector's dolphin (*Cephalorhynchus hectori*), humpback whales, bottlenose dolphins, Atlantic spotted dolphins (*Stenella frontalis*), and botos, males display an erect penis above and below the water (Slooten 1994; Pack et al. 2002; Melillo et al. 2009; Araujo and Wang 2012; Projeto Boto unpubl. data) (Fig. 8.7). This behavior can occur in the presence of other individuals or alone and may be associated with self-pleasure, to attract females, or to demonstrate dominance among competing males. Bottlenose dolphins in Bimini, the Bahamas, were observed exposing the penis while supine at the surface and swimming toward Atlantic spotted dolphins (Melillo et al. 2009).

In addition to exposing the penis, adult male botos were recorded urinating into the air while supine and stationary at the surface. This behavior was observed in two boto populations (Araguaia River and Mamirauá Reserve, Brazil) and has been described as a solitary behavior or involving two or more adults, sometimes drinking the ejected urine (Araujo and Wang 2012; Projeto Boto unpubl. data). Araujo and Wang (2012) suggested that aerial urination has a socialization or communication function with a sensory role.

Masturbation has been observed in many animal taxa and is common in dolphins (Lateefah et al. 2022). This behavior, observed mainly in captive dolphins, is still poorly understood and may be associated with sexual frustration, the elimination of excess semen, or sexual display (Morisaka et al. 2013). Most reports of this behavior are from several species of male dolphins in captivity, such as bottlenose dolphin,

spinner dolphin, killer whale, baiji (*Lipotes vexillifer*), and boto (McBride and Hebb 1948; Mcbride and Kritzler 1951; Harrison and Ridgway 1971; Defran and Pryor 1980; Chen et al. 2001, 2002). The males rubbed their erect penis against the walls, the bottom of the tank, or objects such as brushes left in the tank (Sylvestre 1985).

At the Valencia Aquarium in Venezuela, masturbation and homosexual interactions among captive Orinoco river dolphins (*I. g. humboldtiana*) were commonly observed in females and males from an early age, except when a female was pregnant (Boede et al. 2018). A female boto born at the Valencia Aquarium started interacting sexually with other botos and attempted copulation at the age of 2 years. These behaviors are not hormonally dependent (Boede et al. 2018).

Zhang et al. (2015) described socio-sexual behavior between two female Yangtze finless porpoises in captivity, while Brown (1962) reported this same behavior between different species, such as the pilot whale (*Globicephala* sp.) and striped dolphin (*Stenella coeruleoalba*). Although reports are mainly for captive animals, this behavior also occurs in the wild. Female homosexual behaviors in bottlenose dolphins, Atlantic spotted dolphins, Hawaiian spinner dolphins, and dusky dolphins have been observed (B. Würsig, pers. com.). These socio-sexual behaviors may be associated with companionship, communication, and for providing pleasure. Brennan et al. (2022) described the presence of a highly innervated clitoris in female common bottlenose dolphins and how this structure is functional, sensitive, and stimulated by touch. The females were observed touching each other's genitalia with their rostrum and pectoral and dorsal fin, possibly stimulating the clitoral region.

8.4 Animal Boredom

Boredom may be defined as the state of weariness and restlessness through a lack of interest (Campbell 2007; Burn 2017; Svendsen 2019), but it may motivate exploration and learning (Burn 2017). However, the concept of boredom behavior is not yet well understood in animals and is a problematic behavior to measure or evaluate (Mason and Mendl 1993). The available literature is mainly on animals in impoverished environments resulting in frustration and apparent boredom (Latham and Mason 2010; Burn 2017; Mason and Burn 2017; Meagher 2018). No detailed information exists on this subject for dolphins or other cetaceans in captivity or nature.

Like all animals, cetaceans are sentient and use internal and external sensory information to inform and guide their behavior (Brakes and Simmonds 2011). Some behaviors are learned, and some are innate, enabling creative problem-solving or activity to relieve boredom. Indo-Pacific bottlenose dolphins in Shark Bay use tools such as sponges and shells for foraging and play (Smolker et al. 1997; Wild et al. 2020), similar to the Indo-Pacific humpback dolphin (*Sousa chinensis*) (Parra 2007). This activity was learned from other individuals, generating a cultural behavior in this population. Allen et al. (2017) reported a different use of sponges by the Australian humpback dolphins, in which the object was presented to adult females

as a socio-sexual behavior. Whether this behavior was associated with curiosity or the alleviation of boredom is unknown. According to Burn (2017), boredom might motivate young animals to seek stimulation that helps them learn about their environment.

In the rivers of the Amazon basin, botos are surrounded by abiotic and biotic objects distributed along the river banks with riparian vegetation and seasonally flooded forest. Food is abundant, leaving plenty of time for other activities. There are no records of nonhuman predation of botos, although black caimans (*Melanosuchus niger*), bull sharks (*Carcharhinus leucas*), and jaguars (*Panthera onca*) are potential predators.

Botos were recorded on several occasions and in different areas throwing an electric eel, locally known as poraquê (*Electrophorus* sp.), into the air with their tail or touching this fish several times with the rostrum, thus receiving some degree of electric shock. This fish can reach up to 2 m, producing an electric shock of up to 860 volts (de Santana et al. 2019). There is no record of botos eating electric eels, although they eat smaller gymnotiform fishes, which produce a low-voltage electric discharge (da Silva 1983). The reason adult male botos choose to play with such fish is unknown, but it causes excited activity. In video recordings of this behavior, a single male dolphin repeatedly harasses the fish (portalamazonia.com; @Eliane Jardini).

One of the most intriguing behaviors of botos is male attacks on conspecific calves, with prolonged and repeated pushing, battering, tossing, and forced submergence, which may or may not be lethal (da Silva et al. 2021). Botos have a wide gape and firm bite, which could kill a calf. The motive for this behavior is not clear, and it does not fit the sexual selection hypothesis of killing a calf to have the mother come into estrus (da Silva et al. 2021). Aggression toward calves usually attracts a large group of botos. It can be described as play, a socio-sexual display, or dysfunctional "flash mob" behavior as described in human crowd behavior (da Silva et al. 2021). The aggression of botos toward neonate Amazonian manatees (*Trichechus inunguis*) was described by da Silva et al. (2022) and suggested similar behavior of play or display because there is little or no interaction between these sympatric species and no competition for food or mates. Rescued orphaned Amazonian manatee calves sometimes have the scars of boto teeth, mainly on the tail and the flippers but not on the head, suggesting that the main purpose of the interaction was not killing (da Silva et al. 2022). These aggressive behaviors toward calves have no apparent fitness advantage and may result from boredom or frustration.

8.5 Conclusions

Our general inability to see below the water's surface makes the observation of cetacean behavior challenging. Most interpretations of behavior are difficult to validate, especially with incomplete observations. Many cetaceans are organized into complex social groups, with little evidence of how social behaviors are

structured. Much remains unknown about the evolution of cetacean social behavior and its importance for fitness. Further information on cetacean behavior associated with play, sexual displays, and boredom may be revealed using autonomous aerial underwater drones to observe fleeting and partially obscured behaviors.

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Chapter 9
Sexual Behaviors of Odontocetes in Managed Care

Heather M. Manitzas Hill, Kalthleen M. Dudzinski, Malin K. Lilley, and Jackson R. Ham

Abstract A number of odontocete species have been cared for by humans for multiple decades, including but not limited to pilot whales, killer whales, Commerson's dolphins, bottlenose dolphins (Indo-Pacific and common), and beluga whales (or white whales). Because many of these were breeding, numerous reproductive behaviors have been observed, documented, and investigated in detail. Similarly, sociosexual behaviors exchanged between nonreproductive partners have been examined. This chapter summarizes what has been learned regarding the role of hormones in sexual behavior, seasonality of sexual behavior, reproductive courtship behavior and displays, copulation, non-conceptive sexual behavior, development, social bonds, same-sex interactions, and interspecies interactions. We provide insight to the behavioral systems involved with both reproduction and social bonding for odontocetes. This chapter concludes with areas of future research that have been informed and should continue to be informed by knowledge of odontocete sexual behavior gained from managed care facilities.

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9.1 Introduction

The ability to study sexual behaviors in odontocetes is first and foremost limited by access to the animals. Opportunistic observations of conceptive and non-conceptive sexual behaviors of free-ranging animals have accrued over the years; the contextual information is often limited (e.g., preceding behaviors, relationship between individuals), and the behaviors documented are those that are often more visible and frequent than others. Thus, many of the observations tend to be anecdotal, with years between observations, and/or are reliant upon retrospective sources, such as post-mortem records. While retrospective methods are useful for some topics, they do not capture behavior directly. With advances in technology (e.g., drones and other sample methods), additional insights will be gained but will continue to be limited to the species, and individual animals, that are visible and present at the time of data collection.

Observations from managed care facilities can corroborate details gleaned from free-ranging populations. Data obtained from animals in such facilities can be used to better understand cetacean behavior in more detail and inform studies in the natural habitat. Although there are limitations to managed care facilities (e.g., limited existing populations), there are opportunities for close observation, longitudinal studies, and knowledge of biological state based on veterinary and care staff records. This chapter summarizes the knowledge that has been acquired on sexual behavior from odontocetes in managed care facilities over the past 70 years and how these data complement and expand on studies conducted on free-ranging animals. Research on behavior in managed care facilities aligns well with behavior of free-ranging animals to the extent that specific behaviors are documented within that context. Thus, there is little evidence to suggest the behaviors discussed in this chapter are not comparable to behaviors in free-ranging animals.

9.2 Reproductive Behavior

This section highlights topics related to reproductive behavior. We begin with mechanisms that influence reproductive behavior such as hormones and seasonality, and then we expand to behavioral processes. We defined reproductive behavior as any action of reproduction that promotes fertility and a conceptive outcome. Following this section, we elaborate on nonreproductive sexual behavior.

9.2.1 Hormonal Influences on Reproductive Behavior

Despite the advances in technology and our understanding of odontocete reproductive biology, the world of hormonal influences on reproductive behavior is still in its infancy with few clearly defined links identified between hormone levels and behavior. Many odontocete species have well-defined breeding seasons (e.g., Connor et al. 1996; Shelden et al. 2020), which are also observed for species in managed care (e.g., finless porpoises, *Neophocaena* spp., Daoquan et al. 2006; bottlenose dolphins, *Tursiops* spp. McBride and Kritzler 1951; Samuels and Gifford 1997; Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, Robeck et al. 2009; Commerson's dolphins, *Cephalorhynchus commersonii*, killer whales, *Orcinus orca*, Robeck et al. 1993; false killer whales, *Pseudorca crassidens*, beluga whales [or white whales], *Delphinapterus leucas*, Robeck et al. 2005; harbor porpoises, *Phocoena phocoena*, Desportes et al. 2003) and correspond to spikes in specific hormones for females and for males (Robeck et al. 2005). For all odontocetes studied, whether collected through blood, blow, or fecal samples, testosterone is the primary hormone associated with sexual maturity and sperm production in males (e.g., Robeck et al. 2005; Robeck and Monfort 2006; Katsumata et al. 2017). Female odontocetes present a more complex suite of reproductive hormones than males. Hormonal analysis is further complicated by some species being spontaneous ovulators (e.g., bottlenose dolphins), while others appear to experience induced and/or spontaneous ovulation (e.g., beluga whales, Steinman et al. 2012). Spontaneous ovulators, in which ovulation can occur cyclically, appear to require an increase in estrogen and progesterone to stimulate the hypothalamus to release gonadotropin-releasing hormone (GnRH) (Steinman et al. 2012; Bergfelt et al. 2018). This hormonal increase then stimulates the pituitary to release luteinizing hormone (LH) and follicle-stimulating hormone (FSH) to signal the ovary to release a mature follicle (reviewed by Bergfelt et al. 2018). In contrast, induced ovulators are believed to require physical stimulation through intromission and/or the presence of a biochemical component of semen to promote ovulation (reviewed by Bergfelt et al. 2018).

The production of sperm and the releasing of eggs require increases in reproductively relevant hormones over time. Research has begun to explore the development of sexual maturity in male odontocetes with evidence suggesting that as males approach sexual maturity, testosterone begins to spike in concert with breeding season timing even in the years prior to the concentration necessary to produce sperm (e.g., beluga whales, Richard et al. 2017b; killer whales, Robeck and Monfort 2006; Katsumata et al. 2021; Yangtze finless porpoises, *N. asiaeorientalis*, Wu et al. 2010). Sexual maturity for females appears to be dependent upon relevant ratios of specific hormones, including progesterone and estradiol (e.g., Indo-Pacific bottlenose dolphins, *T. aduncus*, Zhang et al. 2021). However, the interplay between hormone levels and onset of sexual maturity for females is more complex. More work is needed on male and female reproductive biology, in spite of research efforts conducted to develop artificial insemination procedures in females (Robeck et al. 1993; O'Brien et al. 2008, 2019; Katsumata 2010).

There may be evidence of suppressed ovulation in the case of matriarchal societies, such as killer whales (Croft et al. 2017; O'Brien et al. 2019), which suppression has been proposed as a mechanism by which reproductive fitness can be maximized. Research with free-ranging killer whales suggested that older females have less success rearing offspring, which may lead to a menopausal state (Croft et al. 2017; Dalton 2022). Research on killer whales in managed care facilities suggested that not all females cycle during the same breeding period and that cycling may be suppressed in younger females who are not the matriarch (O'Brien et al. 2019). As one of the few mammalian species to exhibit reproductive senescence, killer whales in managed care facilities provide a unique opportunity to track the development of reproductive senescence over time.

Currently, the mechanisms by which males detect a cycling female are unknown. There is recent evidence that bottlenose dolphins can discriminate familiar from unfamiliar conspecifics using urine samples (Bruck et al. 2022) and rostrum-to-genital behaviors have been observed in many different odontocete species (Table 9.1; Dudzinski 1998; Mann and Smuts 1999; Kuczaj and Yeater 2007; Horback et al. 2012). Anecdotal observations suggest that there are some behavioral correlates associated with increases in fertility for females and interest by males, many of which involve genital stimulation (both self- and conspecific-initiated), behavioral displays by males and perhaps females, increased vocalizations, and increased pair swimming between females and males (Table 9.1). However, only two studies have attempted to systematically correlate changes in reproductive hormone levels to behavior with minimal success or insight (two Hawaiian spinner dolphins, *Stenella longirostris*, Wells 1984; a killer whale, Horback et al. 2012; see summary in courtship display section). Despite all efforts made thus far on understanding the reproductive biology of odontocetes, there are many more opportunities for further research.

9.2.2 Seasonality

Seasonality of odontocete reproductive biology has been examined in detail through ultrasound and hormone analysis and corroborated with behavioral observations and the seasonality of when calves are born (beluga whales, O'Brien et al. 2008; Glabicky et al. 2010; Steinman et al. 2012; Richard et al. 2021). The detailed observations of behavior and biological samples from managed care facilities are the same as those documented from free-ranging populations through research and traditional knowledge (Shelden et al. 2020; Hill et al. 2021). Both in free-ranging animals and in managed care facilities, reproductive sex is rarely documented in the literature; however, voluntary husbandry behaviors with animals in managed care facilities have yielded biological samples that can be collected year-round from animals, in concert with known health and behavior records. This set of conditions and information allows additional conclusions to be drawn regarding when sexual behavior is non-conceptive (e.g., sociosexual) in nature and when sexual behavior

Table 9.1 Abbreviated anecdotal observations of sexual behaviors of odontocetes in managed care. For the complete description of observations from each source per observed behavior, please see Supplemental Table 9.1

Category	Behaviors observed*	Sex	Source (representative, facility)
Displays and solicitation	Floating Spasms Trance Rest on bottom	Females	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Immobility Rostrum-to-genitals	Females	Rita Stacy Brookfield Zoological Society
	Eyes closed Shiver Lying on side	Females	Michelle Campbell Dolphin Quest
	Present ventrum	Females	Heather Manitzas Hill
	Vertical hang, slow vertical sink to bottom, rest on bottom in prone position	Females	Kathleen M. Dudzinski
	Attention to female Rostrum-to-genitals Surface swim Appetite drop	Males	Michelle Campbell Dolphin Quest
	Spasms Fast swims Tail slaps	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Rostrum-to-genitals Rubbing	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Chasing Vocalizations Rubbing Hazed stare (trancelike) More than two animals S-posture	Males	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
	Immobility Rest on bottom Observational learning Following	Males	Rita Stacy Brookfield Zoological Society
	Vocalizations	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Vocalizations	Males and females	Michelle Campbell Dolphin Quest
	Vocalizations	Males	Heather Manitzas Hill
	Vocalizations Bubbles S-posture	Males and females	Fabienne Delfour

<div align="right">(continued)</div>

Table 9.1 (continued)

Category	Behaviors observed*	Sex	Source (representative, facility)
	Rubbing Object display Urination		
	Bubble displays S-postures	Males and females	Heather Manitzas Hill
	Floating Rest on bottom	Males and females	Hendrick Nollens
	Female present Female choice Male competition Surface socializing	Males and females	Hendrick Nollens
	Object carrying	Males	Personal communication with animal care staff at SeaWorld of Texas
	Urination	Females	Malin Lilley
Copulation	Copulation	Males and females	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Copulation	Males and females	Fabienne Delfour
	Copulation	Males	Michelle Campbell Dolphin Quest
	Copulation Forceful	Male and females	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
Aggression	Copulation attempt Dominance Aggression Fighting Raking	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
Lack of attention during training sessions	Lack of attention during training Extended attention to female dolphins Not eating	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Lack of attention during training Not eating	Males	Rita Stacy Brookfield Zoological Society
	Lack of attention during training	Males	Michelle Campbell Dolphin Quest
	Lack of attention during training	Males	Heather Manitzas Hill

Table 9.1 (continued)

Category	Behaviors observed*	Sex	Source (representative, facility)
Calves and sexual behavior	Calf sexual with mother	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Calf sexual with mother Penis in blowhole	Males	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
	Sexual with mother Mother sexual with calf	Males and females	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
	Calves sexual with trainers	Males	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
	Touching Calves mounting mothers	Males and females	Michelle Campbell Dolphin Quest
	Rubbing Mother sexual toward calf	Females	Fabienne Delfour
	Role playing	Males	Michelle Campbell Dolphin Quest
	Calf sexual with mother	Males	Heather Manitzas Hill
Sociosexual and nonsocial behaviors	Immobility Rest on bottom Mounting Harassment (chasing)	Males	Fabienne Delfour
	Turn-taking Mounting Role-modeling Social ball	Males	Michelle Campbell Dolphin Quest
	Turn-taking	Males	Heather Manitzas Hill
	Vocalizations	Males and females	Fabienne Delfour
	Rubbing with objects	Males and females	Fabienne Delfour
	Same-sex rubbing Rubbing with objects	Females	Guillermo J. Sanchez Contreras, DVM (Marine Mammal

Table 9.1 (continued)

Category	Behaviors observed*	Sex	Source (representative, facility)
			Specialists, Veterinarians), The Dolphin Company
	Rubbing with objects	Females	Heather Manitzas Hill
	Rubbing with objects	Males	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Rubbing with objects	Male and females	Sunna Edberg, Kolmårdens Djurpark, and Pernilla Mossesson (Founder Animal and Human Inspirations)
	Rubbing with object	Males and females	Fabienne Delfour
	Penis in blowhole Immobility Rest at bottom	Males and females	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company
	Group sexual arousal	Males	Jennifer Moore
Other	Spontaneous ejaculation	Males	Chaka (Tadamichi Morisaka) via friend's personal communication
	Spontaneous ejaculation	Males	Personal communication with animal care staff at Aquatica Orlando
	Synchronous behavior	Males	Rita Stacy Brookfield Zoological Society
	Mentoring	Males	Kathleen M. Dudzinski
	Menopausal state	Females	Guillermo J. Sanchez Contreras, DVM (Marine Mammal Specialists, Veterinarians), The Dolphin Company

*Behaviors observed are categorical identifiers by the chapter coauthors to help summarize and categorize the anecdotal observations provided by the source

can lead to conception. For example, in male beluga whales, testosterone concentrations peak in February to April (Richard et al. 2017a), and in female beluga whales, estrous cycles occur from March to June (Steinman et al. 2012). As described briefly above, female beluga whales may experience spontaneous and induced ovulation (Steinman et al. 2012), although the exact mechanism responsible for inducing ovulation requires further investigation. Even when housed in mixed-sex groups, male beluga whales typically only display pelvic thrusts (Glabicky et al. 2010) and genital presentations toward adult females during their estrous cycle, as confirmed by hormone measurements (Richard et al. 2021; Inyakina et al. 2022).

Ovulation in female bottlenose dolphins in managed care facilities may occur throughout the year and have a less pronounced window of reproduction, although

most conceptions and births occur from spring to fall with a peak in summer months (Zhang et al. 2021). Still, these individual bottlenose dolphins may have narrower windows for reproduction than the norm, which may be related to the population from which they genetically originated (Urian et al. 1996). These patterns are consistent with free-ranging populations (e.g., Connor et al. 1996), even for populations in the southern hemisphere, which also have an austral spring to summer peak.

Killer whales also have a seasonal increase in estrous activity during spring months, but hormonal cycling has been documented throughout the year (Robeck et al. 1993). For Pacific white-sided dolphins found only in the northern hemisphere, ovulation and conception occurs from August to October, and indicators of male fertility (e.g., peak testosterone, sperm production) occur in a similar timeframe from July to October (Robeck et al. 2009).

The above studies on the seasonality of reproductive sex are complemented by knowledge of odontocete non-conceptive sex. In some species, such as beluga whales, non-conceptive sexual behavior is present year-round (Hill et al. 2015; Ham et al. 2022) but varies seasonally in prevalence (Glabicky et al. 2010; Lilley et al. 2020). Seasonal fluctuations were also more apparent during the years when individuals approach sexual maturity (Ham et al. 2021). Behavioral variation corresponds with seasonal variation in hormone levels (Robeck et al. 2005; Richard et al. 2017a; Atkinson et al. 2022; Inyakina et al. 2022). For Yangtze finless porpoises, sociosexual behavior was most frequently initiated by sexually immature males, who engaged in same-sex interactions throughout the year (Wu et al. 2010; Serres et al. 2021). Year-round sociosexual behavior has also been documented for bottlenose dolphins (McBride and Hebb 1948; Brown and Norris 1956), harbor porpoises (Desportes et al. 2003), river dolphins (*Inia* spp. and *Lipotes vexillifer*) (Renjun et al. 1994; Entiauspe-Neto et al. 2022), and killer whales (Sánchez-Hernández et al. 2019). However, the extent to which this non-conceptive sexual behavior varies seasonally has not been examined explicitly for many odontocete species. The year-round, non-conceptive sexual behavior of odontocetes in managed care facilities matches what is known about free-ranging populations (e.g., Connor et al. 1996; Urian et al. 1996; Lomac-Mac Nair et al. 2016; O'Corry-Crowe et al. 2020; Shelden et al. 2020). Non-conceptive sex is discussed further in Sect. 9.3 of this chapter and Ham et al. (2023, this book).

9.2.3 Courtship Behaviors and Displays

Courtship displays are expressed by a number of odontocetes and range from sound emissions (e.g., whistles, clicks) to body postures (e.g., lateral presentations, s-postures, immobile hangs) to high energy swims (e.g., "shark" swims) and aerials (e.g., leaps, twists, spins) (e.g., Tavolga and Essapian 1957; Puente and Dewsbury 1976; Schaeff 2007; Muraco and Kuczaj 2015). In some species, object presentations may also occur (e.g., Amazon river dolphins, Martin et al. 2008; some bottlenose

dolphins, Weaver and Kuczaj 2016; beluga whales, Lilley et al. 2022a, b; killer whales, Table 9.1). As a courtship progresses between a female and a male, the interaction can develop to include paired and synchronous swims, rubbing, and other close-proximity actions, such as pelvic thrusting and genital stimulation (Table 9.1).

Most odontocetes, including species in managed care facilities (e.g., bottlenose dolphins, Commerson's dolphin, porpoises, *Neophocaena* spp., beluga whales, false killer whales), appear to have a polygynandrous mating system where females and males mate with multiple partners within a breeding season (e.g., Joseph et al. 1987). Many species show strong seasonality in their reproductive behavior, corresponding hormones, and anatomical changes to testes and ovaries (Robeck et al. 1993; Richard et al. 2017a, b; Funasaka et al. 2018; O'Brien et al. 2019; Katsumata et al. 2021; see Hormonal Influence section). Correspondingly, courtship behaviors increase in frequency with the onset of the breeding season (e.g., Glabicky et al. 2010). Many courtship behaviors displayed by males during the breeding season also occur during non-breeding seasons but typically with same-sex partners, especially in bottlenose dolphins, porpoises, and beluga whales (Ham et al. 2023, this book).

Courtship behaviors and displays during breeding seasons are more commonly documented for males compared to females of most odontocete species in managed care facilities. While females likely present chemical cues to indicate that an estrous cycle is occurring and at times solicit attention from conspecifics, including genital rubbing, genital presentations, and immobility (Muraco and Kuczaj 2015; Table 9.1), more research is needed to better understand the more subtle cues from females as it is possible that females initiate sexual interactions more frequently than is known due to the less obvious nature of their cues. In bottlenose dolphins, anecdotal reports indicate that males will follow, swim with, vocalize at, and perform many different aerial and fast swim behaviors around a female that appears to be of interest to the male (Table 9.1). Male killer whales, bottlenose dolphins, and beluga whales in managed care facilities swim with a female of interest and refuse to leave her when requested by humans for different activities (Table 9.1). Male beluga whales also engage in directed gazes at a female of interest and match her swim patterns while also increasing variability in vocalizations (H. Manitzas Hill personal observation), presenting static s-postures, and mouthing the female when pair swimming with her (Hill et al. 2015; Lilley et al. 2020). At times, bubbles are released as different types of trails/streams, presumably both in concert with and independent of vocalizations that are emitted. Similar types of behaviors have also been observed with smaller delphinids such as Pacific white-sided dolphins, common dolphins (*Delphinus delphis*), and porpoises (Brown 1962; Nakahara and Takemura 1997).

While little is known of sexual selection strategies of odontocetes, Orbach et al. (2019) extended Schaeff's (2007) review of the literature. Both authors emphasized that female and male choice occurs in all odontocetes. Aside from narwhals (*Monodon monoceros*) and several others (Würsig et al. 2023, this book), most odontocetes do not have obvious ornaments or sexually selected armaments that could be used to discriminate between candidates – rake marks, however, may be used to evaluate how successful others are in conspecific fighting, which may be

used in mate selection (MacLeod 1998; Orbach 2019) – and male odontocetes generally do not engage in head-to-head reproductive competition as is the case in some terrestrial species, such as deer or giraffe (except for narwhals, beaked and larger whales; see Orbach 2019). However, females may select among possible males based on the speed, displays, or other courtship activities presented by the males (Schaeff 2007; Orbach 2019). Furthermore, male courtship displays in addition to certain physical attributes (e.g., postanal ventral hump in Hawaiian spinner dolphins, caudal peduncle in bottlenose dolphins, melon position in beluga whales, dorsal fin in killer whales) and indirect behaviors (e.g., male Atlantic spotted dolphins "babysitting" young calves while the adult females forage) may facilitate female choice (Schaeff 2007; Orbach 2019, H. Hill, personal observations, K. Dudzinski, personal observations). This conclusion remains conjecture as no systematic experimental study has been conducted.

Ultimately, odontocete females have much control in mating as males are less easily able to restrain or coerce them (with the exception of male bottlenose dolphin alliances cooperating to coerce an ovulating female, Scott et al. 2005), unlike many terrestrial species. Aquatic mammals live in a three-dimensional world that allows females to maneuver their genitalia away from males most of the time, even in species selected for sexual dimorphism with larger body size for males (e.g., beluga whales, killer whales, bottlenose dolphins, Pacific white-sided dolphins, false killer whales, harbor porpoises). In some instances, females actively participate in copulation either by soliciting the attention of males or actively joining a male that is displaying toward her but at some distance away (Hill et al. 2022; Lilley et al. 2022a, b; Table 9.1). More work is needed to uncover the mechanisms involved in female mating strategies.

Little is known about male mate choice in odontocetes. Longitudinal work on the role of male alliances and female access in Indo-Pacific bottlenose dolphins in Monkey Mia has suggested that male alliances facilitate male reproductive success, but the characteristics by which the males select females remains poorly understood (Connor et al. 2022).

Since many odontocete species appear to be spontaneous ovulators (e.g., killer whales, bottlenose dolphins; Sawyer-Steffan et al. 1983, Pacific white-sided dolphins; Robeck et al. 2009, false killer whales, reviewed by Bergfelt et al. 2018) and some species appear to be induced ovulators (e.g., beluga whales, Steinman et al. 2012), males could increase their opportunities to breed if they were considered "attractive" to females.

9.2.4 Copulation

Copulation in odontocetes is defined as the intromission or insertion of a male's penis into the vaginal slit of a female. The penis may be inserted partially or completely; however, little is known whether there is a difference in fertilization success rate for partial versus full intromission (Lünen 2020). Intromission is

considered a reproductive act if the function is to fertilize an ovulating female. Despite the prevalence and extended duration of many odontocete sexual interactions, intromission itself is rarely observed in either free-ranging or captive settings (reviewed by Schaeff 2007; Orbach 2019), primarily due to the speed at which it occurs (Table 9.1). Whether it is a killer whale, a bottlenose dolphin, Pacific white-sided dolphin, coastal tucuxi (*Sotalia fluviatilis guianensis*), or beluga whale, the entire act of copulation appears to occur in seconds to no more than a minute (Tavolga and Essapian 1957; Puente and Dewsbury 1976; Terry 1984; Schaeff 2007; Muraco and Kuczaj 2015). Apparent successful copulation has been described for some baleen whales, including male orgasm in southern right whales, *Eubalaena australis* (Würsig 2000).

Often short intromissions, along with the difficulty in determining estrous state and the propensity of many odontocetes to engage in high levels of sociosexual behavior, make the act of copulation difficult to study systematically. Female receptivity is key to successful copulation attempts, regardless of coercive tactics used by some populations of bottlenose dolphins (e.g., in Shark Bay, Australia, Connor et al. 1992; Connor and Krützen 2015). Many descriptions of copulation attempts or completions commonly report the importance of females presenting their ventrum to the male of interest within close proximity (Table 9.1, Fig. 9.1, also reviewed by Schaeff 2007; Orbach 2019). Without this cooperation, males appear to be unsuccessful in their attempts to copulate (e.g., Terry 1984). Other behaviors reported in Table 9.1 that warrant further systematic investigation are the specific vocalizations associated with copulation, spasms (which could be similar to

Fig. 9.1 After the adult male beluga whale (on left) displayed an s-posture, the adult female beluga whale (on right) swam over to the adult male and positioned herself, ventrum up, next to the adult male. Image taken from video footage collected by H. Manitzas Hill

orgasms), and object carrying. Among odontocetes, female choice, male competition, and courtship behaviors are important driving forces in mating behaviors.

9.3 Non-conceptive Sexual Behavior

One common form of behavior observed in odontocetes is non-conceptive sexual behavior or actions where conception is not possible. This may include behaviors between two animals of the same sex, two different species, sexually immature and mature animals, or masturbation. Often characterized as sociosexual behavior (when exhibited within a social domain), these behaviors are frequently observed in animals in managed care facilities and nature. For beluga whales, a well-documented species, this behavior is exhibited from a young age and develops slowly (Glabicky et al. 2010; Hill et al. 2015; Lilley et al. 2020; Ham et al. 2022). As male beluga whales approach adulthood, they engage in sociosexual behavior relatively frequently, making up around 5–10% of their time budget (when considering "solo," "affiliative," "agonistic," and "sociosexual" behavior, Lilley et al. 2020). Though studied systematically in a few species, most reports of non-conceptive sexual behavior are anecdotal; but together, these studies suggest there are multiple functions and types of non-conceptive sexual behavior in Odontoceti. Ham et al. (2023, this book) review what is known about cetacean non-conceptive sexual behavior.

9.3.1 Development

One suggested function of non-conceptive sexual behavior in odontocetes is that such activities contribute to the development and practice of reproductively functional behavior (Mann 2006; Bailey and Zuk 2009; Lilley et al. 2020). Sociosexual behavior, which is often similar to copulatory behavior (Hill et al. 2015), may be repeated or practiced before sexual maturity and may even require repeated practice to develop full copulatory behavior patterns (Ham et al. 2022). Sociosexual behavior is common among young male bottlenose dolphins beginning with neonates and has been reported in both managed care and nature (e.g., Connor et al. 2006; Sakai et al. 2006; Dudzinski and Ribic 2017; all chapter coauthors, personal observations, Table 9.1). The extent to which sexual behavior is innate or learned is not known. Some courtship- and reproductive-specific behaviors likely emerge innately (e.g., genital stimulation for both sexes or erections in males); however, there is a growing body of evidence that observational learning and direct mentoring may improve reproductive success (Dudzinski et al. 2022; Ham et al. 2022; Hill et al. 2022; Table 9.1; see Fig. 9.2). Even if mentors or role models are not crucial, conspecific partners may provide opportunities for sociosexual behavior exchanges during which motor skills are developed.

Fig. 9.2 A subadult male beluga whale displaying an s-posture and erection toward a juvenile male beluga whale. This image was taken from a bout of sociosexual behavior that lasted several minutes with the two male beluga whales taking turns reciprocating the behavior. Image taken from video footage collected by H. Manitzas Hill

9.3.2 Social Bonds

Non-conceptive sexual behavior may aid in bond formation and bond maintenance (Connor et al. 1992, 2001, 2006; Dudzinski and Ribic 2017; Lilley et al. 2020) and likely also serves as a form of tactile communication (Gaskin 1982; Dudzinski and Ribic 2017; Tyack 2019). For example, in bottlenose dolphins living in Shark Bay, Australia, same-sex sexual interactions between sexually immature males seem to facilitate, at least in part, bond and alliance formations (Connor et al. 1992, 2001, 2006); these interactions have been documented for bottlenose dolphins in managed care facilities with similar behaviors and functions confirmed (Dudzinski and Ribic 2017; Table 9.1). Indeed, young male bottlenose dolphins likely exchange these sociosexual behaviors (e.g., mounting peers, rubbing body and erections on peers, etc.) when establishing their bonds with other males. Connor et al. (1992) and Dudzinski and Ribic (2017) suggest that sociosexual exchanges in which three to four young males (sexually immature) take turns in active and passive roles that include much body contact, rubbing peers with erect penises, active rubbing of body parts, and whistle and squawk vocals may be critical in establishing bonds and maintaining those relationships into adulthood. These actions serve to signal to close affiliates that the individuals have a tight bond and to let others in a group know that those particular individuals are associated. Similar non-conceptive sexual functions have been suggested for beluga whales and killer whales in managed care facilities and nature (Sánchez-Hernández et al. 2019; Lilley et al. 2020; Sanvito and Galimberti 2022).

9.3.3 Masturbation and Sexual Object Play

Many species of odontocetes in managed care facilities rub their ventrums and more specifically their genitals, on the environment in which they are housed, as well as on conspecifics, non-reciprocating species (e.g., turtles, sharks, fish), and/or items found within their environment (Table 9.1). These behaviors, though not functionally reproductive, likely provide some form of sexual tension relief or physical pleasure (Dudzinski et al. 2012). With increased research on the genitals of both female and male odontocetes (Orbach et al. 2019), it is becoming clear that odontocetes have functional anatomy for feeling sensations (Brennan et al. 2022). However, for males, ejaculation is rarely observed in nonreproductive sexual behavior (Table 9.1). As part of masturbation, odontocetes sometimes engage in playful sexual behavior with objects (Burghardt 2005; Greene et al. 2011; Hill et al. 2016, 2017), using their genitals to move or manipulate objects (Table 9.1). For males, this may mean thrusting toward an environmental enrichment device (e.g., buoy, hose, towel, pipe) with an erect penis. Females may rub their genitals on objects such that the object externally rubs the genital slit or penetrates the slit. In both sexes, it is likely that this rubbing is pleasurable in a sexual (Brennan et al. 2022) and playful domain (Kuczaj and Eskelinen 2014).

9.3.4 Same-Sex Sexual Interactions

One of the most commonly described non-conceptive sexual behavior in odontocetes is same-sex non-conceptive behavior (Ham et al. 2023, this book). This may occur between two females or between two males (Table 9.1), but in either case it is very clearly not reproductively functional. Same-sex sexual interactions are sometimes described as playful and often occur between same-aged individuals. This behavior likely functions in a multitude of facets from practice (Mann 2006; Lilley et al. 2020) to managing social relations (Dudzinski and Ribic 2017; Harvey et al. 2017; Lilley et al. 2020, 2022a, b). As noted in Table 9.1, many same-sex sexual interactions often involve more than two individuals, which can take the form of all behaviors directed toward one recipient or can involve group members being both an initiator and recipient (sometimes simultaneously) of sexual behavior. These triads or larger groups are sometimes referred to as "group social balls" (Miller et al. 2010, 2021; Fig. 9.3). Once thought to be rare among nonhuman animals or only found in highly socially complex species (Furuichi et al. 2014), same-sex interactions are becoming increasingly well-documented across taxa, including cetaceans.
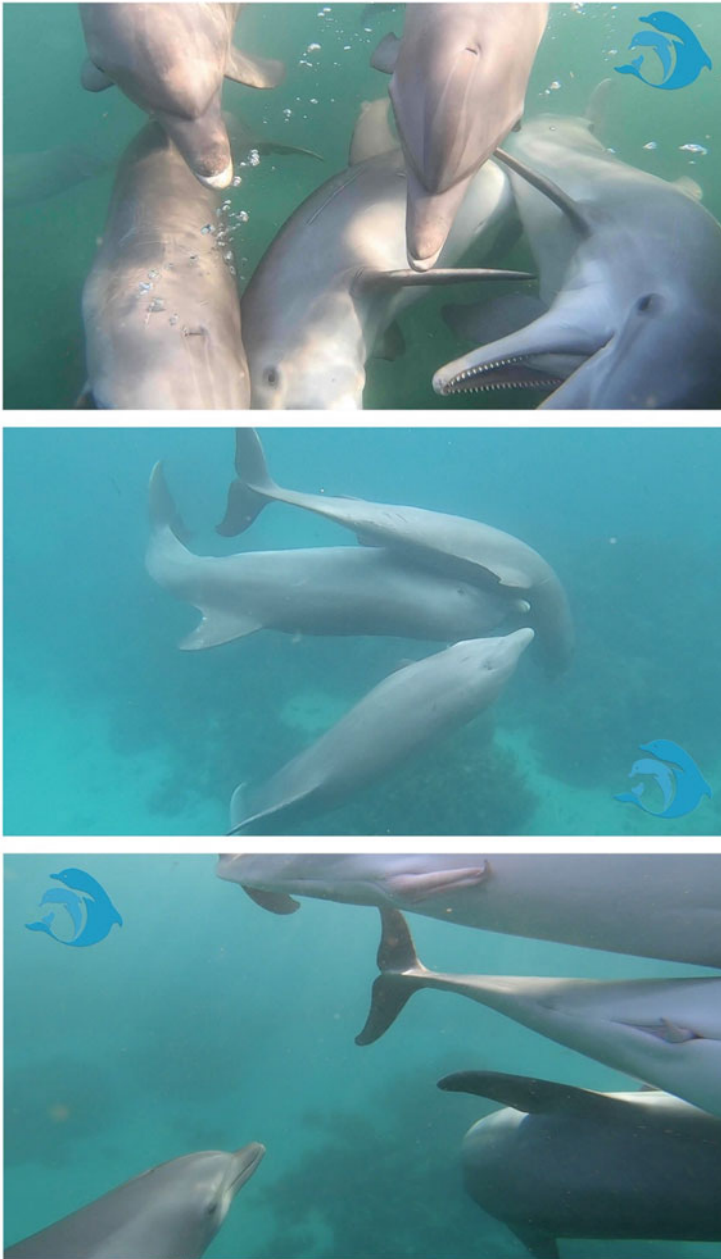
Fig. 9.3 This panel displays several angles of what is frequently labeled a group social ball. Several, usually male, bottlenose dolphins engage in sociosexual behavior with behaviors directed at one or more recipients within the group. Photo courtesy of Dolphin Communication Project

Fig. 9.4 Two male beluga whale calves and one adult female Pacific white-sided dolphin engage in sociosexual behavior. As the male calves displayed presentations of their ventrums, the adult female Pacific white-sided dolphin oriented at their genital regions, pushed them at the surface, and reciprocated with positioning her ventrum closer to the male beluga whale. Image taken from video footage collected by H. Manitzas Hill

9.3.5 Interspecies Sexual Interactions

Interspecies sexual interactions can occur when multiple species share space in nature or managed care facilities. Occurring between same-sex and mixed-sex pairings, conspecific sexual behavior may function to manage social bonds or as a way of establishing social dominance hierarchies. In some cases, these interspecies sexual interactions yield hybrid species in nature (e.g., Baird et al. 1998; Schaeff 2007; Herzing et al. 2013; Skovrind et al. 2019; K. Dudzinski, personal observation – hybrid of dusky and common dolphins confirmed morphologically) and managed care facilities (e.g., Caballero and Baker 2010). Observations of interspecific sexual exchanges have been made when mixed species are housed together; for example, immature male beluga whales have directed sexual behavior toward mature female and male Pacific white-sided dolphins who reciprocated the sexual behavior (Fig. 9.4). That is, the female Pacific white-sided dolphin exhibited a surface body spasm in response to the immature beluga whale male presents (H. Manitzas Hill and M. Lilley, personal observations). This suggests that even when individuals present to nonspecific peers, the response is behaviorally correct for the context.

9.3.6 Lessons from Managed Care and Free-Ranging Populations

Studies on non-conceptive sexual behavior can yield important information on the social structure of animals (e.g., Connor et al. 2001) and how reproductive behaviors

develop (e.g., Lilley et al. 2020; Ham et al. 2022) and may even provide clues on the welfare of species living in managed care and nature (Clegg and Delfour 2018; Miller et al. 2021). Given the information described above, chemical and noise pollution could impact gustatory, olfactory, and/or vocal cues for mating and impair reproduction, thus affecting not only the welfare of free-ranging odontocetes (de Vere et al. 2018) but also, potentially, their population numbers, which could be the case for the endangered Cook Inlet beluga whale population or Southern Resident killer whales off Vancouver Island. Non-conceptive sexual behavior comprises a substantial part of many odontocetes' behavioral repertoire. Access to appropriate social partners may impact welfare in managed care settings and may also impact future reproductive success for free-ranging populations.

9.4 Future Research

Studies of the physiology and behavior of odontocetes in managed care facilities can yield unparalleled insights into their reproductive physiology and both conceptive and non-conceptive sexual behavior. Voluntary husbandry behaviors for biological samples and measurements and the opportunity for frequent behavioral observations over the lifespan of individual animals have the potential to address a number of currently unanswered questions. For example, to what extent are reproductive behaviors socially learned? Do sexually immature individuals need adult "role models" to learn the behavior? Does practicing sexual behavior in a sociosexual context either with peers or adult role models improve reproductive success later in life? In addition, questions can be answered regarding courtship displays and copulation. What are the factors involved in both female and male mate choice? How do different social group compositions affect mating systems? What role does reproductive and nonreproductive sexual behavior play in the welfare of individuals?

One question that should be investigated further is how can a male become attractive to females? This is a question that is rarely asked as most research focuses on how females make themselves more attractive to males, though, of course, both sides of the coin are important, depending on the species. No study to date provides clear evidence of a strong relationship between select behaviors and possible ovulation in females. Such studies may elucidate mechanisms of mate choice in odontocetes and thereby provide additional direction for animal management of species both in their natural habitats and in managed care facilities.

Most research on sexual behavior has centered on bottlenose dolphins, killer whales, and beluga whales. Although there is still much to learn, there are many opportunities to study the larger range of odontocete species currently living in managed care facilities by documenting sexual behavior and physiology when possible (e.g., Webber et al. 2023, this book). With advances in drone technology, behavioral observations and physiological (e.g., hormone analyses) measurements can also be conducted for free-ranging cetaceans (Ramos et al. 2023, this book).

Findings from both settings can complement each other (Dudzinski 2010; Hill et al. 2021) and be used to inform best practices for conservation and welfare. As an example, the importance of role models in the development of sexual behavior and the role of mate choice in breeding success could play a crucial role for populations currently facing extinction.

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Chapter 10
Infanticide and Sexual Conflict in Cetaceans

Molly H. F. McEntee, Meredith MacQueeney, Diana Alvarado, and Janet Mann

Abstract Infanticide by adult males is a striking example of sexual conflict; males can increase their reproductive success by killing an unrelated infant and accelerating the mother's return to breeding condition. Reports of infanticide in cetaceans have quadrupled in the past decade, and infanticide has now been documented in six species of toothed whale, including multiple populations of common bottlenose dolphins (*Tursiops truncatus*). Evidence of infanticide in these species is consistent with the sexual selection hypothesis; perpetrators are predominantly adult males and targets are neonates. Toothed whales have long lactation periods that suppress estrus, making infanticide potentially adaptive for adult males. However, it remains unclear if infanticidal males are likely to sire the mother's subsequent offspring. Here, we provide an overview of infanticide in cetaceans, evaluate the evidence for the sexual selection hypothesis, and propose a framework to predict infanticide risk in this clade. Toothed whales do not typically have dominance hierarchies, stable social groups, or monopolizable mating opportunities, all hallmarks of infanticide risk in terrestrial species. Instead, we hypothesize that infanticide risk in toothed whales is modulated by encounter rates with unfamiliar males.

Keywords Aggression · Cetacean · Coevolution · Dolphin · Infanticide · Reproduction · Sexual conflict · Sexual selection

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10.1 Introduction

Infanticide is broadly defined as any behavior by a conspecific that contributes directly and significantly to the death of an infant and has been described in a diverse array of taxa and a wide range of social contexts (Palombit 2015). No single hypothesis explains the diversity of observed infanticidal behaviors, and drivers of infanticide vary within and among species. For example, male chimpanzees (*Pan troglodytes*) increase their territories after killing extra-community infants (Watts et al. 2002), and some species of male rainbowfish (*Telmatherina sarasinorum*) gain nutritional benefits by cannibalizing their broods when paternity is uncertain (Gray et al. 2007). Dominant female meerkats (*Suricata suricatta*) maximize the alloparental care their offspring receive by killing the offspring of close kin (Clutton-Brock et al. 1998), and elephant seal (*Mirounga angustirostris*) males appear to accidentally trample and kill infants in the course of male-male competition (Le Boeuf and Briggs 1977). Our understanding of the numerous drivers of infanticide has advanced substantially since the adaptive benefits of infanticidal behavior became a subject of study in the 1970s (Sommer 2000). However, due to the logistical challenges of observing marine mammal behavior in the wild, infanticide was not described in cetaceans until the late 1990s. Increases in observational effort have now yielded evidence of infanticide in six species of cetaceans, all toothed whales (Fig. 10.1). Here, we review reports of infanticide in cetaceans to date and bring the cetacean literature into a comparative framework with terrestrial mammals.

Out of numerous hypotheses, infanticide driven by sexual selection has received particular attention in the literature both due to its widespread occurrence and as a notable illustration of sexual conflict. This hypothesis posits that an adult male can increase his reproductive success by killing an unrelated infant and siring the mother's subsequent offspring (Hrdy 1974). Mammalian females often cease estrous cycling during nursing, a phenomenon called lactational amenorrhea; premature death of a nursing infant can end lactational amenorrhea, causing the mother to return to estrus and providing a reproductive opportunity for the infanticidal male (Hrdy 1974; Altmann et al. 1978). Infant death, of course, comes with tremendous costs to the mother, resulting in a coevolutionary arms race between the sexes as females evolve counterstrategies to male infanticidal aggression. Adaptations to counter infanticide risk, and subsequent adaptations to overcome female resistance, can profoundly shape reproductive physiology and social behavior. The discordance between male and female reproductive interests has led sexually selected infanticide by adult males to be considered an "archetype of sexual conflict" (Palombit 2015).

The sexual selection hypothesis makes three basic predictions. First, infanticide is committed by adult males who target infants that are not their own offspring. Second, the mother is likely to return to estrus faster or in better condition than if she had successfully weaned the infant. Third, the infanticidal male has an opportunity to sire the mother's next offspring (Hrdy 1979; Ebensperger 1998). The systems that have generated compelling evidence for sexually selected infanticide
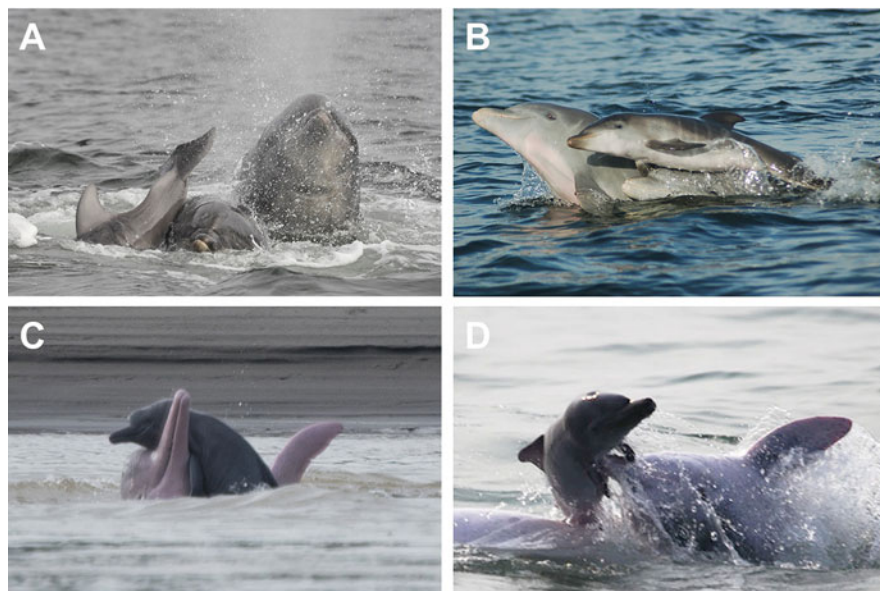
Fig. 10.1 Infanticidal behaviors appear consistent across multiple species of odontocetes. They include separating the mother from the infant, ramming the infant from below such that the infant is lifted or thrown out of the water, and forced submergence. (**a**) *Tursiops truncatus*, the Moray Firth, Scotland (Robinson 2014). (**b**) *T. truncatus*, Turneffe Atoll, Belize (Ramos et al. 2022). (**c**) *Inia geoffrensis*, Napo River, Peru (Bowler et al. 2018). (**d**) *Sousa chinensis*, Pearl River Estuary, southeast China (Zheng et al. 2016)

are characterized by high levels of male-male competition and high reproductive skew, in which one or several males obtain a disproportionate number of paternities (Palombit 2015). In langur monkeys (*Presbytis entellus*), an early and foundational study system for infanticide, male leaders of multi-female troops monopolize the majority of matings (Hrdy 1974). Takeovers (the displacement of the resident male by an immigrant male) are associated with infanticidal aggression and high infant mortality (Hrdy 1974), and infanticidal males father the subsequent troop offspring (Borries et al. 1999). Further observations of infanticide in primates, carnivores, and rodents support the hypothesis that male replacement of previous dominant breeders is a key risk factor for infanticide. In groups with female-biased adult sex ratios, in which a male or group of males can take over and displace resident males (e.g., langur monkeys, gelada monkeys (*Theropithecus gelada*), lions (*Panthera leo*)), male takeovers result in high rates of infanticide (Packer 2000; Beehner and Bergman 2008). In multi-male multi-female groups (e.g., Japanese macaques (*Macaca fuscata*) (Soltis et al. 2000), colobus monkeys (*Colobus vellerosus*) (Teichroeb and Sicotte 2008), savannah baboons (*Papio* spp.) (Zipple et al. 2017)), infanticide rates increase after immigrant males rise in the dominance hierarchy, replacing previous dominant males. In two species of deer mice (*Peromyscus* sp.) that nest alone or in male-female pairs, dispersing males kill pups they encounter outside of their home

range (Wolff and Cicirello 1991). These observations are further supported by phylogenetic analyses; infanticide by adult males is most likely to evolve in stable bisexual groups, groups that have female-biased adult sex ratios, and groups with high paternity skew and short male breeding tenures (Lukas and Huchard 2014).

10.2 Cetaceans

Cetaceans provide a useful parallel system to terrestrial mammals for examining both interspecific and interpopulation variation in infanticide. Most odontocetes have exceedingly long lactation periods (Whitehead and Mann 2000) that are likely substantially shortened by the death of a nursing offspring. On the other hand, the social factors that we know result in increased infanticide risk in terrestrial mammals do not apply neatly to cetacean social systems. Cetaceans are often wide-ranging and highly migratory with diffuse social networks and community boundaries that are rarely as delineated as they are in primates (Tsai and Mann 2013; Rendell et al. 2019). In primates and lions, short breeding tenures may refer to a period of years; for cetaceans, habitat overlap can be seasonal and associations in fission-fusion groups can last just a few minutes (Galezo et al. 2018). Bottlenose dolphins (*Tursiops* sp.), the most intensively studied genus of cetacean, do not have stable male dominance hierarchies (Samuels and Gifford 1997). The classic examples of male takeovers of multi-female groups or male changes in dominance position do not occur in cetaceans; while there is evidence of intense sexual conflict in multiple species, it remains unclear if and how males monopolize mating opportunities. In the fission-fusion social system of Indo-Pacific bottlenose dolphins (*T. aduncus*), alliances of males cooperate to harass and mate-guard females (Connor et al. 2022); females are consorted by up to 13 males in a breeding season (Connor et al. 1996), suggesting males are not able to completely monopolize mating. In species with modular social structures, such as killer whales (*Orcinus orca*), mating occurs outside the social group during temporary associations (Pilot et al. 2010). While life history factors make toothed whales excellent candidates for sexually selected infanticide, the social factors that stabilize infanticidal behavior could differ substantially from those in terrestrial species.

10.2.1 Baleen Whales

No evidence of infanticide has been reported in baleen whales. While this does not preclude the possibility that infanticide occurs and has not been observed yet, the seasonal breeding systems and short lactation periods of baleen whales could explain the lack of infanticide in this clade. Sexually selected infanticide is strongly associated with non-annual breeding (Lukas and Huchard 2014). When lactation lasts less than a full year and seasonal changes cue the commencement of estrus, the death of

dependent offspring will not result in earlier estrous cycling and will therefore not provide an adaptive benefit for infanticidal males. Baleen whale interbirth intervals range from 2 to 3 years, but nearly all baleen whales wean their offspring within a year of birth (Bannister 2009). In a sample of Antarctic humpback whales (*Megaptera novaeangliae*), 55% of females were simultaneously pregnant and lactating (Pallin et al. 2018), suggesting postpartum estrus may have been a common feature of mysticete reproduction in healthy pre-whaling populations. If postpartum estrus was common historically, sexually selected infanticide would be very unlikely to evolve. It has been proposed that male infanticide can be adaptive in annual breeding systems if the death of a dependent offspring results in better maternal condition and higher fecundity in the subsequent breeding season (Hrdy and Hausfater 1984). However, even if infanticide reduced a mysticete mother's interbirth interval or improved her condition, the diffuse social structure, polygynandrous mating system, and spatiotemporal expanse of movements (Rendell et al. 2019) mean that an infanticidal male may be unlikely to encounter the same female, let alone sire her offspring, in the next breeding season. Finally, mysticete females are larger than males and can effectively defend their offspring (Ralls 1976; Pitman et al. 2017). The lack of evidence for infanticide in mysticetes is consistent with the hypothesis that seasonal breeding, postpartum estrus, migratory lifestyle, and polygynandrous mating system all make baleen whales unlikely candidates for the evolution of sexually selected infanticide by adult males.

10.2.2   Toothed Whales

In contrast to baleen whales, toothed whale reproduction is characterized by slow calf growth and long lactation periods (Mann 2019), life history characteristics that make them prime candidates for the evolution of sexually selected infanticide. Bottlenose dolphins typically wean around age 4, but in exceptional cases, calves can nurse for up to 8 years (Karniski et al. 2018). While simultaneous lactation and gestation occur, interbirth intervals are long and females appear to begin estrous cycling only within a year of weaning (Mann et al. 2000; Karniski et al. 2018). Many odontocetes exhibit seasonal peaks in mating and birthing, but females seem to be able to reproduce throughout the year and long interbirth intervals are likely shortened by the death of a dependent calf (Robeck and O'Brien 2018). While these life history characteristics may predispose toothed whales to the evolution of sexually selected male infanticide, species- and population-specific social structure, mating system, and migratory tendencies likely interact to determine the actual risk of infanticide. Here, we review reported evidence for infanticide by species and date (Table 10.1).

Table 10.1 Published reports of evidence of infanticide in cetaceans by species and date. The age of victims and identity of attackers are consistent with the sexual selection hypothesis. Individuals are classified as neonates if they are estimated to be under 3 months old, roughly the age at which fetal lines disappear. Female defense reactions suggest both individual defense and social defense are important in these systems

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
T. truncatus	The Moray Firth, Scotland	Five out of eight necropsied calves showed evidence of infanticidal attacks; all five were estimated <1 year old. An attack on a freshly dead calf of unknown age was observed.	The aggressor was an adult of unknown sex. No other individuals besides the mother and calf were present.	Unknown	The presumed mother remained close to the calf but did not contact the calf or the aggressor.	Patterson et al. (1998)
T. truncatus	Virginia, USA	Nine out of 20 necropsied calves showed evidence of infanticidal attacks. Nine were estimated <1 year old; five of those were < 2 months old.	N/A	N/A	N/A	Dunn et al. (2002)
T. truncatus	St. Augustine, Florida, USA	An attack on a calf <2/3 the size of the adult animals was observed. Authors state that the injuries the calf sustained were likely fatal, but death was not confirmed.	At least two of the aggressors were male, confirmed by observations of erections. The sexes and total number of other aggressors were unknown. Group size varied from 2 to >18 individuals throughout the event.	Unknown	No dolphins appeared to intervene.	Kaplan et al. (2009)
T. truncatus		An attack on a neonate "several days old" was	One adult male was the aggressor. The event	Both the mother and aggressor were well-	The mother and several female associates	Robinson (2014)

	The Moray Firth, Scotland	observed. The neonate survived the initial attack but developed a spinal deformity that was not previously obvious, likely as the result of injuries sustained during the attack. The calf live stranded and died ~8 months after the attack.	occurred within a sub-group of a large, mixed-sex group of 41 individuals.	known to researchers but were not known associates. They were observed together 2 weeks after the attack.	intervened and recovered the calf from the aggressor several times. The mother positioned herself between the calf and the aggressor and held the calf on her back. Several other males encircled and obstructed the aggressor as the mother and infant escaped with female associates.	
T. truncatus	Savannah, Georgia, USA	A birth and a subsequent attack on the neonate (4 minutes old) were observed. The neonate was sighted alive the following day; long-term survival status is unknown.	Two adult males were the primary aggressors; sex was confirmed by observation of erections. Group size varied from five to ten individuals.	The mother and aggressors were known to researchers, but no previous association between them was reported. The male aggressors were presumed alliance partners. The mother, calf, and aggressors were seen together the day after the attack.	The mother lifted and carried the neonate on her back and head. The mother also engaged in potentially defensive behaviors including "thrashing her flukes through the air, lunging, and a high-arch dive".	Perrtree et al. (2016)
T. truncatus	Galician coast, Spain	Case 1: an attack on a live neonate was observed; the neonate was killed in the attack. Case 2: an attack on an already dead neonate was observed; the body was recovered, and a necropsy confirmed the neonate was a few days	Case 1: six adults of unknown sex were the aggressors. The group included only the aggressors and mother-calf pair. Case 2: the group included the mother-calf pair and two adult males. One adult male was the	Case 1: no individuals were identified from previous work in the area. Case 2: all individuals were identified from previous work in the area; the adult male aggressor had never been seen with the mother before, while	Case 1: the mother was separated from the calf by the aggressors and later surfaced with the calf, presumed dead, on her head. Case 2: the mother held the dead calf on her head and repeatedly positioned herself between	Díaz López et al. (2018)

(continued)

Table 10.1 (continued)

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
		old and that the infanticidal attack was the cause of death. Case 3: the dead body of a neonate was recovered; a necropsy indicated that the neonate was a few days old and died from an infanticidal attack.	primary aggressor, while the other adult male remained nearby but did not participate. Case 3: unknown	the bystander male was a known associate of the mother. Case 3: unknown	the dead calf and the aggressive male. Case 3: unknown	
T. truncatus	Sabine Lake, Texas and Louisiana, USA	An attack on a neonate was observed; the neonate survived the attack, but its long-term survival status is unknown.	One adult of unknown sex was the aggressor. The group included ten dolphins.	The aggressor was known to researchers and had been previously observed in the area; the mother, calf, and one other individual in the group had not been observed in the area before.	The mother intervened in the attack, positioning herself between the calf and the aggressor. The mother and calf continued to travel in same direction as the group but put some distance (~100 m) between themselves and the group.	Ronje et al. (2020)
T. truncatus	Turneffe Atoll, Belize	An attack on a neonate (< 2 months from fetal lines) was observed; observation ended while aggression was ongoing with the neonate still alive. The calf was not reidentified within the next 2 years.	Three individuals were the primary aggressors: one adult male and two adults of unknown sex. Two more adults of unknown sex participated in the attack, and one adult female performed both aggressive and	Individuals were all known to researchers. Participants were a mix of full-time and part-time local residents, but individual association history was not reported.	One adult female was heavily involved in the attack and may have been the mother but performed both aggressive and helping behaviors toward the calf. Another adult of unknown sex also	Ramos et al. (2022)

I. geoffrensis	Napo River, Peru	An attack on a neonate (<1 week old, suspected a few hours old) was observed. The neonate survived the attack but was swimming poorly at the end of the observation.	helping behaviors. Five other adults were present. One adult male was the aggressor. Three additional individuals were in the group but did not participate.	Unknown	performed helping behaviors. The mother repeatedly positioned herself between the calf and the aggressor and made potentially defensive contact with the aggressor.	Bowler et al. (2018)
I. geoffrensis	Japurá River, Brazil	Five attacks on neonates were observed. Case 1: the neonate was dead when the observation began. Case 2: the neonate was dead when the observation began and appeared to have been dead for at least a day. Case 3: the neonate survived the attack, but its long-term survival status is unknown. Cases 4 and 5: the neonates survived the attacks and were observed alive several months later. Additionally, five necropsied neonates showed evidence of infanticidal attacks.	Case 1: three adult males were the primary aggressors; eight more adult males also participated. About 20 individuals were in the area. Case 2: one adult male and one subadult male were among the primary aggressors; the other two to four aggressors were described as males. About 18 dolphins were in the area. Case 3: six adult males were the aggressors. An estimated 37 individuals were in the area. Case 4: one subadult male was the aggressor. About seven additional individuals were in the area. Case 5: five adult males and one juvenile of	Case 1–4: several individuals were known to researchers, but association history was not reported. Case 5: one aggressor was the adult maternal brother of the targeted calf.	Case 1: no dolphins appeared to intervene. Case 2: no dolphins appeared to intervene. Case 3: a group of adult females occasionally swam close to the calf and lifted it to the surface on their heads. Case 4: mother did not intervene. Case 5: mother intervened to protect the calf toward the end of the attack.	da Silva et al. (2021)

Table 10.1 (continued)

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
			unknown sex were the aggressors. Up to 25 individuals were in the area.			
S. guianensis	Sepetiba Bay, Brazil	An attack on a neonate was observed; the neonate was presumed to have been killed in the attack.	Six adult males were the aggressors. No other individuals besides the mother and calf were present.	Unknown	The mother was separated from the calf by the aggressors and repeatedly aggressed on when she tried to reunite with the calf.	Nery and Simao (2009)
S. chinensis	Pearl River Estuary, China	Three attacks on neonates were observed. Case 1: the neonate was killed in the attack. Case 2: the neonate was alive at the end of observation. Case 3: the neonate was killed in the attack. Additionally, 3 out of 25 calf carcasses that were necropsied showed evidence of infanticidal attacks.	Case 1: 11 adults were the aggressors. Case 2: two adults and one subadult were the aggressors. Case 3: three adults were the aggressors. The aggressors in all cases were presumed males based on their behavior. No other individuals besides the mother, calf, and aggressors were present.	Case 1–3: the authors describe "infrequent and casual" associations between the perpetrators and presumed mothers before and after the attacks. Case 3: two of the aggressors were seen with the mother 2 days before the attack.	Case 1: the presumed mother tried to protect the neonate and charge the aggressors but was repeatedly separated from the neonate by the aggressors. Case 2: the presumed mother used echelon position to successfully block the aggressors from accessing the calf. Case 3: the presumed mother unsuccessfully tried to block the aggressors from accessing the calf.	Zheng et al. (2016)
O. orca		An attack on a neonate (< a few days old) was	One adult male and his postreproductive mother	The mother and male aggressor had been seen	The mother and her female kin apparently	

	Vancouver Island, Canada	observed; the neonate was killed in the attack.	were the aggressors. The mother-calf pair was accompanied by five members of their matriline.	together on two prior occasions.	tried to separate the aggressors from the neonate by forming two groups. The mother rammed the male aggressor, and the male and his postreproductive mother suffered tooth rakes.	Towers et al. (2018)
L. obliquidens	Mutsu Bay, Japan	An attack on a neonate (~2 months old) was observed; the neonate was alive at end of the observation.	The first group of aggressors included two adult males and two individuals of unknown sex. The second group included two adult males, one possible male, and three individuals of unknown sex. About 24 total individuals were present.	Unknown	The presumed mother charged and aggressed on the attackers.	Rosser et al. (2022)

10.2.2.1   Bottlenose Dolphins (*T. truncatus*)

The first evidence of infanticide in cetaceans came from a residential population of bottlenose dolphins in the Moray Firth, Scotland, in the mid-1990s (Patterson et al. 1998). Five of eight necropsied bottlenose dolphin calves were found to have significant internal injuries likely caused by intraspecific aggression (Patterson et al. 1998). Additional necropsy evidence from dolphins stranded on the coast of Virginia, USA, supported these findings (Dunn et al. 2002). Internal injuries indicated that attacks came from multiple directions and were concentrated on the head and thorax of the calves (Dunn et al. 2002). One calf had an external bite mark consistent with the tooth placement of an adult bottlenose dolphin, and some calves showed evidence of being subject to multiple traumatic injuries over several weeks (Dunn et al. 2002).

Patterson et al. (1998) observed one interaction in which an adult dolphin repeatedly attacked an already dead calf, lending credence to the hypothesis that intraspecific aggression is a significant cause of infant death in the Moray Firth population. Since then, reports of calf-directed aggression and apparent infanticidal attacks have accelerated. Aerial footage collected off the coast of Florida, USA, captured extensive and likely fatal attacks by multiple adult bottlenose dolphins on a calf over the course of 51 minutes (Kaplan et al. 2009). In the Moray Firth, where long-term research effort means that some of the dolphins' individual histories are known, Robinson (2014) reported an event in which a large adult male was seen repeatedly attacking a calf that was just a few days old. The mother of the calf appeared to try to intervene in the attack, positioning herself between the aggressive male and the calf (Robinson 2014). A female associate accompanied the mother, and other adult males obstructed the aggressive male's access to the calf by encircling him, facilitating the mother and calf's escape (Robinson 2014). The first published observation of a bottlenose dolphin birth, off the coast of Georgia, USA, was accompanied by an observation of an infanticidal attack. Just minutes after the calf was born, two males repeatedly attacked and attempted to submerge the neonate (Perrtree et al. 2016). The two male aggressors were presumed alliance partners and had been seen together several times before; they were seen flanking the pregnant female hours before the birth, indicating that they could have been tracking her impending parturition (Perrtree et al. 2016). Despite the increase in observations of calf-directed aggression, so far there is only one case in bottlenose dolphins in which a complete successful infanticide attack was observed. Off the coast of Galicia, Spain, Díaz López et al. (2018) observed six dolphins coordinating an attack on a neonate that resulted in the infant's death. Additional bouts of intense calf-directed aggression by bottlenose dolphins have been observed in Sabine Lake in the Gulf of Mexico (Ronje et al. 2020) and off the coast of Belize (Ramos et al. 2022). A survey of dolphin researchers working in the Gulf of Mexico revealed extensive records of calf-directed aggression, though no successful infanticidal attacks were observed (Ronje et al. 2020).

Several unpublished incidences of aggression toward calves indicative of infanticidal attempts have been observed in the Potomac River and Chesapeake Bay,

USA, despite only a few years of detailed observation (Ann-Marie Jacoby pers. comm. November 2022; JM pers. obs.). Dolphins inhabiting these waters overlap with the dolphin population(s) observed off the coast of Virginia Beach, USA (Dunn et al. 2002), so observations of infanticide were not unexpected. Two unsuccessful infanticidal attempts on neonates by suspected adult males (based on physical and behavioral features) were observed. One occurred immediately postpartum, similar to the case described by Perrtree et al. (2016). The calf was chased, tossed into the air several times, and held underwater by a suspected male before the mother was able to intervene and flee with the calf. The other case involved a neonate that was estimated to be 5 to 10 days old (Mann and Smuts 1999); the calf was repeatedly charged and chased, and in one incident was tossed out of the water. The mother and a juvenile (possibly her weaned offspring) appeared to defend against the attackers by repeatedly positioning the calf less than one-half meter alongside the research boat, effectively preventing the males from accessing the calf. Every time they separated from the vessel, the males resumed chasing, and the mother, neonate, and juvenile returned to the vessel. Both calves were observed with their mothers at least 1 month later and appeared to be healthy.

10.2.2.2 Amazon River Dolphins (*Inia geoffrensis*)

Amazon river dolphins are the only species besides bottlenose dolphins in which there are multiple published observations of infanticidal behavior and the only cetacean species outside of the delphinid family in which infanticide has been observed. In Peru, a newborn Amazon river dolphin was attacked by a large adult male, while the mother tried to intervene and keep the male away from the infant (Bowler et al. 2018). Five additional observations of infanticidal aggression were reported in Brazil (da Silva et al. 2021). In one case, one of the male aggressors was the maternal brother of the neonate target, and the authors suggest that this event is not consistent with the sexual selection hypothesis. For several of the attacks, there were large numbers of dolphins in the area, and da Silva et al. (2021) suggest that this behavior could be a form of sociosexual display (discussed further below).

10.2.2.3 Guiana Dolphins (*Sotalia guianensis*)

One observation of infanticide has been reported in Guiana dolphins in Brazil; a mother and neonate were separated and both repeatedly attacked by a group of six individuals of unknown sex (Nery and Simao 2009). The calf disappeared and seemed to have been killed within 12 minutes of the attack starting (Nery and Simao 2009).

10.2.2.4 Indo-Pacific Humpback Dolphins (*Sousa chinensis*)

Among Indo-Pacific humpback dolphins in southeast China, three infanticidal attacks have been reported, two of which resulted in the death of the infants

(Zheng et al. 2016). In all three cases, neonates were targeted, and the presumed mothers repeatedly tried to shelter the infant from aggression, even charging and attacking the aggressors. The number of attackers ranged from 3 to 11 dolphins all believed to be male (Zheng et al. 2016). Necropsy data on three additional calves indicate that the cause of death was blunt force trauma, implicating infanticide.

10.2.2.5 Killer Whales (*O. orca*)

One notable observation of infanticidal behavior occurred in mammal-eating killer whales off British Columbia, Canada (Towers et al. 2018). In 2016, an adult male and his postreproductive mother engaged in a long chase and eventual killing of a neonate. The mother of the neonate and her matrilineal kin apparently tried to separate the attackers from the neonate by forming two groups. When the attackers caught up to their target, the mother of the neonate defended her calf, aggressing on and ramming the infanticidal male. The neonate was killed quickly, and defensive behavior did not persist. While the infanticidal male and neonate's mother had been sighted together twice before (in 2005 and 2007), they were not regular associates. It was not reported if the infanticidal male was seen in association with the mother after the attack, but at the time of publication she had not yet been seen with a new calf, suggesting that a successful pregnancy was not immediate.

10.2.2.6 Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)

Recently, a group of male and unknown-sex Pacific white-sided dolphins were seen repeatedly attacking a neonate in Mutsu Bay, Japan (Rosser et al. 2022). A separate group of dolphins displaced the first aggressive group and continued the attack, a behavior that has not been described in any other accounts. The authors noted that it is unusual to see neonates in this location; this was the first neonate sighting in 5 years (Rosser et al. 2022).

10.3   The Sexual Selection Hypothesis in Cetaceans

10.3.1   Prediction 1: Infanticide Is Committed by Adult Males Who Target Infants That Are Not Their Own Offspring

Overall, cases of infanticide in odontocetes are consistent with the sexual selection hypothesis. First, where age and sex are known, the perpetrators are by and large adult males (Table 10.1). However, there are several reports of subadult males participating in infanticide attempts (Zheng et al. 2016; da Silva et al. 2021). Even though subadult males are unlikely to sire a female's next offspring, engaging in

attacks may serve as practice, particularly if these attempts are relatively low cost for males. In one case, a female who could have been the calf's mother was involved in both aggressive and helping behaviors (Ramos et al. 2022), which is unusual but difficult to interpret without confirmation that the female was the mother. In the most conspicuous example of a female participating in an infanticidal attack, in which an adult female killer whale assisted her adult son, the exception may prove the rule (Towers et al. 2018). Postreproductive killer whale females provide fitness benefits to their adult offspring, particularly their sons (Foster et al. 2012; Brent et al. 2015). If a mother's assistance in an infanticidal attack results in her son being more likely to sire offspring, the sexual selection hypothesis applies to both mother and son.

Previous social association between the infanticidal individuals and their victim's mothers is often not known, but when it is reported, infanticidal males appear to be socially unassociated with the female and unlikely sires of the targeted infant (Table 10.1). In several cases, the males were not frequent associates of the mother (Robinson 2014; Zheng et al. 2016; Díaz López et al. 2018; Towers et al. 2018), and in others, the attackers and the mothers seemed to be from different subpopulations (Ronje et al. 2020; Ramos et al. 2022). The conspicuous exception to this is a case in the Amazon river dolphin, in which one attacker was the maternal brother of the targeted calf (da Silva et al. 2021). Given the large number of individuals who were involved in this attack, it seems relatively unlikely that the male would father his mother's next offspring; however, inbreeding rates are high in some dolphin species (Frère et al. 2010; Ford et al. 2018), and it is not impossible. While attacking one's sibling certainly seems detrimental to inclusive fitness, observations of adaptively neutral or maladaptive infanticide events do not necessarily represent evidence against the sexual selection hypothesis (Hrdy 1979). These behaviors are cued by complex circumstances that involve long-term individual recognition and memory, and occasional maladaptive attacks are probable. Overall, the evidence to date suggests that adult male cetaceans target infants that they are unlikely to have sired.

10.3.2 Prediction 2: The Mother Is Likely to Return to Estrus Faster, or in Better Condition, than if She Had Successfully Weaned the Infant

The second prediction of sexually selected infanticide is also met in all cases reported herein; the odontocete species that engage in infanticidal behavior have long lactation periods and no known postpartum estrus. The death of a dependent offspring is very likely to accelerate the return to conceptive estrus in these species (Robinson et al. 2017; Karniski et al. 2018; Martin and Da Silva 2018; Nattrass et al. 2019; Bezamat et al. 2020). Lactation requires large energetic investments in milk production (Cheal and Gales 1991), and losing a very young calf may be less costly to mothers than losing an older calf. Mothers who lose a neonate appear to conceive rapidly within a few weeks or months, while mothers who lose older calves can

sometimes take over a year to conceive again (Mann et al. 2000). Infanticidal males who kill a very young calf may only have to maintain an association or consortship with the mother for a period of a few weeks to sire her next offspring. An infanticidal male who kills an older calf would have to ensure that he is in contact with the mother after she has recovered sufficient body condition to return to estrus, which may take months or years. The potential benefit of killing a young calf is therefore much higher than killing an older calf, and it is salient that the vast majority of the targets described in the literature are neonates (Table 10.1). In multiple cases, attacks occurred within minutes or days of birth, and in two cases, males may have been tracking the female before she gave birth (Perrtree et al. 2016; Ann-Marie Jacoby pers. comm. November 2022). While neonates may be particularly vulnerable and easier to kill than older calves, the size differential and fact that attacks often involve multiple adult aggressors suggest that adult males could kill older calves as well. Given the transitory association patterns in some of these migratory populations, however, targeting neonates may help maximize the likelihood of subsequent conceptive mating. Feticide, male aggression against a pregnant female that induces abortion, could also operate in these systems, given that males seem able to determine a female's reproductive state (Wallen et al. 2017). Whether pregnancy loss results in a rapid return to estrus is not known, although it seems likely. Rates of feticide would be difficult to assess in wild cetaceans, but male aggression toward pregnant females would be telling.

10.3.3 Prediction 3: The Infanticidal Male Has an Opportunity to Sire the Mother's Next Offspring

The third prediction of the sexual selection hypothesis remains uncertain in all cetacean cases reported herein; no studies reported mating or association during estrus between infanticidal males and the mothers of their victims. In terrestrial systems, the monopolizability of mating and the likelihood that an infanticidal male will sire the next offspring have been highlighted as important modulators of infanticide risk (Lukas and Huchard 2014). In cetaceans, however, most species have polygynandrous mating systems (Würsig et al. 2023, this book), and mating monopolizability is likely relatively low. In cetacean species in which male-female associations are seasonal and unpredictable, the likelihood of a male siring a female's next offspring without committing infanticide could be zero. If costs of infanticidal behavior to males are low, it may be adaptive to commit infanticide for even a small chance of siring the subsequent offspring. In one case in bottlenose dolphins, the mother and calf who survived the initial attack were seen with the aggressor several weeks later (Robinson 2014), demonstrating the plausibility of males maintaining an association with the mother long enough to mate. Still, this key requirement of the sexual selection hypothesis is yet to be demonstrated in cetaceans.

10.3.4 Cooperation During Infanticide

Infanticidal attacks in toothed whales often involve multiple males launching highly coordinated attacks against a victim (Table 10.1). While early accounts of sexually selected infanticide in langurs and lions note that groups of males can be involved in takeovers and infanticide attempts (Hrdy 1974; Packer and Pusey 1984), to our knowledge the number of males and the level of coordination described in cetaceans represent an extreme of this behavior. Many of the events involved between 3 and 6 attackers, with 1 event involving 11 (Table 10.1), and coordinated behaviors including "sandwiching", in which the mother or infant was trapped between two attackers, were described by multiple observers (Zheng et al. 2016; Díaz López et al. 2018; Rosser et al. 2022). In two cases, the observers described what seems to be strategic coordination, in which a subgroup of attackers sequestered the mother, preventing her from reaching her calf, while another subgroup focused their aggression on the infant (Díaz López et al. 2018; Rosser et al. 2022). The presence of multiple attackers poses an obvious challenge to the sexual selection hypothesis; if males cooperatively kill infants, not all infanticidal males can benefit by siring the female's next offspring. At the same time, cooperative attacks may reduce the cost for each individual male. In some cases, males could be cooperating with relatives, as in the killer whale event (Towers et al. 2018). Cooperation between related (Parsons et al. 2003; Diaz-Aguirre et al. 2018) or unrelated (Gerber et al. 2020) males in alliances that compete over access to paternity, an indivisible resource, is a characteristic feature of bottlenose dolphin mating systems (Gerber et al. 2022). While it remains unclear how paternity is divided between alliance partners, strong cooperative bonds appear to provide a reproductive benefit (Gerber et al. 2022). Cooperation during infanticide attempts may be an extension of male-male cooperation to gain access to mating opportunities, and thus consistent with the sexual selection hypothesis.

10.3.5 Alternative Hypothesis for Infanticide

Numerous other hypotheses for adaptive infanticide are supported in a variety of systems (Ebensperger 1998; Palombit 2015), but so far there is little evidence for them in cetaceans. None of the cases of infanticide described in cetaceans are consistent with the predation hypothesis, as none of the infants were eaten after being killed. Killer whales are one of only a few cetacean species that eat mammals, and even in the killer whale infanticide case, the dead infant was not consumed (Towers et al. 2018). The resource competition hypothesis posits that individuals kill unrelated infants to increase their or their offspring's access to resources (Ebensperger 1998), but cetacean prey are typically non-monopolizable, and competition over prey or territory is not obvious. The adoption avoidance hypothesis posits that infanticide can prevent individuals from investing alloparental care

into unrelated infants (Ebensperger 1998). While alloparental behavior has been documented in sperm whales (*Physeter macrocephalus*) (Konrad et al. 2019), infanticide has not. All of these hypotheses predict that adult females will be equally or more likely than males to attack infants, which has not been reported in cetaceans.

Nonadaptive hypotheses for infanticide are divided between neutral and pathological explanations. The neutral generalized aggression hypothesis suggests that infants can be killed incidentally in the course of male competition or male aggression on females (Palombit 2015). This does not fit observed patterns in cetaceans as all cases involved extensive, repeated, and highly directed aggression against an infant. While aggression and sexual behaviors against the mother did occur during infanticidal attacks, the infant was always the primary target. Since the 1960s, nonadaptive or pathological explanations for infanticide have been proposed (e.g., Curtin and Dolhinow 1978) and dismissed (Hrdy 1979; Packer 2000). Pathological hypotheses focus on the idea that infanticide can be a maladaptive response to anthropogenic disturbance and stress. While there is no evidence supporting the idea that human disturbance results in aberrant aggressive behavior, there is some suggestion that disturbance can indirectly impact infanticide via demographic variables such as immigration or male turnover rates (Sterck 1999; Swenson et al. 2001). Anthropogenic induced stress in cetaceans is pervasive, but there is little evidence linking human disturbance to infanticidal aggression. The one potential exception is in Amazon river dolphins, where the population is in severe decline. Despite constant research effort since 1998, all five observations of infanticidal aggression described by da Silva et al. (2021) occurred after 2010. It is possible that population decline may have disrupted social structure and resulted in decreased access to females in estrus and increased infanticide rates, but this has not been proven.

One hypothesis in the literature is unique to cetaceans. Da Silva et al. (2021) suggest that infanticide in Amazon river dolphins could be a form of sociosexual display, akin to the object carrying that males perform in this species (Martin et al. 2008). The fact that a maternal relative engaged in an infanticidal attack leads the authors to conclude that sexually selected infanticide is unlikely. Observations of males handling a neonate who had been dead for at least a day, along with the large number of dolphins present during attacks, supports the display hypothesis. Still, it seems equally maladaptive to kill a half-sibling to obtain a display object as it would be to obtain a mating opportunity, and it is possible that sexually selected infanticide and sociosexual display of the dead neonate could occur sequentially in this species.

10.4   Interspecific Infanticide

While the sexual conflict literature defines infanticide as a behavior committed by conspecifics (Palombit 2015), interspecific attacks are a prominent feature of reports of cetacean infanticide. Non-predatory interspecific aggression has been reported in a number of odontocetes (e.g., Shane 1995; Weller et al. 1996; Orr and Harwood 1998), with bottlenose dolphins featuring heavily as aggressors (Ross and Wilson 1996; Herzing et al. 2003; Wedekin et al. 2004; Barnett et al. 2009; Puig-Lozano

et al. 2020). At first glance, these attacks are inconsistent with the sexual selection hypothesis and raise the possibility of an alternative underlying driver of both intraspecific and interspecific attacks. Details of some of these aggressive interactions, however, are consistent with sexually selected infanticide. Harbor porpoises are similar in size to dolphin neonates, and porpoise-directed aggression could be a form of object-oriented play that allows males to practice infanticidal behaviors or to reinforce social bonds and improve coordination between male social partners during aggression (Patterson et al. 1998). In "porpicide" events observed off the coast of California, bottlenose dolphin aggressors were confirmed or putative males, supporting the hypothesis that this behavior is linked to sexually selected infanticide (Cotter et al. 2012). One observation of three male Indo-Pacific bottlenose dolphins harassing a dead spinner dolphin (*Stenella longirostris*) neonate and its assumed mother closely resembles accounts of conspecific infanticidal behavior (Estrade and Dulau 2017). While no bottlenose x spinner dolphin hybrids are known, bottlenose dolphins do hybridize with other sometimes less closely related species (Herzing et al. 2003; Crossman et al. 2016; Estrade and Dulau 2017) suggest that the sexual selection hypothesis could apply in this and other interspecific attacks. Alternative hypotheses for interspecific attacks have been raised, including aberrant aggression, sexual frustration, and aggressive tendencies driven by testosterone (Ross and Wilson 1996; Patterson et al. 1998). In practice, it would be difficult to differentiate between males expressing general aggressive tendencies on a low-cost target and males practicing aggressive behavior on a low-cost target, and these explanations represent potentially compatible proximate and ultimate hypotheses. Alternatively, interspecific resource competition may be relevant in some cases and would generate distinct predictions from the sexual selection hypothesis, including the prediction that females would be involved in attacks. Non-predatory interspecific aggression likely has different drivers in different species, and research targeting the social and ecological circumstances of these events will help determine if they are compatible or at odds with sexually selected infanticide.

10.5   Female Counterstrategies to Infanticide

Infanticide risk has been hypothesized to influence virtually every aspect of female reproductive biology and social behavior, including physiology, mating strategies, territoriality, group sizes, and social bonds (Agrell et al. 1998; Palombit 2015). Phylogenetic analysis suggests that multi-male mating, measured by relative testes size, has evolved in response to infanticide by adult males in multiple lineages (Lukas and Huchard 2014). Males who have mated with the mother of an infant are less likely to target that infant in attacks, as the cost of potentially killing their own offspring is very high (Palombit 2015). Polyestrous cycling and multi-male matings that confuse or "dilute" paternity occur in many odontocetes and may be important for reducing infanticide risk (Connor et al. 1996). Many odontocetes breed seasonally, likely to ensure calves are born during warm months. Breeding

synchrony between females may also serve to reduce male monopolization of mating opportunities, further confusing paternity. However, polygynandrous mating and synchronous estrus appear insufficient to deter infanticide completely in these species, likely because extra-group males, or males with whom the female has little or no prior association, are still unlikely to have mated with the mother and are therefore more likely to target her infant.

Other types of reproductive and sexual anti-infanticide strategies are less likely to operate in cetaceans. Concealed ovulation, postconception sexual behavior, and pseudoestrus can all confuse paternity and dilute infanticide risk in species where males cannot accurately judge female reproductive state (Ebensperger 1998). However, toothed whales have sophisticated echolocation and appear to readily detect early pregnancy (Wallen et al. 2017). Spontaneous abortion following exposure to an unfamiliar male, the "Bruce effect," occurs in rodents and primates (Beehner and Lu 2013); females terminate their pregnancies (i.e., "cut their losses") when the offspring is likely to be killed after birth. Due to stable social grouping, females cannot avoid the newly immigrant infanticidal male, and ending the pregnancy reduces the cost of infanticide. This is an unlikely scenario for cetaceans because novel males rarely establish tenure in a female group.

Deterrence tactics from the mother were prominent in many of the events described in cetaceans. Mothers often tried to place themselves between attackers and their infants, and several mothers aggressed on their attackers. Female cetaceans rarely engage in aggressive behavior compared to males (e.g., Scott et al. 2005), and the few cases of female aggression that have been reported in cetaceans are in defense of their offspring (e.g., Mann and Barnett 1999). In classic infanticidal species, where males take over or rise to dominance in stable social groups, females are unlikely to be able to fully avoid infanticidal males, and their infant may be at risk of infanticide for months. In the fission-fusion social system of odontocetes, females who successfully fend off infanticidal males may be able to avoid those males until their calf is less vulnerable. Limited sexual size dimorphism in some dolphins may also enable females to better defend against males. While in the killer whale event the mother's attempts to defend her calf failed, both the infanticidal male and his mother suffered injuries in the attack (Towers et al. 2018), suggesting maternal aggression can be costly for infanticidal attackers.

Social strategies likely also play a role in infanticide deterrence in cetaceans. In several descriptions of attacks, mothers were assisted in infant defense by female kin, female associates, or male associates (Robinson 2014; Towers et al. 2018; da Silva et al. 2021). Large group sizes are characteristic of mothers with newborn infants (Mann et al. 2000), and groups of females with calves might deter infanticidal attacks or inflict injury on the perpetrators, as in the killer whale event (Towers et al. 2018). Females might also travel with residential males with whom they commonly associate. Polygynandrous mating could result in multiple potential fathers that could provide infant protection, though this is dependent on fathers remaining in association with mothers when the calf is vulnerable. While there is no known paternal care in cetaceans, it is possible that dyadic male-female relationships could result in fathers or male associates providing infant protection. In one

described case in which a male attacked an already dead calf, a different male who was present at the infanticide attempt but not involved in the aggression was seen with the mother in the weeks following the attack (Díaz López et al. 2018). While the authors hypothesized that the male could have been involved in the attack and benefited by fathering the female's next offspring, it is also possible that as a known associate of the mother, he provided the mother support or intervened in the attack before the calf's death.

10.6   Summary and Future Directions

The instances of infanticide described in cetaceans are most clearly consistent with the sexual selection hypothesis. While much remains unknown about the relative costs and benefits of sexually selected infanticide in cetaceans, this group can provide an important comparative system to study the evolutionary drivers of infanticidal behavior and defense. Descriptions of infanticide in these highly mobile, multi-male mating systems challenge previous findings that infanticide occurs in stable bisexual groups in which few males monopolize mating opportunities (Lukas and Huchard 2014). Instead of being associated with male takeovers or changes in dominance status, we hypothesize that infanticide risk in cetaceans is largely determined by contact with unfamiliar males. We expect infanticide to occur when populations experience seasonal influxes of unfamiliar males or when multiple subpopulations interact and males encounter females with whom they have had little to no previous contact.

There is substantial evidence for infanticide in multiple bottlenose dolphin populations. However, several long-term bottlenose dolphin sites have *not* reported infanticide. In residential populations of bottlenose dolphins with bisexual philopatry in Shark Bay, Australia, Doubtful Sound, New Zealand, and Sarasota, Florida, USA, infanticide has not been reported. Calf-directed aggression has been described in Sarasota, but it is unclear if those events meet the standard of intense, highly directed infanticide attempts (Ronje et al. 2020). In Shark Bay, where there has been intensive research effort for over 38 years, there is no evidence of infanticide or calf-directed aggression. Infanticide events are always rare and often relatively brief, and it is possible that unobserved infanticide does occur in these populations. Even in extremely well-studied populations of primates with strong demographic evidence for infanticide, the behavior has never been witnessed (Zipple et al. 2017). However, the lack of observed infanticide could be the result of effective female counterstrategies to male infanticidal aggression. Females in stable, socially integrated, residential groups (Tsai and Mann 2013) with polygynandrous mating systems and polyestrous cycling (Connor et al. 1996) are surrounded by males with whom they have social histories and have likely mated with (Foroughirad et al. 2022), potentially minimizing infanticide risk.

We see several promising areas for future research. First, as research effort and researcher interest in infanticide in cetaceans increase, anecdotal reports of

infanticidal behavior and necropsy evidence will likely continue to accelerate. These anecdotal reports are extremely valuable, and standardization of vocabulary to describe these behaviors will facilitate comparison over different research programs and species. Second, in populations where infanticide has been described, researchers can explicitly investigate the risk of infanticide based on the presence of unfamiliar males who are unlikely to have sired current offspring. Third, continued long-term monitoring of cetacean populations is likely to yield further information about the post-infanticide patterns of association between infanticidal males and females, and increases in the use of high throughput sequencing technologies will improve our understanding of male reproductive success. Determining the realized benefit of infanticide (i.e., the likelihood of an infanticidal male fathering the mother's next offspring) is a key component for advancing our understanding of the evolution of infanticide in these systems. Fourth, researchers can examine mating and association patterns that may reduce infanticide risk, both in sites where infanticide has been observed and where it has not been. Increased attention to low-level calf-directed aggression and maternal protective behaviors will further our understanding of infanticide, even in the absence of conspicuous attacks. Cetaceans provide an exciting opportunity to investigate the drivers of infanticide in mating and social systems that differ substantially from their terrestrial counterparts. Continued research effort will elucidate how infanticide evolved in species without dominance hierarchies or stable social groups, providing insight into the evolution of infanticide overall.

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Chapter 11
Drone Perspectives on Cetacean Mating and Sex

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Abstract Mating and sociosexual behaviors of cetaceans are challenging to study in nature because most species spend only brief periods of time at the surface and most copulation and courtship occurs underwater. Recent advancements in technology have enabled a new perspective on these behaviors. Drones, or unoccupied aerial systems, have revolutionized studies of marine mammals by providing unparalleled aerial perspectives on the behaviors of whales, porpoises, and dolphins, including their use for investigating questions concerning the sexual behaviors and mating habits of species in near-surface waters. Drones offer numerous benefits over traditional boat- and land-based observational methods for studying mating in free-swimming cetaceans, including the ability to continuously film in high resolution for fine-scale tracking of activity and mating behaviors at and near the water's surface. This paper outlines various ways in which drone data can be used to understand mating in cetaceans, including novel drone-based video observations of six species of dolphins and whales. These examples illustrate specific sociosexual and mating behaviors and how drone-based data can be used to address questions

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11.1.1 Aerial Perspectives

The use of unoccupied aerial vehicles (UAVs)/drones in marine mammal studies has significantly increased in recent years due to their versatility and multiple benefits. Drones consist of a multirotor or a fixed-wing aircraft equipped with cameras and other sensors, which are piloted remotely or autonomously. Drones have been used in a wide range of marine mammal research including photogrammetry to assess body size, health, and energetics (Christiansen et al. 2016; Torres et al. 2022), estimations of population or group size (Fettermann et al. 2022), tracking interactions with humans (Fiori et al. 2020; Pirotta et al. 2022), and observing the behaviors of cryptic species (Baird et al. 2022). Small (< 5 kg) multirotor drones flown over cetaceans may provide overhead views of behaviors inaccessible from boat-based observers or capture rare events, foraging patterns, socializations, and mother-calf interactions (Ramos et al. 2021). Drones can also facilitate the collection of blow samples for genetic, microbiome, and hormonal studies (Raudino et al. 2019; Centelleghe et al. 2020) and provide a means of photo-identifying taxa (Koski et al. 2015; Hartman et al. 2020; Landeo-Yauri et al. 2021). When combined with other methods of data collection, drones may provide valuable insights about the mating grounds of large whales (Cole et al. 2013) and the behavior of pelagic cetaceans (Smultea et al. 2018). Yet observations of mating are often brief and opportunistically gathered during surveys dedicated to estimating population distribution and abundance (Kingsley and Reeves 1998), often in remote and inaccessible regions (Angliss et al. 2018).

The widespread use of drone technology for behavioral studies in cetaceans requires careful consideration and adaptation to different contexts. A growing body of literature has been published on the disturbance impacts of drones on marine mammals, particularly on bottlenose dolphins and manatees (Ramos et al. 2018; Giles et al. 2021; Landeo-Yauri et al. 2021). The type of drone needed depends on the research question and target species. Numerous recent comprehensive reviews and synthesis of the benefits and pitfalls of drone use for marine megafauna studies provide insights of broad and specific applications (e.g., Nowacek et al. 2016; Raoult et al. 2020; King and Jensen 2022). We emphasize the value of drones compared to boat-based research when applied to studying sociosexual and mating behavior in cetaceans (Table 11.1).

11.2 Drones Applied to Assess the Sociosexual and Mating Behavior of Cetaceans

An increasing number of studies have reported sociosexual and mating behaviors of cetaceans using drones (e.g., Ramos et al. 2021; Hill et al. 2022; Lonati et al. 2022). The use of aerial drones for enabling direct overhead views of cetaceans and for gathering high-resolution videos of their interactions provides numerous benefits to

Table 11.1 Comparison of different aspects of boat- and drone-based methods for studying mating and sexual behavior in cetaceans

Characteristic	Boat	Aerial drone
Data sampling	Visual observations of animals at the surface and submerged near the surface (<1 m)	Surface and subsurface observations
Animal visibility	Visible primarily at the surface and possibly just beneath the surface	Visible for the duration of time within <1–3 m of the surface
Scale of observations	Within <200 m of the vessel or several km from shore	Fine-scale of meters to hundreds of meters across field-of-view
Follow type	Focal animal or focal group	Focal animal or focal group
Sampling strategy	Variety of sampling types (e.g., all event, ad libitum, scan, point) implemented by observer to account for need to track different numbers of individuals engaged in different activities	High-resolution recording enables resampling of videos to conduct multiple sampling types. For example, focal follows of all individuals paired with scan sampling every 30 sec to account for activity of the group
Duration of observation	At the surface for minutes to hours depending on the target species and other factors. Animals regularly go out-of-sight. Recording of the activity of multiple animals is often restricted by the number of observers	Each flight is limited in battery time (e.g., 20–45 min). Multiple flights can be flown back-to-back to overcome this
Behavioral activity	Observers tracking surface activity of subsets of animals and sampling sexual and mating behaviors	Detailed video record of all near-surface behavior in target animals. Videos can be scored for behaviors and associated factors (e.g., position, orientation, sex identification, quantification of mating behaviors)
Individual identification	Photo-identification using high-resolution cameras equipped with telephoto lenses to capture images of the dorsal fins, bodies, or flukes of individuals	Photo-identification feasible for species with sufficient scarring detectable
Tracking movements	Estimates between surfacings, measured by speed of surface movements	Tracked at fine-scale with onboard GPS sensor providing spatially and temporally fine-grained location and time data

Table adapted from King and Jensen (2022)

the study of cetacean mating behavior (Table 11.1). By enabling continuous observations of behavior at the surface and subsurface, it is possible to track individuals and groups and detect specific mating behaviors. High-resolution drone footage demonstrated that the sex-specific mating behaviors of dusky dolphins (*Lagenorhynchus obscurus*) varied with context (Orbach et al. 2020b); detailed analysis of footage enabled precise counts of mating behaviors, swimming speeds, bearing changes, and the percent of time dolphins spent at the surface (Orbach et al. 2020b). One male rough-toothed dolphin (*Steno bredanensis*) was video-recorded

copulating with another dolphin on at least seven occasions within 7 minutes (Ramos et al. 2021). For some species like harbor porpoises (*Phocoena phocoena*), their tendency to avoid boats makes them particularly challenging to observe in nature; yet drone footage has captured mating attempts (Webber et al. 2023, this book).

Drones have captured non-conceptive mating, which occurs in several species of cetaceans (Ham et al. 2023, this book). Non-conceptive male-male sexual interactions (swimming belly-to-belly with erect penises) were video-recorded between an adult male killer whale and a calf (Sanvito and Galimberti 2022); aerial imagery enabled identification of the animals from an established photo-identification catalog. Non-conceptive copulatory behavior has also been video-recorded by drone for North Atlantic right whales (*Eubalaena glacialis*; Lonati et al. 2022); the penis of an adult male was recorded entering a calf's genital slit (Lonati et al. 2022; Brown and Sironi 2023, this book). Distinguishing conceptive from non-conceptive mating is important to understand social bonding, dominance relationships, and social learning (Ham et al. 2023, this book).

The rapidly growing literature on applications of aerial drones to cetacean research supports their use for capturing unparalleled views of cetacean behavior in nature. However, the application of drones to explore sociosexual and mating behaviors is largely unexplored.

11.3   New Data Documented with Drones

To demonstrate the capabilities of drones to advance exploration of the mating behavior of cetaceans, we analyzed a selection of aerial footage from six different species of cetaceans (common bottlenose dolphins (*Tursiops truncatus*), rough-toothed dolphins, pygmy killer whales (*Feresa attenuata*), Risso's dolphins (*Grampus griseus*), dusky dolphins (*Lagenorhynchus obscurus*), and gray whales (*Eschrichtius robustus*)). We employed various models of small (< 5 kg) multirotor DJI drones, ensuring compliance with all local laws and regulations for drone operations in Belize, Mexico, New Zealand, the USA, and Portugal (Table 11.2). All videos were filmed in 4 K resolution during manually operated flights at a maximum duration of ~20 mins (Table 11.2).

Videos collected by drone were analyzed, and a subset that included repeated sociosexual or mating behaviors were reviewed in BORIS behavioral analysis software (Friard and Gamba 2016). To provide examples of different data acquired by drones, we reviewed video footage and conducted focal group follows using ad libitum sampling (Mann 1999). Sexual behaviors associated with different mating tactics of each sex were characterized according to behavioral ethograms (Table 11.3; Orbach 2016, 2019). Due to the limited duration of our follows and our overall dataset, we likely only captured a fraction of the sexual behaviors displayed by any of our study species.

Table 11.2 Information on the six species of cetacean filmed using small aerial DJI drones during focal group follows

Scientific name	Common name	Location	Body of water	Drone type	Flight altitudes (m)	Habitat type	Mean depth (m)	No. flights
Tursiops truncatus	Common bottlenose dolphin	Turneffe Atoll, Belize	Caribbean Sea	Phantom 4 Pro v2	20–35	Shallow lagoon	3	24
Lagenorhynchus obscurus	Dusky dolphin	Kaikoura, New Zealand	South Pacific Ocean	Phantom 4 Pro v2	10–20	Open sea	900	3
Eschrichtius robustus	Gray whale	San Ignacio Lagoon, Mexico	Eastern North Pacific Ocean	Inspire 2	20–40	Shallow lagoon	2–30	3
Steno bredanensis	Rough-toothed dolphin	Bay of Petatlan, Mexico	Eastern Tropical Pacific Ocean	Mavic Pro 2	20–40	Open sea	25	6
Feresa attenuata	Pygmy killer whale	Hawai'i, USA	Eastern Tropical Pacific Ocean	Mavic Pro 2	25–50	Open sea	1300	3
Grampus griseus	Risso's dolphin	Azores, Portugal	North Atlantic Ocean	Phantom 4/Mavic Pro 2 Zoom	15–40	Open sea	800	3

Table 11.3 Mating tactics and associated precopulatory behaviors in male and female cetaceans identifiable by drone observations

Sex	Mating tactic	Measurable from a drone	Example in our data
Male	Display competition	Measure body size and shape in sexually dimorphic species. Determine dominance relationships through group position (e.g., leaders)	Stereotypic copulation position in rough-toothed dolphins perpendicular to the female who swam ventrum-up
Male	Contest competition	Compare and quantify competitive behaviors and intrasexual competition in individual males during mating behavior	Male gray whales simultaneously jostled for position against the female during copulation attempts. Males interfered with the copulation attempts of rival males
Male	Endurance competition	Track individual male mating behaviors subsurface and over fine-spatial scales. Identify roles in consortships and occurrences of cooperative mating tactics (i.e., herding)	Two adult male bottlenose dolphins herded a sexually immature female to prevent her from leaving the area and copulating with other males
Male	Scramble competition	Measure individual male speed during mating chases and compare between successful and rejected copulations between rival males	Female dusky dolphins led multiple males on energetically costly chases involving deep dives, leaps, and abrupt changes in swim speeds and directions.
Female	Signal discrimination	Measure characteristics of male chases (e.g., maneuverability, speed)	Female gray whale behavior in response to multiple different males
Female	Evasive behaviors	Sex identification and fine-scale behavior of individuals including the detection and frequency of behavioral events	Female dusky dolphins avoided males with reorientation leaps, accelerated swim speed, and reorientation ventrum-up to prevent genital access
Female	Polyestry and multiple matings	Identify male roles in infanticide associated with social networks and measure synchrony and inter-animal distances	Multiple matings in bottlenose dolphins and Risso's dolphins of known age and sex to track reproductive status in relation to individual mating partners

Table is modified from Orbach (2016, 2019)

11.3.1 Sex Identification

Observations of the genitals of cetaceans, which are a necessity to verify the sex of an individual in the absence of genetic analyses, were often possible during post hoc video review of sociosexual interactions and mating behaviors (Fig. 11.1). All cetaceans analyzed rotated numerous times during sexual interactions, exposing their ventra at the surface (Fig. 11.1). Males were identified in videos of all six species based on observation of their everted penises (Fig. 11.1). It was

Sex identification
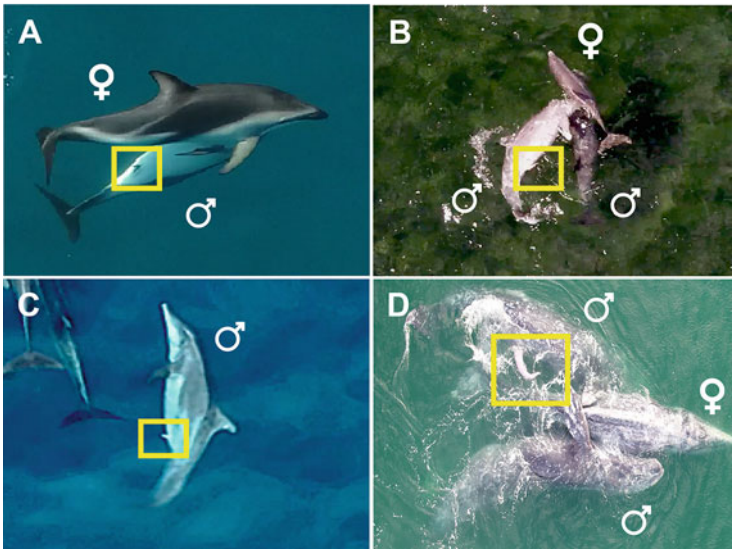
Fig. 11.1 Examples of sex identification of cetaceans from aerial drone observations. The extruded penis of males provides the most reliable indicator of sex in a wild cetacean from aerial drone observations. (**a**) Dusky dolphins (*Lagenorhynchus obscurus*), (**b**) common bottlenose dolphins (*Tursiops truncatus*), (**c**) rough-toothed dolphins (*Steno bredanensis*), (**d**) gray whales (*Eschrichtius robustus*). ♀ = female; ♂ = male

comparatively easy to observe the large penises of large odontocetes and baleen whales (Fig. 11.1d).

Differences in mating behaviors within and across species resulted in varying degrees of visibility of the act of intromission (penile penetration). For instance, intromission was rarely visible in dusky dolphins as females swam ventrum-down and belly-to-belly with a male, thereby obscuring views of copulation from the overhead view of the drone (Fig. 11.1a). In contrast, intromission was sometimes visible for common bottlenose dolphins as males had a perpendicular orientation to a female while thrusting their pelvises toward her genitals (Fig. 11.1b). Males of all species we analyzed approached females with their penises extruded during copulation attempts, sometimes successfully achieving intromission (Fig. 11.2). Successful intromission was not observed in gray whales although it should be overt as mating occurs primarily at the surface and the penis is sizeable and highly visible (Fig. 11.1d). The gray whale penis may be sufficiently large to detect ejaculation from aerial drone footage. Caution may be warranted in determining sex based on behaviors alone during mating interactions since homosexuality is common among cetaceans (Ham et al. 2023, this book; Würsig et al. 2023, this book).
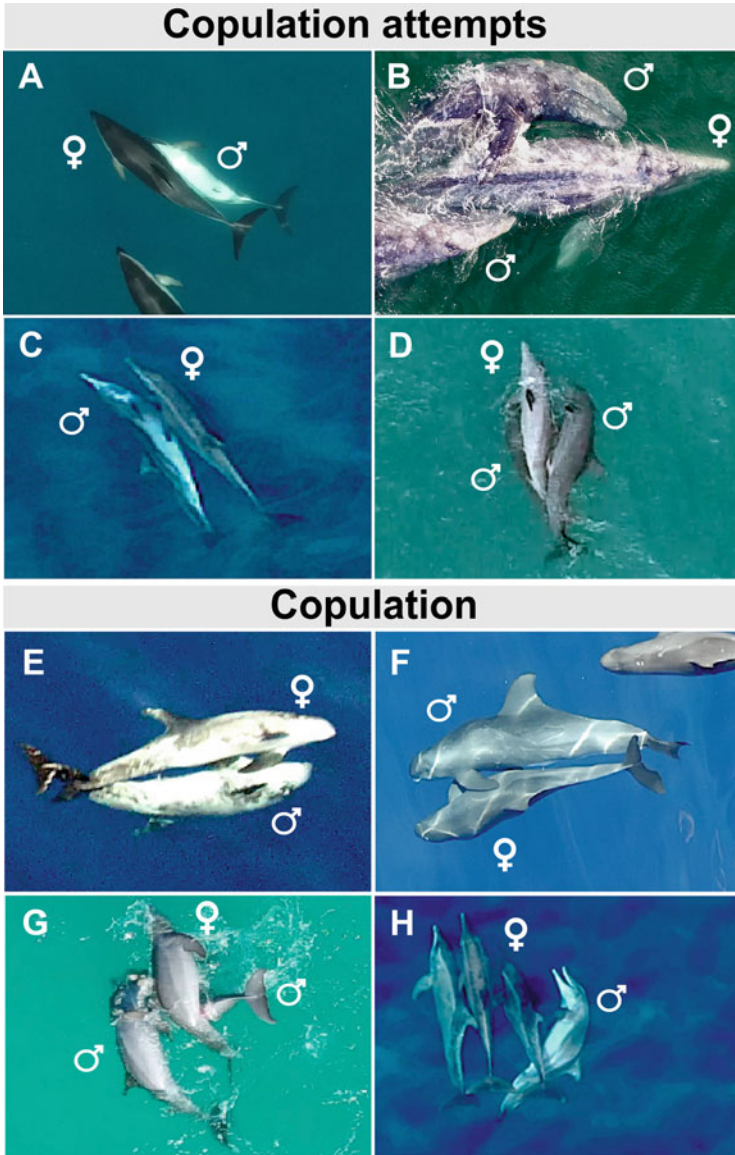
Fig. 11.2 Copulation attempts and copulations involving intromission in six species of cetaceans. Copulation attempts varied across species in orientation, intensity of approach, and receptivity of females. (**a**) Dusky dolphins (*Lagenorhynchus obscurus*), (**b**) gray whales (*Eschrichtius robustus*), (**c**) rough-toothed dolphins (*Steno bredanensis*), (**d**) common bottlenose dolphins (*Tursiops truncatus*), (**e**) Risso's dolphins (*Grampus griseus*), (**f**) pygmy killer whales (*Feresa attenuata*), (**g**) common bottlenose dolphins, (**h**) rough-toothed dolphins. ♀ = female; ♂ = male

11.3.2 Individual Identification

The ability to identify particular individuals during mating encounters can yield insights into sexual selection pressures. For example, certain males may have a particular attribute that is desirable to a female or increases copulation opportunities. Drones offer the potential for photo-identification or tracking of cetaceans that have scarring or unique body markings and features that are discernible from an aerial perspective (Hartman et al. 2020; Ramos et al. 2021). Rough-toothed dolphins, Risso's dolphins, pygmy killer whales, and gray whales had individually identifiable features visible in drone footage that provided the ability to distinguish individuals in mating interactions. For example, we could distinguish which male gray whales pursued females and count the frequency at which a male interrupted a rival's copulation attempt (Fig. 11.3). ImageJ (Abràmoff et al. 2004) was used to alter the color scheme of images to make scars appear prominent, and the measure particle tool was used to extract prominent features (Fig. 11.3c).

We caution that the overhead angle of drones can reduce visualization of certain body features typically used for photo-identification (e.g., perpendicular photographs of dorsal fins, undersides of flukes). However, body scarring can often be used to match individuals to identification photos taken from a boat simultaneous to drone operations. When flown at a steep angle to one side of a group, it may be possible to photograph the dorsal fins of cetaceans with sufficient quality images to match boat-based photo-identification images (e.g., dwarf sperm whales, *Kogia sima*, Baird et al. 2022). While drones are unlikely to serve as an alternative to boat-based photography during behavioral follows, they serve as a complementary tool.

11.3.3 Female Cetacean Mating Tactics

Cetacean mating tactics are diverse and vary between the sexes, ecological conditions, and social contexts (Orbach 2019). The mating strategies and tactics used by female cetaceans to control paternity are not well understood nor known for most species (Boness et al. 2002). Given the energetic costs associated with producing large gametes and investing in parental care (Trivers 1972), females likely play an active role in the selection of mating partners to improve the fitness of their offspring (Orbach 2019). However, male intrasexual competition and sexual coercion can obscure female preferences, leading to the historic belief that females have more passive roles in paternity control than males (Clutton-Brock and McAuliffe 2009). Thus, research has largely focused on understanding the temporal and energetic investments females make in rearing viable offspring (Whitehead and Mann 2000). However, female cetaceans may use several mating tactics to control paternity.

Of the five female mating tactics characterized for cetaceans (i.e., signal discrimination, mate choice copying, evasive behaviors, polyestry/multiple matings,
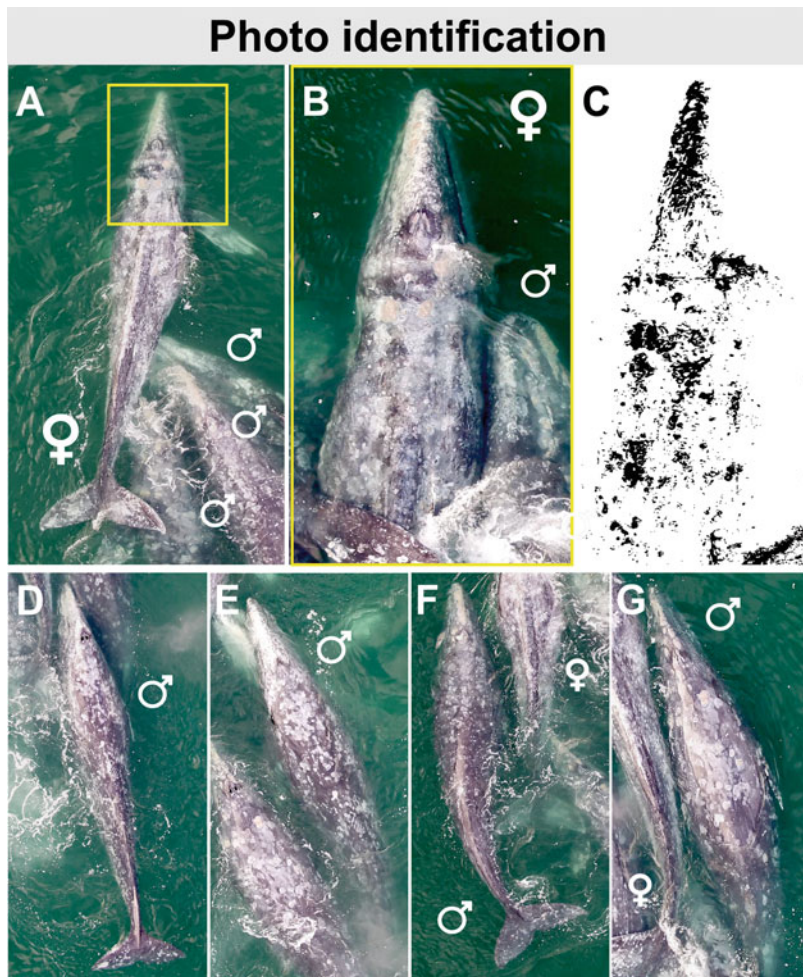
Fig. 11.3 An example of photo-identification of individual female and male gray whales (*Eschrichtius robustus*) during mating behavior in a group of adults observed in San Ignacio Lagoon, Mexico. Whales are covered in markings that enable reidentification of individuals throughout drone-based focal follows and in future sightings. (**a**) A female gray whale as multiple males nuzzle her genitals with their rostrums. (**b**) The head and anterior body of the same female zoomed in (yellow box in A). (**c**) Features extracted from B using the analyze particle feature in ImageJ (Abràmoff et al. 2004) to illustrate some features for use in photo-identification. (**d–g**) Different male gray whales observed in a mating chase in pursuit of a single female. ♀ = female; ♂ = male

modified genitalia; Orbach 2019), we focus on examples of evasive behaviors, signal discrimination, and polyestry/multiple matings because of the possibilities to detect evidence of these tactics using aerial videos collected by small multirotor drones (Table 11.3).

11.3.3.1   Evasive Behaviors

To ensure the reproductive success of their progeny, females assess the quality of potential mates before selecting preferred mates and rejecting undesirable mates. Behavioral studies using drones could identify and quantify female responses to copulation attempts and levels of proceptivity, receptivity, or resistance to males. Thus, drone footage can provide a valuable tool to improve understanding of the complex and nuanced ways in which females express their mate choice. Our data demonstrate that female cetaceans display many short-duration, easily detectable evasive behaviors during mating chases that can be examined in aerial drone video across different species and environmental conditions.

Females may prevent copulations by changing their body position to make their genitalia inaccessible to suitors. Female dusky dolphins repeatedly make deep dives and swim inverted at the surface so that their genital opening is inaccessible to pursuing males (Orbach et al. 2015). Similarly, we observed from drone footage that female bottlenose dolphins frequently rolled while stationary to turn their ventra away from approaching males (Fig. 11.4c). We observed a single female repeatedly roll to her left and right to avoid copulation attempts from three pursuing males (Figs. 11.2d, 11.4c). In contrast, female rough-toothed dolphins sometimes evaded approaching males by rapidly swimming forward.

In most species for which we observed evasive female displays, females also exhibited receptive behaviors to mating attempts. In a group of 12 pygmy killer whales, a single female was not observed actively maneuvering or turning her ventrum to block male access to her genitals (Fig. 11.2f). Similarly, a female rough-toothed dolphin did not resist copulations by multiple males and maintained her swimming speed.

11.3.3.2   Signal Discrimination

Female selection of desired mates involves choices of heritable characteristics that can include access to ample resources, morphological traits, behavioral displays, and overall competitive abilities (Darwin 1871). Signal discrimination of secondary sexual characteristics is a common tactic used by females to choose high quality mates. For example, female dusky dolphins swim ventrum-down, which may regulate copulations by restricting the breathing rate of competing ventrum-up males attempting to copulate (Markowitz et al. 2010; Orbach et al. 2015). These behaviors seem to drive extended mating chases during which females may assess the fitness of potential mates based on their agility and behavior.

Our analysis revealed that several cetacean species display behaviors consistent with female signal discrimination in mating contexts. Dusky dolphins and gray whales engaged in long mating chases, with multiple males pursuing a female that was swimming ventrum-down (Fig. 11.2a, b). During copulation attempts, male dusky dolphins briefly approached females and maintained a ventrum-up posture to
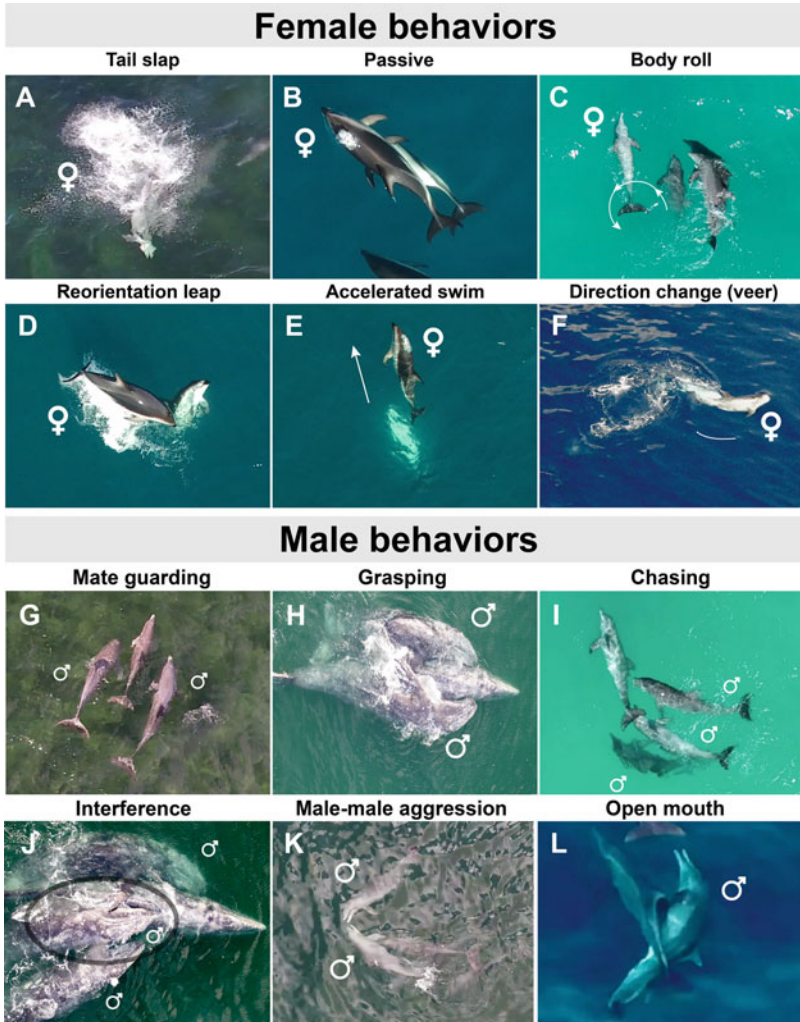
Fig. 11.4 Examples of different mating behaviors of female and male cetaceans identified in aerial drone observations. (**a**) Common bottlenose dolphins (*Tursiops truncatus*), (**b**) dusky dolphins (*Lagenorhynchus obscurus*), (**c**) common bottlenose dolphins, (**d–e**) dusky dolphins, (**f**) Risso's dolphins (*Grampus griseus*), (**g**) common bottlenose dolphins, (**h**) gray whales (*Eschrichtius robustus*), (**i**) common bottlenose dolphins, (**j**) gray whales, (**k**) common bottlenose dolphins, (**l**) rough-toothed dolphins (*Steno bredanensis*). ♀ = female; ♂ = male

align themselves with a female and match her swim speed (Figs. 11.1a, 11.2a). Male dusky dolphins also leaped multiple times while in pursuit of females, which may function as a behavioral display; mating attempts may provide females with opportunities to assess potential suitors' characteristics such as swim speed and body size (Markowitz et al. 2010). Male gray whales also actively competed to be proximate to

the female and copulate, pushing away other males and grasping the female with their flippers (Figs. 11.1a, 11.2b); a female gray whale may evaluate a male's ability to remain proximate to her. In rough-toothed dolphins, food sharing may have played a role in maintaining females nearby during copulation attempts (Ramos et al. 2021).

Alternatively, photogrammetric measurements of the size of individual males may help reveal mate choice driven by body characteristics of different possible mates (e.g., the choice of a large male). We did not consistently collect data on animal size, but future studies using drones equipped with a GPS/LiDAR sensor payload (e.g., Dawson et al. 2017) would enable precise measurements of male and female sizes to associate with behavioral data on individual success at copulation.

11.3.3.3 Polyestry and Multiple Matings

In some species and populations in which male cetaceans coerce females to mate, females may exert control over paternity through polyestrous cycling and multiple mating (Connor et al. 1996). Polyestry is hypothesized to obscure calf paternity, reduce sexual harassment, and prevent infanticide by conspecifics (Hrdy 1979; Connor et al. 1996; McEntee et al. 2023, this book). Repeated estrous cycles, coupled with limited periods of ovulation and mating with multiple males, may aid a female in siring the offspring of a desired mate while obscuring the paternity of her calf. Infanticide (intentional killing of non-descendent young) may induce lactating females to begin estrous cycling and thereby increase the potential for a male to sire an offspring (Hrdy 1979). Multiple species of dolphins commit infanticide (McEntee et al. 2023, this book).

Polyestry is a physiological mechanism and cannot be identified directly from drone observations. However, tracking individuals with drones paired with information on the estrous cycling of specific females could facilitate investigation of cetacean reproduction and heredity. Detailed behavioral observations of cetaceans during mating chases and infanticide attempts could be used to identify evidence of males driving specific non-receptive females into estrus (Table 11.3). Target populations require extensive photo-ID and life history information where observations of female choice of mates could be associated with behavioral data and genetic information on dolphins (Connor 2000).

Multiple matings were readily detectable from aerial drone observations with all species we observed, sometimes involving possible signaling of receptivity to copulation with one or multiple males at a time. In contrast to the ventrum-up orientation of female gray whales typically observed during evasive mating chases (Swartz 2018), the female we observed maintained a ventrum-down position during a mating chase, possibly indicating receptivity to the mating attempts by numerous competing males (Figs. 11.1d, 11.3). Male Risso's and rough-toothed dolphins individually approached females resulting in multiple mating attempts (Fig. 11.5). In Risso's dolphins and dusky dolphins, copulation attempts occur in quick succession with multiple males (Hartman et al. 2023, this book; Markowitz et al. 2023, this
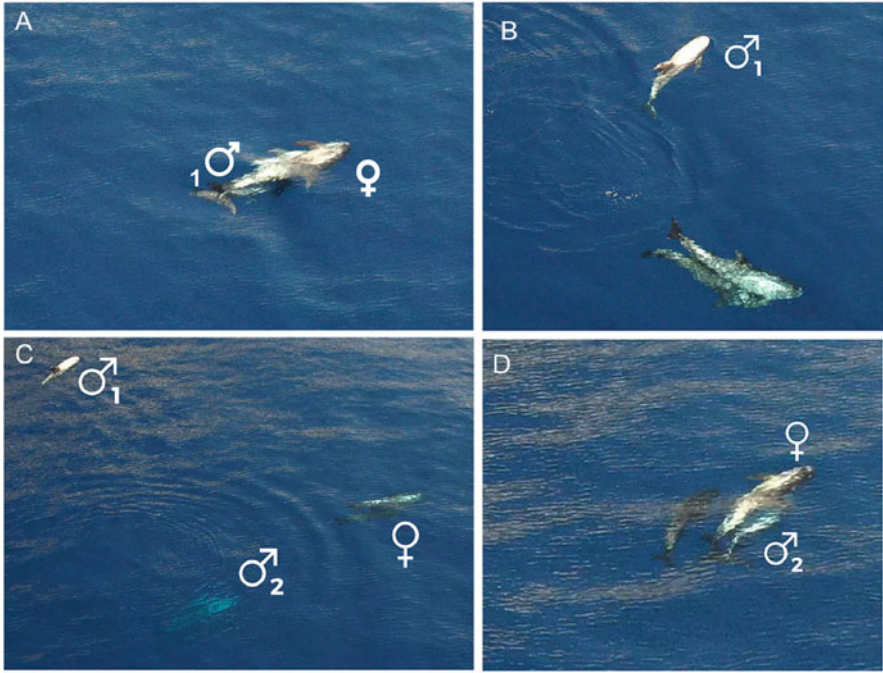
Fig. 11.5 One example from mutual mating in Risso's dolphins (*Grampus griseus*) captured by a drone in 2022 (Mavic Pro 2). (**a**) Copulation between Male 1 and female. (**b**) Male 1 leaves the female and her calf. (**c**) The distance increases between Male 1 and the female with her calf as Male 2 approaches. (**d**) Male 2 in mating position beneath the female with the calf nearby. ♀ = female; ♂ = male

book). Data on the estrous cycling of these species could be associated with drone-based mating observations to disentangle the dynamics of mating.

11.3.4 Male Cetacean Mating Tactics

Male cetaceans primarily use five competitive mating tactics: display, scramble, contest, endurance, and sperm competition. These tactics can be observed visually and are more amenable to drone-based studies compared to the covert tactics used by females (Table 11.3).

11.3.4.1 Display Competition

In display competition, males engage in courtship displays that use morphological or behavioral signals to attract the attention of females. These displays can reflect

dominance, genetic quality, readiness to breed, and access to resources. For example, male humpback whales (*Megaptera novaeangliae*) have elaborate songs, and Amazon river dolphins (*Inia geoffrensis*) carry sticks (Martin et al. 2008; Allen et al. 2018). The improved vantage point provided by drones enables capturing rarely seen displays and allows for detailed tracking of male and female interactions, which is not possible from a boat perspective (Fig. 11.4).

Although we did not observe cetacean males displaying overt behaviors that were interpretable as evidence of display competition, males frequently pursued females with their penises extruded prior to attempting copulation. An everted penis may increase the chances of intromission when near a female and could also serve as a signal to females of readiness to mate (Keener et al. 2018). In gray whales, an extruded penis would likely be visible to females during mating chases and may partially explain why males maintained their erections while swimming in pursuit of females instead of only immediately prior to attempting intromission (Fig. 11.1d).

11.3.4.2 Contest Competition

Contest competition involves one or more males attempting to prevent other males from approaching reproductive females through aggression, sometimes escalating into violent intrasexual interactions (Tyack and Whitehead 1982; Orbach 2019). For some species, detailed and repeated observations of contest competition are available from boat-based studies (e.g., humpback whale competitive groups), as they typically occur near the surface and in clear water (Clapham et al. 1992). Common and Indo-Pacific bottlenose dolphins in many populations display aggression and violent behavior during male-male competition and sexual coercion, typically resulting in dolphins biting each other and leaving extensive tooth rake markings across bodies (Connor et al. 2006). Similar aggressive male-male interactions are reported in Risso's dolphins, including headbutting (Hartman et al. 2023, this book).

Intense competition among males was seen in multiple species we examined based on drone footage. Several male common bottlenose dolphins and Risso's dolphins engaged in aggressive exchanges with each other in the presence of a single female being pursued. Two male bottlenose dolphins in a group of eight engaged in repeated head-on charges, during which both males had their mouths open and attempted to hit each other with their flukes while passing each other (Fig. 11.4k). Multiple competing male gray whales repeatedly interfered with the copulation attempts of other males by using their rostrums to wedge between rivals and the female and pushing the competing male out of the way while occupying its previous position (Fig. 11.4j).

11.3.4.3 Endurance Competition

In endurance competition, multiple males attempt to outlast their competitors for durations long enough to cause major energetic and temporal costs. Male

Indo-Pacific bottlenose dolphins in Shark Bay, Australia, work with alliance members to sequester and isolate the female for up to several months and aggressively copulate with her (Connor et al. 1992). Allied males coordinate to "herd" a female and restrain her movements by producing loud and threatening "pop" sounds (Smolker and Connor 1996) and aggressively charging, biting, and colliding with her. Alliance formation among bottlenose dolphins is reviewed in this book (Brightwell and Gibson 2023, this book) as is endurance competition in Risso's dolphins (Hartman et al. 2023, this book).

We observed common bottlenose dolphins engaged in sociosexual behaviors in small (group size = 3) to large groups (group size = 16); some included male cooperative mate guarding and herding of females and intense aggressive fights between multiple males competing for access to the female (Fig. 11.6). Mating behaviors frequently involved high-energy chases of females and frequent surface displays (Fig. 11.6).

11.3.4.4 Scramble Competition

Scramble competition manifests as males rapidly finding and mating with as many reproductively ready females as possible over a short time. Males fight for the closest position to the reproductively ready female to mate with her, providing her opportunities to exert selection over mates during extended chases (Clapham et al. 1992). During scramble competition, male cetaceans typically engage in energetic chases or surface displays in pursuit of females, changing their swimming speed and direction frequently and incurring energetic costs for both sexes (Orbach et al. 2014). For example, groups of four sexually mature male dusky dolphins typically chased a single female for 10 minutes (Orbach et al. 2015).

In our data, evidence of scramble competition was most salient in mating interactions of dusky dolphins. Dusky dolphin males engage in high-speed chases and rapid copulation attempts with a target female, often including surface-active behaviors and leaps. Male gray whales display numerous behaviors associated with scramble competition. Most baleen whales, including humpback whales and North Atlantic right whales, migrate to breeding grounds annually (Clapham et al. 1992; Kraus and Hatch 2001). Similarly, gray whales are commonly observed in surface-active groups engaging in vigorous sexual activity during their breeding season. Drone footage captured many surface-active groups including multiple gray males simultaneously pursuing a single female (Fig. 11.4h, j). It is unclear from our observations alone if multiple males pursue multiple females over short times in the other four species of cetacean we observed, as most observations involved a single female pursued by multiple males. In Risso's dolphins, scramble competition filmed with a drone showed that not all males participating during a chase were able to mate or obtain access to a female.
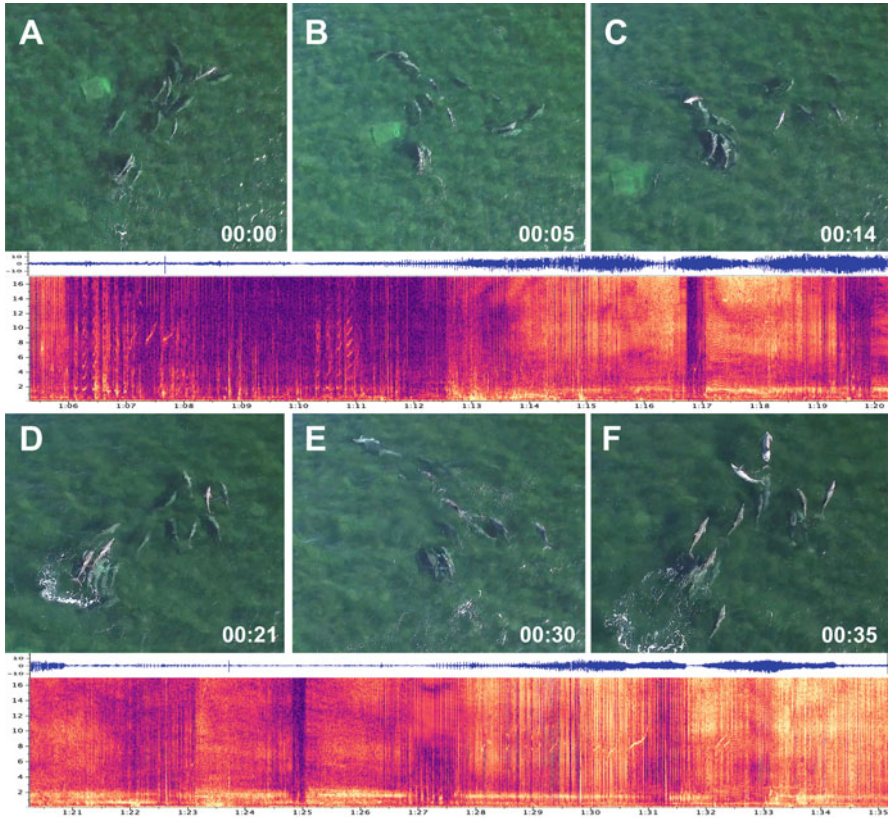
Fig. 11.6 Aerial drone observations of common bottlenose dolphins (*Tursiops truncatus*) engaged in sociosexual behavior during concurrent boat-based acoustic recordings of their sounds. (**a–f**) The interactions involved active chases, surface displays, numerous copulation attempts, and aggressive intrasexual interactions among 16 dolphins. The timestamps are in mm: ss. The waveform and spectrograms below the panels depict the sounds recorded during this 35 second clip, primarily consisting of the vocalizations of dolphins (bright orange). Sounds were graphed using Raven 1.6.3 (K. Lisa Yang Center for Conservation Bioacoustics 2023)

11.4   New Mating Behaviors Documented via Drone

Drones hold immense potential to capture new mating behaviors among cetaceans. Continuous observations of cetacean mating interactions revealed a variety of behaviors that were previously undetected from a boat or any other platform of observation. For example, a rough-toothed dolphin that copulated repeatedly with a female displayed an open mouth behavior, moving its jaw up and down with its mouth agape while aligned perpendicularly with the female (Fig. 11.4l); the open mouth behavior occurred eight times within 12 minutes of video footage during a single focal follow, indicating it may be commonly associated with mating in this

species or population. Open mouth displays may signal threats to the female, as open mouth behaviors have typically been reported during agonistic interactions between conspecifics and heterospecifics in multiple species of cetaceans (Herzing 1996). The use of open mouth behaviors during copulation attempts could signal to the female potential negative consequences of resisting copulation attempts or signal to other nearby males to stay away.

We documented a variety of mating behaviors involving close physical contact between animals at the surface and subsurface. For example, male gray whales regularly used their pectoral flippers to grasp the female across her peduncle, appearing to slow her movement and prevent evasion (Fig. 11.4h). Similar behaviors were observed in multiple bottlenose dolphin males sandwiching a female between them (Figs. 11.1b, 11.4g) and during individual male approaches in pygmy killer whales (Fig. 11.2f). Grasping behavior may function to constrain female evasion, prevent copulations from rival males by limiting access to the female, be part of a male display to the female or other male, or aid in intromission by enabling the male to direct its penis more effectively toward the female's genital slit (Fig. 11.1d). Male cetaceans may orient their bodies in specific positions to align their genitalia with females as physical alignment of genitalia at specific angles is essential for high likelihood of fertilization success (Orbach et al. 2020a).

In gray whales, common bottlenose dolphins, and pygmy killer whales, we observed males repeatedly nuzzling their rostra against the genital region of females and engaging in close physical contact with females; these sociosexual behaviors may play an important role in mating and were detected because of the overhead view from the drone coupled with high-resolution video recording. Clitoral stimulation is likely pleasurable to common bottlenose dolphins (Brennan et al. 2022). Dolphins of other species and populations engage in genital stimulation, sometimes coupled with a buzzing with the melon against the genital area of a conspecific (Herzing 1996). Dolphin echolocation sounds have high energy, which could provide extensive vibration and stimulation of the genitals.

11.5 Understanding Sound Production and Mating Behavior

The sounds produced by cetaceans can play an important role in mating and reproduction, sometimes functioning in sexual displays and competition (Clapham et al. 1992). During cooperative mate herding, pairs of male Indo-Pacific bottlenose dolphins consort females through aggression and produce "pop" vocalizations that threaten her to stay close (Smolker and Connor 1996; Vollmer et al. 2015). Associating specific sounds with behavior and attributing calls to specific individuals are often limited to classifying behaviors of individuals or a group during brief surfacings and comparing these with recorded sounds (Tyack 2000). Drones provide a valuable observational tool to identify behaviors associated with acoustic production

in cetaceans and enhance our ability to contextualize the use of different sounds. Drones used to observe dolphin behavior during acoustic playback experiments have enhanced understandings of social associations of male Indo-Pacific bottlenose dolphins (King and Jensen 2022). Concurrent flights of multiple drones, some equipped with passive acoustic recorders (Frouin-Mouy et al. 2020), are a promising area of future research to associate acoustic sounds with mating specific behaviors.

We demonstrate an example of acoustic recordings of the vocalizations of a group of 16 common bottlenose dolphins with concurrent aerial observations in the lagoons of Turneffe Atoll, Belize, on August 1, 2016. An SQ26-08 (Cetacean Research Technology) hydrophone was suspended 1 m under the water's surface from the boat, recording to a Tascam DR-05 digital recorder with a 96 kHz sample rate in 16-bit to WAV format files. Spectrograms of acoustics recordings were reviewed by EAR in Raven 1.6.3 (K. Lisa Yang Center for Conservation Bioacoustics 2023) to identify and classify dolphin vocalizations as tonal whistles, burst-pulse calls, or echolocation clicks (Tyack 2000).

The bottlenose dolphins engaged in vigorous mating and sociosexual behavior throughout multiple flights (Fig. 11.6). Numerous dolphins pursued a single individual within the group (possibly a female), swimming fast to stay close to each other as the group collectively turned in the same direction (Fig. 11.6a). Half of the group appeared to pursue the single dolphin, while the other half oriented toward the possible mating chase (Fig. 11.6c). The fleeing dolphin leaped several times (Fig. 11.6d) and accelerated to swim ahead of its pursuers close behind (Fig. 11.6e).

We plotted the waveform and spectrogram of a 35 second clip of sounds recorded in the time series of aerial imagery of the dolphin group (Fig. 11.6). Multiple dolphins produced longs bouts of low- and high-frequency burst-pulse signals, repeated bouts of echolocation clicks, and numerous frequency-modulated narrowband whistles (Fig. 11.6). Several low-frequency sounds have been associated with allied male bottlenose dolphin aggression toward females during consortships, such as "pops" (Smolker and Connor 1996; King et al. 2019; Casoli et al. 2022), and with attempted infanticides perpetrated by males (Perrtree et al. 2016).

The above observations illustrate the power of aerial drone video to identify the surface and subsurface activity of cetacean mating groups associated with their sound production. For instance, most of the bottlenose dolphins recorded were completely underwater during our observations and largely out-of-sight to surface observers (Fig. 11.6). Paired subsurface observations and underwater recordings of animal sounds provide a previously unattainable capacity to identify the behavioral context of sound production.

11.6 Conclusions

The improvement of our understanding of the diversity of mating strategies, tactics, and behaviors that evolved across whales, dolphins, and porpoises encourages the development of novel methods to quantify animal behavior in nature. We

demonstrate how drone-based imaging can be applied to the study of sociosexual and mating behavior of free-ranging cetaceans, providing increased observational power in capturing behavior and enabling detailed animal tracking. The inclusion of aerial drones as a data collection tool allows for unparalleled views of animals, their behavior, and collection of robust video and imagery for multiple uses. The use of drones for observing the behavior of cetaceans paired with traditional methods of field data collection and laboratory analyses has the potential to help contextualize the activities of rarely observed species and optimize limited surface times with difficult to study species. Advancements in drone and imaging technologies continue to rapidly improve the flight time and resolution of imagery while decreasing in costs; growing commercial popularity makes drone purchases and use more available to the global community of scientists.

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Chapter 12
Inter- and Intrapopulation Variation in Bottlenose Dolphin Mating Strategies

Kristin Brightwell and Quincy Gibson

Abstract Bottlenose dolphins (*Tursiops* spp.) live in complex societies with high fission-fusion dynamics and exhibit a polygynandrous mating system in which both sexes mate with multiple partners. The benefits of polygynandry vary between the sexes; males likely increase their reproductive success by maximizing the number of mating partners, whereas females may reduce infanticide risk and/or increase the genetic quality of offspring by mating with multiple males. Socio-ecological theory states that mating strategies are dictated by the distribution of females and the ability of males to monopolize them. However, the tactics that males use to achieve reproductive success vary within and across populations. Although some male bottlenose dolphins appear to use a solitary approach to gain mating access, males in several populations demonstrate a relatively rare mating tactic: cooperative mate guarding within alliances. Male alliances generally consist of a pair or trio of males that work together to sequester a fertile female. However, nested or multilevel alliances have been documented in two populations to date (i.e., Shark Bay, Australia, and Jacksonville, Florida). The complexity of male alliances may vary in response to a suite of specific ecological, demographic, and/or morphological variables that promote male-male cooperation and reduce intrasexual competition. In this chapter, we review population-specific examples of male bottlenose dolphin mating tactics and examine several hypotheses that may explain inter- and intrapopulation variation in alliance complexity. We also explore the sociosexual behavior and potential countertactics used by females.

Keywords Bottlenose dolphin · Cooperation · Male alliance · Male-male competition · Mate guarding

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12.1   Introduction

Bottlenose dolphins (*Tursiops* spp.) live in complex societies with high fission-fusion dynamics including fluid changes in group size and composition (Connor et al. 2000b). Within this fluid structure, preferences for same-sex associates are common (Wells 2014; Ermak et al. 2017; Galezo et al. 2018; Ham et al. 2023, this book; but see Lusseau et al. 2003 and Wiszniewski et al. 2010) and likely reflect sex-specific reproductive strategies. Due to long gestation and lactation periods (Whitehead and Mann 2000), individual female bottlenose dolphins are unavailable to breed for several years at a time. The resulting male-biased operational sex ratio can lead to high variation in male reproductive success and intense male-male competition (Connor et al. 2000b; Karniski et al. 2018; Gerber et al. 2022; Würsig et al. 2023, this book). Male mating strategies are then constrained by the ability of males to monopolize either females or the resources that are valuable to them (Emlen and Oring 1977). Dolphins' food resources are often patchily distributed and highly mobile, making territorial defense difficult (Connor et al. 2000b). Females, however, are defensible resources, and mate guarding can be effective at ensuring paternity and increasing reproductive success (Wells 1991; Connor et al. 1992). Although some male bottlenose dolphins appear to use a solitary approach to gain mating access, in several populations, males demonstrate a relatively rare mating tactic – cooperative mate guarding within long-term alliances (Table 12.1). Male alliances generally consist of a pair or trio of males that cooperate to sequester a fertile female (Connor et al. 1992; Owen et al. 2002). While mating can be shared, fertilization is an indivisible resource, making intrasexual reproductive cooperation paradoxical and recurring cooperation among the same individuals uncommon among animals (Díaz-Muñoz et al. 2014). Yet, cooperative mate guarding likely increases male reproductive success as it improves the odds of winning contests against other males and of successfully sequestering fertile females (Connor et al. 1992).

Despite mate guarding attempts by males, bottlenose dolphins have a polygynandrous mating system; both sexes mate with multiple partners in a given breeding season (Connor et al. 1996; Boness et al. 2002). The benefits of polygynandry vary between the sexes; males likely increase their reproductive success by maximizing the number of mating partners (Bateman 1948), whereas females may reduce infanticide risk (Wolff and Macdonald 2004) and/or increase the genetic quality of offspring by mating with multiple males (Stockley 2003). Populations vary with respect to the seasonality of reproduction. Conceptions and births may occur year-round, but diffuse seasonal peaks corresponding with warm water temperatures are common (e.g., Urian et al. 1996; Mann et al. 2000). Mating can occur in a variety of positions, but males mounting along the side (lateral-ventral) or dorsum (dorsoventral) of the female are more commonly documented than ventrum-ventrum (Tavolga and Essapian 1957; Connor et al. 2000b). Mounting and goosing (rostrum to genital area contact) are the most conspicuous sociosexual behaviors, with intromission more difficult to observe and not necessarily indicative of reproduction (Connor et al. 2000b; Connor and Vollmer 2009; Furuichi et al.

Table 12.1 Summary of social structure studies conducted on *Tursiops* spp. that specifically indicated male social complexity. Populations are listed in order of increasing population density; interbirth intervals (IBIs) are provided for additional context

Study site	Male social complexity	Population density (dolphins/km²)	IBIs
Normano-Breton Gulf, France[1]	Probable first-order alliances	0.05[a]	N/A
Cardigan Bay, Wales	No male alliances[2]	0.07[b][3]	3.4[3]
Gulf of Trieste, Slovenia	No male alliances[4]	0.07[c][5]	N/A
Inner Moray Firth, Scotland	No male alliances[6]	0.07[a][7]	3.7[8]
Bahía San Antonio, Argentina	No male alliances[9]	0.09[10]	3.5[10]
Kvarnerić, Croatia[11]	Probable first-order alliances	0.10	N/A
Aeolian Archipelago, Italy	No male alliances[12]	0.12[d][12]	3.5[13]
Sado Estuary, Portugal[14]	No male alliances	0.12	N/A
Gulf of Guayaquil, Ecuador	First-order alliance[15]	El Morro community[b][15]: 0.12 Posorja community[b][15]: 0.49	El Morro community[16]: 2.16 Posorja community[16]: 4.28
Shannon Estuary, Ireland	No male alliances[17]	0.21[d][18]	2.7–3.5[18]
San Luis Pass, Texas	Probable first-order alliances[19]	0.25[20]	N/A
Sardinia[21]	No male alliances	0.28	N/A
Swan Canning Riverpark, Perth, Australia	First-order alliances[22]	0.29[23]	N/A
St. Andrews Bay, Florida	First-order alliances[24]	0.41[25]	N/A
Moreton Bay, Australia	Probable first-order alliances[26]	0.43[27]	N/A
Golfo Dulce, Costa Rica	Probable first-order alliances[28]	0.44[28]	3.4[29]
Abaco[30] and Northern Little Bahama Bank[31] communities, Little Bahama Bank, Bahamas	First-order alliances	East Abaco[32]: 0.60 South Abaco[33]: 1	South Abaco[33]: 3.6
Bay of Islands, New Zealand	No male alliances[34]	< 0.61[35]	4.3[36]
Doubtful Sound, New Zealand	Agonistic coalitions[37]	0.67[38,39]	4.4[40]

(continued)

Table 12.1 (continued)

Study site	Male social complexity	Population density (dolphins/km^2)	IBIs
Sein Island, France[41]	No male alliances	0.93^e	N/A
Cedar Key, Florida[42]	Probable first-order alliances	0.96^f	N/A
Port Stephens, Australia	First-order alliances[43]	0.96^d[44,45]	3–5^g[46]
North Inlet-Winyah Bay, South Carolina[47]	No male alliances	1	N/A
Patos Lagoon Estuary, Brazil	No alliances[82]	1.05[49]	3.0[50]
Indian River Lagoon	First-order alliances[51]	1.15[52]	N/A
Coffin Bay, Australia	Probable first-order alliances[53]	1.16[54] Inner area^c = 1.64	N/A
Sarasota, Florida	First-order alliances[55]	1.28[56]	4–5[57]
St. Johns River, Florida	Second-order alliances[58]	1.65^b[59] 6.76^d[58]	3.03^g[60]
Alvarado, Mexico	First-order alliance[61]	1.75[62]	N/A
Shark Bay, Australia	Third-order alliances[63]	2.67[64]	4.25[65]
Amakusa-Shimoshima Island, Japan[66]	First-order alliances	N/A	N/A

^{a}Calculated from general geographic area of study

^{b}Per linear km

^{c}Average annual density calculated from publication

^{d}Summer abundance

^{e}Calculated using community home range (km^2)

^{f}Average individuals in a year/km^2 calculated from publication

^{g}Unpublished data

[1]Louis et al. (2015) [2]Thomson (2021) [3]Lohrengel et al. (2018) [4]Genov et al. (2019) [5]Genov et al. (2008) [6]Wilson (1995) [7]Cheney et al. (2018b) [8]Arso Civil et al. (2017) [9]Vermeulen (2018) [10]Vermeulen and Bräger (2015) [11]Rako-Gospić et al. (2017) [12]Blasi and Boitani (2014) [13]Blasi et al. (2020) [14]Augusto et al. (2012) [15]Félix et al. (2017) [16]Félix and Burneo (2020) [17]Baker et al. (2020) [18]Baker et al. (2018) [19]Maze-Foley and Würsig (2002) [20]Ronje et al. (2020) [21]Frau et al. (2021) [22]Chabanne et al. (2022) [23]Chabanne et al. (2017) [24]Bouveroux and Mallefet (2010) [25]Bouveroux et al. (2014) [26]Chilvers and Corkeron (2001) [27]Ansmann et al. (2013) [28]Moreno and Acevedo-Gutiérrez (2016) [29]Castro (2021) [30]Parsons et al. (2003) [31]Elliser and Herzing (2011) [32]Fearnbach et al. (2012) [33]Coxon et al. (2022) [34]Mourão (2006) [35]Tezanos-Pinto et al. (2013) [36]Tezanos-Pinto et al. (2015) [37]Lusseau (2007) [38]Lusseau et al. (2003) [39]Currey et al. (2007) [40]Henderson et al. (2014) [41]Louis et al. (2017) [42]Quintana-Rizzo and Wells (2001) [43]Möller et al. (2001) [44]Möller et al. (2002) [45]Wiszniewski et al. (2012a) [46]Möller (2012) [47]Brusa et al. (2016) [48]Genoves et al. (2018) [49]Fruet et al. (2015a) [50]Fruet et al. (2015b) [51]Brightwell et al. (2020) [52]Durden et al. (2021) [53]Diaz-Aguirre et al. (2018) [54]Passadore et al. (2017) [55]Owen et al. (2002) [56]Wells (2014) [57]Wells (2000) [58]Ermak et al. (2017) [59]Mazzoil et al. (2020) [60]Gibson, unpublished data [61]Morteo et al. (2014) [62]Bolaños-Jiménez et al. (2021) [63]Connor et al. (2022) [64]Bejder et al. (2006) [65]Karniski et al. (2018) [66]Nishita et al. (2017).

2014). Nonreproductive sociosexual behaviors also occur throughout the year and may facilitate pleasure, learning, and establishing or mediating relationships (Connor et al. 2000b; Brennan et al. 2022; da Silva and Spinelli 2023, this book; Ham et al. 2023, this book).

Both sexes likely use conditional, rather than fixed, strategies with alternative mating tactics to optimize reproductive success. Conditional mating tactics are shaped by a combination of morphological, demographic, environmental, and social variables (Gross 1996), which vary greatly among populations of *Tursiops* spp. The following sections review population-specific examples of male bottlenose dolphin mating tactics and hypotheses that may explain variation in alliance complexity. The sociosexual behavior and potential countertactics used by females are also reviewed.

12.2   Male Mating Tactics

Male bottlenose dolphins engage in agonistic endurance competitions in which they compete for mating opportunities by roving among females; they either depart soon after mating or follow/herd the female to prevent other males from mating with her (i.e., mate guarding; Wells 1991; Connor et al. 1992). Copulation does not guarantee fertilization nor siring offspring if females have multiple mating partners. The degree of sperm competition in a species is typically correlated with testis size relative to body size and sperm count per ejaculate (Harvey and Harcourt 1984; Connor et al. 2000a). Bottlenose dolphins have relatively small testis mass and a moderate degree of sexual size dimorphism compared to other delphinids (Connor et al. 2000a), suggesting sperm competition may not be important, especially if males mate guard (Perrin and Reilly 1984). Mate guarding duration ranges from a few minutes to several months to competitively exclude rival males from copulation during the female's estrus (Connor et al. 1992, 1996). The predicted number of receptive females and male competitors may influence the length of time males spend guarding individual females (Magnusson and Kasuya 1997). This mate guarding tactic can be temporally costly to males as ensuring paternity with one female may reduce the time available to mate guard others. However, if males do not guard a female for long enough, the likelihood of paternity may be greatly reduced. Connor et al. (1996) observed that females in Shark Bay, Australia, were guarded (and presumably mated) by up to 13 males in a single breeding season. Mate guarding and male-female associations may also be longer than the typical estrus period and/or begin prior to the breeding season as males may be preemptively mate guarding before a female reaches peak attractiveness (Connor et al. 1996; Owen et al. 2002; Robeck et al. 2005).

When cooperatively mate guarding, allied male dolphins frequently travel abreast behind the female or flank her on either side and slightly behind (i.e., a consortship; Fig. 12.1, Connor et al. 1992). Males pursue a female by angling out on either side of her, a feat more difficult to accomplish alone or in deep waters where a female has depth as an escape route (Connor et al. 2000b). The term herding describes

Fig. 12.1 Two adult male first-order allies surfacing synchronously in herding formation behind an adult female and her dependent calf in the St. Johns River, Florida. Photo taken by Q. Gibson under authorization of NOAA Fisheries GA LOC 14157

coercively maintained consortships (Connor et al. 1996). Mate coercion is a common component of polygynandrous mating systems without strong or long-term intersexual bonds (Smuts and Smuts 1993). To constrain a female's movements and prevent extra-pair copulations, males threaten females through posture, vocalizations, and charges or by aggressively biting or colliding into females (Connor et al. 1992, 2000b; Connor and Smolker 1996). Intersexual aggression has also been documented through analysis of conspecific tooth-rake marks. In Shark Bay, cycling females have more new rake marks than non-cycling females (Scott et al. 2005), and younger females may receive more aggression from males than do older females, suggesting male preferences for females with high calving success (Watson 2005; Karniski et al. 2018). There is currently no evidence of forced copulation, as females have been observed rolling away from mounting males; however, males may use intimidation tactics to coerce females into copulating (Connor and Vollmer 2009). In Sarasota, Florida, mate coercion occurs less frequently, and allied and non-allied males increase associations with females in the nonbreeding season compared to the breeding season, suggesting males may attempt to form affiliative relationships to influence future mating success through female choice (Owen et al. 2002).

Intrasexual (male-male) aggression is also evident from tooth-rake marks and opportunistic sightings of violent interactions (Connor et al. 1992, 2000b; Scott et al. 2005; Hamilton et al. 2019). However, the rates and severity of aggression may be underestimated as internal wounds from body slamming may not be externally visible and tooth-rake mark scars typically regain pigmentation within 20 months

(Lockyer and Morris 1990; Ross and Wilson 1996). Several studies have found a significant sex difference in the prevalence of conspecific tooth-rake marks on bottlenose dolphins; more males have rake marks than females (Scott et al. 2005; Marley et al. 2013; Lee et al. 2019). This consistent sex-specific pattern suggests that aggression occurs in the context of male-male competition for access to mates. Patterns of rake mark coverage appear to vary among populations. In Sarasota, there was no observed sex difference in rake mark coverage (Tolley et al. 1995), whereas in Scotland, males had greater rake mark coverage than females (Marley et al. 2013). This sex difference may reflect the lack of male-male cooperation (i.e., alliances) in Scotland, resulting in increased competition and aggression (Marley et al. 2013).

12.2.1 Variation in Male Mating Tactics

Significant variation in male cooperation exists as not all populations of bottlenose dolphins exhibit reproductive cooperation (i.e., no alliances; Wilson 1995; Lusseau et al. 2003), males within a population may utilize different tactics (i.e., solitary vs. allied; Owen et al. 2002; Wiszniewski et al. 2012a), and alliances may be multilevel (i.e., first-order vs. second-order; Ermak et al. 2017; Connor et al. 2022; Table 12.1). Quantitative measures used to identify alliances differ among researchers (Table S1), which likely influences some of this variation. Qualitatively, first-order alliances are consistently defined as enduring relationships among males with repeated instances of cooperation within a reproductive context (i.e., jointly sequestering and coercing reproductive females; de Waal and Harcourt 1992). In contrast to more opportunistic coalitionary relationships, alliance associations occur year-round during all behavioral states, can last over seasons or years, and are more stable than other ephemeral relationships within dolphin societies (Wells et al. 1987; Connor et al. 1992, 1996; van Hooff and van Schaik 1994). This complex behavior is distinct in that individuals exhibit mutual tolerance, cooperation, and partner preferences to reduce intrasexual competition (Díaz-Muñoz et al. 2014). To mediate social bonds and potentially reduce tensions during consortships, allied males regularly engage in synchronous surfacing (Fig. 12.2; Connor et al. 2006), with the degree of synchrony increasing between partners with weaker bonds (McCue et al. 2020).

12.2.1.1 Populations Without Confirmed Male Alliances

To our knowledge, there is currently no published evidence of confirmed male alliances in populations at the northern and southern limits of bottlenose dolphins' range (e.g., Scotland, Wilson 1995; New Zealand, Lusseau et al. 2003). Table 12.1 details populations where male alliances have been noted as absent. In Doubtful Sound, New Zealand, no direct mating competition or mate guarding has been

Fig. 12.2 Two adult male first-order allies surfacing synchronously in the St. Johns River, Florida. Photo taken by Q. Gibson under authorization of NOAA Fisheries GA LOC 14157

observed; Lusseau (2007) hypothesized that mate guarding may be too costly due to both increased female maneuverability in the fjord's depths and difficulties excluding rivals in the large group sizes ($x^- = 17.2$). Male-male aggression, however, is regularly documented; males with higher intrasexual associations were less likely to suffer from aggression (i.e., headbutting) from other males, and they maintained bonds with potential coalition partners through affiliative behavior (i.e., mirroring; Lusseau 2007). While these coalitions function in a non-mate guarding context, coalitions had heterogenous association rates with receptive females and new mothers, suggesting that the maintenance of intrasexual relationships may still be important in this population (Lusseau 2007).

Solitary male mating tactics may not be as conspicuous as the cooperative mate guarding behavior of allied males, so less is known about the variation in solitary tactics across populations (Connor et al. 2000b). It is currently unknown whether individual males consort or attempt to mate guard females, but it is likely that solitary males employ similar tactics to allied males (e.g., roving, mate following/guarding, aggression, and/or displaying to influence female choice). In Sarasota, Florida, "roving" non-allied males have secured paternities, albeit fewer than allied males (Wells 2000; Duffield and Wells 2002; Owen et al. 2002). Stable associations with females may allow a male to be selected as a preferred mate during the breeding season (i.e., female choice; Owen et al. 2002). Although uncommon across populations, preferred male-female associations are a prominent feature of social structures in Ireland (Baker et al. 2020), the Gulf of Trieste, Slovenia (Genov et al. 2019), and Doubtful Sound (Lusseau et al. 2003), where alliance formation has not been documented. Intersex affiliation may play a strong role in determining reproductive success in small populations where alliances are absent and where strong male-female bonds occur (Lusseau et al. 2003; Augusto et al. 2012; Blasi and Boitani 2014; Louis et al. 2017; Baker et al. 2020).

12.2.1.2 Populations with Probable First-Order Male Alliances

Several study sites have indicated probable alliance occurrence based on strong male-male associations but are pending further behavioral analyses or longer study durations to determine the nature of these male bonds (Cedar Key, Florida: Quintana-Rizzo and Wells 2001; Moreton Bay, Australia: Chilvers and Corkeron 2001; San Luis Pass, Texas: Maze-Foley and Würsig 2002; Normano-Breton Gulf, France: Louis et al. 2015; Golfo Dulce, Costa Rica: Moreno and Acevedo-Gutiérrez 2016; Cres-Lošinj archipelago, Croatia: Rako-Gospić et al. 2017). Researchers in Coffin Bay, Australia, identified interconnected male social clusters ranging in size from two to five males resemblant of second-order alliances (Diaz-Aguirre et al. 2018). These preferred associates likely function as alliances, although neither mate guarding nor coercion was documented and male-male aggression appeared to be absent (Diaz-Aguirre et al. 2018). Similarly in Alvarado, Mexico, male dyads and trios had moderate bonds between them; however, researchers noted that detailed behavioral observations to determine the nature of these associations were limited (Morteo et al. 2014).

12.2.1.3 Populations with Confirmed First-Order Male Alliances

The presence and complexity of male alliances vary considerably within and among populations depending on their socio-ecological environments. Males in several nearshore populations cooperatively mate guard through an alliance to decrease intrasexual competition and increase reproductive success (Wells et al. 1987; Connor et al. 1992; Wiszniewski et al. 2012b). To our knowledge, first-order alliances have been reported in Florida (Owen et al. 2002; Bouveroux and Mallet 2010; Ermak et al. 2017; Brightwell et al. 2020), the Bahamas (Parsons et al. 2003; Elliser and Herzing 2011), Ecuador (Félix et al. 2019), Japan (Nishita et al. 2017), and Australia (Smolker et al. 1992; Möller et al. 2001; Chabanne et al. 2022). Table 12.1 provides a list of bottlenose dolphin populations with confirmed alliances.

The size and stability of first-order alliances vary. Across populations, pairs are the most commonly documented alliance size (Owen et al. 2002; Parsons et al. 2003; Elliser and Herzing 2011; Nishita et al. 2017; Félix et al. 2019; Brightwell et al. 2020). In Shark Bay, Australia, trio formation is the preferred alliance size (Connor et al. 1999), but the number of partners participating in a consortship is influenced by the habitat's ecological variation (Connor et al. 2017). Greater intrapopulation variation has been observed in Port Stephens, Australia, and the St. Johns River, Florida, where alliances ranged from pairs to quads, with pairs most common (Wiszniewski et al. 2012a; Ermak et al. 2017; Fig. 12.3). Wiszniewski et al. (2012a) documented considerable variation among Port Stephens alliances that encapsulates the continuum of alliance tactics across populations: males in strong highly stable alliances, males in weaker and more labile alliances, and males that
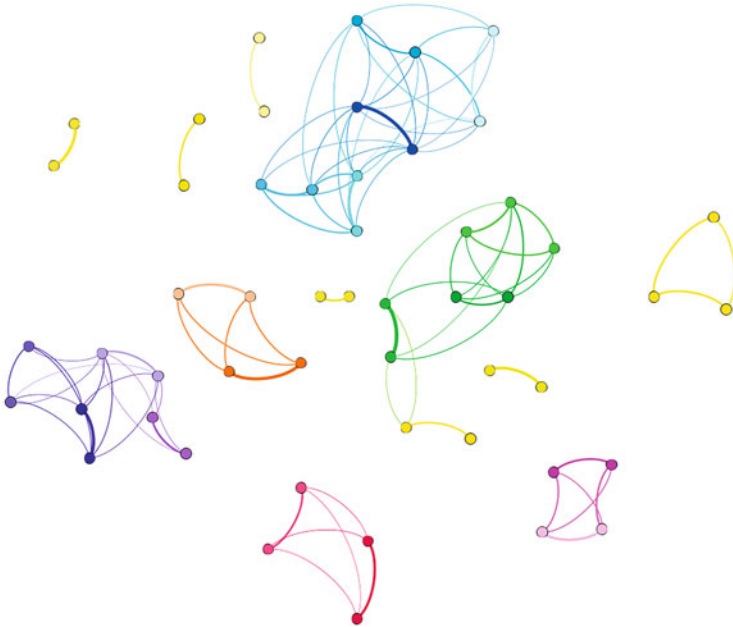
Fig. 12.3 Social network of 23 dyadic and 2 triadic alliances in bottlenose dolphins (*Tursiops truncatus*) in the St. Johns River, Jacksonville, Florida, from April 2011 to March 2018. Edge weights correspond to association strength calculated using the simple ratio index (SRI). Associations less than twice the nonzero male mean (SRI = 0.114) were removed. Node colors denote first-order alliance membership with second-order alliances sharing similar colors: yellows are the 6 dyads and 1 trio that form only first-order alliances; pinks, oranges, and reds are the 6 dyads that only form 1 second-order alliance each; and purples, blues, and greens are the 11 dyads and 1 trio that are part of larger second-order complexes wherein some (but not all) of the first-order alliances form multiple second-order alliances. SRIs were calculated in SOCPROG 2.9 (Whitehead 2009) and nodes arranged using the Force Atlas 2 algorithm in GEPHI (Bastian et al. 2009)

were allied for a short duration. At the longest running behavioral study sites, Sarasota, Florida, and Shark Bay, Australia, researchers have documented alliances ranging in duration from labile (e.g., changing each season or consortship) to stable partnerships lasting decades (Wells 1991; Connor et al. 1999, 2001; Connor and Krützen 2015). Disappearances can cause partner changes on shortened timescales, and males may form new alliances with unallied males whose partners may have also disappeared (Connor et al. 2000b). However, partner switches also occur when a previous alliance partner remains present in the same geographic area, indicating changes in association preferences (Wiszniewski et al. 2012a, Karle 2016; Brightwell et al. 2020).

In populations where alliances have been documented, solitary (unallied) males are also present. The relative percentage of allied vs. unallied males varies; in some populations, solitary males are as prevalent, or more so, than allied males (≥50% unallied males in Little Bahama Bank, Bahamas, Elliser and Herzing 2011; St. Johns

River, Ermak et al. 2017; Indian River Lagoon, Florida, Brightwell et al. 2020). In other populations, most males form alliances (<30% unallied males in Shark Bay, Smolker et al. 1992; Port Stephens, Möller et al. 2001; Sarasota, Owen et al. 2002). It is possible that solitary males are successfully using an alternative mating tactic. For example, Krützen et al. (2004) found that unallied juvenile males sired offspring.

12.2.1.4 Populations with Documented Multilevel Male Alliances

Second-order alliances consist of multiple first-order alliances that cooperate in contests over females (e.g., attempted thefts or defense of females from rival males; Connor et al. 1992). Quantitatively, the social bonds among members of second-order alliances are more moderate in strength than those among first-order alliance partners (Connor et al. 1992, 1999; Ermak et al. 2017; Table S1). This level of male social complexity is extremely rare; multilevel bottlenose dolphin alliances have been documented in only two populations to date: Shark Bay, Australia, and the St. Johns River, Florida. The majority of Shark Bay males are members of second-order alliances ranging in size from 4 to 14 members, with alliance size potentially related to the members' foraging tactics (Connor and Krützen 2015; Bizzozzero et al. 2019; O'Brien et al. 2020). Second-order alliances are believed to be the core male social unit in the Shark Bay population (Connor and Krützen 2015), as males choose their first-order (herding) partner(s) from within their second-order alliances (Connor et al. 2011; King et al. 2021). While the identity of some first-order pairs and trios is stable (i.e., high partner fidelity), many second-order alliances demonstrate much greater flexibility in the formation of pairs and trios (Connor and Krützen 2015). This frequent partner switching is believed to maintain cooperative relationships within a larger group (Connor et al. 1999). Second-order alliances can endure for 20 years, ending due to gradual attrition more often than relationship changes (Connor and Krützen 2015). Surviving members of second-order alliances that have dissolved to the size of a first-order alliance ("lone trios") still form relationships with other alliances, but at the association level of third-order alliances (Connor et al. 2011).

In contrast, second-order alliances do not appear to be the core male social unit in the St. Johns River, as males in this community exhibit a variety of mating tactics. As shown in Fig. 12.3, males may be unallied, form only a first-order alliance, form only one second-order alliance, or form multiple second-order alliances (Ermak et al. 2017). Among allied males, partner fidelity is high with most alliances dissolving due to a partner's death or disappearance (Brightwell and Gibson, unpublished data). However, some alliances have reduced associations despite partners remaining in the area (Karle 2016). Switching herding partners between consortships, as observed in Shark Bay, has not been documented in the St. Johns River. Second-order alliance duration also appears to be more variable within the St. Johns River than in Shark Bay.

A third level of alliance formation, cooperation among multiple second-order alliances, has also been reported (Connor and Krützen 2015). Although the functions

of first- and second-order alliances differ (i.e., consortships vs. female theft/defense), Connor and Krützen (2015) proposed that second- and third-order alliances are functionally similar. Third-order alliances in Shark Bay increased consortship duration by increasing the likelihood that allies were nearby (Connor et al. 2022). While there have been observations of groups containing multiple second-order alliances in the St. Johns River (Fig. 12.3), it is not yet clear if third-order alliances are present.

12.2.2   Cooperation Benefits

Populations with bisexual philopatry (i.e., both sexes remain in the same area postweaning) allow for association and affiliative bonding with kin postweaning (van Hooff and van Schaik 1994; Tsai and Mann 2013; Wells 2014; Wallen et al. 2017). As fertilizations cannot be shared, cooperation among individuals can provide direct (i.e., increased reproductive success) and/or indirect (e.g., kin selection) fitness benefits (Hamilton 1964; Würsig et al. 2023, this book). Although relatedness is not yet documented for many populations, where it has been studied, there does not appear to be a clear pattern across populations. Mean genetic relatedness was higher within than between alliances off Abaco, Bahamas (Parsons et al. 2003). Similarly, in Coffin Bay, Australia, preferential associates were more likely to be related than by chance (i.e., probable alliances; Diaz-Aguirre et al. 2018). In contrast, alliance members in Port Stephens, Australia (Möller et al. 2001), and Sarasota (Duffield and Wells 2002), were primarily unrelated, despite the presence of male relatives in the population. Findings from Shark Bay are mixed; early reports indicated that males in small, stable first- and second-order alliances were more related than those in a large second-order alliance with more labile herding partners (i.e., first-orders within a "super-alliance," Krützen et al. 2003). Recent Shark Bay analyses evaluated individual male relatedness, as opposed to average group relatedness, and found that while kinship explained adolescent associations, similar ages between males were a better predictor of adult associations (Gerber et al. 2021), similar to the patterns observed among allied pairs in Sarasota (Wells 2014).

Alliance partner preferences for close relatives may not be a successful tactic given differences in sexual and social maturity among siblings due to demographic constraints (i.e., single births, extended interbirth intervals), and joint skill may be a more important driver than relatedness in partner selection (Möller 2012; Diaz-Aguirre et al. 2018; Gerber et al. 2021). However, depending on the population, partner choice is likely influenced to varying degrees by a mixture of kin selection and a form of reciprocity or by-product mutualism based on the availability of similar sexually and socially mature individuals (Trivers 1971; West-Eberhard 1975; Díaz-Muñoz et al. 2014). The adaptive benefits of reproductive cooperation, in the shape of increased reproductive success, likely offsets any incurred costs due to sharing copulations with unrelated allies.

Alliance membership is believed to be advantageous to reproductive success in populations that exhibit this male mating tactic. In Sarasota, both solitary and allied

males sired offspring, with allied males siring disproportionately more calves despite appearing to associate equally with females (Wells 2000; Duffield and Wells 2002; Owen et al. 2002). In Shark Bay, non-allied males sired few, if any, offspring (Krützen et al. 2004), as males with more homogenous social bonds with second-order partners obtained the most paternities (Gerber et al. 2022). In Port Stephens, paternities were positively correlated with the number of males in an alliance and evenly distributed among members (Wiszniewski et al. 2012b), yet alliance social bond strengths were not predictors of success. Wiszniewski et al. (2012b) hypothesized that the variance in male reproductive success was attributed to mate guarding within a diffuse breeding season.

While alliances function in a reproductive context, they may also provide additional advantages through protection (e.g., reduced predation risk; Wells 1991; Hill and Lee 1998). Allied males in Sarasota, Florida, had larger home ranges, and although they acquired more shark bite scars, they lived longer than solitary males (Wells 1991). This pattern suggests that alliance partners may provide increased predator detection or enable cooperative defense (Wells 1991). Predation risk can be approximated through documentation of shark bite scars in field observations or through postmortem reports, as relatively few predation attempts have been directly observed by researchers (e.g., Gibson 2006). However, predation risk is likely underestimated in all areas; typically only survivors of predation attempts are observed by researchers in the field, and carcass recovery may not be feasible. Males may also guard a partner during recovery from an injury (Wells 1991). This hypothesis was supported by observations that alliances remained stable after anthropogenic injuries were incurred, with the exception of a male that died post-injury (Greenfield et al. 2021). In contrast, two Gulf of Guayaquil, Ecuador, alliances dissolved during a partner's entanglement in fishing gear, and did not resume alliance status with their original partner after disentanglement (Félix 2021).

12.3 Hypotheses on Differences

We examine several socio-ecological factors that may help explain the variation in male bottlenose dolphin alliance complexity among populations. Encounter rates, in concert with the operational sex ratio and sexual size dimorphism, likely affect a male's choice of mating tactic. In populations with a high rival encounter rate, limited availability of breeding partners, and minimal intersexual size differences, alliance formation should be favored if it leads to increased mating opportunities for allied males that can outcompete lone males or smaller alliances (Whitehead and Connor 2005). In contrast, in populations with low encounter rates, with stable availability of receptive females, and where males are large enough to effectively monopolize a female, alliance formation may not confer any significant reproductive benefits (Connor et al. 2000b; Möller 2012).

12.3.1 Sexual Size Dimorphism

Without a large degree of sexual size dimorphism (SSD), it may be difficult for a lone male to sequester and monopolize a female in a three-dimensional environment. Alliances are likely beneficial in that males can coordinate their spatial positions to effectively restrict female movements, while more robust males may be able to intimidate females on their own and not need assistance in mate guarding (Connor et al. 2000a). Bottlenose dolphin SSD is constrained, particularly with respect to body shape and size variations, possibly due to the energetic costs associated with increasing drag (Connor et al. 2000a). If SSD is present, the most pronounced differences are in robustness and modes of propulsion (males 11–47% heavier than females; Tolley et al. 1995; McFee et al. 2010); however, differences in mass (kg) are less often reported. Population differences in the degree of SSD and alliance formation tend to follow this predicted pattern (Connor et al. 2000a). There is minimal SSD in Shark Bay, Australia (van Aswegen et al. 2019), where multilevel alliances are present; slight-to-moderate SSD in Florida (Tolley et al. 1995; McFee et al. 2010), which has first-order alliances; and more moderate SSD in Scotland (Cheney et al. 2018a) and Brazil (Fruet et al. 2012) where alliances are absent. Although this comparison may be confounded by species-specific (*T. truncatus* vs. *T. aduncus*) differences in morphology, second-order alliances have been documented in both *T. aduncus* (Shark Bay; Connor et al. 1992) and *T. truncatus* (St. Johns River, Florida; Ermak et al. 2017). In the Bahamas, bottlenose dolphins are much larger than the sympatric spotted dolphins (*Stenella frontalis*), and bottlenose dolphin males attempt interspecific matings without the assistance of alliance partners (Elliser and Herzing 2016).

12.3.2 Operational Sex Ratio

Alliance formation would be expected in populations with a strongly male-biased operational sex ratio (OSR) as a tactic to reduce male-male competition (Daly and Wilson 1983; Whitehead and Connor 2005). Although the ratio of reproductively available males to females can be difficult to assess directly, the average interbirth interval (IBI) of females in a population can serve as a proxy for the OSR. Due to long gestation and lactation periods (Mann et al. 2000; Henderson et al. 2014), individual female bottlenose dolphins are unavailable to breed for several years at a time which can influence the degree of male-male competition. Few studies have reported a mean IBl of <3 yr for surviving calves, with most documented IBIs ranging between 3 and 4 years (Table 12.1). Among the populations with mean IBIs >4 yr, which suggests high levels of male-male competition, the full continuum of male social complexity (from no alliances to multilevel alliances) is observed. Thus, a male-biased OSR (and longer IBIs) may be a contributing factor for alliance formation, but it is unlikely to be the primary driver. However, calf mortality rates

should also be considered due to their impacts on IBIs and the OSR (Mann et al. 2000; Karniski et al. 2018).

12.3.3 Encounter Rates

The encounter rate with rival males, which is often estimated using population density (dolphins/km^2; Connor et al. 2000b), likely impacts alliance formation; however, density can vary among and within study sites as it may be influenced by demographics, predation pressure, resource availability, and habitat (Heithaus and Dill 2002; Wiszniewski et al. 2012a; Connor et al. 2017). Theoretically, given a set population density within a community, an increase in daily travel distance could increase the male-male encounter rate with adjacent communities, and a more open habitat would increase the detectability of rivals through better sound propagation (reviewed in Connor et al. 2000b). When the likelihood of encountering potential rivals is high, males may reduce competition and increase reproductive success via cooperative mating tactics (i.e., alliance formation; Connor and Whitehead 2005). The costs of sharing mating opportunities would be lower than the accrued benefits of gaining and maintaining access to fertile females. As population density and thus competition increase, cooperation benefits and alliance sizes should increase as well. However, the spatiotemporal distribution of male-male competition varies; clusters of increased competition may lead to the formation of clusters in the distribution of alliance sizes (e.g., pairs and trios; Whitehead and Connor 2005). An alternative explanation for this potential correlation between population density and alliance formation is that social complexity is easier for researchers to document in populations with high density. Table 12.1 summarizes male alliance complexity with respect to population density across populations.

The two locations with the greatest alliance complexity (i.e., multilevel alliances and multiple/shifting tactics [intrapopulation variation]) also have some of the highest reported population densities (Shark Bay, Australia, Bejder et al. 2006; St. Johns River, Florida, Ermak et al. 2017 and Mazzoil et al. 2020). In Shark Bay, alliance range overlap increases during the breeding season, and consortship size (male pairs vs. trios) and aggression (new tooth-rake marks) increase at the study site's transition from shallow banks to open habitat, suggesting alliance size is being driven by both encounter rate and rival detection (Whitehead and Connor 2005; Connor et al. 2017; Hamilton et al. 2019). St. Johns River dolphins also demonstrate seasonal shifts in habitat use during the breeding season, which coincides with a large influx of transients and seasonal residents whose core areas are concentrated near the mouth of the river (Mazzoil et al. 2020; Szott et al. 2022). Upriver range expansion is limited due to low salinity levels which compacts dolphin density within the river despite seasonal habitat shifts (Ermak et al. 2017; Mazzoil et al. 2020).

Encounter rates in Sarasota, Florida, may be affected by home ranges in a shallow and fragmented habitat, where rival detectability can be restricted. Allied males have

larger ranges compared to unallied males (Wells et al. 1987; Owen et al. 2002), and males occasionally leave the study area for months at a time, thereby increasing their encounters with males in adjacent communities (Wells 1991; Urian et al. 2009). Further, range overlap among communities can increase competition in those areas (Wells et al. 1987). In Port Stephens, Australia, males with more labile alliance partners, larger group sizes, and larger social networks relative to the population's averages concentrated their spatial use close to the entrance of the embayment where they would encounter males from the coastal population (Wiszniewski et al. 2010, 2012a). As with the fluid first-order alliances within Shark Bay's larger second-order alliances, Port Stephens males with a large social network likely have reduced costs of partner switching due to maintenance of social bonds among potential partners (Connor et al. 1999; Whitehead and Connor 2005; Wiszniewski et al. 2012a). In the Gulf of Guayaquil, Ecuador, the two communities with the most survey effort demonstrate a male-biased OSR (3:1 and 2:1; Félix and Burneo 2020) with sightings concentrated at channel mouths (Félix et al. 2017). Alliances with low male-female associations had wider home ranges than the alliance with stronger male-female bonds (Félix et al. 2019), suggesting these males may be forced to rove between communities for mating opportunities.

Bottlenose dolphin alliance formation on the Little Bahama Bank, Bahamas, is likely influenced by both intra- and interspecific encounter rates with the sympatric spotted dolphin (*Stenella frontalis*) population. Cross-species mating and suspected hybridization have been reported in the Bahamas (Herzing et al. 2003; Herzing and Elliser 2013), effectively doubling the population density and increasing male-male competition in this area (average 100 individuals of each species per season; Volker and Herzing 2021). Bottlenose dolphin alliance members are often observed alone during mixed-species encounters (Elliser and Herzing 2016), as their larger size allows them to outcompete the small spotted dolphin males for mating opportunities. Herzing and Johnson (1997) found that it takes six spotted males to chase away one bottlenose dolphin.

In populations with relatively stable population density and low encounter rates, alliance formation is less commonly reported (Table 12.1; Connor and Whitehead 2005). Doubtful Sound, New Zealand, is a small, closed population wherein density remains relatively stable and there is no need to restrict resident females from accessing males from other communities (Lusseau et al. 2003). Moray Firth, Scotland, is also composed of a small population that has increased in abundance from approximately 100 to 200 individuals since the 1980s. Yet dolphins have also expanded their range along the east coast of Scotland (Wilson et al. 2004), keeping encounter rates low.

12.4 Female Mating Tactics

The mating tactics of female bottlenose dolphins have received relatively little research attention compared to those of males; in many cases, female mating tactics can be masked by male-male competition and sexual coercion (Clutton-Brock and McAuliffe 2009), and there are likely more female tactics than are currently reported. The cost of poor mate choice is higher for females than males given the discrepancy in parental investment; female bottlenose dolphins have a yearlong gestation period, produce a single offspring per reproductive event, and exhibit extended interbirth intervals due to long lactation periods (Table 12.1; Whitehead and Mann 2000). Firstborn offspring of young adult females tend to have low survival rates, potentially due to inexperience in parenting, mate choice, or toxic offload (Wells 2000; Schwacke et al. 2002). Calf survival also decreases with maternal age due to reproductive senescence (Karniski et al. 2018). Although physiological factors play a strong role in female reproductive success, social factors such as associations with kin and other females in the same reproductive state can influence fitness as well (Mann et al. 2000; Möller and Harcourt 2008). Mate guarding by males can be costly to females by altering their foraging patterns and energetic budgets due to range and habitat shifts during consortships (Wallen et al. 2016), and it likely also limits their ability to select a preferred mate, at least outside those consorting her. Non-mutually exclusive female countertactics to mate guarding involve polygynandrous mating, preferential association with potential mates, and male avoidance.

Paired with polygynandry, repeated estrus cycles can counteract conception monopolization and reduce harassment, obscure paternity, and improve the genetic quality of offspring (Robeck et al. 2005; Watson 2005; Furuichi et al. 2014). Mate fidelity is uncommon (Duffield and Wells 2002; Wiszniewski et al. 2012b), and the risk of rejecting males can increase harassment, aggression, and injury during herding (Scott et al. 2005; Watson 2005). Mothers with calves may also attempt to avoid adult and juvenile males to reduce the threat of infanticide or aggression; in Shark Bay, sexual segregation is driven by female avoidance of aggressive males (Gibson and Mann 2008; Galezo et al. 2018). Calf-directed aggression and infanticide are favored in species with seasonal breeding, where lactation duration exceeds gestation duration, and year-round intersexual association occurs (Connor et al. 2000a). Males may be less likely to commit infanticide when there is a possibility that calves may be their offspring; thus, it is in a female's best interest to mate with multiple males and not exhibit mate or alliance fidelity (van Schaik and Kappeler 1997; Wiszniewski et al. 2012b; Chap. 11) and in a male's best interest to exert paternity control through mate guarding.

Multiple estrus cycles may enable females to mate with non-preferred males during one cycle and a preferred male during the next (Connor et al. 1996; Robeck et al. 2005). Males may have imperfect fertility detection, as suggested by the finding that male habitat use and ranging patterns shift during consortships, regardless of the female's cycling status (Wallen et al. 2016). Consortships occur year-round, even

though there can be seasonal peaks in reproduction (Connor et al. 1996; Mann et al. 2000; Karle 2016). However, both sexes may use these opportunities to strengthen bonds and utilize countertactics. Males may consort non-cycling females to strengthen male-male bonds and provide consortship practice prior to the mating season; females may be attempting to confuse paternity and/or evaluate males' fitness (Connor et al. 1996; Furuichi et al. 2014). Connor et al. (1996) proposed that females may attempt escapes during consortships to test a male's physical fitness.

Preferentially seeking out or associating with preferred males can facilitate female mate choice (Watson 2005). Females' associations with males were high during breeding seasons in which the female was cycling (Wells et al. 1987; Smolker et al. 1992), and both non-agonistic and preferred female-male associations have been observed (Connor et al. 1996; Owen et al. 2002; Lusseau 2007; Wiszniewski et al. 2010). Sarasota alliances begin associating with females in the middle of the nonbreeding season, potentially to create affiliative relationships to influence female choice (Owen et al. 2002); this is further supported by the relatively low observations of mate coercion in this population (Tolley et al. 1995). Synchronous surfacing and displays by males facilitate social bonding among males (Fig. 12.4) but may also indicate mate quality to females (Connor et al. 2006; Sakai et al. 2010). Australian alliances (i.e., Shark Bay and Swan Canning Riverpark) have been observed conducting displays near female consorts, suggesting females may utilize these displays as a choice criterion among alliance members (Connor et al. 1992, 2000b; Chabanne et al. 2022).

In bisexually philopatric populations, evasion of related males can reduce the cost of inbreeding. Inbreeding can reduce fitness through lower calving success and extended weaning age (Frère et al. 2010). Mating with unrelated males can increase the chances of better genetic compatibility by obtaining genetically diverse sperm (Jennions and Petrie 2000). Shark Bay females almost never associate with their sons while cycling but do preferentially associate with sons compared to non-sons during anestrous periods, suggesting they may be mitigating for inbreeding risk during estrous (Wallen et al. 2017).

When sexual coercion occurs, modified genitalia may provide females with a mechanism for cryptic female choice and the ability to evade fertilization (Eberhard 1996). While ventrum-ventrum mating has been observed (Tavolga and Essapian 1957), males attempting mating alongside females at the surface or by lateral-ventral or dorsoventral mounting may have better fertilization success (Connor et al. 2000b). Optimal copulatory fit corresponds to a dorsoventral positioning, and penile penetration may be curtailed by a vaginal fold (Orbach et al. 2016, 2017); females can subtly shift position and may obstruct a male's fertilization success by redirecting sperm or the penis from non-preferred partners into vaginal recesses.

Fig. 12.4 Three adult dolphins performing a synchronous display in the St. Johns River, Florida; the placement of the pectoral fin on the dorsal body of another dolphin is an indication of bonding. Photo taken by Q. Gibson under authorization of NOAA Fisheries GA LOC 23796

12.5 Conclusions and Future Directions

Within the polygynandrous mating systems of bottlenose dolphins, each sex exhibits conditional mating tactics to optimize sex-specific reproductive success. In estuarine or nearshore coastal populations, males rove between receptive females, solitarily or cooperatively mate guard females, or form preferential intersex bonds (Wilson 1995; Lusseau et al. 2003; Connor and Krützen 2015). Females counteract mate guarding through multi-male mating, evasive behaviors, and preferential intersex bonds (Boness et al. 2002; Galezo et al. 2018; Baker et al. 2020). Less is known about the sexual strategies of offshore dolphins. Offshore studies provide logistical challenges, and larger group sizes can make it difficult to maintain proximity to specific individuals; it is hypothesized that larger groups and deeper depths make it difficult for males to sequester and monopolize a female (Gowans et al. 2008).

Further research on contiguous study sites using similar methodological approaches to each other would be beneficial for modeling predictive parameters of alliance formation, while filling in data gaps on morphological, genetic, demographic, and socio-environmental differences (e.g., SSD, OSR/IBI, population density) would enhance a global comparison. Technological advances can reduce some of these data gaps. For example, laser photogrammetry can be used to assess sexual size dimorphism, and drones can provide greater context during behavioral studies (Cheney et al. 2018a; King et al. 2021). Where possible, focal follows should be conducted on individuals of both sexes to provide a more thorough understanding of

the context in which alliances form and insight into both solitary male and female mating tactics.

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Chapter 13
Sex and Sexual Strategies in Deep-Diving Risso's Dolphins

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Abstract Risso's dolphins (*Grampus griseus*) in the Azores maintain a sexually stratified community with males forming stable clusters, whereas females tend to associate in temporally stable units when calving and nursing. Large relative testes size indicates a mating system based on sperm competition. Small sexual size dimorphism and long interbirth intervals may facilitate male cooperation. We describe mating tactics observed in a resident population of Risso's dolphins based on data collected over 8 consecutive years. We distinguished groups by sex and age class and analyzed peaceful and aggressive behaviors using an ethogram. Males displayed a variety of mating tactics described in cetaceans, spanning display, contest, endurance, and scramble competition, in the assumed context of sperm competition. We observed rare behaviors including male care for neonates but also intense aggression toward newborn calves, leading to possible infanticide. Females' mating tactics included evasive behaviors and signal discrimination. We hypothesize that male mating tactics of Risso's dolphins are related to age class. For females, the polygynandrous mating system may serve to improve fertility, reduce sexual harassment, and reduce the risk of infanticide. Adult females seem to prefer older over younger male groups, suggesting that some level of female mate choice exists in this species.

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13.1   Introduction: Risso's Dolphin Life History and Social Structure

The Risso's dolphin (*Grampus griseus*) is a medium sized (3.6–4 m), deep-diving oceanic delphinid, feeding mainly on mesopelagic cephalopods (Hartman 2018). Both sexes have three to seven oval teeth present in the lower jaw, and their presence may have a specific social function in this species: they leave unpigmented linear scars on the skin, mostly during aggressive intraspecies interactions. This causes, especially in males, the distinctive light or white skin appearance, which may serve as an indicator of male quality (MacLeod 1998). The distinctive scarring marks are also visible on the dorsal fins and provide a unique opportunity for individual identification through standard photo-identification methods (Würsig and Jefferson 1990; Wells 2018). In Risso's dolphins, the changes in skin coloration over time can be used to classify an individual's life history stage, which can be linked to sex, social structure, and specific reproduction stages and strategies (Hartman et al. 2016). Besides having a more scarified skin, adult male Risso's dolphins have more bulbous heads, a more muscular body, and they tend to grow on average 10–15% larger than females. Thus, there is some degree of sexual size dimorphism in this species, impacting Risso's dolphin's social ecology and mating strategies.

Across populations, it appears that Risso's dolphins have medium-to-long interbirth intervals, based on a gestation period of 13–14 months (Amano and Miyazaki 2004; Bloch et al. 2012), followed by a period of up to 4 years of maternal care (Hartman 2018). During a successful nursing period, during which the female is presumably not in estrus, she is not available for reproduction for a period of up to 4–5 years. This contributes to a skewed operational sex ratio, which in combination with the sexual size dimorphism (Cox 2017) may lead to the formation of stable multi-male clusters (Möller 2012). This may be one of the drivers for the formation of stable groups of adult males, with clusters composed of 3–12 individuals of the same age class, reported from one single study site in the Azores (Hartman et al. 2008). In contrast to males, adult females of this population merge seasonally and form temporally stable units when calving and nursing. This particular social structure has been described as a "sexually stratified community" (Hartman et al. 2008, 2014).

Risso's dolphin males display a behavior of "synchronous breathing" in pairs or trios. Synchrony in free-ranging cetaceans is defined as two or more individuals who simultaneously break the surface to breathe, often in close proximity (less than 50 cm) of each other (Sakai et al. 2010). It has been reported for bottlenose dolphins (*Tursiops* spp.) and pilot whales (*Globicephala melas*) (Senigaglia and Whitehead

2012). Among Indo-Pacific bottlenose dolphins (*T. aduncus*), synchronous surfacing by allied males was linked to intense social behavior with female consorts (Connor et al. 2006; McCue et al. 2020). Male Risso's dolphins in the Azores bond with various or fixed "synchrony" partners, indicating a complex intragroup structure (Hartman et al. 2020). In addition, male Risso's dolphins have large testes in relation to body mass, which is a robust indicator of a mating system based on sperm competition (Connor et al. 2000). Stable and highly associated male groups may enhance their chances of having access to females in competition with other groups.

Little is known about social behavior and mating tactics in Risso's dolphins (Bearzi et al. 2011; Visser et al. 2011; Cipriano et al. 2022). There are aggressive inter-animal contacts (Kruse 1989) and potential hybridism between free-ranging Risso's dolphins and bottlenose dolphins (*Tursiops truncatus*) in UK waters (Hodgins et al. 2014). This chapter describes and interprets behavior in the context of mating tactic in one population of free-ranging Risso's dolphins studied off Pico Island, Azores, Atlantic Ocean, for which detailed long-term behavioral data are available.

13.2 Methods

13.2.1 Study Area

The volcanic islands of the Azores archipelago, central North-East Atlantic Ocean, are surrounded by deep waters. There is virtually no continental shelf, as steep submarine walls cause a rapid descent of the ocean floor within 5 km from the shore. This, in combination with the upwelling of nutrient-rich waters, results in high productivity and predictable food resources for marine megafauna (Morton et al. 1998). Over 25 species of cetaceans have been recorded in the Azores, and many species use these waters as breeding, nursing, and feeding grounds (Silva et al. 2014; Cascão et al. 2019). Because of the deep waters nearshore, several deep-diving species such as Risso's dolphins occur relatively close to the coast, creating unique opportunities for in-depth studies.

13.2.2 Data Collection

Data were collected off southeast Pico Island (central group, Azores), covering a survey area of approximately 540 km^2, 2004–2011. Field effort varied from year to year, with most sightings between May and September. Risso's dolphins were first detected from a land-based lookout at 45 m above sea level (38.4078 N, 28.1880 W-covering approximately 370 km^2), at Santa Cruz das Ribeiras, using 20 × 80 binoculars (see Visser et al. (2011) for an overview of land-based methods). Research

vessels (rigid-hull inflatables 4.2–5.2 m long and a 6.7 m fiberglass motorboat) were then directed from land toward dolphin groups.

During surveys, we applied focal group follows (Altmann 1974; Mann 1999) and general individual photo-identification (Würsig and Jefferson 1990; Wells 2018). A group was defined at the start of each survey, applying the 15 m "chain rule" proposed by Smolker et al. (1992), considering social interaction and coordination of activities among individual group members (Whitehead 2003) at the start of each group observation. Two observers estimated group size at sea and refined this estimate after processing photo-identification data. Photographs were matched with the existing catalog, consisting of 1250 unique identifications (Hartman et al. 2008, 2015); new individuals were added to the database. For the present study, only the age class and sex classification per individual were used.

13.2.3   Sex and Age Class Determination

An individual was assumed female if observed on more than two separate days with the same calf. In other cases, sexing was based on photography of the genital area. For male individuals, additional characteristics were used, including long-term absence of calves in stable units, as well as skin coloration (Hartman et al. 2016). For 114 animals, the sex of individuals was later confirmed using molecular genotyping methods (Hartman, in review). For newly observed individuals, often younger animals, it was not always possible to define sex; hence, we classified these animals as "sex unknown."

We assigned age classes per year based on scarification patterns as described in Table 13.1 (after Hartman et al. (2016); Fig. 13.1). Figure 13.2 shows three examples of long-term followed individuals of confirmed sex, displaying the changes and differences in scarification between males and females. In this species, these are important visual clues for the determination of sex and age classes.

For known individuals that we encountered every year, it was possible to assign intermediate age classes. As an example, a male halfway in age class M4 would be

Table 13.1 Skin stages based on scarification patterns, maturity stages, and age classes, after Hartman et al. (2016)

Skin stage	Scarification	Maturity stage		Age class	
		Males	Females	Males	Females
1	Unscratched	Nursing calf[a]		1[a]	
2	Limited	Juvenile[a]		2[a]	
3	Moderate	Subadult		M3	F3
4	Severe	Adult 1		M4	F4
5	Marbled	Adult 2		M5	F5
6	White	Adult 3	–	M6	–

[a]The sex of calves and juveniles is generally unknown, with the exception of a few individuals ($n = 11$; eight males and three females)

Fig. 13.1 Six categories for male and female age class determination based on skin coloration after Hartman et.al (2016): (**a**) calf (1), (**b**) juveniles (2), (**c**) subadult (M3/F3), (**d**) adult-phase 1 (M4/F4), (**e**) adult-phase 2 (M5/F5), and (**f**) adult-phase 3 (M6)

assigned a numerical age class value of 4.5. The numerical age class value assigned to unknown individuals was always "halfway" the age class (e.g., 3.5 for subadults, 4.5 for M4 males, etc.). Females in age class F4 were all assigned the numerical value 4.5, since for females the scarring pattern does not allow a more detailed age classification (Fig. 13.2). We calculated average age classes per group and per year using these numerical values.

13.2.4 Underwater Video Recordings

We used a handheld underwater camera (GoPro 4 and 6) attached to a 1.5 m pole, when the engine was still or at low speed, to record underwater behavior on video.

Fig. 13.2 Life history patterns illustrated by three resident individuals, displaying the changes and differences in the scarification process between males and females, captured over a period of 11–18 years. Left column: the resident female M32a, first observed in 2004 as a subadult of unknown sex, approximately 7–8 years old. In 2009, at the age of 12–13 years, her first (female) calf was born, followed in 2014 by a male calf. Her third calf (unknown sex) was born in 2019, suggesting an interbirth interval of approximately 5 years. Overall, her scarring pattern increased little over time. Center column: M32a_c1, a female who left her mother's side in 2014 at the age of 5. She was seen with her first newborn calf in 2021, when she was 12 years old. In 2022, M32a_c1 was sighted without her calf. Her scarring patterns increased little over time, with large areas of unscarred skin. Right column: M1d_c1, a male born in 2003. At the age of 9 (2012), his skin was already severely scarred

13.2.5 Synchrony

We recorded the occurrence of "synchronous behavior" when two or more individuals swam next (<50 cm) to each other and simultaneously broke the surface for breathing (Sakai et al. 2010; Hartman et al. 2020).

13.2.6 Selection of Groups and Behavioral Data Scoring

Data for this analysis were selected from observations including previously identified male or female clusters (Hartman et al. 2008). We included groups with more than 75% individuals of known sex and more than 75% individuals of known age class. Unknown sex often concerned juveniles and calves, whereas unknown age class concerned infrequently sighted individuals. We considered the following group types: all-female (100% of individuals of known sex were females), all-male (100% males), and mixed-sex groups (containing males and females). Within the mixed-sex groups, we made a further distinction based on the average age class of the males: M3 (the average age class of the males with known age class was subadult), M4

Table 13.2 Overview of group descriptions, according to composition and restrictions of sex and male age class, with indications of individuals' appearance

Composition	Group description	Restrictions	Appearance
All-female	100% females	Females, including their calves	Limited scarification
Mixed male/ female	Subadult males	Average age class of males M3	Limited/moderate scarification
	Adult male stage 1	Average age class of males M4	Severe overlapping scarification
	Adult male stage 2/3[a]	Average age class of males M5/M6[a]	Marbled/white, overlapping scarification
All-male	100% males	Males, all age classes	Limited scarification to white

[a]Groups with average age class M6 were combined with M5, since the number of groups with average age class M6 ($n = 13$) was insufficient to make any statistically significant analysis. References to M5 in this study therefore include individuals from age class M6

(average age class adult-phase 1), and M5 combined (average age class adult stages 2 and 3; Table 13.2).

13.2.7   Ethogram Definitions

We scored specific behavioral states for the selected all-female, all-male, and mixed-sex groups, using an ethogram. "Main" and "secondary" behaviors were determined for the first 20 minutes of each observation, of four behavior types: resting, traveling, socializing, and foraging (Altmann 1974; Shane 1990; Visser et al. 2011; Hartman 2018). "Main behavior" was defined as the behavior observed most frequently during the first 20 minutes of an observation and "secondary behavior" as the second most frequently observed behavior. We focused on socializing behavior. Displays (e.g., aggression) were noted. Observations were classified as "aggressive" in case any aggressive interaction (see below) was recorded over the timespan of the observation or as "peaceful" in all other cases.

For situations in which females associated with males, we considered the following types of groups:

1. Confirmed female(s) swimming synchronized with a male "partner" (paired consortship)
2. Confirmed female(s) swimming freely close to or surrounded by males, <15 m distance (loose consortship)
3. Confirmed female(s) swimming freely with no interaction with males, >15m distance (no consortship)
4. Males present in, or following, a nursery with females and calves (no consortship)

Females meeting the descriptions 1 and 2 were marked as "targets."
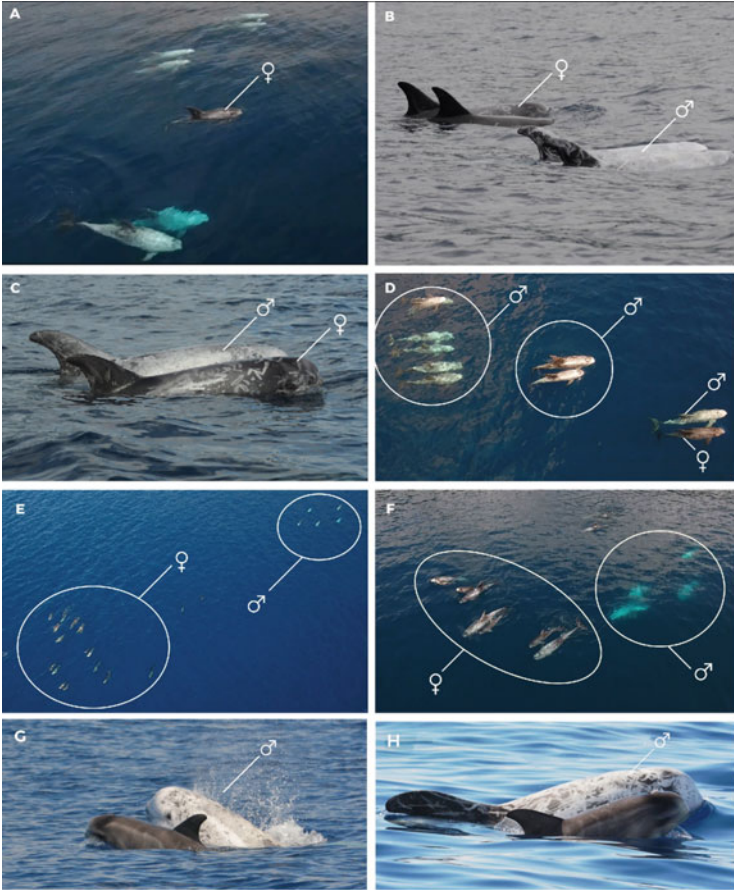
Fig. 13.3 Examples of peaceful male-female association types and exceptional male-neonate behavior: (**a**) a female swimming free (non-escorted) in the center of a male cluster (loose consortship), (**b**) two females swimming synchronously within a male cluster (loose consortship), (**c**) a young female and an adult male swimming synchronously (sync consortship), (**d**) a female and male swimming synchronously in a frontal position in the group (sync consortship), (**e**) a male cluster following a nursery at a distance >15 m (no consortship), (**f**) males mixed in a nursery (no consortship), (**g–h**) an M4 male accompanying a newborn after the mother left her calf when diving, during a mixed-sex group foraging event

Examples of "peaceful" associations are given in Fig. 13.3.

Aggressive behavior was defined as individuals engaging in physical contact and performing combinations of the following displays: handstands, flipper slaps, tail slaps, tail strikes, breaches, frequent opening of mouths, biting, ramming heads (head butting) into one another, and/or chasing one or more individuals. For displays of aggressive behavior, a distinction was made between male-only events and female-directed aggression by males. Aggression directed at females with nursing calves was recorded as a distinct behavior. A specific type of aggressive behavior,
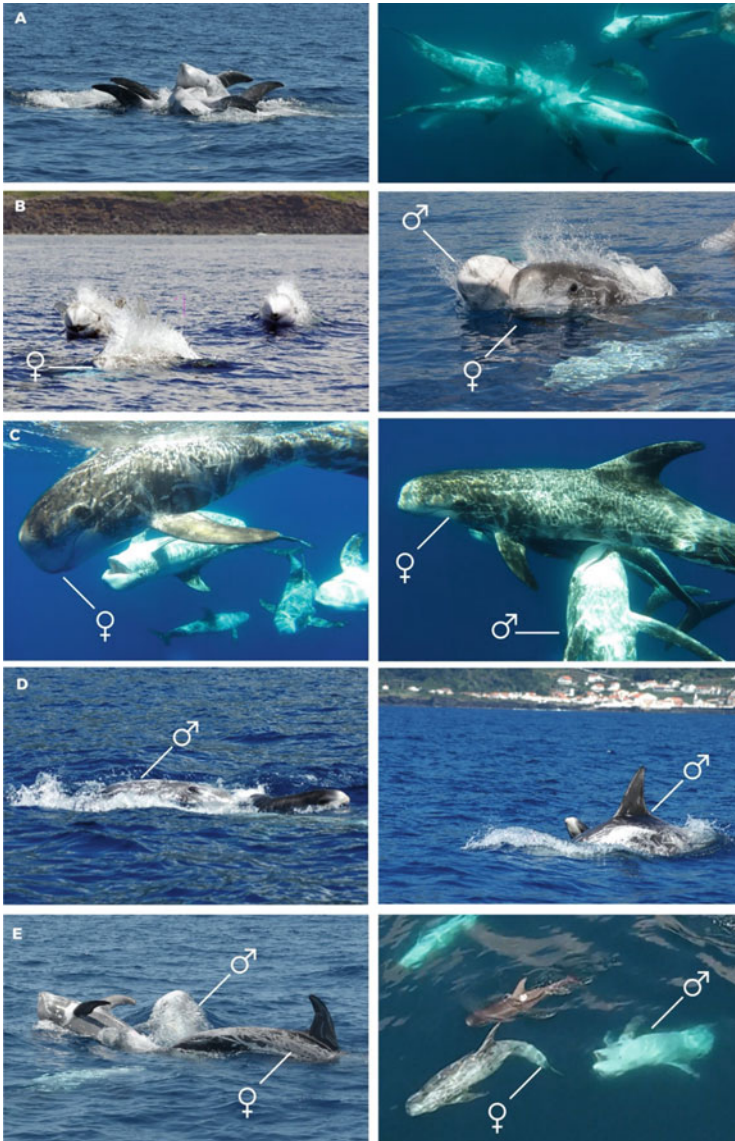
Fig. 13.4 Examples of aggressive behavior: (**a**) male individuals headbutting in "star formation" at the surface and underwater, (**b**) males chasing a female during a bull chase, (**c**) a female being exposed to aggressive behavior such as biting, (**d**) a male chasing a newborn calf, (**e**) males harassing females with older calves

noted as "bull (male) chasing," was defined as male individuals chasing a female at high speed for prolonged periods of time, often including the displays described above and mating events. Examples of aggressive behavior are given in Fig. 13.4. Females who were the object of male aggression were also marked as "targets."

13.2.8 Mating

Mating in aquatic mammals is difficult to observe in the wild. However, based on underwater video footage of copulations with clear intromission, we recognized mating events from the surface by the characteristic belly-to-belly movement and brief "logging" (resting at the surface) by the male after copulation (unpublished data KL Hartman). "Multi-male mating" was recorded when several males mated frequently one after the other with the same female, during one continuous observation (Fig. 13.5).

13.2.9 Data Analysis

For statistical significance (further referred to as "significant"), we applied a p-value <0.05. We calculated average group sizes, numbers of males and females, number of males per female and per target, and number of females in consortships across different male age classes (M3, M4, and M5). For behavioral data, we calculated the percentage of observations during which the behavior was observed, per male
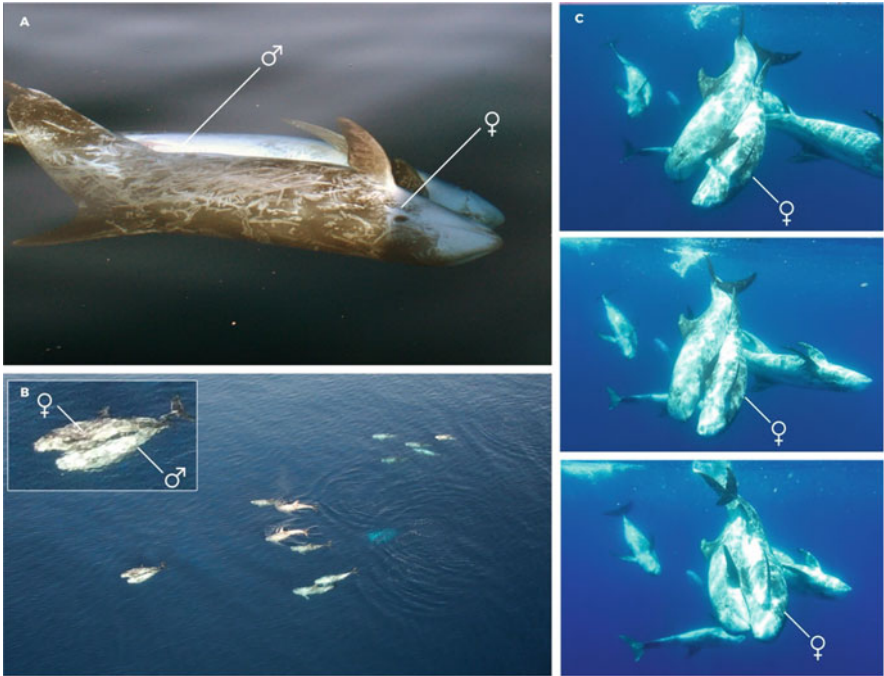
Fig. 13.5 Examples of mating events. (**a**) Mating observed from the surface, (**b**) captured by a drone (outside the duration of this study), and (**c**) captured with an underwater camera

age class. All model calculations were performed using R statistical software (R core team 2022), with two main statistical tests used depending on data to be compared. Behavioral data expressed as percentages were compared using a Bayesian proportions test by means of the *bayes.prop.test* function of the *BayesianFirstAid* package (Bååth 2014). Ninety-five percent confidence intervals (95% CI; presented in square brackets) were given for the estimated differences between groups. Second, for comparisons of count averages (e.g., numbers of males or females per male age class group), sample distribution was described and assessed for count data using the *descdist* function from the *fitdistrplus* package (Delignette-Muller and Dutang 2015) and also visually assessed by means of a histogram and the *fitdist* function. The best fitting distribution (either Poisson or negative binomial) was used to fit a linear model (GLM) by group, and the *Anova* function in the *car* package (Fox and Weisberg 2019) was used to evaluate the deviance of the model residuals. Finally, a post hoc analysis was conducted with the *emmeans* package (Lenth 2023) to estimate marginal means from the linear model and obtain 95% CI of the count averages.

13.3 Results

13.3.1 Survey Effort and Data Collection

For this study, we used data collected between 2004 and 2011 during 925 sea-based surveys in 591 days. We conducted 2367 hours of focal follows of Risso's dolphins, of which 309 hours (first 20 minutes for each selected group) were used for further analysis. We identified 1246 groups, of which 925 met the criteria described in Sect. 13.2.6 (at least 75% individuals of known sex and age class present per group) and were selected for further analysis, comprising 11,789 individuals (including resightings). The average percentage of individuals of unknown sex was 4%; the average percentage of individuals of unknown age class was also 4%. Mean group size was 13.1 dolphins (range, 4–45; SD, 10.1; mode, 9; median, 10.0). The average similarity tests and Bayesian proportion tests of the differences between age classes are presented in Supplementary Material Table 13.1.

13.3.2 Group Types

13.3.2.1 All-Female Groups Including Calves

We observed 91 groups exclusively consisting of females and calves. Average group size was 9.81 individuals, including 5.4 females (55%), 2.6 calves (26%), 1.7 juveniles of unknown sex (18%), and 0.13 subadults of unknown sex (1%).

Table 13.3 Composition and specific behavior of all-female groups. Percentages are calculated against the number of observations

# Observations	91	
# Individuals	893	
Average group size	9.81	
Composition	**#**	**%**
Average # subadult females (F3)	0.57	6%
Average # reproducing females (F4-F5)	4.80	49%
Average # juveniles	1.73	18%
Average # calves	2.58	26%
Average # subadults unknown gender	0.13	1%
Socializing	20	22%

Table 13.4 Composition and specific behaviors of all-male groups, per age class. Percentages are calculated against the number of observations

Group type	M3		M4		M5	
# Observations	95		184		76	
# Individuals	672		1521		608	
Average group size [95% CI]	7.07 [6.07, 8.25]		8.27 [7.42, 9.20]		8.0 [6.76, 9.47]	
Behaviors	**#**	**%**	**#**	**%**	**#**	**%**
Socializing	35	37%	36	20%	11	14%
Male-male aggression	1	1%	4	2%	0	0%

Socializing behavior was recorded during 20 observations (22%); no aggression was observed in all-female groups (Table 13.3).

13.3.2.2 All-Male Groups

We observed 355 groups consisting exclusively of males, of which 95 were subadult (M3) groups, 184 were of stage 1 adult male (M4) groups, and 76 were mature adult male (M5) groups. The average number of males per age class varied from 7.1 (M3) to 8.3 (M4) and 8.0 (M5). No significant differences occurred among age classes. Socializing behavior decreased with age, from 37% of observations in M3 groups, to 20% in M4 groups, and 14% in M5 groups. Estimated group differences among M3 versus both M4 and M5 were significant, whereas the estimated group differences between M4 and M5 were not. Male-male aggression was higher in M4 groups (2% of observations), compared to M3 groups (1%), and M5 groups, where aggression was not observed, but the estimated group differences were not significant among groups (Table 13.4; Supplementary Material Table 13.1).

Table 13.5 Composition, key data, and behaviors of mixed-sex groups, per average male age class

5a Group type	M3		M4		M5	
# Observations	135		225		113	
# Individuals	2031		4352		1578	
Average group size	15.04		19.34		13.96	
5b Composition	#	[95% CI]	#	[95% CI]	#	[95% CI]
Average # males	8.89	[7.72, 10.24]	10.46	[9.40, 11.64]	6.13	[5.20, 7.23]
Average # females	3.23	[2.73, 3.82]	3.87	[3.42, 4.38]	4.50	[3.80, 5.34]
Average # males per female	4.50	[3.67, 5.43]	4.61	[3.97, 5.39]	2.51	[1.99, 3.20]
Average # females in consortship	1.75	[1.04, 2.95]	1.58	[1.22, 2.04]	2.35	[1.73, 3.18]
Average # males per target	7.69	[6.11, 9.58]	8.25	[7.39, 9.16]	4.10	[3.32, 5.05]
Average age class females	F3		F4		F4	
5c Consortships	#	%	#	%	#	%
Consortships	15	11%	62	28%	31	27%
Peaceful	13	10%	43	19%	29	26%
Aggressive	0	0%	17	8%	0	0%
# Targets	25		100		71	
Average # targets	1.92		1.67		2.45	
Average # males per target	4.62		6.27		2.50	
Targets paired with male *	7	28%	51	51%	6	8%
Targets non-paired *	18	72%	49	49%	65	92%
Nursery present	8	6%	61	27%	32	28%
5d Behaviors	#	%	#	%	#	%
Peaceful behavior	126	93%	208	92%	110	97%
Females free, no consortship	113	84%	165	73%	81	72%
Peaceful consortship	13	10%	43	19%	29	26%
Female-directed aggression	9	7%	17	8%	3	3%
Of which bull chase	9	7%	12	5%	3	3%
Socializing	67	50%	104	46%	23	20%
Male-male aggression	4	3%	16	7%	3	3%
*Percentage calculated against # targets						

A target was defined as a consorted female. Unless indicated otherwise, percentages are calculated against the number of observations. Definitions are described under 2.7

13.3.2.3 Mixed-Sex Groups

We observed 473 groups of both males and females. We split these groups according to average male age class, resulting in 135 M3 groups, 225 M4 groups, and 113 M5 groups (Table 13.5a). The average number of male individuals was significantly higher in mixed-sex groups compared to all-male groups, for M3 groups (8.9 vs. 6.4)

and for M4 groups (10.5 vs. 7.9). For M5 groups, however, the average number was lower, though not significantly, in mixed groups (6.1 vs. 7.8). The average number of males per female was significantly similar for M3 and M4 groups (4.50 and 4.61, respectively) but significantly lower (2.51) for M5 groups (Table 13.5b; Supplementary Material Table 13.2).

13.3.3 Peaceful Associations and Consortships

Significantly similar numbers were found for the average number of females in mixed-sex groups for M3 (3.2) and M4 (3.9) and for M4 vs. M5 (4.5), whereas M3 vs. M5 group averages were significantly different. The average number of "targets" (females in consortships) was much lower: 1.8 in M3 groups, 1.6 in M4 groups, and 2.4 in M5 groups (see Fig. 13.4); but the differences between age classes were not significant (Table 13.5b-c; Supplementary Material Table 13.1).

A total of 108 observations were classified as "consortships," involving 196 females. The majority (79%) of consortships were peaceful. The highest percentage of targets paired with a male (sync consortships) was observed in M4 groups (51%), followed by 28% in M3 and 8% in M5 groups. Estimated differences were significant among all age class groups. Non-paired targets (loose consortships) were predominantly observed in M5 groups (92%) but also frequently in M3 (72%) and in 49% of all observations of consortships in M4 groups. The number of males per target ranged from 7.7 in M3 groups to 8.3 in M4 groups (difference not significant) and 4.1 in M5 groups (significantly different from both M3 and M4; Table 13.5c; Supplementary Material Table 13.1). The average age class of males varied according to the composition of mixed-sex groups; when >50% of individuals were male, the average age class of the males was M4, whereas for groups composed of ≥50% females, the average age class of males was M5. M3 groups were present in or following nurseries in 6% of observations, versus 27% and 28%, respectively, for M4 and M5 groups. The estimated group differences between M3 and both M4 and M5 groups showed significantly lower proportions in M3, but no significant differences were found between M4 and M5 groups (Table 13.5c; Supplementary Material Table 13.1).

13.3.4 Socializing and Aggression

Male-male aggression was infrequently observed but higher in mixed-sex groups than in all-male groups. We recorded male-male aggression in 1% of observations in all-male M3 groups and in 3% of observations in mixed-sex M3 groups. For M4 males, the percentages were 2% for all-male groups and 7% for mixed-sex groups and for M5 males, 0% and 3%, respectively (Fig. 13.5a). Only the difference for M4 groups was significant. Similarly, socializing was seen more frequently in mixed-sex

groups than in all-male groups. For M3 groups, the percentages were 50% and 37%, respectively, compared to 46% and 20% for M4 groups and 20% and 14% for M5 groups. Significant estimated differences between mixed-sex and all-male groups were found in M3 and M4 groups, but for M5 groups, the estimated difference was not significant (Table 13.5d; Supplementary Material Table 13.2).

13.3.5   Female-Directed Aggression

Within the mixed-sex groups, we recorded 444 observations of peaceful behavior (no aggression observed; 94% of the observations). Clear aggression by males directed at females was observed on 29 occasions, notably in the M3 (7% of observations) and M4 groups (8%), compared with 3% in M5 groups (Fig. 13.5c +e). The estimated differences between M3, M4, and M5 groups were however not significant. Among the aggressive interactions, we recorded 24 bull chases (Fig. 13.5b). M3 groups were observed chasing a female in 7% of the observations, followed by M4 groups (5%). The lowest percentage was found in M5 groups (3%), but here again, the estimated differences between M3, M4, and M5 groups were not significant (Table 13.5d; Supplementary Material Table 13.1).

Figure 13.6 shows the durations of observed bull chases in relation to group size. Durations of bull chases varied from 8 minutes to 1 hour 11 minutes, with an average of 23 minutes. Male group sizes involved in bull chases varied from 5 to 38 male individuals (mean 13.4, SD 6.5). During all of these events, only one female was chased. The average travel speed ranged between 18 and 32 km/h (boat speed travelling alongside the group taken as a proxy).
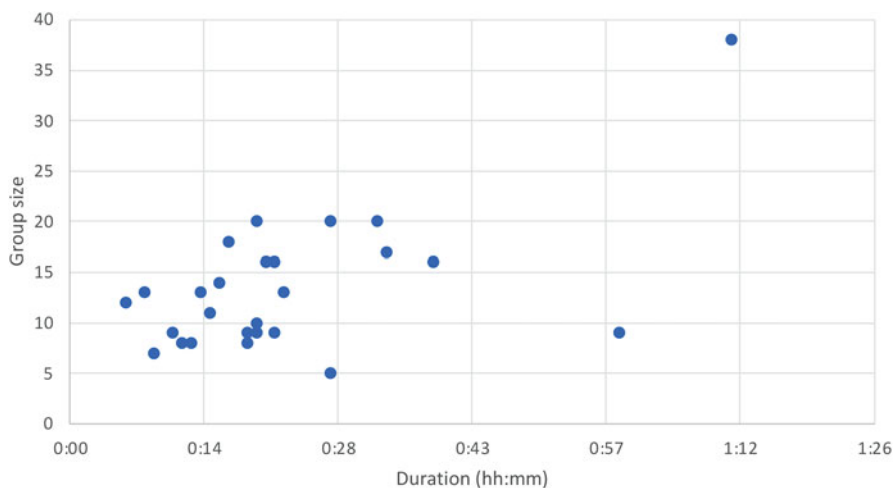
Fig. 13.6 Distribution of the durations of observed bull chases in relation to group size

13.3.6   Mating Events

Male Risso's dolphin chases often led to intense mating sessions, during which the targeted female could be violently pushed and squeezed between males (Fig. 13.4b and c). Mating was also observed in more peaceful settings, usually taking place when a female was consorted by one single male group (in which the female was swimming in synchrony with one male (size, 3–12; Hartman et al. 2008), and no competing male pods were involved or nearby (Fig. 13.5a and b). Copulation was observed during 38% of the bull chases (Fig. 13.5c).

13.3.7   Rare Observations

13.3.7.1   Males Associating Peacefully with Neonates

On four different occasions, we observed four different (confirmed) males (3x M4, 1x M3) associating with four different neonate calves for short periods of time. This behavior only occurred during mixed-sex foraging events. Calves were observed in "calf-position" next to the male, on three occasions within 10 seconds and on one occasion within 16 seconds after the mother had disappeared from the surface to forage. During the interaction, the male was swimming at low speed (less than 2.5 km per hour). The calf was retrieved by the mother after 8–12 minutes, with the male calmly swimming in the vicinity of the group (Fig. 13.3g–h).

13.3.7.2   In-Nursery and Calf-Directed Aggression by Males

We only occasionally ($n = 4$) witnessed males harassing females and calves in nurseries. These events lasted for less than a minute, with females avoiding interactions by performing shallow dives, surfacing after some minutes at 150–300 m from the males.

However, on two occasions, we observed males displaying highly aggressive behavior toward neonates (Fig. 13.4d–e). Confirmed resident males were seen chasing a single neonate at high speed, during which attempts to bite, slap, or jump on top of the neonate were recorded. Some of these displays clearly made it difficult for the neonate to breathe. During 1 occasion (group size, 32 animals), a mother was chased by 6–8 males of the same social male unit, separating the female from her calf and preventing the mother from protecting her offspring. Two older male pods were following but not interfering and seemed occupied with other females. Other nursing females and some subadult units were staying close to the aggressors, without interfering. The male aggression may have led to its death, although we did not observe an actual kill during this occasion. Nevertheless, the neonate was not resighted the following days, and the mother was seen without this

calf on several occasions after the event (and for the rest of the particular season), so we assumed it had died. On another occasion, males chased a female with a neonate without separating them. We observed highly aggressive and coordinated behavior with around five to six males trying to bite, headbutt, and beat both the mother and the calf. Chasing lasted for at least two sessions of 30 minutes during this observation. This group was a nonresident pod including 45–50 individuals, organized in subunits of similar age classes. The mother and calf were not resighted in the following days or years.

13.4 Discussion

13.4.1 Mating Tactics

The social ecology and mating system of Risso's dolphins studied off Pico Island appear to be diverse and complex, considering the range of patterns observed in this dataset. Table 13.6 lists the observed behaviors in this study, distinguishing peaceful and aggressive behaviors in relation to male and female mating tactics observed in mixed-sex groups.

13.4.2 Contest Competition

Although intense male-male aggression was observed on multiple occasions, these only represented a small percentage of all observations: male-male aggression was only recorded in 3% ($n = 28$) of all observations ($n = 834$) of all-male and mixed-sex groups combined. Individuals may avoid intense aggressive events, given the risk of injury and the high energetic costs. In contrast, females never exhibited or initiated aggressive behaviors against other females or during social events involving male individuals. During aggressive events among males, "headbutting" was regularly observed. The fact that within the M4 age class male-male aggression occurred significantly more frequently in mixed-sex groups than in all-male groups suggests that the presence of females increased the competitive pressure. These fights may be related to competition between dominant and competing male pods and individuals (Clutton Brock 2016). Similar contest behavior has been reported in male northern bottlenose whales (*Hyperoodon ampullatus*; Gowans and Rendell 1999).

Subadult (M3) male groups socialized more than males in older age classes, although the difference was only significant with M5 groups. This might be explained by the fluid association patterns of subadults, illustrated by weak to moderate associations between pairs (Hartman et al. 2008). We hypothesize that during the stage when male groups are formed, it may be useful for subadult males to assess relationships with their peers in social events that include fighting. In subsequent life stages, this "testing" of relationships may continue to be a useful tool for

Table 13.6 Ethogram with definitions of peaceful and aggressive behavior states in Risso's dolphins off Pico Island, classified according to mating tactics (after Orbach 2019)

Group composition	Definition	Behavior type	Male mating tactic	Female mating tactic
Peaceful behaviors				
All-male/ all-female	Calm, paired or non-paired, often resting/travelling, few interactions	Calm		
Mixed	General socializing events with frequent semi-peaceful to moderately aggressive interactions	Socializing		
Mixed	Confirmed female(s) swimming synchronized with a male "partner," no aggressive interactions	Consortship (sync)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming synchronized with a female "partner," no aggressive interactions	Consortship (loose)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming freely close to or surrounded by males, <15 m distance	Consortship (loose)	Endurance competition	Mate choice
Mixed	Confirmed female(s) swimming freely with no interaction with males, >15 m distance	No consortship	Endurance competition	Mate choice
Mixed	Males present in, or following, a nursery with females and calves	No consortship	Endurance competition	Mate choice
Mixed	Several males (repeatedly) attempting to mate with the female, who may cooperate or evade	Mating	Sperm competition	Mate choice/ evasive behavior
Mixed	Male individuals taking care of a neonate during mixed foraging events	Neonate care	Endurance competition	Mate choice
Aggressive behaviors				
All-male	General aggressive displays	Aggression	Contest competition	-
All male	Individuals turn backward at the surface and headbutt/bite one another in star formation	Headbutting/ biting	Contest competition	-
All male	Individuals strike tails at one another at the surface	Tail striking	Contest competition	-
Mixed	Males chasing (a) female(s) at high speed (25–32 km/h) for prolonged periods getting access to/isolating/or stealing females from other males	Bull chase	Scramble competition	Signal discrimination
Mixed	Aggressive displays toward female observed (e.g., biting, pushing, tail striking, enclosing, and squeezing)	Female-directed aggression	Scramble competition	Evasive behavior

Table 13.6 (continued)

Group composition	Definition	Behavior type	Male mating tactic	Female mating tactic
Mixed	Males chasing females and calves for short periods, often females with larger calves	Male harassment of nursery	Scramble competition	Signal discrimination/evasive behavior
Mixed	Actual mating	Mating	Sperm competition	Signal discrimination/evasive behavior
Mixed	Males chasing neonates highly aggressively, frequent body contact	Potential infanticide	Contest competition	Signal discrimination/evasive behavior

individuals in assessing the costs and benefits of belonging to a specific cluster, but it seems to reduce with age, as is illustrated by the significant difference in socializing between M4 and M5 groups. Male Risso's dolphins from all age classes engaged in intense fights, displaying aggression toward each other through tail striking, biting, and/or headbutting. Fresh and bloody scars were often visible after these events.

13.4.3 Endurance Competition, Display Competition, and Female Mate Choice

The two types of consortships (synchronized and loose formation) in this study are interpreted as manifestations of endurance competition. This, together with synchronized mixed-sex couples during consortships, has not been described before in this species. During consortships, not all females in mixed-sex groups were consorted; the average number of consorted females was much lower than the average number of females present, across all male age classes. This may be related to the paucity of fertile females as a result of the male-biased operational sex ratio, but it could also reflect the number of males required to control a female. Average number of males per female in consortships varied strongly with male age class, suggesting that factors related to age play a stronger role than the operational sex ratio. The highest number of sync consortships (52%) was observed in M4 male groups, comprising both subadult and adult females. This group type also shows the highest average number of males. The significantly higher level of male-male aggression compared to all-male M4 groups is an indicator of intense competition for access to females. Females may thus be more motivated to escape male aggression, which may require closer control of the females and a higher number of cooperating males to prevent females from escaping or defend against "theft" of these females by competing male

groups. Similar patterns of male aggression toward females during consortships occur in Indo-Pacific bottlenose dolphins (Connor et al. 1992, 1996), where they are also indicated by numerous tooth marks on both sexes (Scott et al. 2005).

In the M3 groups, males and females tended to be subadults. Average number of males was lower than in M4 groups, and even though M3 groups engage significantly more in socializing than the older age classes, they show the lowest (though not significantly lower) percentage of male-male aggression. M3 groups spend more time and energy on socializing. This may explain why the percentage of sync consortships is significantly lower than in M4 groups that appear to be more focused on gaining access to, and guarding, females.

In contrast, M5 groups had the highest percentage of loose consortships and the lowest number of males per consorted female, suggesting a more relaxed group behavior compared to the sync consortships. The lowest number of males per female was observed in these mature male groups. This can be an indication of female (mate) choice, allowing older males to gain access to females in smaller numbers. Earlier theoretical models predicted that female individuals prefer to mate with older males, who would pass on so-called good genes to their offspring through viability selection (Trivers 1972; Kokko and Lindström 1996; Kokko 1998). In contrast, other models predicted the evolution of female preference for young males, since fertility reduces with male age (Beck and Promislow 2007), while yet other studies highlight the importance of other factors than age (Scauzillo and Ferkin 2019; Aich et al. 2020). Our findings suggest that, apart from the possible selection of higher genotypic quality, there could be other reasons why female Risso's dolphins may favor older over younger males. For one, mature males are overall more peaceful, reflected by the lowest percentage in time spent on socializing and on female-directed aggression compared to the younger age classes. Given the risk of injury (also for offspring), and the energetic costs involved, females may prefer to be around nonaggressive older males rather than frisky subadults and M4 males. Besides, the skin coloration of Risso's dolphin males has been suggested to serve as an indicator of male quality (MacLeod, 1998), and a whiter color may also assist to deter conspecific competitors. It is also possible that potential fathers may be present among these M5 groups, who by guarding a group may defend their possible offspring through display competition. Similar patterns of male protection have been suggested in Indo-Pacific bottlenose dolphins (Lusseau 2007). Finally, M5 groups maintain stable associations (Hartman et al. 2008), an indication for successful cooperation among individuals. Overall, the maintenance of social relationships in groups with male mammal individuals is complex given the intragroup rivalry for reproduction (De Waal and Tyack 2009; Clutton Brock 2016). Hence, mature M5 male groups may not only provide a safer environment but also display desirable qualities for viable offspring and therefore be attractive to females.

A remarkable finding in this study is the regular presence of multiple (consorted) females in mixed-sex units of Risso's dolphins. In Indo-Pacific bottlenose dolphins over a 30-year study, only one case was reported of a male trio herding two females simultaneously (Connor and Krützen 2015). The group sizes in Risso's dolphins are greater, with 4.10 (M5 groups) to 8.25 (M4 groups) males per target, compared with

the two or three males in the first order alliances in Indo-Pacific bottlenose dolphins, but the presence of multiple Risso's dolphin females in male groups may also be related to female choice, especially in the older ones. An alternative explanation would be the occurrence of synchronous interbirth cycles, in combination with the temporally stable associations between non-nursing and nursing females (Hartman et al. 2008, 2014; Mann 2019).

13.4.4 Scramble Competition, Signal Discrimination, and Evasive Behavior

Male Risso's dolphin chases, an example of scramble competition, were only occasionally observed (in 4.6% of observations of mixed-sex groups), which is probably due to the high energetic costs for a species that has to save energy for deep foraging dives. It is unknown whether this mating tactic is initiated by males or females. It is plausible that these events were initiated by males (potentially following the escape of a female), since they were generally characterized by aggression toward the female by the male participants. During chases, not all male individuals were "in the frontline," and only a subset of male individuals involved in a chase were close to the female during mating events, indicating that not all males could mate with the female. We observed clear signals of stress and exhaustion in the female target, as well as attempts to avoid mating (evasive behavior). Nevertheless, the phenomenon might also be an instance of the female signaling a discrimination mating tactic, allowing the fittest males to mate (Orbach, 2019), as illustrated by the longest chase observed in this study, involving 38 males. During such long contests, the targeted female stands a good chance to mate and become fertilized by the fittest individual (Markowitz et al. 2010).

During or at the end of such chases, intense multi-male mating sessions often took place once the female was exhausted. In 1 observation in 2017, more than 80 mating events were recorded with an underwater camera involving 10 males and 1 female during 1h 15 min (K.L. Hartman, personal observation). Most of the male group members displayed aggressive behavior toward the female, including biting, tail striking, headbutting, and mating. Between mating sessions, the female tried to escape from the group but during 2 hours of observation did not succeed (Supplementary Material Video).

13.4.5 Mating

Mating occurred among male individuals from competing clusters or from the same cluster, usually in response to a mating event between another male and a female during a consortship. However, these intragroup mating events were often peaceful. Males consecutively mated with the same female one after the other. Figure 1a–b in

Supplementary Materials shows two occasions of intragroup multiple mating events captured.

13.4.6 Male Care of Calves

Our dataset comprised four observations of peaceful interactions between single males and neonates. Like most mammals, long-term parental care in cetaceans is generally provided by females (Whitehead and Mann 2000; Mann 2019). However, a limited number of observations concerning males taking care of calves have been recorded in killer whales (*Orcinus orca*; Bigg et al. 1990), involving care for related calves within a family pod. In bottlenose dolphins, males may escort females with calves to prevent infanticide of their (possible) offspring by outsiders (Lusseau 2007; Brightwell and Gibson 2023, this book; McEntee et al. 2023, this book), whereas in Atlantic spotted dolphins (*Stenella frontalis*), males may be involved with young to teach "desired behavior" (Weinpress and Herzing 2015). Furthermore, in long-finned pilot whales (*Globicephala Melas*), sporadic male care has been suggested to be a by-product of their matrilineal social structure and by another strategy described as "social prestige" (Zahavi 1975, 1995), where males show their mating potential to females through calf care (Augusto et al. 2017).

Risso's dolphins seem to have a polygynandrous mating system, where male care of calves is unlikely to be inspired by paternity, and the observations of several individual males guarding neonates in this study are viewed as extraordinary. This behavior was only observed during mixed-sex foraging behavior, when female Risso's dolphins regularly left their offspring in the care of allied females (and, occasionally, males). One explanation might be that males and females of the same age class had spent the first years of their lives together in a nursery, which may have created a basis for female-male trust in a later stage of their lives. Other explanations include the possibility that the male and female are (half-) siblings or that the male displays a "social" behavior, hoping to improve his chances of mating in the future (Zahavi 1975, 1995; Augusto et al. 2017), a form of endurance competition.

13.4.7 Calf-Directed Aggression

Based on the sexual selection hypothesis, male mammals commit infanticide to enhance their fitness, since after having killed a calf the female stops lactating and may become fertile again, which enhances mating opportunities, and in addition infanticide removes unrelated males from the gene pool (Hrdy 1979). In cetaceans, conspecific infanticide is relatively rare, but it has been described in various dolphin species: common bottlenose dolphins (Patterson et al. 1998; Dunn et al. 2002; Kaplan et al. 2009; Robinson 2014; Perrtree et al. 2016; Díaz López et al. 2018), Indo-Pacific humpback dolphins (*Sousa chinensis*; Zheng et al. 2016), Guiana

dolphins (*Sotalia guianensis*; Nery and Simão 2009), and killer whales (Towers et al. 2018; McEntee et al. 2023, this book).

Overall, calf-directed aggression by male Risso's dolphins has rarely been observed, with only two documented occasions over an extended research period that may have led to infanticide. On both occasions, several males attacked the female and calf, giving the impression of an organized action to eliminate the calf. It is impossible for male Risso's dolphins to be sure of their paternity, but it is plausible that males know whether they have mated with a female or not. Thus, it is possible that calf-directed aggression is initiated by males who have not had the opportunity to mate with the mother. For this reason, female Risso's dolphins may reduce the risk of infanticide by mating with as many males as possible, as has been suggested for Indo-Pacific bottlenose dolphins (Connor et al. 1996).

13.5 Conclusions and Future Directions

Previous studies reported the existence of genetically distinct populations of Risso's dolphins (Gaspari et al. 2007; Chen et al. 2018), highlighting that social ecology may vary between (sub-) populations. This study presents data coming from one field site. Therefore, it is highly recommended to compare present results with data from other populations. For example, the chases observed in the Mediterranean Sea (Cipriano et al. 2022) may be an indication of similar scramble competition tactics in another population. However, at present, there are not sufficient data available from other study sites.

Risso's dolphins observed off Pico Island display a range of mating strategies, influenced by big testes, 4- to 5-year interbirth intervals, and small sexual size dimorphism, which cause a male-biased operational sex ratio. Their pelagic habitat may require a robust number of "allies" to gain and maintain access to females, and this may have contributed to the formation of stable male groups of the same age class and presumably of similar strength. In females, a diet based on deep-sea cephalopods and avoidance of male aggression may have promoted the formation of temporally stable female clusters in the same reproductive stage, a system in which they gain protection for neonates and young calves through babysitting when foraging (Hartman et al. 2014; Hartman 2018).

Mating tactics (and success) seem related to age class, reproductive stage, and possibly the strength of association between individuals. Mating tactics in this study correspond to those of different cetacean species (Orbach 2019; Würsig et al. 2023, this book), ranging from two types of peaceful consortships to aggressive male chases. Mating behavior regularly involved multiple mating sessions where the same female mates with different males. These events could be either aggressive (typically when multiple groups were involved and there was intergroup competition) or peaceful (generally when one social unit was involved and there was only intragroup competition). Rare behaviors included male care for neonates and, in contrast, intense aggression from males toward newborn calves, leading to possible

infanticide. The apparent preference of females for mature over younger male groups, combined with the peaceful character of these interactions, suggests some level of female mate choice.

Present findings invite further research. Long-term association data analyzed at individuals' level may clarify the evolution of male group structures and their drivers. For females, preference for certain males or male clusters may clarify the degree of mating choice. Future studies should include investigation of synchronous mixed-sex couples during consortships, as it seems a striking behavior. Furthermore, studies focusing on the degree of kinship may reveal if kinship is a driver for stable male units and forms a basis for potential matrilineal group formation.

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Chapter 14
Sociosexual Behavior of Nocturnally Foraging Dusky and Spinner Dolphins

Tim M. Markowitz, Wendy J. Markowitz, Bernd Würsig, and Dara N. Orbach

Abstract Dusky and spinner dolphins are small-bodied odontocetes that show variation in socioecology across their range. New Zealand dusky dolphins and Hawaiian spinner dolphins of deep nearshore waters feed nocturnally upon prey species associated with the deep scattering layer, leaving the daytime free for rest and social interaction, often close to shore. In this chapter, we investigate relationships between foraging ecology, diel activity patterns, and sociosexual activities of dusky and spinner dolphins in breeding and nonbreeding contexts. We review similarities and differences between dusky and spinner dolphins related to mating strategies and tactics, socioecology, and evolution. We examine the effects of breeding season and variation in male testis mass and female receptivity on mating behavior. We further explore the influence of sociosexual behavior on female social grouping and calf rearing.

Keywords Dusky dolphin · Female choice · Hawai'i · Male-male competition · Mating behavior · New Zealand · Socioecology · Sociosexual · Spinner dolphin

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14.1 Introduction

Animal ecology profoundly influences social structure and reproduction (Clutton-Brock and Harvey 1977; Emlen and Oring 1977; Trivers 1985; Clutton-Brock 2016). Environmental factors affect animal social grouping patterns and behavior (Vehrencamp 1983; Kappeler and van Schaik 2002). Cetacean social structures have evolved in different ecological circumstances, resulting in intraspecific and intrapopulation variability in response to environmental challenges and opportunities (Bearzi and Stanford 2007). Odontocete mating systems, sexual behavior, and reproductive strategies are often a result of evolutionary history and environmental pressures (Norris and Schilt 1988; Whitehead and Mann 2000; Gowans et al. 2007; Orbach 2019). Spatiotemporal variation in prey availability and/or predation pressure can influence cetacean group size (Wells et al. 1999) as well as social unit size in fission-fusion societies (Dunbar 1992). Norris (1994) described dolphin socioecology in terms of dynamic social and behavioral responses to environmental changes. For dolphins, spatial and temporal predictability of resources and predation pressure are important drivers influencing group size, social structure, and mating interactions (Wells et al. 1999; Gowans et al. 2007; Acevedo-Gutiérrez 2009; Würsig et al. 2023, this book). Socioecological interactions of dolphins occur in three-dimensional space, perhaps with similarities to small primates that live in the three-dimensional rainforest canopy (Würsig and Pearson 2014). Much can be learned about delphinid sociality and evolutionary ecology by comparing behavior and mating systems among species living in similar or different habitats (Würsig and Pearson 2015). Herein, we compare and contrast the sociosexual behavior of spinner dolphins (*Stenella longirostris*) of Hawai'i and dusky dolphins (*Lagenorhynchus obscurus*) of New Zealand.

Despite living in different hemispheres and being connected by only distantly shared ancestry, Hawaiian spinner dolphins and New Zealand dusky dolphins have much in common. Both are small-bodied odontocetes ranging in length from 1.4 m to just over 2 m (Table 14.1), with spinner dolphins slightly larger than dusky dolphins. Dusky dolphins and Hawaiian spinner dolphins show little sexual size dimorphism, with maximum length at maturity varying <5% between the sexes for

Table 14.1 Reproductive life history parameters of spinner and dusky dolphins[a]

Parameter	Hawaiian spinner dolphin	New Zealand dusky dolphin
Gestation length	10.7 months	11.4 months
Lactation duration	15–18 months	18 months
Calving season	Spring-fall	Spring-summer
Age at first reproduction	7 years	7–8 years
Size at birth	0.77 m	0.97–1.02 m
Size of adults	Female, 1.39–2.04 m Male, 1.60–2.08 m	Female, 1.60–1.78 m Male, 1.65–1.86 m

[a]From: Norris and Dohl (1980), Leatherwood and Reeves (1983), Cipriano (1992), Würsig et al. (1997), Jefferson et al. (2015)

Fig. 14.1 A female dusky dolphin (left) engages in a high headfirst reentry leap, followed closely by a male dolphin (right) with penis extended. Dusky dolphins have minimal sexual dimorphism, with the male often leaping second during a chase. (Photo by: B. Würsig)

both species (dusky dolphins 4%, spinner dolphins 2%; Table 14.1). These two dolphin species live in large, fission-fusion societies and demonstrate considerable behavioral flexibility (Lammers 2019; Pearson 2019). They share similar life history traits with respect to reproduction, including age at first reproduction, gestation length, size of newborns relative to adults, and age at weaning (Table 14.1). Both species are also known for their aerial behaviors such as acrobatic head-over-tail leaps in dusky dolphins (Würsig et al. 1994, 1997) and spins along the body axis in spinner dolphins (Norris and Dohl 1980). Backslaps, tail slaps, and nose-out behaviors are also exhibited in small and large groups of dusky and spinner dolphins (Norris and Dohl 1980; Würsig and Würsig 1980; Norris et al. 1994; Markowitz 2004). Headfirst reentry leaps by dusky dolphins are commonly associated with feeding and mating behavior (Markowitz et al. 2004, 2010; Fig. 14.1). Similar arched leaps occur in spinner dolphins (Norris et al. 1994) but are not as commonly described in the context of mating interactions (Norris and Dohl 1980).

Spinner dolphins along the coast of the Big Island of Hawai'i and dusky dolphins along the coast of Kaikoura, New Zealand, are similar in their foraging ecology and diel activity patterns. Both species feed nocturnally upon prey associated with the deep scattering layer in deep nearshore waters, leaving the daytime free for resting, social interactions, and very rare feeding close to shore (Würsig et al. 1994, 1997;

Markowitz 2004). Diurnal use of nearshore habitats by these two populations is particularly conducive to the study of sociosexual interactions, which are readily observed during the daytime, especially during the breeding season. We review research from the past 40 years on the sociosexual behavior of spinner and dusky dolphins, highlighting commonalities and differences within and between the species.

14.2 Mating Systems: Anatomical, Behavioral, and Social Context

Much can be inferred about the mating systems of cetaceans, particularly the degree and form of male-male competition, based on relative testis mass and sexual size dimorphism (Dines et al. 2015). Among spinner dolphins, divergent sexual selection based on differences in mating systems may be an evolutionary force driving population subdivision (e.g., between ecotypes in the Eastern Tropical Pacific; Andrews et al. 2021). Anatomical comparisons based on sexual size dimorphism and testis mass suggest variability in mating systems among different populations of spinner dolphins (Perrin and Mesnick 2003). For example, spinner dolphins of the Eastern Tropical Pacific (presently listed as *Stenella longirostris orientalis* and *S. l. centroamericana*) exhibit sexual dimorphism. Small relative testis mass and sperm content are associated with forward-canted dorsal fins and an enlarged postanal hump, indicating polygynous mating with aggressive male-male behavioral competition (Perrin and Mesnick 2003). In contrast, the Gray's spinner dolphins (*S. l. longirostris*), the most common worldwide form, are characterized by relatively large testis mass (>700 g) and a lack of marked sexual dimorphism. The latter characteristics are indicative of sperm competition and a polygynandrous mating system (multi-mate for both sexes) with less aggressive male-male behavioral competition than those of the Eastern forms. Gray's spinner dolphins include the Hawaiian and whitebelly spinner dolphin. The whitebelly spinner dolphin is an intermediate form between those with less sexual dimorphism and is presently not recognized as a subspecies (Perrin and Mesnick 2003; Lammers 2019). Observations of multiple partners mating in small groups of just a few individuals and in large groups of dozens of individuals appear to support polygynandry in these latter spinner dolphin forms (Norris and Dohl 1980; Norris 1994).

Although dusky dolphins show some variation in body size among populations, they do not display the evident sexual size dimorphism characterizing some spinner dolphin populations. Adult male dusky dolphins have somewhat different dorsal fin morphology than adult females. Male dorsal fins appear larger, thicker, and more curved than female dorsal fins (Van Waerebeek and Würsig 2009). Male dusky dolphins have exceptionally large testes for their body size. The maximum reported testis mass (5120 g) and high ratio of testis-to-body mass (0.085) in sexually mature males are one of the highest of any mammal. The large testis-to-body mass ratio

Fig. 14.2 Dusky dolphins copulating belly-to-belly at the surface, with the male underneath and the female on top. The characteristic "U-shaped" position is held by the female at the surface during copulation (Photos by W.J. Markowitz)

indicates an important role for sperm competition (Cipriano 1992; Van Waerebeek and Read 1994). Although lower than the maximum testis mass of dusky dolphins, the maximum testes mass of Gray's (whitebelly) spinner dolphin (1354 g) also indicates a role for sperm competition (Perrin and Mesnick 2003).

Behavioral field observations of spinner and dusky dolphins indicate that although aggressive interactions occur between males in a mating context, they are relatively rare when compared to other delphinid species; for example, common bottlenose dolphins (*T. truncatus*) routinely engage in physically aggressive contest competition (Johnson and Norris 1994; Markowitz et al. 2010; Markowitz 2012; Orbach 2019). This does not mean, however, that these smaller-bodied, low aggression spinner and dusky dolphins are non-discriminate breeders. Field observations indicate polygynandrous mating systems for Hawaiian spinner and New Zealand dusky dolphins. Mating tactics include postcopulatory sperm competition and precopulatory male-male competition, such as scramble competition (Johnson and Norris 1994; McOmber 1999; Markowitz et al. 2010; Orbach et al. 2015a; Lammers 2019). For example, male dusky dolphins rarely interfere overtly or aggressively with other males copulating with females; however, the copulation rate per male decreases as group size increases, indicating that males are in competition (Orbach et al. 2015b, c).

As with most delphinids and other social mammals, social and sexual behavior occurs in episodes or bouts in spinner and dusky dolphins. Caressing of the pectoral fin, flukes, and full body contact in the mating posture often occur in mixed-sex interactions involving the entire subgroup (Johnson and Norris 1994; Markowitz et al. 2010). Dolphins within these groups are active with frequent ventral flashes toward partners of both sexes, possibly signaling an invitation to join (Norris 1994; Markowitz 2012). Male and female spinner and dusky dolphins can mate with multiple partners within a few minutes (Johnson and Norris 1994; Würsig 1999; Orbach et al. 2015a). Spinner and dusky dolphins mate ventrum-to-ventrum. Male dusky dolphins typically approach and mate ventrum-up from beneath the female (Markowitz et al. 2010; Fig. 14.2). Spinner dolphins show more variation, with

females at times approaching males from below, leading to copulation (Norris and Dohl 1980).

Sexual interactions can be social as well as reproductive and include same sex pairings (Norris and Dohl 1980; Markowitz et al. 2010; Ham et al. 2023, this book). Dusky dolphins sometimes engage in sociosexual interactions with common dolphins (*Delphinus delphis*; Markowitz et al. 2010) in mixed-species assemblages (Cords and Würsig 2014). Apparent hybrids of the two species have been observed in New Zealand (Markowitz 2004) and Peru (Reyes 1996).

14.3 Influence of Habitat Structure on the Social Context of Sexual Interactions

Deep waters not far from shore provide abundant food resources for Hawaiian spinner and New Zealand dusky dolphins, and both species capitalize on this prey availability while also minimizing predation risk. In the evening, dolphins in both populations move offshore into waters ranging in depth from 200 m to >2000 m to feed on prey that become more accessible with the nightly vertical migration of the deep scattering layer (Benoit-Bird and Au 2004, 2009; Benoit-Bird et al. 2004, 2009; Au and Benoit-Bird 2008). During the day, they move inshore to rest, play, and socialize in relatively shallow habitats of <50 m depth that likely provide protection from predators (Norris and Dohl 1980; Markowitz 2004; Thorne et al. 2012). However, they may encounter more frequent anthropogenic disturbances in these areas (Courbis and Timmel 2009; Lundquist et al. 2013; Heenehan et al. 2017; Tyne et al. 2017, 2018). Daytime observations have revealed many similarities in social and sexual behaviors of spinner dolphins in Hawai'i and dusky dolphins in New Zealand waters. These behaviors, including mating, likely help strengthen social bonds in these night-foraging societies with many complex associations (Norris 1994; Würsig and Pearson 2014).

Whether in remote atolls or where islands and atolls are within a few kilometers of each other, spinner dolphins associated with shorelines prefer to rest during daylight in shallow habitats adjacent to deep water (within 1.5–2.5 km) where nocturnal foraging occurs (Norris and Dohl 1980; Norris 1994). Hawaiian spinner dolphins exhibit site fidelity to island coastlines where they rest during the day; however, they frequently reassociate in small groups and in different bays from one day to the next, resulting in shifting fission-fusion associations within and among days (Lammers 2019). Active leaping, surface behaviors, and sociosexual behaviors are most common in the early morning while dolphins begin to move toward the coast from offshore feeding grounds. The transition to full rest once dolphins enter shallow bays can take as long as 2 hours, with groups predominantly resting at around midday (Johnson and Norris 1994). Social and other active behaviors then decrease as tight-knit groups rest close to shore with little sociosexual activity (Norris 1994). Spinner dolphins spend at least 30% of their time in caressing bouts

in the morning and afternoon, but do not engage in caressing or sexual behavior while resting during midday in shallow sandy areas of the bay (Johnson and Norris 1994). Coming out of rest in the afternoon, spinner dolphins become more active, "zig and zag," and begin to associate sexually, with mating occurring in groups of one dozen or more individuals (Johnson and Norris 1994; Würsig et al. 1994). Spinner dolphin sociosexual behavior increases as they become active in preparation for moving offshore for nighttime foraging, with most sociosexual activity occurring in deep water or bay entrances in the afternoon or evening (Norris and Dohl 1980; Norris 1994).

Spinner dolphins in the main Hawaiian Islands show strong site fidelity, a fission-fusion society, and genetic differentiation among some islands (Andrews et al. 2010). In more remote atolls, such as Midway Atoll and other locations in the Northwestern Hawai'i Archipelago (100+ km apart), spinner dolphins do not show the same daily fluid fission-fusion social structure (Karczmarski et al. 2005). Site fidelity for spinner dolphins in remote atolls is very high, and competition for atolls can be intense. This difference in social structure and habitat use is likely related to habitat structure. Remote atolls likely do not provide opportunities for large scale day-to-day fission-fusion associations since there is only one resting place available (Karczmarski et al. 2005; Gowans et al. 2007).

Like Hawaiian spinner dolphins, dusky dolphins live in a fission-fusion society (Markowitz 2004; Pearson 2009; Orbach et al. 2018). In contrast to spinner dolphins, New Zealand dusky dolphins move large distances seasonally (Markowitz et al. 2004). Despite differences in seasonal residency and habitat use, New Zealand dusky dolphins show no sign of population subdivision (Harlin et al. 2003). In the deep waters of the Kaikoura Canyon, dusky dolphins feed at night on prey associated with the deep scattering layer (Würsig et al. 1997; Dahood and Benoit-Bird 2010). Although dusky dolphins are present in the Kaikoura Canyon year-round, photo-identification records indicate individual dolphins remain in the area seasonally, with different assemblages of individuals in summer and winter seasons. Winter movements take some dolphins to other shallow water habitats in the Marlborough Sounds where they feed diurnally in coordinated groups on schooling fishes (Markowitz et al. 2004), similar to daytime foraging by dusky dolphins in shallow waters off Argentina (Würsig 1975, 1989; Würsig and Würsig 1980; Degrati et al. 2019). The shallow bays of the Marlborough Sounds provide a winter habitat for primarily male dusky dolphins, with some nonbreeding sociosexual behavior observed between bouts of daytime feeding (Markowitz et al. 2010).

14.4 Breeding Seasonality, Circadian Rhythm, and Reproductive Physiology

Among marine mammals, female delphinids generally have relatively long seasons of receptivity, averaging 4 months (Boness et al. 2002; Boness 2009). Spinner and dusky dolphins are seasonal breeders with female receptivity, male testis mass and

testosterone levels, and conception peaking in the summer-autumn season (Cipriano 1992; Van Waerebeek and Read 1994; Perrin and Mesnick 2003; Perrin 2009; Markowitz et al. 2010; Table 14.1). Like other dolphins (e.g., bottlenose dolphins, Schroeder 1990), female spinner and dusky dolphins are seasonally polyestrous (Cipriano 1992; Van Waerebeek and Read 1994; Wells and Norris 1994). Seasonal polyestry may be an adaptive strategy to guarantee conception (McEntee et al. 2023, this book). Seasonal breeding is timed such that calves are born, following just under 1 year of gestation, at a time when sea surface temperatures rise in spring and summer, reducing thermal demands on small neonates (Weir et al. 2010).

While sociosexual activity occurs year-round in spinner and dusky dolphins, it is most pronounced during the breeding season, coinciding with peak testosterone levels in males and receptivity in females (Johnson and Norris 1994; Markowitz et al. 2010). In a breeding context apparently tied to seasonal changes in hormone profiles, increased sexual activity coincides with spinner and dusky dolphins gathering in small, tight-knit, highly active mating groups (Johnson and Norris 1994; Markowitz et al. 2010; Markowitz 2012). A captive study of Hawaiian spinner dolphin behavioral endocrinology found that genital-to-genital contact occurred only between male and female spinner dolphins when male testosterone levels were high; mutual ventral presentations were correlated with both male testosterone levels and female estradiol levels (Wells and Norris 1994). Male New Zealand dusky dolphins show large seasonal variation in testis mass, peaking at >3 kg in the spring and remaining high in summer through autumn (Cipriano 1992). Sociosexual activity is relatively uncommon during the winter in both the deep-water habitat off Kaikoura where dolphins feed primarily at night and in the shallow habitat of the Marlborough Sounds where they feed during the day (Markowitz et al. 2010; Markowitz 2012). Thus, seasonal changes in female receptivity, male testis mass, and sex hormones are correlated with sociosexual activity for both species (Wells and Norris 1994; Markowitz et al. 2010).

Mating, which occurs in nonbreeding and breeding contexts, can be playful and relaxed as well as competitive. Frequent intromission among spinner dolphins is most observed during the breeding season (Wells and Norris 1994), similar to dusky dolphins (Markowitz et al. 2010). However, sociosexual behavior among spinner dolphins occurs throughout the year and is described as a "marked" feature of this species' society outside of the breeding season (Norris 1994). For dusky dolphins, sexual behaviors, even in competitive mating groups during the breeding season, occur alongside play behaviors (e.g., playing with kelp; Markowitz 2012). Outside the breeding season, sociosexual interactions among dusky dolphins are less frequent and often take on a "lazy" quality that appears to be part of the fluid suite of interactive behaviors that include other forms of touching and play (Markowitz et al. 2010). These sexual interactions likely serve to strengthen social bonds, as seen in many primate species and other mammals (Würsig and Pearson 2015; da Silva and Spinelli 2023, this book).

Sexual activity of Hawaiian spinner dolphins and New Zealand dusky dolphins is not uniformly distributed throughout the day. Rather, it follows predictable circadian rhythms of rest and social interaction. Both populations rest predominantly during

midday with high activity levels early in the morning following offshore feeding and late in the day prior to returning offshore to nocturnally feed (Würsig et al. 1994; Markowitz 2004). Sociosexual behavior of Hawaiian spinner dolphins often occurs in the morning before resting in nearshore waters (Würsig et al. 1994). Spinner dolphins off the Brazilian coast also engage in reproductive activity most often during the morning (Silva and Da Silva 2009). Similarly, dusky dolphins off Kaikoura, New Zealand, exhibit high levels of sociosexual activity in the morning followed by predominant midday rest but exhibit even higher sociosexual activity levels late in the day prior to moving offshore to feed at night (Markowitz et al. 2010). While sociosexual activity occurs at all times of day among dusky dolphins, it is least frequent around the midday rest period (Markowitz 2004).

In contrast, dusky dolphins in Golfo San José, Argentina, and Admiralty Bay, New Zealand, feed during the day in shallow bays where low predation pressure appears to have released them from assembling in large groups (Würsig and Pearson 2014). Daytime social and sexual interactions of dusky dolphins in these habitats occur within a diel activity schedule that includes diurnal foraging and feeding (Vaughn et al. 2010). In these habitats, most social and sexual interaction occurs following a successful feeding bout (Würsig and Würsig 1980; Würsig and Pearson 2014).

14.5 Competition, Collaboration, and Choice

Male spinner and dusky dolphins have high testis-to-body mass ratios and high brain-to-body mass ratios (Kelley et al. 2014; Ridgway et al. 2016). Their large gonads and brains play a role in sociosexual interactions. The mating system of spinner dolphins is serial polygynandry, with multiple males mating with a single female in quick succession and those males then mating with other females as well, but not necessarily in the same male groupings as before (Johnson and Norris 1994). While mating behavior of Hawaiian spinner dolphins often occurs in pairs and trios, during the estrus season, it also occurs in larger, bunched, interweaving groups of a dozen or more dolphins termed "wuzzles" (Johnson and Norris 1994; Würsig 1999). Similarly, mating in dusky dolphins is sometimes observed in pairs or trios but more commonly occurs in tight groups that engage in particularly frenzied activity during the breeding season. The average dusky dolphin mating group size is five dolphins comprised of four male dolphins chasing a lone female (Markowitz et al. 2010; Orbach et al. 2015a). Neither spinner nor dusky dolphin males engage in the overtly aggressive male-male physical competition or mate guarding observed in bottlenose dolphins (Wells and Norris 1994; Connor et al. 2000; Markowitz 2004; Brightwell and Gibson 2023, this book). Unlike bottlenose dolphins, male spinner and dusky dolphins appear unable, either singly or cooperatively, to monopolize females (Wells and Norris 1994; Markowitz et al. 2010). Male dusky dolphins appear to engage in "mating of the quickest" (Markowitz et al. 2010), a form of scramble competition in which not all participants succeed in copulating with the female (Orbach et al. 2014).

Fig. 14.3 Dolphin social contact in the context of mating is shown. One dolphin is performing a "rollover" in an attempt to break up a mating pair. A fourth dolphin is approaching from behind the group (Photo by W.J. Markowitz)

While overtly aggressive physical interactions among dusky dolphin males are rare, males jostling for position at times collide midair or engage in a "rolling over" behavior in which one male separates a copulating female and male at the surface (Markowitz 2012; Fig. 14.3). Similar competitive mating behavior occurs in spinner dolphins (Norris and Dohl 1980).

Close social associations frequently occur within male spinner dolphin groups off Hawai'i and male dusky dolphin groups in New Zealand; this suggests the possibility of collaboration among male dolphins during competitive sexual encounters (Östman 1994; Markowitz et al. 2004; Pearson et al. 2019). While male Hawaiian spinner dolphins maintain close associations and often swim side-by-side, sociosexual behavior, including touching, rubbing, and nuzzling of the genital area, occurs most often among males and females (Östman 1994). In New Zealand, a group of closely associated male dusky dolphins that chased females together off Kaikoura in the summer breeding season also engaged in coordinated diurnal fish feeding in Admiralty Bay during the winter nonbreeding season; this suggests that these males most likely use "team mates to get mates" (Markowitz et al. 2010). Although male-male competition generally decreases copulation rate per male (Orbach et al. 2015b, c), observations of apparent mate sharing in small mating groups with the first male copulating longest suggest that male dusky dolphins may allow rivals opportunities to mate but that the sharing may not be equal (Markowitz 2012). Such mate sharing among alliance partners is common among primate societies and has also been observed in male alliances of bottlenose dolphins engaged in more aggressive competition and mate guarding (Connor et al. 1992).

As is common in large-brained mammals where females invest most heavily in offspring and provide most parental care (Trivers 1985), female choice plays a major role in the mating system of many social odontocetes (Orbach 2019). Among cetaceans, where some aspects of matrilineal cultures often occur (e.g., Betty et al. 2023, this book), females play a key role in shaping social structure, behavioral biology, and sexual interactions (Whitehead and Mann 2000). Female mate choice, hormonal state, libido, and prowess appear to be key components in sexual interactions (Würsig et al. 2023, this book). There is strong sexual selection for those traits that make males successful in their attempts to copulate with females and females successful in copulating with the highest-quality males. Females appear to actively engage in mate selection, including exhibiting extensive evasive behaviors (Orbach et al. 2015a). Females appear to pay attention to the mating behaviors of males and adjust their responses accordingly, providing strong evidence of discrimination in mates (Orbach et al. 2015a). Female vaginal morphology of spinner and dusky dolphins also supports an active female role in controlling paternity. Female cetaceans possess vaginal folds that create a labyrinth for the penis and sperm inside their reproductive tracts (Orbach et al. 2019, 2020a). Research with captive spinner dolphins showed that females initiated sociosexual beak-to-genital interactions with males when their estradiol levels were highest (Wells and Norris 1994). Underwater observations of Hawaiian spinner dolphins in nature found that social contact behaviors were more common in female-male pairs than in male-male pairs, with the females most often initiating these behaviors including social rubbing, "hitchhiking" (assisted locomotion), and genital rubbing (Östman 1994).

In some cases, female choice may occur indirectly in the form of females encouraging male-male competition (Boness et al. 2002), often by making it difficult for males to access a female who is ventrum-up at the surface, as in right whales (*Eubalaena* spp., Brown and Sironi 2023, this book), bowhead whales (*Balaena mysticetus*, Koski et al. 2023, this book), and gray whales (*Eschrichtius robustus*, Swartz et al. 2023, this book). In addition to initiating sociosexual interactions, female odontocetes often engage in a variety of elusive behaviors, probably to ensure that they mate with the highest-quality prospective mates (Orbach 2019). This appears to be the case for dusky dolphins off Kaikoura during the breeding season (Markowitz et al. 2010; Markowitz 2012), where mating chases in small groups occur in fits and starts with the female engaged in evasive behaviors at the front of the group (Orbach et al. 2015a). Females may prolong mating chases to improve the likelihood that only the most adept male chasers successfully copulate. This notion is supported by copulation rate decreases with reorientation rate in mating groups during the breeding season (Markowitz 2012). With frequent changes in direction, the swimming speeds of dolphins engaged in mating chases vary considerably more than in groups traveling in a linear direction or resting, reaching top speeds exceeding 20 km/h (Markowitz et al. 2010). In such mating groups, female dusky dolphins extend chases by frequently changing direction and head-up braking maneuvers (Markowitz et al. 2010), as well as deep dives and inverted swimming (Orbach et al. 2015a). Reentry leaps are common among mating groups of dusky dolphins, occurring more often than in other social groups, and often associated with high-speed

surface chasing (Markowitz 2004, 2012). Typically, the female in the group leaps first and is often followed immediately by one or more of her male suitors (Fig. 14.1). High rates of reentry leaping are correlated with reduced copulation rates, suggesting that females may use reentry leaps to break away from chasing males near the surface and extend mating chases in three-dimensional space down through the water column (Markowitz et al. 2010). Drone footage of subsurface activities has revealed that chasing continues during dives, with male dolphins following the female throughout the dive sequence (Orbach et al. 2020b). In form, and perhaps also in function, female dusky dolphins are leaders in sociosexual interactions.

14.6   Sociosexual Development and Learning

Spinner and dusky dolphins have opportunities to learn about sociosexual interactions long before they reach sexual maturity at about 7 years of age (Norris and Dohl 1980; Cipriano 1992; Table 14.1). In spinner dolphins, sociosexual behavior commonly occurs in mixed age class resting groups (Johnson and Norris 1994). Dusky dolphin calves may witness their mothers and/or other adult companions engage in sociosexual behavior (Markowitz et al. 2010). One function of dusky dolphin nursery groups may be the reduction of harassment by males during the breeding season (Weir et al. 2008). Calves and their mothers also frequently join large groups, where more relaxed sociosexual interactions are common (Markowitz 2012). As they mature into juveniles, reproductive behavioral patterns are practiced in social interactions among spinner dolphins (Norris 1994) and may also occur in playful subgroups of dusky dolphins (Markowitz 2004).

14.7   Summary and Future Directions

Hawaiian spinner dolphins and New Zealand dusky dolphins live in large societies in which associations change frequently despite evidence of preferred companions (Markowitz 2004; Andrews et al. 2010; Pearson et al. 2016; Orbach et al. 2018). Sexual interactions occur in busy, ever-changing social environments within these two populations, both of which forage nocturnally (Johnson and Norris 1994; Markowitz et al. 2010). Off Kaikoura, New Zealand, large groups of dusky dolphins, typically numbering in the hundreds, facilitate diverse social interactions that require social rules and communication relative to organizing group movements (Markowitz 2004). Small subgroups, including mating groups, split off from the large groups and rejoin them throughout the day. This results in a busy network of social interactions that can change seasonally, daily, and from one moment to the next (Markowitz 2012). Although spinner dolphins in the main Hawaiian Islands show strong general site fidelity (Andrews et al. 2010; Lammers 2019), different groups come and go

from individual bays with much social mixing (Würsig and Pearson 2015). In their shallow (< 50 m), sandy, daytime resting habitat along the shores of the main Hawaiian Islands, spinner dolphin group sizes do not reach the numbers observed in dusky dolphins inhabiting deep nearshore waters of the Kaikoura Canyon during daytime. However, group size and membership can change throughout the day, and sociosexual behavior is observed in both small groups and large "wuzzles" (Johnson and Norris 1994).

Dusky and spinner dolphins appear to have two different modes of exhibiting sexual behavior: an active competitive form involving multiple partners and a more relaxed, "lazy" form. Both these forms of sociosexual behavior can include intromission, although their function appears to be quite different. In a breeding context, high activity levels among dusky dolphins show a role for sexual selection in male-male competition and female choice (Markowitz et al. 2010). Copulations in small groups of spinner dolphins tend to involve two successful males mating with one female; these interactions are not particularly active with minimal chasing and no leaping. Females are not isolated from the large group for long and mating occurs quite briefly (Johnson and Norris 1994). Sexual behavior also occurs in large interactive groups of spinner dolphins with high activity levels (Johnson and Norris 1994; Würsig 1999). In a nonbreeding context, sex also plays an important role, strengthening social bonds within fission-fusion societies of nocturnally foraging dolphins that depend on one another for survival (Norris and Schilt 1988; Markowitz 2012).

In this chapter, we reviewed research conducted over the past 40 years on the sexual behavior of night-foraging spinner and dusky dolphins and how mating fits into their circadian and seasonal rhythms, rich social lives, and fission-fusion societies. These studies were facilitated by a combination of ingenuity and technological advances that improved the ability to better understand the mysterious and complex social and sexual lives of dolphins. In Hawai'i, spinner dolphin groups were monitored in Kealakekua Bay from research vessels and by theodolite tracking from shore stations (Würsig et al. 1994). Some vessel-based work included observations of spinner dolphin social behaviors from underwater viewing platforms, yielding a better and extended view of subsurface behavior including sociosexual interactions (Norris and Wells 1994; Östman 1994). Captive research has provided invaluable insights into the role of hormone levels in sociosexual behavior of male and female spinner dolphins (Wells and Norris 1994). In New Zealand, early work relying on stopwatches, datasheets, and photo-identification using film photography gave way to digital video, digital audio, and high-resolution digital SLR photography (Markowitz et al. 2003; Markowitz 2012). Within dusky dolphin mating groups, high-resolution video and photography provided improved quality information on individual identity and roles in sexual encounters and also the sex of the participants using anogenital digital records (AGDRs, Markowitz et al. 2010). Recently aerial drones were used to provide both a broader view of group interactions from above and a view of behavior underwater as seen from above (Orbach et al. 2020b; Ramos et al. 2023, this book).

New research approaches have given us previously unavailable glimpses into the social and sexual lives of spinner and dusky dolphins, but much remains to be discovered. Important questions to be explored include: how do spinner dolphin "wuzzles" and dusky dolphin mating groups influence reproductive success and fitness for females and males? What is the relationship between nocturnal foraging success and diurnal sexual activity? How do sociosexual interactions influence other socioecological interactions and vice versa? What can similarities and differences in the sex lives of spinner dolphins, dusky dolphins, and other cetaceans teach us about the roles of sex in shaping complex cetacean societies? We expect much will be learned in the future regarding these and other questions as new methodological approaches are incorporated into research efforts. For example, further photo-iden-tification and behavioral research, facilitated by ever-improving technology (Markowitz et al. 2003; Orbach et al. 2020b), will provide new insights into social partnerships in sexual and other interactions for both populations. Future work using drones might include hormonal sampling from exhaled air (Abele 2021) to provide real-time field data on the hormonal states of dolphins engaged in sociosexual interactions. The use of noninvasive tags for dive records, underwater video capture, and documentation of other parameters also shows great promise for future advances in our understanding of dolphin sociosexual interactions (Pearson et al. 2017, 2019).

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Chapter 15
Life History Parameters, Sociobiology, and Reproductive Strategies of Pilot Whales

Emma L. Betty, Elizabeth M. J. Zwamborn, Mieke Weyn, Emma Luck, and Filipe Alves

Abstract Two species of pilot whales are globally distributed, the long-finned (*Globicephala melas*) in cold-temperate waters and the short-finned (*G. macrorhynchus*) in tropical and warm-temperate latitudes. Two subspecies of the long-finned pilot whale are recognized, *G. m. melas* in the North Atlantic and *G. m. edwardii* in the Southern Hemisphere. In addition, three types have been proposed in short-finned pilot whales. In general, it is assumed that pilot whales live in matrilineal societies composed of stable units/pods displaying bisexual natal philopatry, but inter- and intraspecific variabilities in the sociality of these units have been described worldwide. Moreover, there is inter- and intraspecific heterogeneity in life history and reproductive parameters, which supports geographic variation. To investigate life history parameters, sociobiology, and reproductive

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strategies within different populations of pilot whales, we reviewed the current literature and compiled novel data. We cover populations from both hemispheres and combine life history characteristics from strandings with field-/behavioral-based information such as long-term photographic-identification, social analysis with molecular sexing, and drone technology. This chapter contributes to improving our knowledge of the life history parameters between sexes and populations, interactions between animals of different sexes within units, social structures, and reproductive strategies in pilot whales. We explore pilot whales' sexual group dynamics and social system and discuss whether they are strictly matrilineal in comparison with other "matrilineal" species.

Keywords *Globicephala* · Matrilineal · Naisa type · Post-reproductive lifespan · Reproduction · Shiho type · Social structure

15.1 Introduction

There are two species of pilot whales currently recognized (Fig. 15.1), the temperately distributed long-finned pilot whale (*Globicephala melas*; herein LFPW) as well as the tropically and subtropically distributed short-finned pilot whale (*G. macrorhynchus*; herein SFPW). LFPWs are split into two subspecies—one in the North Atlantic (*Globicephala melas melas*; herein North Atlantic LFPW) and the other in the Southern Hemisphere (*G. melas edwardii*; herein Southern Hemisphere LFPW) (Olson 2018). Recent genomic work suggests three SFPW types within the species: (1) an Atlantic Ocean (Atlantic Naisa) type, (2) a western/central Pacific and Indian Ocean (Pacific Naisa) type, and (3) an eastern Pacific Ocean and northern Japan (Shiho) type (Van Cise et al. 2019). There is evidence of interbreeding between these species, including post-F1 hybrids recorded in studies of both Iberian Peninsula and Faroe Islands genetic samples (Miralles et al. 2013, 2016).

Both pilot whale species have pronounced sexual dimorphism. Males grow to around 1.3 times the length of females and have taller dorsal fins, longer pectoral fins, more pronounced melons, and wider flukes than adult females of similar body lengths (Fig. 15.1, Table 15.1; Kasuya 2017; Betty et al. 2022a). The biological significance of sexual differences in adult male dorsal fin shape and size is not well understood, but they may serve a thermoregulatory function and/or act as a visual signal in mating interactions, while the longer and broader flukes and pectoral fins may function to give more propulsion compared to females (Mesnick and Ralls 2018). There are differences in the relative degree of sexual shape dimorphism of the dorsal fin between species, subspecies, and types, which is likely due to variations in ecology and sociality—with immature individuals having proportionally smaller fins (and lighter coloration) than mature pilot whales (Fig. 15.2). In LFPWs, sexes can be distinguished by distinctive urogenital markings from a young age; the light gray ventral stripe on females flares out to encompass the mammary slits before
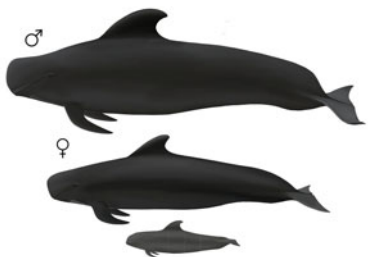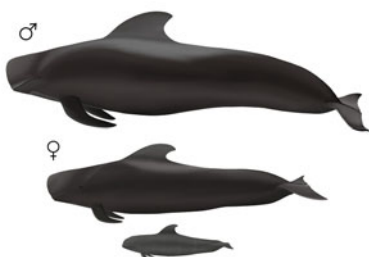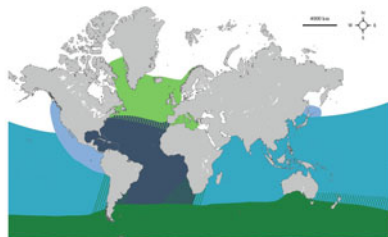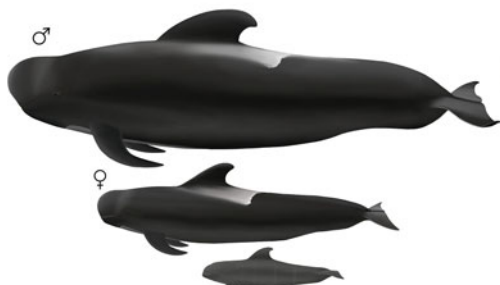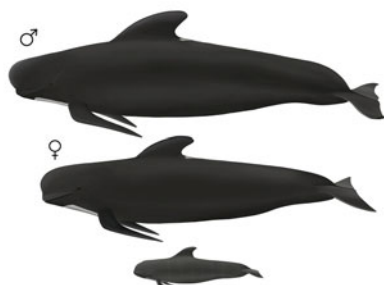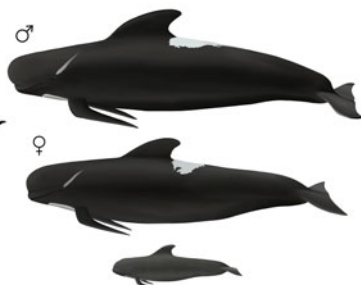
Fig. 15.1 Long-finned pilot whale (*Globicephala melas*) subspecies and short-finned pilot whale (*G. macrorhynchus*) types showing sexually dimorphic characteristics, with global distribution map

truncating off rather abruptly, while in males there is no distinctive flare and the light gray patch tapers off gradually before the caudal end of the genital slit (Fig. 15.3). While pilot whales share several reproductive characteristics with other large odontocetes (e.g., long lifespan, delayed maturity, bimaturism, sexual dimorphism, extended calving intervals, etc.), many of these differ significantly between species, subspecies, and types (Tables 15.1 and 15.2).

Table 15.1 Summary of total body length and age data available for the short- (*Globicephala macrorhynchus*) and long-finned (*G. melas*) pilot whales

	G. macrorhynchus		*G. m. melas*				*G. m. edvardii*	
Location	Japan		Britain[4]	Faroe Islands[5,6]	Iceland[7]	Newfoundland[8,9]	Argentina[10,11]	New Zealand[12]
Type	Pacific Naisa[1,2]	Shiho[3]						
Source	Drive fishery	Drive fishery	Stranding	Drive fishery	Stranding	Drive fishery	Stranding	Stranding
Sampling period	1983–1988	1982–1988	1982–1985	1986–1992	1982–1986	1951–1959	1982, 2009	1948–2017
Average length-at-birth (cm)	140[a]	185[b]		177[a]		♂ 178[c] ♀ 174[c]		170[a]
Asymptotic length (cm) ♂	474[d]	650[e]	550–600[f]	580[g]		557[h]		570[i]
Asymptotic length (cm) ♀	364[d]	467[e]	400–450[f]	445[g]		489[h]	441[j]	438[j]
Sexual size dimorphism ratio	1.3	1.4		1.3		1.1		1.3
Age at asymptotic length (years) ♂	27[d]	25–30	>20[k]	>46		21–25[l]		40
Age at asymptotic length (years) ♀	22[d]	25–30	>20[k]	32		21–25[l]		30
Maximum length (cm) ♂	525	720	630	625	595	617	538	622
Maximum length (cm) ♀	405	510	546	512	475	511	483	500
Maximum age (years) ♂	45.5	44.5	20[k]	46	34	35.5[l]	16	31
Maximum age (years) ♀	62.5	61.5	25[k]	59	34	56.5[l]	35	38

[a] Estimated by logistic regression
[b] estimated from relationship of mean neonatal length and mean TBL of females at sexual maturation
[c] estimated as mean of overlapping fetus and neonate TBL
[d] estimated from growth curve "drawn by eye"
[e] estimated as mean TBL of individuals >30 years
[f] estimated from length frequency distribution
[g] estimated using a single Gompertz growth model
[h] estimated as mean TBL of individuals >25 years
[i] estimated using a two-phase von Bertalanffy growth model
[j] estimated using a single von Bertalanffy growth model
[k] estimated using less reliable method: acid etching
[l] estimated using less reliable method: transverse tooth sections

Sources: [1]Kasuya and Matsui (1984), [2]Kasuya and Marsh (1984), [3]Kasuya and Tai (1993), [4]Martin et al. (1987), [5]Bloch et al. (1993), [6]Lockyer (1993), [7]Sigurjónsson et al. (1993), [8]Sergeant (1962), [9]Kasuya et al. (1988), [10]Crespo et al. (1985), [11] Soto et al. (2017), [12]Betty et al. (2022a)

Fig. 15.2 Examples of coloration and dorsal fin proportional differences between age classes for North Atlantic long-finned pilot whales (*Globicephala melas melas*), including a juvenile (front), calf (center), and adult (back)
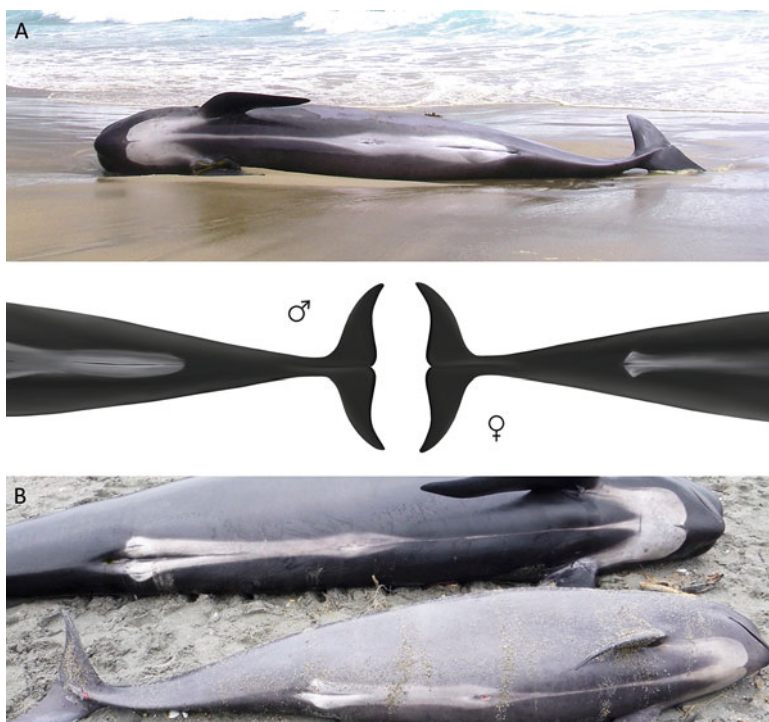
Fig. 15.3 Long-finned pilot whale (*Globicephala melas*) urogenital marking patterns with examples of both A) male and B) female *G. m. edwardii* stranded on the Aotearoa New Zealand, coast

15.2 Social Structure and Reproductive Strategies

Pilot whales are well-known for their multilevel and highly cohesive social structure, which is a contributing factor toward their tendency to strand en masse. Often referred to as one of the most gregarious cetaceans, pilot whales are commonly found in temporary aggregations of up to several hundred individuals. The average reported group size is around 20 whales (Jefferson et al. 2008), though this varies by population. There is also some evidence that pilot whale "groups" are comprised of several smaller "units" of constant companions (Heimlich-Boran 1993; Ottensmeyer and Whitehead 2003; de Stephanis et al. 2008; Alves et al. 2013; Mahaffy et al. 2015; Augusto et al. 2017). Pilot whales are one of the few mammals that appear to have a matrilineal social structure (Amos et al. 1993a; Alves et al. 2013), along with sperm whales (*Physeter macrocephalus*; Cantor et al. 2015), killer whales (*Orcinus orca*; Bigg et al. 1990), elephants (*Elephas maximus*; Berger et al. 2021), some primates (Greenwood 1980), and humans (Behar et al. 2008). There are unique differences in how matrilines are structured, such as the lack of sex-biased dispersal from the natal groups in some ecotypes of killer whales (Ford 2019), male dispersal before sexual maturity to live primarily solitarily or with other males in sperm whales (Best 1979), and a possible mixture in pilot whales that is not fully understood (Amos et al. 1993a; Hill et al. 2019). Both pilot whale species have been reported to form long-term stable units consisting of several generations of maternally related individuals (with an increase in local relatedness with age), as well as strong mother-offspring associations with long periods of dependency (Marsh and Kasuya 1990; Brent et al. 2015; Croft et al. 2017; Nichols et al. 2020). There is some genetic evidence that groups of both LFPWs and SFPWs can contain multiple matrilines (Alves et al. 2013; Oremus et al. 2013; Nichols et al. 2020; Ball et al. 2021). It has been suggested that both pilot whale species form temporary associations comprising multiple matrilineal units, as supported by studies of SFPWs (Alves et al. 2013; Mahaffy et al. 2015) and North Atlantic LFPWs (Ottensmeyer and Whitehead 2003; de Stephanis et al. 2008; Augusto et al. 2017) where long-term stable units are smaller than the average observed group size.

The mating strategies and tactics of pilot whales are not well understood. Both LFPWs and SFPWs are assumed to have a polygynous mating system due to their sexual dimorphism. However, there is a lack of evidence for male combat in pilot whales. North Atlantic LFPWs have the fourth largest residual testes-to-body mass ratio when compared to 30 other cetacean species (MacLeod 2010). The lack of a trade-off with testis size indicates that male pilot whales (1) are not able to monopolize access to females to the same extent as those who compete by combat and (2) may invest in postcopulatory sperm competition (MacLeod 2010; Dines et al. 2015). For both pilot whale species, there is agreement that males mature about 7–9 years later than the females (Table 15.2), which concurs with the general delphinid pattern of bimaturism (Perrin and Reilly 1984). Male and female North Atlantic LFPWs have been documented engaging in sociosexual behavior from a very young age (see Case Study 3.1).

Table 15.2 Estimated reproductive parameters for short—(*Globicephala macrorhynchus*) and long-finned (*G. melas*) pilot whales

	G. macrorhynchus		G. m. melas			G. m. edwardii	
Location	Japan		Britain[4]	Faroe Islands[5,6]	Newfoundland[7,8]	Argentina[9]	New Zealand[10,11]
	Pacific Naisa[1,2]	Shiho[3]					
Type	Drive fishery	Drive fishery	Stranding	Drive fishery	Drive fishery	Stranding	Stranding
Source	Drive fishery	Drive fishery	Stranding	Drive fishery	Drive fishery	Stranding	Stranding
Sampling period	1983–1988	1982–1988	1982–1985	1986–1992	1951–1959	2009	2008–2017
Sexual maturity							
Average length at sexual maturity (LSM; cm) ♂	422	560		516	c. 460		472
♀	316	390–400	c. 300–400[a]	375	356	366	356
Average age at sexual maturity (ASM; years) ♂	17	17		16.8	c.12		13.5
♀	9	8–9	c. 7[a]	8.3	c. 6-7[a]	8	6.7
Reproductive cycle							
Mean ovulation rate (year^{-1})	0.70–0.14 (7–39 years)			0.25	0.3–0.5	0.41	0.4
Annual pregnancy rate, all ages (%)	12.8	14–20		24	13.2		19
Gestation period (mo.)	14.9	c.15		12	15.5–16		13.6
Mean lactation length (years)	2.23[b]	2–2.78[b]		3.4	1.75–1.83		1.6
Mean calving interval (years)	5.21[b]	4.5–5.7[b]		4–5	3.3		5.3
Post-reproductive females (% of mature)	25		14	<5	≤5	0	0
Lifetime reproductive output	4–5			3–4	9		5

[a]Estimated from evidence of first ovulation

[b]For reproductive females

Sources: [1]Kasuya and Marsh (1984), [2]Marsh and Kasuya (1984), [3]Kasuya and Tai (1993), [4]Martin et al. (1987) [5]Martin and Rothery (1993), [6]Desportes et al. (1993), [7]Sergeant (1962), [8]Kasuya et al. (1988), [9]Soto et al. (2017), [10]Betty et al. (2019), [11]Betty (2019)

Pilot whale groups are mainly stable, with the young growing to maturity in their natal group and most remaining there for life. In a few populations, it has been suggested that young male pilot whales might disperse from their natal unit/pod to aggregate in other matrilines and/or form male-only groups (Kasuya and Marsh 1984; Desportes et al. 1992). Genetic and long-term photographic-identification studies suggest that males breed outside their family group and that they can remain with their group for decades (Kasuya and Marsh 1984; Amos et al. 1993b; de Stephanis et al. 2008; Alves et al. 2013; Mahaffy et al. 2015; Augusto et al. 2017; Van Cise et al. 2017; Boran and Heimlich 2019; Hill et al. 2019; Nichols et al. 2020). Therefore, mating must occur when two or more pods meet or when adult males visit other groups. This type of social structure where adult males stay with their female kin and mate elsewhere is unusual among mammals. Studies on males' stability have covered only specific populations, such as the North Atlantic LFPW (Nova Scotia and Gibraltar; de Stephanis et al. 2008; Augusto et al. 2017) and the Pacific Naisa SFPW (Hawai'i and Mariana archipelagos; Mahaffy et al. 2015; Hill et al. 2019). There are still gaps in our understanding of the role of male pilot whales within the social structure of other subspecies/types; see Case Study 3.2 with discussion on male-only groups and natal philopatry in the Atlantic Naisa SFPW.

In general, fertility and reproductive success are low in newly mature female cetaceans, reaching a peak in young mature animals, followed by a plateau until they (often) decline with age (Best et al. 1984; Martin and Rothery 1993; Boyd et al. 1999). Females are defined as reproductively senescent, or post-reproductive, if conceiving or sustaining a successful pregnancy is no longer possible because of age-related changes to the reproductive system (Marsh and Kasuya 1986). The occurrence of reproductive senescence is contradictory to classical life history theory (Ellis et al. 2018a) and has been observed in females of several odontocete species including sperm whales (Best 1980), killer whales (Foster et al. 2012), false killer whales (*Pseudorca crassidens*; Photopoulou et al. 2017), beluga whales (Ferguson et al. 2020), narwhal (*Monodon monoceros*; Garde et al. 2015), and SFPWs (Marsh and Kasuya 1984). A detailed examination of ovarian aging in the Pacific Naisa SFPW showed an age-specific decline in the pregnancy rate, paralleled by a decline in the ovulation rate and a high incidence of infertile ovulations (atresia) in old females (Marsh and Kasuya 1984). Approximately 25% of mature female SFPWs examined ($n = 298$) had senescent ovaries, and it was concluded that SFPWs appear to cease ovulating before 40 years of age but may live up to 30 years (14 years on average) after the birth of their last calf (Marsh and Kasuya 1984). Curiously, post-reproductive females were observed much less frequently in the North Atlantic LFPW ($< 5\%$ of mature females; Sergeant 1962; Kasuya et al. 1988; Martin and Rothery 1993), and it has been reported that LFPWs do not appear to have a significant post-reproductive lifespan (Ellis et al. 2018a, Betty 2019, Nichols et al. 2020; see Case Study 3.3). Potential explanations for post-reproductive lifespan include the mother and grandmother hypotheses, where old nonreproductive mothers avoid reproductive competition with their daughters, and instead maximize their inclusive fitness, by aiding and enhancing the survival of their offspring (Johnstone and Cant 2010; Foster et al. 2012; Brent et al. 2015; Croft et al. 2017;

Nichols et al. 2020). For reproductively active females of both pilot whale species, the calving interval is estimated to be about 4–5 years (Table 15.2). However, the calving interval and duration of lactation increase with maternal age, which may mean (1) higher calf survival, (2) milk is provided to calves other than the mother's own, and (3) increased investment in calves with advancing age of the mother (Marsh and Kasuya 1984, Martin and Rothery 1993). Overall, there remains much to learn about pilot whale social structure, reproductive strategies, and life history.

15.3 Case Studies

This chapter presents three case studies from one Atlantic Naisa SFPW and two LFPW (both North Atlantic and Southern Hemisphere) populations, utilizing both strandings-based and field-/behavioral-based data. The case studies provide novel insights that further our understanding of (1) sociosexual behavior in immature North Atlantic LFPWs, (2) male natal group philopatry in Atlantic Naisa SFPWs, and (3) reproductive senescence in female Southern Hemisphere LFPWs.

15.3.1 Sociosexual Behavior in Immature North Atlantic LFPWs

LFPWs are thought to be matrilineal, with the Northern Hemisphere subspecies composed of mixed-sex social units that include females with their offspring (Augusto et al. 2017). These social units frequently associate with other matrilines and form large groups, suggesting that there are often both related and unrelated sexually immature pilot whales near each other. The sociosexual behaviors of LFPWs have not yet been studied nor formally described. Here we provide the first description of non-conceptive sexual behavior for immature North Atlantic LFPWs from a population that summers off Cape Breton Island, Nova Scotia, Canada.

While on research surveys for a study on North Atlantic LFPW behavioral ecology, we noticed several clusters of sexually immature individuals engaged in sociosexual behaviors within different groups that were followed for approximately 1 hour. Aerial footage was collected using a DJI Inspire 1 V2 drone fitted with a DJI X5 camera and Olympus Zuiko 25 mm f1.8 lens launched off a chartered vessel on August 17, 2020. Just over 21 minutes of video (from two different clusters of individuals) were analyzed frame-by-frame to categorize and count sociosexual behaviors based on an ethogram modified from Ham et al. (2022; Table 15.3).

Seven different types of sociosexual behavior were documented (Fig. 15.4). Age categories were assigned based on natural markings following Auger-Méthé and Whitehead (2007), with calves classified as newborns (nb; up to a couple months in

Table 15.3 Sociosexual behaviors in immature North Atlantic long-finned pilot whales (*Globicephala melas melas*) and their definitions

Behavior	Definition
Genital rub	An individual drags its genital region along the body of a receiver
Ventral present	An individual presents its ventral surface to a receiver that it is interacting with in a parallel position
S position	An individual thrusts its genital region forward toward the receiver while holding its body in a curved or "s"-shaped position for 2–3 seconds
Avoidance	A receiver maneuvers to avoid the attentions of the giver (e.g., an individual rolling over to prevent intromission)
Thrust	An individual quickly moves its genital region in the direction of the receiver
Ride	An individual positions themselves above the back of the receiver—this can be done simultaneously with a genital rub or a thrust
Erection	A male individual everts his penis
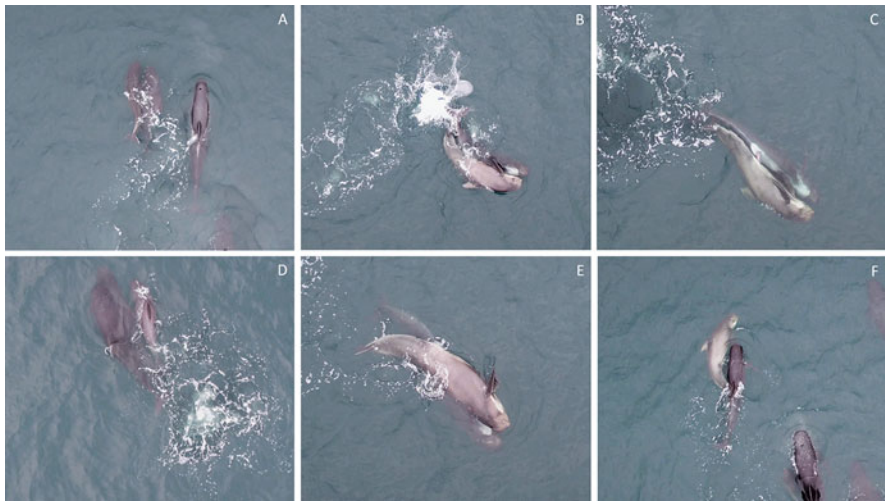
Fig. 15.4 Examples of sociosexual behaviors documented in immature long-finned pilot whales (*Globicephala melas melas*) including (**a**) S position (left whale), (**b**) thrust, (**c**) erection and genital rub, (**d**) ride (left whale), (**e**) avoidance, and (**f**) ventral present (left whale)

age), fetal folds (ff; a few months to a year), or gray calves (gc; 1–3 years of age). The sexes of calves were determined by examination of the genital region when whales rolled over. Sociosexual behaviors were observed in LFPWs across ff and gc age cohorts and for both sexes (Table 15.4), as has been documented in other species of cetaceans (Ham et al. 2022; Lonati et al. 2022; Sanvito and Galimberti 2022; Ham et al. 2023, this book). As ff were involved in some of the sociosexual interactions, sexual play begins relatively early in the development of LFPWs. We did not observe any sexually mature LFPWs engaging in sociosexual behaviors during these encounters, though they were often in close proximity to the individuals engaged in non-conceptive sexual play (two to six sexually mature LFPWs per

Table 15.4 Rates of sociosexual behaviors for long-finned pilot whales (with the presence of erection denoted as "X" if present for males)

Obs.	Individual ID	Rate (behavior/minute)						Erection
		Genital rub	Ventral present	S position	Avoidance	Thrust	Riding	
1	Calf (ff) 1 ♂	1.2	1.3	0.2	1.5	–	–	
	Juvenile 1 ♂	2.0	1.9	–	–	1.8	0.1	X
2	Calf (gc) 2 ♂	4.6	5.2	–	–	3.9	–	X
	Juvenile 2 ♀	–	–	–	2.6	–	–	N/A
	Juvenile 3 ♂	4.6	4.6	–	–	4.6	0.7	X

cluster). While male calves of several age cohorts were involved in sociosexual play, only juvenile males exhibited riding behavior (Table 15.4). Each receiver of these behaviors displayed avoidance of the pursuing males' efforts at some point during the encounters. Rates of sociosexual behaviors varied between the two clusters, but some behaviors were observed consistently more often than others (e.g., genital rubs vs. riding behaviors).

15.3.1.1 Functions of Sociosexual Behavior in LFPWs

There are several hypothesized reasons for non-conceptive sexual behaviors in cetaceans (reviewed by Ham et al. 2023, this book). Practice may increase success once individuals reach sexual maturity (Mann 2006; Furuichi et al. 2014). Sociosexual behaviors may establish and strengthen bonds between conspecifics within and across age cohorts (Connor et al. 2006; Lilley et al. 2020), which may be especially important when sexually immature individuals bond with more dominant or socially connected conspecifics (Lilley et al. 2020). Sociosexual behaviors could also be a by-product of sexual physiology and drives. The sole female filmed in these interactions did not display any sociosexual behaviors aside from avoidance, perhaps being an unwilling participant. Body rolling avoidance behavior has been observed in female dusky dolphins (*Lagenorhynchus obscurus*) to avoid copulatory attempts by pursuing males (Orbach et al. 2015; Markowitz et al. 2023, this book). While our observations of sociosexual play in sexually immature North Atlantic LFPWs do not give concrete evidence for a specific function, they likely train individuals in sexual and social skills (Ham et al. 2022).

This study provides some preliminary evidence for the development of behavior over time, as seen in immature beluga whales (*Delphinapterus leucas*) (Ham et al. 2022). Only juvenile North Atlantic LFPWs were documented displaying riding of the individuals they were pursuing, which could be because (1) this behavior develops later than other non-conceptive sexual behaviors, (2) riding is more frequently used by older individuals or (3) the drivers and function of sociosexual behaviors change as a pilot whale approaches sexual maturity. The development and

accumulation of sociosexual behaviors over time have been well documented in both beluga whales and bottlenose dolphins (Mann 2006; Ham et al. 2022), providing a likely explanation for the subtle differences in behaviors seen across different age classes of North Atlantic LFPWs.

Further studies into the non-conceptive sexual play of both immature and mature LFPWs are needed, particularly to determine whether these change across behavioral contexts and whether adults are sometimes engaged in sociosexual behaviors with younger age cohorts, as is observed in other cetacean species (Lilley et al. 2020; Lonati et al. 2022; Sanvito and Galimberti 2022). Recent technological advances may soon help lead to discoveries of additional pilot whale reproductive and non-conceptive sexual behaviors, particularly for behaviors that occur at depth or are not as readily observable as the ones documented here.

15.3.2 Stability and Fluidity of Naisa SFPW Social Groups of Known Sex off Madeira Island

Current knowledge supports the theory that pilot whales have a stable matrilineal kin-based structure, but it is unknown how much variation there is between species, subspecies/types, or even populations. Here we provide information on the stability of Atlantic Naisa SFPW social structure, using animals with known sex in social groups off Madeira Island, Portugal, to infer sex-biased dispersal. These data improve our knowledge on the debated natal group philopatry of males, given that some studies suggest males can have a non-kin-based social structure or question the stability of male associations due to the existence of multiple matrilines in closely associated groups and/or individuals (Oremus et al. 2013; Hill et al. 2019).

Atlantic Naisa SFPWs with several different residency patterns, but no genetic differentiation, are found in the coastal waters off Madeira Island (32° N 017° W), including both nomadic animals passing through sporadically and island-associated whales (i.e., seasonal visitors, residents) that occasionally visit the neighboring archipelagos of the Azores and Canaries (Alves et al. 2013, 2019; Boran and Heimlich 2019; Servidio et al. 2019). There have been over 100 island-associated whales documented off Madeira encompassing several matrilineal pods (akin to units in LFPWs), each with a mean size of 15 individuals (SD = 9) (Alves et al. 2013). These pods are made up of individuals that share documented long-lasting relationships (on a scale of decades), and genetic relatedness has been shown to be higher within groups than between them (Alves et al. 2013; Esteban et al. 2022). Atlantic Naisa SFPWs off Madeira have a high survival rate and the population size is stable (Alves et al. 2015; Verborgh et al. 2022). Although some degree of natal philopatry has been proposed for Atlantic Naisa SFPWs, the analyses of long-term stability of sexed animals within pods were inferred from a limited dataset of whales of known sex (Alves et al. 2013).

We used long-term photographic-identification data of 1275 Atlantic Naisa SFPWs off Madeira, complemented with biopsies of 51 individuals to genetically determine sex following Alves et al. (2020). Hierarchical cluster analysis was used to classify and illustrate relationships between the genetically sexed and distinctive whales captured on ≥4 encounters with high or full coverage (e.g., when the proportion of captured individuals per encounter was ≥0.8; Alves et al. 2013) and where documented pods had >1 animal of known sex. The truncated dataset used in the analysis selected 42 sexed/distinctive whales (24 females, 18 males) and 362 encounters collected year-round between 2003 and 2020. We defined the sampling period (and associations) as all individuals grouped within an encounter. Permutation tests were performed to understand whether preferred associations existed (Bejder et al. 1998; Whitehead 1999). Associations were calculated using the average-linkage method due to presenting the highest cophenetic correlation coefficient (CCC = 0.986). The association index corresponding to the maximum modularity was used to define community division by clusters (Whitehead 2008), and all analyses were carried out in SOCPROG 2.9 (Whitehead 2009).

Significantly high coefficients of variation (observed CV = 3.223, random CV = 3.064, $p < 0.001$) of all association indices indicate (according to Whitehead 1999, 2009) that individuals have long-term preferred companions. A Mantel test showed no significant differences in association strength within or between sexes ($p > 0.4$). The cluster diagram divided the individuals into six pods of mixed sexes and two pods containing only females (males may have been present but were not photographed or biopsied; Fig. 15.5). Males first documented in 2003–2005 were repeatedly captured together in their respective pods over the entire duration of this study (e.g., ID0089, ID0112, and ID0271 were captured 67, 89, and 94 times, respectively). A presumed mother-calf pair first captured in 2005 (male calf ID0271 in association with adult female ID0088) has been documented together over the course of 16 years. Although the mean association for all individuals was low (0.05 ± 0.02), the maximum association index for each individual was relatively high (mean = 0.68, SD = 0.19, range = 0.12–0.92); 33% of individuals displayed a maximum association index >0.80, indicating strong dyadic associations. Only one male (ID0114) in this study, with a maximum association index of 0.12, was not assigned to a specific pod due to not being regularly captured ($n = 6$) associated with the same individuals.

15.3.2.1 Sex-Biased Dispersal and Social Dynamics

This study confirms that Atlantic Naisa SFPWs off Madeira exhibit long-lasting and stable groups of mixed sexes, as suggested by Alves et al. (2013) and Esteban et al. (2022). Such female and male natal group philopatry complements the positive correlation between association indices and genetic relatedness coefficients previously described for this population (Alves et al. 2013), thus supporting the hypothesis that SFPW social groups are primarily matrilineal. A lack of male-biased dispersal has also been described in a population of killer whales (Ford 2019) and

Sex	Ind. ID	1st Year (# Capt.)
M	ID0707	2015 (06)
F	ID0082	2005 (12)
F	ID0083	2005 (18)
M	ID0080	2005 (15)
F	ID1185	2017 (07)
F	ID0261	2006 (11)
F	ID0253	2006 (08)
F	ID1337	2018 (06)
F	ID0995	2016 (07)
F	ID0234	2006 (09)
M	ID0628	2009 (19)
F	ID0501	2007 (18)
M	ID0499	2009 (14)
F	ID0630	2011 (07)
M	ID0272	2011 (07)
M	ID1106	2014 (13)
M	ID1034	2014 (22)
M	ID0896	2015 (35)
F	ID0228	2004 (45)
M	ID0217	2004 (28)
F	ID0133	2004 (43)
M	ID1412	2018 (05)
F	ID1255	2018 (10)
M	ID1254	2018 (10)
M	ID0114	2005 (06)
F	ID1090	2016 (27)
M	ID0089	2004 (69)
M	ID0112	2003 (87)
F	ID0110	2003 (76)
M	ID0271	2005 (94)
F	ID0088	2004 (88)
M	ID0723	2012 (12)
M	ID0761	2015 (22)
F	ID0141	2005 (26)
F	ID1234	2016 (06)
F	ID0054	2005 (38)
F	ID0036	2007 (35)
M	ID0854	2015 (38)
F	ID0034	2003 (50)
F	ID1505	2019 (04)
F	ID1167	2017 (07)
F	ID0862	2014 (06)

Fig. 15.5 Dendrogram constructed using average-weight linkage hierarchical cluster analysis for 42 genetically sexed and distinctive Atlantic Naisa short-finned pilot whales (*Globicephala macrorhynchus*) captured on ≥4 encounters with high or full coverage and > 1 animal with known sex, between 2003 and 2020, off Madeira Island. The sex, ID of the individual, and year of the first capture (and the total number of captures) are shown for each whale

is known to benefit the inclusive fitness of living with kin by improving access to resources that require coordination and provide alloparental care or defense from predators (Boran and Heimlich 2019).

Pods composed of only males were not recorded in the present case study, nor have they been observed at sea (following Yahn et al. 2023) during nearly two decades of intensive fieldwork off Madeira. Although other studies have mentioned the possibility of all-male pilot whale groups, such anecdotal records are based on (1) strandings or drive fisheries that may not reflect natural group stability, (2) in situ

visual sex determination, or (3) molecular sexing that might be influenced by (statistical) unit division criteria (Desportes et al. 1992; Mahaffy et al. 2015). To avoid inbreeding, it is possible that males may temporarily leave their natal group to mate, and therefore previously reported male individual/group sightings could represent short-term disassociations from their matrilines. This could be the case of ID0114, who was captured in association with different stable pods throughout the course of our study. Although this information advances our knowledge of social structure in Atlantic Naisa SFPWs and sheds new light on pilot whale social organization in general, additional genetic analyses are needed to clarify whether associated individuals are mothers and offspring, or siblings, to confirm matrilineality.

15.3.3 Examination of Reproductive Senescence in Female Southern Hemisphere LFPWs off Aotearoa New Zealand

Prolonged post-reproductive lifespans are rare in mammalian species. In contrast with the closely related SFPW, female North Atlantic LFPWs do not appear to have a significant post-reproductive lifespan (Martin and Rothery 1993; Ellis et al. 2018a). Reproductive senescence has not been previously examined in female Southern Hemisphere LFPWs. However, given that population variability in life history parameters exists for this species (Tables 15.1 and 15.2), it is important to investigate the potential existence of a significant post-reproductive lifespan in the Southern Hemisphere LFPW, specifically. Here we present the first investigation of female reproductive senescence for the Southern Hemisphere LFPW, through examination of reproductive data opportunistically collected from stranding events on the Aotearoa New Zealand, coast.

   As part of a study investigating the life history of the Southern Hemisphere LFPW (Betty 2019), postmortem reproductive data were collected from 166 females following 14 independent stranding events on the coast of Aotearoa New Zealand (2008–2017). Where possible, teeth were collected for age determination, and reproductive organs (ovaries and uteri) were removed in situ via standard postmortem procedures (Geraci and Lounsbury 2005). Age was estimated by examining decalcified and stained tooth sections and counting growth layer groups in the dentine (Betty et al. 2022a). Assessment of female reproductive status was determined through ovarian, uterine, and mammary gland examination (Betty 2019). Sexual maturity was determined by the presence of a least one corpus luteum (CL) or corpora albicantia (CA) on the ovary and/or evidence of pregnancy or lactation, with sexually mature females further classified into one of three reproductive states (i.e., pregnant, lactating, resting). To investigate evidence of reproductive senescence, ovaries were examined for absence of (1) a CL, (2) young or medium CAs, and (3) macroscopic follicles (Fig. 15.6) following Marsh and Kasuya (1984).
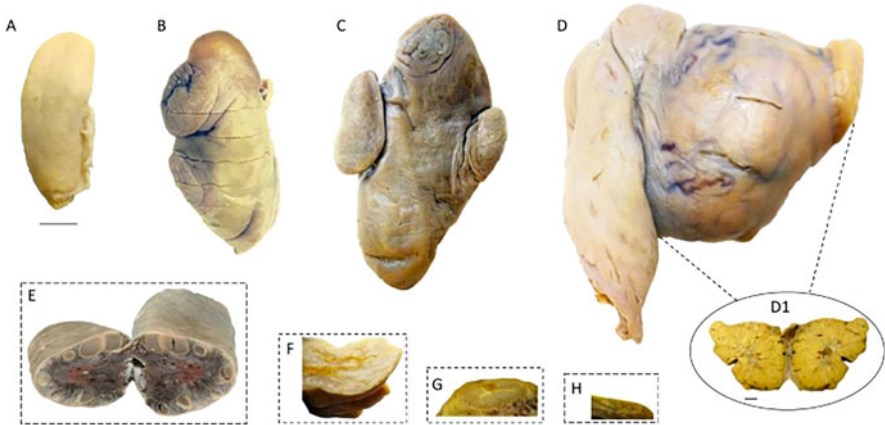
Fig. 15.6 Examples of long-finned pilot whale (*Globicephala melas edwardii*) ovaries: (**a**) left ovary of sexually immature female with no ovarian corpora scars; (**b**) left ovary of a resting mature female with a large fluid-filled follicle and a young, medium, and an old corpora albicantia (CA) visible; (**c**) left ovary of a lactating female with one young and two medium CAs visible; (**d**) right ovary of a pregnant female with a corpus luteum (CL) of late pregnancy, a medium, and an old CA visible with a (D1) median slice through the CL; (**e**) median slice through the left ovary of a lactating female, multiple follicles visible; (**f**) median slice through a young CA on the left ovary of a resting female; (**g**) median slice through a medium CA on the left ovary of a lactating female; and (**h**) median slice through an old CA on the left ovary of a resting female. All ovaries formalin fixed. Scale bar = 1 cm

As reported by Betty (2019), none of the 114 sexually mature females for which both ovaries were examined showed evidence of being post-reproductive (i.e., would not ovulate again). Where both the age and full reproductive status were available for sexually mature individuals ($n = 102$), the proportion of pregnant, lactating, and resting mature individuals was determined for six age groups (5–10, 11–15, 16–20, 21–25, 26–30, 31–35 years) to identify any changes in reproductive status with increasing age (Fig. 15.7). For the age class 5–10 years, a very small proportion of sexually mature pilot whales were resting (14%), and the majority of individuals were either pregnant (50%) or lactating (36%). A decreased proportion of pregnant and an increased proportion of resting individuals were noted in age classes >10 years (compared to the 5–10 year age class), except the single female in the oldest age class (31–35 years), which was aged at 33 years and was pregnant with a 23.5 cm fetus.

15.3.3.1 Lack of Evidence for a Post-reproductive Lifespan in LFPWs

The observation that pregnancy rates decrease and the duration of the resting periods increases in Southern Hemisphere LFPWs older than 10 years suggests that there is a reduction in fecundity with age, as also reported for the North Atlantic LFPW
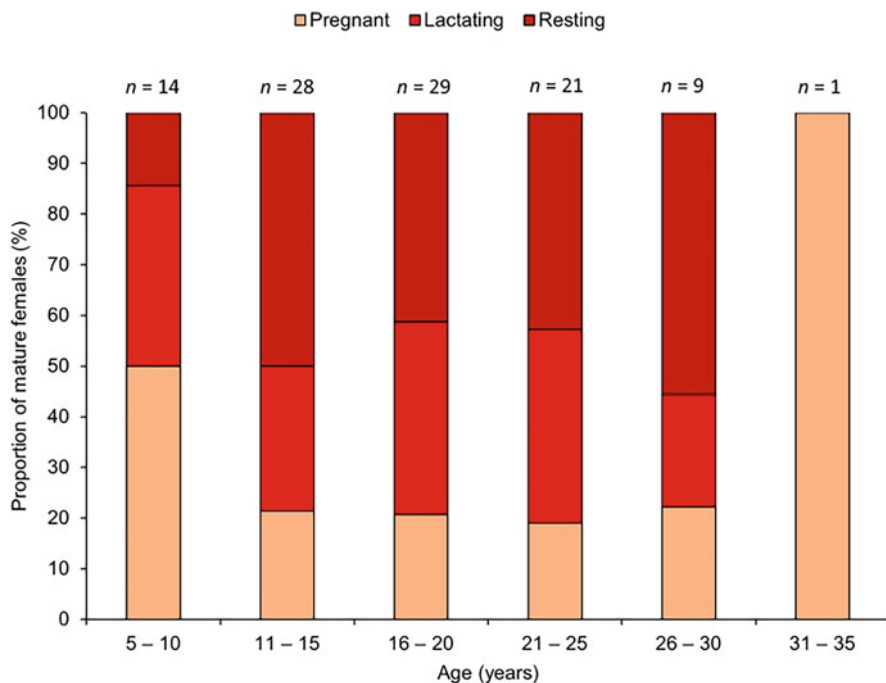
Fig. 15.7 Proportion of pregnant, lactating, and resting mature female long-finned pilot whales (*Globicephala melas edwardii*) stranded on the coast of Aotearoa New Zealand (2008–2017), by age group (*n* = 102)

(Martin and Rothery 1993). In contrast to the North Atlantic LFPW, reproductive senescence was not evident in Southern Hemisphere LFPWs. However, the maximum female age estimated for Southern Hemisphere LFPWs in this study (33 years) was much lower than that recorded for North Atlantic LFPWs in the Faroe Islands (59 years; Martin and Rothery 1993) and Newfoundland (56.5 years; Sergeant 1962; Kasuya et al. 1988), where longevity exceeded 50 years (Table 15.1). The smaller sample size in this study, compared with the availability of much larger datasets from North Atlantic drive fisheries (e.g., *n* = 1402; Martin and Rothery 1993), decreased our probability of sampling the rare old (possibly senescent) females. However, even if true reproductive senescence does occur in a small proportion of the oldest females, few live long enough to enter this phase (e.g., approximately 10% of females reach 40 years of age in Faroese studies; Bloch et al. 1993) that it is unlikely to represent a significant and functional part of the life history or social ecology of this species (Martin and Rothery 1993; Ellis et al. 2018a). Fewer than 5% of female North Atlantic LFPWs are reported to become reproductively senescent, and pregnancy can potentially continue throughout life (oldest pregnant female 55 years; Martin and Rothery 1993).

It has been suggested that the demographic consequences of certain life history characteristics are important in the evolution of post-reproductive lifespans

(Johnstone and Cant 2010; Croft et al. 2015; Ellis et al. 2018a; Nichols et al. 2020). However, such characteristics do not appear to necessitate the evolution of post-reproductive lifespans (Ellis et al. 2018a). Available evidence suggests that LFPWs exhibit similar life history characteristics and social structure to SFPWs and the other three odontocete species for which a substantial post-reproductive lifespan has been identified (resident killer whales, beluga whales, and narwhal; Ellis et al. 2018a; Nichols et al. 2020). For example, these species are all sexually dimorphic and highly social, have low lifetime productivity, and are known or believed to exist in stable matrilineal groups of closely related females with increasing local relatedness as females age, strong mother-offspring associations, and a long period of dependency (Bigg 1982; Kasuya and Marsh 1984; Heimlich-Boran 1993; Palsbøll et al. 1997; Whitehead and Mann 2000; Marcoux et al. 2009; Colbeck et al. 2013; O'Corry-Crowe et al. 2018; Nichols et al. 2020). However, no significant post-reproductive lifespan has been observed in LFPWs, but instead an acceleration in mortality rate (Bloch et al. 1993; Martin and Rothery 1993; Ellis et al. 2018a, b; Betty 2019; Betty et al. 2022b).

Although the social structure is thought to be similar for both pilot whale species, the observed variation in post-reproductive life history strategies may be due in part to the social organization within stable social groups and the relative costs and benefits of cooperative foraging and intergenerational transfer of information. To have an evolutionary benefit, post-reproductive females must be able to contribute to increasing the fitness of relatives in their group. In both SPFWs and killer whales, inclusive fitness is increased by late-life helping and post-reproductive females fulfilling mother and grandmother roles within their group (Kasuya and Marsh 1984; Brent et al. 2015; Croft et al. 2017). Late-life helping has not been observed in LFPWs, though it is acknowledged that empirical data are very limited and difficult to collect. However, genetic studies of LFPWs from the North Atlantic (Faroe Island drive fishery) have revealed that the probability of pregnancy declines with the number of philopatric daughters (but not sons), implying females may refrain from breeding when they come into reproductive competition with their daughters (Nichols et al. 2020). It has been proposed that this apparent plasticity in the cessation of reproduction could represent a step toward the evolution of a post-reproductive lifespan or an alternative strategy to a fixed (and irreversible) post-reproductive lifespan (Nichols et al. 2020), though further investigation is required. Overall, there remains much to be discovered regarding the occurrence, evolution, and function of post-reproductive lifespans in pilot whales and other toothed whales.

15.4   Conclusions and Future Directions

This chapter summarizes what is currently known about the life history, sociobiology, and reproductive strategies of both LFPWs and SFPWs. We have added significantly to what is known of sex in pilot whales by documenting non-conceptive reproductive behaviors in sexually immature North Atlantic LFPWs, providing

evidence for male natal philopatry in Atlantic Naisa SFPWs, and reporting an apparent absence of post-reproductive lifespan in Southern Hemisphere LFPWs. However, there is much that remains unknown; we understand very little about conceptive and non-conceptive sexual behavior in free-ranging pilot whales. Up and coming drone studies may help assist, along with the collection of in situ morphometric data. In addition, genomic analyses of stable units/pods within different populations are needed to confirm if strict matrilineality occurs broadly across both species. Biologging several individuals of known sex in the same unit/pod will be useful to study behavior, fine-scale movements, how both sexes with stable associations interact, and whether males disperse (even briefly) for mating. Further, the evolutionary reason for the apparent differences in post-reproductive lifespans and mortality rate acceleration between LFPWs and SFPWs has not been established and warrants further investigation. Empirical data needed to examine reproductive senescence are often difficult to gather for long-lived species such as cetaceans. Longitudinal data are required to test hypotheses about how a post-reproductive lifespan might increase inclusive population fitness. However, mass stranding events provide valuable opportunities to investigate the interplay between social structure and life history strategies (e.g., the existence of post-reproductive females) across populations of both pilot whale species.

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Chapter 16
Sex in Killer Whales: Behavior, Exogamy, and the Evolution of Sexual Strategies in the Ocean's Apex Predator

Brianna M. Wright, Eva H. Stredulinsky, and John K. B. Ford

Abstract We present the current available knowledge about sexual behavior and mating systems in the killer whale, *Orcinus orca*, focusing primarily on the most well-studied ecotype, the Residents of the eastern North Pacific. Resident killer whales display lifetime natal philopatry of both sexes and thus form stable social groupings organized along maternal lines. Inbreeding is minimized via exogamous mating during multigroup aggregations that are diffusely seasonal. Male reproductive success in Residents is highly skewed, likely as a result of female mate choice or possibly intrasexual contest competition (or both), with only the largest and oldest males siring offspring. Female choice for males with large body and appendage sizes likely explains why killer whales as a species have evolved a high degree of sexual dimorphism. Scarring patterns and dorsal fin injuries indicate that breeding-aged males may occasionally engage in aggressive intrasexual competition to secure mates. Young male Residents appear to practice courtship behaviors by engaging in sociosexual play with other males. Coercive mating or mate-guarding in this species has not been observed and appears to be unlikely. Relative testes size, penis length, and penis tip morphology indicate that some sperm competition presumably exists in killer whales and likely co-evolved with female polyandry. Thus, both pre- and postcopulatory sexual selection may occur simultaneously in killer whales, and this species probably has a polygynandrous mating system in which both males and females can breed with multiple partners. Genetic pedigree studies of killer whale ecotypes besides Residents are needed to provide currently lacking but valuable information about mating patterns in other populations.

Keywords Exogamy · Female mate choice · Intrasexual aggression · Killer whale · Male-male sociosexual play · Matrilineal · Polygynandry · Sexual dimorphism · Sperm competition

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16.1 Introduction

Killer whales (*Orcinus orca*) occur in all major oceans and are the most cosmopolitan of cetaceans (Forney and Wade 2007). Generally, killer whales are most abundant in higher latitudes, with a preference for productive colder waters (Morin et al. 2015). Although currently considered a single species, several distinct forms or "ecotypes" of killer whale have been described (Ford et al. 2000; Pitman and Ensor 2003; Foote et al. 2009; Pitman et al. 2010; Durban et al. 2016). These ecotypes are genetically isolated and are distinguished by differences in diet, habitat preferences, foraging strategies, social organization, vocalizations, and morphology/color patterns (Morin et al. 2010, 2015). Ecotypes are also socially isolated from one another, with no intermixing even when their geographic ranges overlap (Ford et al. 1998, 2000; Matkin et al. 2007; Zerbini et al. 2007; Filatova et al. 2019). As relatively few killer whale populations around the world are well known enough to allow for ecotypic classification (de Bruyn et al. 2013), our primary focus in this chapter is on the ecotypes and populations of the eastern North Pacific. The killer whales of this region have received the longest-running and most extensive research attention and thus provide the best available information relevant to sexual strategies and mating systems.

16.1.1 Population Structure, Genetic Diversity, and Gene Flow

The three sympatric killer whale ecotypes that occur in the eastern North Pacific are exceptional in their long-standing and steadfast ecological divergence and social segregation. Although killer whales as a species are generalist apex predators, with varying degrees of dietary diversity, flexibility, and niche partitioning among populations, eastern North Pacific ecotypes exhibit rigid and disparate dietary specializations. Bigg's killer whales [1] are marine mammal eaters, while the Resident and Offshore ecotypes are both piscivorous, with Residents having a strong preference for salmon (*Oncorhynchus* spp.) and offshores appearing to specialize in shark predation (Ford et al. 1998, 2011a, 2014; Ford and Ellis 2006; Dahlheim et al. 2008). There is no evidence of social mixing or interbreeding among these ecotypes, despite their sympatric ranges (Hoelzel 1998; Barrett-Lennard 2000; Pilot et al. 2010). They diverged genetically from one another tens to hundreds of thousands of years ago (Morin et al. 2010) and are now reproductively isolated due to extreme social segregation and culturally inherited behavioral differences (e.g., dietary specialization and vocal dialects), which likely drive assortative mating (Barrett-Lennard

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[1] Bigg's killer whales were formerly known as Transient killer whales. Here we will use the term "Bigg's" to refer to the ecotype as a whole but retain "Transient" when referring to specific populations within the Bigg's ecotype, for instance, the AT1 Transients.

2000). This reproductive isolation has persisted for long enough that Bigg's killer whales are proposed to be a unique species (Morin et al. 2010).

Multiple populations can exist within an ecotype. For example, the Resident ecotype of the eastern North Pacific comprises three known populations: the southern, northern, and southern Alaska Residents. While these populations do not usually associate with one another, there is evidence of occasional interbreeding (Barrett-Lennard 2000; Ford et al. 2011b). For instance, microsatellite genotypes point to possible but rare instances of breeding between the northern Residents of British Columbia (BC) and the southern Alaska Residents (Barrett-Lennard 2000). However, these genetic patterns could also be due to historical associations and founding events, rather than being driven by contemporary mating patterns. Similarly, there is evidence of occasional gene flow in Bigg's killer whales between the inner West Coast Transient population (ranging coastally from southeastern Alaska to California) and the Gulf of Alaska Transient population (Barrett-Lennard 2000). Nevertheless, the vast majority of mating occurs within rather than between putative killer whale populations in the eastern North Pacific, and some of the smaller, more fragmentary populations are completely reproductively isolated (e.g., the endangered southern Residents and AT1 Transients) (Barrett-Lennard 2000; Pilot et al. 2010; Ford et al. 2011b; Parsons et al. 2013).

16.2 Life History Characteristics Relevant to Sexual Behavior in Killer Whales

Interpretation of the behavioral and social aspects of sexual interactions in killer whales requires an understanding of their physical characteristics, life history parameters, and reproductive physiology. Most detailed information on killer whale life history has been derived from long-term photo-identification studies of the two Resident populations in BC and Washington State (northern and southern Residents, respectively) (Olesiuk et al. 1990, 2005). The reliability and completeness of this information are due to the extremely stable matrilineal social structure of Residents, in which emigration from the natal group does not normally take place and individual mortalities can be documented with high confidence. Recent studies suggest that the life history parameters of these populations are also typical of at least one Resident population in Alaska (Matkin et al. 2014) and of sympatric Bigg's killer whales (Nielsen et al. 2021). Details of reproductive physiology in killer whales have mostly been obtained from studies on captive whales (Robeck et al. 1993; Duffield et al. 1995; Robeck et al. 2004; Katsumata et al. 2006; Robeck and Monfort 2006; Robeck et al. 2015; Katsumata et al. 2021) and may not always reflect patterns in wild populations.
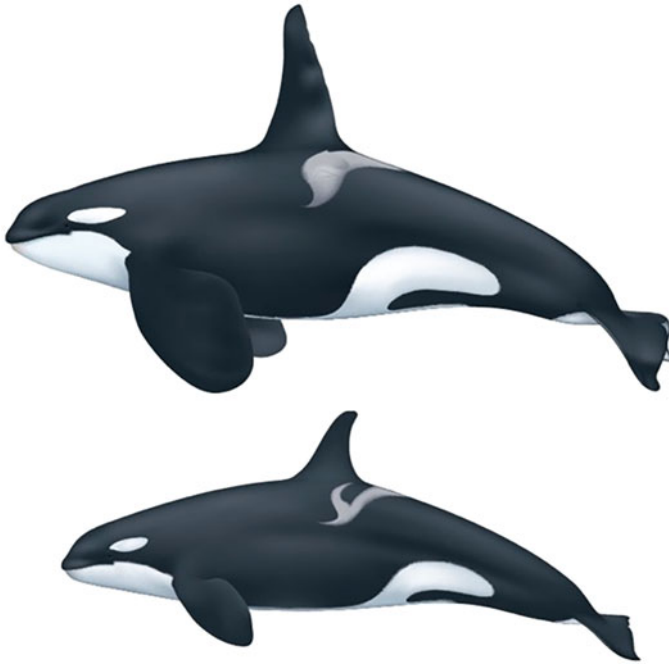
Fig. 16.1 Relative sizes of male (top) and female (bottom) Resident killer whales in coastal eastern North Pacific waters. Illustration courtesy of Uko Gorter

16.2.1 Sexual Dimorphism

Among the family Delphinidae, killer whales are noted for their body size and pronounced sexual dimorphism. They are the largest of the dolphins, with males attaining a maximum length of about 9.0 m and females 7.9 m, although average sizes are somewhat smaller in many populations (Pitman et al. 2007; Ford 2009; Groskreutz et al. 2019; Durban et al. 2021). Mature males are typically about 15% longer than females, but more significantly, males develop disproportionately larger appendages than females (Figs. 16.1 and 16.2). This includes the pectoral flippers, tail flukes, and dorsal fin, which may reach a height of 1.8 m in males, about twice that of females (Ford 2009). As discussed later, sexual dimorphism in killer whales is likely related to the mating system of these large dolphins.

16.2.2 Female Life History Characteristics

Like many cetaceans, female killer whales have a prolonged maturation period before becoming reproductive. They reach sexual maturity at about 10–11 y of

Fig. 16.2 Breaching adult male southern Resident killer whale, showing the disproportionately large pectoral flipper characteristic of this sexually dimorphic species. Photograph by Brian Gisborne, taken under research permit issued by Fisheries and Oceans Canada

age, when they begin estrous cycles averaging 41 d in duration (Robeck et al. 2004). Ovulation in killer whales is spontaneous rather than induced (Katsumata et al. 2006). After conception and a gestation period of 17–18 months, they give birth to a single calf (Duffield et al. 1995; Robeck et al. 2015). Hence, a female's first calf is typically born when she is 12–14 years old (Olesiuk et al. 1990, 2005). In Resident killer whales, calving appears to be diffusely seasonal with a peak in late autumn or winter. Given the gestation period, this suggests a peak in conceptions in late spring through summer. Seasonal variation in estrous cycling activity supports this conclusion, as slight increases are observed between March and August (Robeck et al. 1993). Neonate mortality is high, with one-third or more of calves estimated to die within their first six months (Olesiuk et al. 1990). Calves are nursed for at least one year but may start taking solid food from their mother while still nursing. The typical age at weaning in wild killer whales is not known but is likely between one and two years. Juveniles continue to be provisioned by their mothers and other close kin for many years post-weaning and, in the case of male offspring, potentially for the rest of their lives (Wright et al. 2016).

Calving intervals can be as short as two years but more typically average about five years (Olesiuk et al. 2005, Matkin et al. 2014). Females continue to produce calves through their 20s, but by their late 30s to early 40s, they become reproductively senescent (Olesiuk et al. 2005). Because of high neonate mortality, females only have an average of about five surviving calves over their average 25-year reproductive life span (Olesiuk et al. 2005). Female longevity is about 50 years on average, but some may live to 70–80 years (Olesiuk et al. 2005). Thus, their post-reproductive period averages about 10 years but may extend to 30–40 years (Olesiuk et al. 2005). By the time a female becomes an elderly matriarch, she may have three or four generations of living descendants within her matriline.

16.2.3   Male Life History Characteristics

As with females, male killer whales spend a prolonged period as juveniles or subadults before becoming sexually mature. In the wild, males appear to reach sexual maturity on average at about 13 years, as indicated by a period of rapid growth of the dorsal fin (Olesiuk et al. 2005). Puberty, marked by an increase in serum testosterone, likely starts about two years before this accelerated fin growth (Robeck and Monfort 2006). Serum testosterone also fluctuates seasonally in both pubertal and sexually mature males, with the highest concentrations occurring during the spring and early summer (Robeck and Monfort 2006; Katsumata et al. 2021). This seasonal pattern, similar to that seen in female estrous cycles, probably corresponds to diffuse seasonality in mating opportunities. Sperm concentrations, however, appear to be relatively consistent regardless of season (Robeck and Monfort 2006). Body mass and dorsal fin size continue to increase in males until they reach physical maturity at about 19–20 years Males may be sexually mature for many years before they become reproductively active and successfully mate when in their mid to late 20s. Average life expectancy for males is estimated to be about 30 years, with maximum longevity of about 50–60 years (Olesiuk et al. 2005).

16.3   Killer Whale Sociality

Many stages of mammalian reproduction are influenced by social structure and dynamics, including mate selection, sexual behavior, mating success, and parental investment. Killer whales are gregarious mammals that exhibit matrilineal social organization, where core social units are composed of closely related females and their offspring. These maternal groups are considered the foundation of all described killer whale societies despite significant ecological differences among them, including fish-eating populations in the western North Pacific (Ivkovich et al. 2010), eastern North Pacific (Bigg et al. 1990; Matkin et al. 1999), and eastern North Atlantic (Bisther and Vongraven 1995; Esteban et al. 2016), mammal-eating populations in the eastern North Pacific (Baird and Whitehead 2000) and eastern North Atlantic (Beck et al. 2012), and generalist populations in subantarctic waters (Guinet 1991; Tosh et al. 2008; Tixier et al. 2021). This kin-based organization benefits an animal's inclusive fitness through cooperative behaviors promoting division of labor (e.g., shared rearing of offspring (Sear and Mace 2008; Konrad et al. 2019) and sharing of resources such as prey (Wright et al. 2016)). In Resident killer whales, females have been shown to markedly improve the survival of their offspring and grandoffspring (Foster et al. 2012a; Nattrass et al. 2019), thus enhancing their inclusive fitness, particularly during their post-reproductive life span. Matrilineal social systems commonly arise when females mate with multiple males per estrous cycle; thus paternity is uncertain and consequently there is often little or no investment in offspring by fathers (Greene 1978). Males may increase inclusive

benefits by investing in the offspring of close matrilineal kin (i.e., a male investing in his sister's offspring instead of his own) (Wu et al. 2013). This bias in male investment may be particularly beneficial if resources are shared among the natal groups.

Generally, killer whales form fission-fusion societies, with temporally stable groups of maternally related individuals that may preferentially (i.e., nonrandomly) but temporarily associate with other groups. In fish-eating populations, these intergroup associations can result in multitiered social structures, where preferential but nonhierarchical, casual associations exist among groups (Tavares et al. 2017) or where preferential associations among groups are hierarchical, strong, long-lasting, and often predicted by maternal relatedness (Bigg et al. 1990; Matkin et al. 1999; Parsons et al. 2009; Ivkovich et al. 2010; Esteban et al. 2016). Conversely, more fluid social organization is also observed in some killer whale societies and is common in mammal-eating killer whales, where no definitive social structure beyond the core maternal unit exists and where social associations among groups are often weak and not necessarily predicted by kinship (Baird and Whitehead 2000; Beck et al. 2012; Reisinger et al. 2017; Denkinger et al. 2020). The social structure and dynamics of killer whale societies exhibit plasticity, often influenced by a population's ecology, as well as fluctuations in prey availability and demographics (Lusseau et al. 2004; Williams and Lusseau 2006; Parsons et al. 2009; Foster et al. 2012b; Esteban et al. 2016; Busson et al. 2019; Jordaan et al. 2021; Stredulinsky et al. 2021). For example, foraging strategies may dictate optimal group sizes, resulting in the core social units of mammal-eating populations being generally composed of fewer individuals than those of fish-eating populations (Baird and Dill 1996; Pitman and Ensor 2003; Zerbini et al. 2007; Beck et al. 2012; Higdon et al. 2012; Travers et al. 2018; Denkinger et al. 2020).

Killer whales exhibit natal philopatry, where individuals of both sexes remain with their natal group. The longevity of this group fidelity varies among killer whale populations and sexes. For example, in Bigg's populations, individuals of both sexes have been known to leave their natal groups at or near maturity (Baird and Dill 1996; Baird and Whitehead 2000). Dispersal in Bigg's killer whales appears to occur via female-biased budding events, with a decline in close social associations between daughters and their mothers as daughters age, beginning after a daughter has had at least one calf (Nielsen et al. 2023). Unlike females, male Bigg's killer whales tend to maintain strong social bonds with their mothers throughout life and are considered partially or fully philopatric (Nielsen et al. 2023). In contrast to Bigg's killer whales, Residents exhibit extreme bisexual social philopatry, where both sexes remain with their natal group throughout life and individual dispersal is exceedingly rare (Matkin et al. 1999; Ford et al. 2000; Parsons et al. 2009). Resident killer whales thus live in highly stable groups composed of a female, her offspring, and up to five generations of her descendants through maternal lines (Bigg et al. 1990). These maternal groups are the foundation of Resident killer whale society, which is hierarchically organized (Table 16.1). Since group size is not moderated by individual dispersal in Resident killer whales, matrilineal splitting provides the only mechanism by which new groups can form (Bigg et al. 1990; Stredulinsky et al. 2021).

Table 16.1 Resident killer whale social organization

Term	Definition
Maternal group	Individuals descended from a common direct maternal ancestor (matriarch) that always travel together (Bigg et al. 1990). Maternal groups are named after the most recent matriarch of the group and are the core social unit of Resident killer whales.
Pod	An assemblage of maternal groups that, on average, spend more than 50% of their time together (Bigg et al. 1990). Pods are composed of one or more maternal groups. Maternal groups found in the same pod likely share a common maternal ancestor (i.e., belonging to the same matriline). New pods form when group splitting occurs. Pod membership is typically stable but not permanent (Parsons et al. 2009); this social grouping may only maintain cohesion for a decade or less, depending on group size, demographics, relatedness, and/or ecological factors (Stredulinsky et al. 2021).
Clan	Maternal groups with vocal dialects that include shared call types. Call repertoires of clans can persist for at least 60 years and likely longer. Different clans are acoustically distinct and may represent separate matrilines (Ford 1991).
Population	A community of one or more clans that associate with one another. May be sympatric with but does not mix socially with other populations (Bigg et al. 1990).

A matriline denotes all individuals descended from a common maternal ancestor. Direct maternal ancestors refer to individuals from whom one descends in a direct line through mothers (i.e., mother, maternal grandmother, maternal grandmother's mother, etc.). Adapted from the "Social Groupings" section of Table 16.1 by Stredulinsky et al. (2021) – footnotes removed, used under CC BY

16.4   Exogamy and Inbreeding Avoidance in Eastern North Pacific Ecotypes

Little is known about mate choice and inbreeding in killer whales outside of the well-studied Resident ecotype of the eastern North Pacific, and so we focus on them here as a case study. We also briefly touch on possible mechanisms of inbreeding avoidance in the sympatric Bigg's killer whale. Despite neither sex dispersing from the natal group, Resident killer whales largely avoid inbreeding by mating with unrelated individuals during temporary multigroup associations (Barrett-Lennard 2000). These aggregations are sometimes termed "superpods" (Matkin et al. 1997) and are characterized by high levels of acoustic and social activity (Ford 1989) and reduced foraging rates (Hoelzel 1993). In northern Residents, the probability of encountering aggregations of whales from multiple acoustic clans increases during the summer and into the early autumn (Fig. 16.3). The majority of mating therefore likely occurs between June and October, a pattern that is also reflected in the seasonality of female estrous cycles, male serum testosterone levels, and calving. Copulation itself is rarely (if ever) observed in killer whales, likely because it happens underwater, can be hard to distinguish from other active social or play behaviors, and is thought to be very brief. Cetaceans have a fibroelastic (rather than vascular) penis, and thus it has been suggested that intromission is rapid and only lasts between 1 and 30 seconds; limited observations of mating behavior in wild
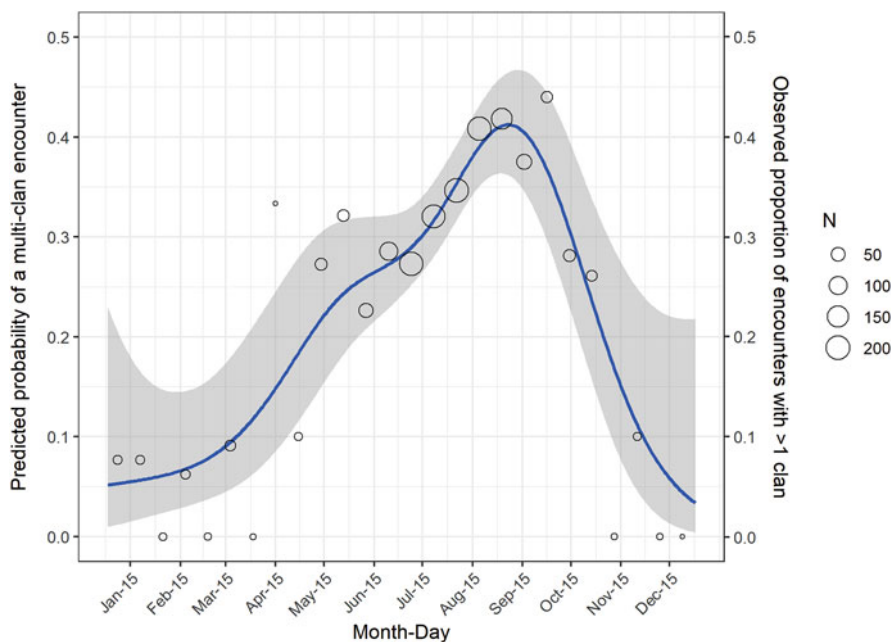
Fig. 16.3 Predicted probability (blue line) of multi-clan northern Resident encounters as a function of day of the year, modeled using photo-identification data collected by the Fisheries and Oceans Canada between 1973 and 2021. Gray shading indicates 95% confidence intervals, and open circles indicate the proportion of observed encounters in each two-week bin that included whales from more than one clan (circle size indicates the total number of encounters per bin). Model uncertainty is greater in the winter months due to the paucity of winter encounter data; however, the available data indicate that multi-clan encounters are much less likely during this season

and captive delphinids appear to support this claim (Slijper 1966; Markowitz et al. 2023, this book).

Similar large, multi-pod, or multi-clan aggregations are also reported in southern Alaska (Olsen et al. 2020) and Russian Far East (Filatova et al. 2009) Resident killer whale populations. Social interactions are frequent and energetic during these aggregations, while time spent foraging and resting decreases (Filatova et al. 2009; Olsen et al. 2020). In southern Alaska Residents, observations of social interactions increase with the overall number of pods and number of rarely encountered pods present (Olsen et al. 2020), and in Russian Far East Residents, social activity increases with both number of pods and number of acoustic clans present. This suggests that large aggregations of other fish-eating killer whale populations provide outbreeding opportunities for unrelated individuals to mate with one another (Filatova et al. 2009; Olsen et al. 2020), just as they do in northern and southern Residents. Rarely encountered groups of southern Alaska Residents that travel long distances beyond their normal home ranges may do so for this purpose (for instance moving between southeastern Alaska and Prince William Sound, a distance of more than 800 km) (Matkin et al. 1997). During such aggregations, mature males often

temporarily abandon their natal groups to closely follow reproductive females from other groups (Matkin et al. 1997). As in the northern Resident multi-clan model (Fig. 16.3), southern Alaska Residents form multi-pod aggregations from May to October (Olsen et al. 2020) but most often in July and August (Matkin et al. 1997), and Far East Russian Residents aggregate in large groups from late June to early September (Filatova et al. 2009).

Bigg's killer whales also socialize more and forage less as group size increases, probably for the same reason as Residents. Large aggregations of multiple maternal groups likely provide increased mating opportunities and facilitate outbreeding (Baird and Dill 1995). Outbreeding in Bigg's killer whales is also promoted by (or potentially drives) this ecotype's greater fluidity in social group membership relative to Resident killer whales, and consequently, Bigg's killer whales have a higher level of genetic diversity (Barrett-Lennard 2000). Dispersing from the natal group either permanently or temporarily, which is observed in both sexes of Bigg's but is especially prevalent in females (Nielsen et al. 2023), may reduce intragroup sexual competition and increase the probability of finding unrelated mates (Baird and Dill 1996; Baird and Whitehead 2000; Towers et al. 2019). Dispersing male Bigg's that travel alone rather than integrating themselves into other social groups (also known as "roving" males; Baird 1994) may do so to increase their chances of encountering and mating with as many unrelated females as possible; however, only eight instances of this type of permanent dispersal have been documented so far for males with living mothers (Nielsen et al. 2023). Other Bigg's males may become solitary without dispersing, since some Bigg's social groupings consist of only a post-reproductive matriarch and her adult son, who travels alone after his mother's death (Towers et al. 2019). Bigg's killer whales do not have kin-specific dialects at the matriline or pod level (Deecke et al. 2005; Ford 2019); hence, they lack the potential benefit of an acoustic outbreeding mechanism as is believed to exist in Residents (Barrett-Lennard 2000).

Exogamous mating is assumed in many Resident killer whale populations based on increases in sociosexual behavior during multi-pod and multi-clan aggregations and has been proven to occur in northern Residents. Paternity analyses revealed that northern Resident calves are sired by males from maternal groups other than their own and are usually sired by males from different pods as well as different acoustic clans (Barrett-Lennard 2000). Females are likely to benefit by selecting the least related males as mates, as these pairings produce offspring with the lowest likelihood of deleterious mutations, which may reduce calf survival. Exogamous mating is evident in the negative inbreeding coefficients calculated at pod (-0.112) and clan (-0.064) levels, which indicate that individuals from the same northern Resident pod or clan are more heterozygous than expected if mating was random (Barrett-Lennard 2000). Conversely, mating in southern Residents appears to be random in terms of the maternal groups that breeding pairs belong to (Ford et al. 2018), which may be due in part to small population size (i.e., limited number of potential mates). In a recent genetic pedigree of southern Residents, intra-pod matings were relatively common, and of 81 offspring for which both parents had been identified, 4 were inbred (Ford et al. 2018). These individuals were the products of two parent/

offspring, one half-sibling and one uncle/half-niece mating. A weak relationship was detected between multi-locus heterozygosity and survival in southern Residents, suggesting that inbreeding depression could be impacting this population (Ford et al. 2018). The lack of discernible exogamy in southern Residents, as well as the occurrence of inbreeding and intra-pod mating, is probably due to this population having only a single acoustic clan and a relatively small number of reproductive individuals. Male reproductive success in northern and southern Residents is highly variable and positively related to body size (Fearnbach et al. 2011), with the oldest, physically mature males siring the vast majority of offspring (Barrett-Lennard 2000; Ford et al. 2011b; Ford et al. 2018). For instance, over half of sampled southern Residents born since 1990 were sired by one of only two males, and the median male age at successful reproduction was 31 years (range = 16–59 years) (Ford et al. 2018). Thus, the small number of physically mature males of prime breeding age may also play a role in the prevalence of inbreeding in the southern Residents.

Mating decisions in Resident killer whales are likely guided by various social cues that allow individuals to distinguish between kin and nonkin, thus facilitating outbreeding. These cues include visual recognition of close maternal kin through associative learning (i.e., familiarity), as well as acoustic recognition of individual (Nousek et al. 2006) and group-specific call repertoires (Ford 1989, 1991; Barrett-Lennard 2000). Because vocal dialects are learned within maternal groups, they do not provide a means of identifying paternal kin, as fathers belong to different groups than their offspring and therefore do not share acoustic repertoires. Despite this, father-daughter matings have never been detected in northern Residents (Barrett-Lennard 2000) and only one such mating has occurred in southern Residents (Ford et al. 2018), so heritable mechanisms of paternal kin recognition may also exist. Conversely, Resident killer whales may have no system of paternal kin recognition, and father-daughter matings are largely prevented because older males engage in the majority of breeding. It is probable that most fathers have died by the time their daughters become reproductively mature (Wright et al. 2016; Ford et al. 2018).

16.5 Sexual Strategies and Mating Systems in Killer Whales

The highly skewed reproductive success of male Resident killer whales suggests that some selective mechanism prevents all but a few males from siring offspring. Variable male reproductive success could be driven either by intrasexual selection (such as contest competition, mate-guarding, coercive mating, and sperm competition) or by intersexual selection in which females choose mates based on specific traits (i.e., signal discrimination). We discuss the current scientific evidence for these possible mating tactics as they relate to Residents and other killer whale populations.

16.5.1 Female Mate Choice and the Evolution of Sexual Dimorphism and Modified Genitalia

The sexual dimorphism in body length and mass in killer whales indicates that there is a selective advantage conferred on males that attain large body sizes. This advantage is likely the driving factor behind provisioning behavior by northern Resident matriarchs, who preferentially share fish with their adult sons, probably as a form of kin selection that enhances the body condition of sons and thus bolsters their likelihood of reproductive success (Wright et al. 2016). While large body size could benefit males during aggressive contest competition, as large males are expected to be more successful in physical confrontations, it is more likely that large males experience greater reproductive success due to female mate choice (Ford et al. 2011b; Caspar and Begali 2022). Female preference for large body and appendage size (i.e., signals of male quality) probably initiated runaway selection favoring males that exhibit these traits, which are energetically costly to maintain. Large appendages (flukes, pectoral flippers, and dorsal fins) may reduce male maneuverability (Fig. 16.2) during aggressive interactions and thus may have evolved as a result of display competition rather than contest competition. Female mate choice explains the large degree of skew in male Resident killer whale reproductive success (Barrett-Lennard 2000; Ford et al. 2011b), with females allowing only the oldest and largest males to sire their offspring. This skew would be further enhanced if females engage in mate choice copying (as suggested for another matrilineal species, the sperm whale (Orbach 2019)). It is not known whether mate choice copying exists in female killer whales, but paternity analysis for similar aged calves belonging to the same maternal groups could provide more evidence to prove or refute this hypothesis. In addition to visual signals of male quality, female mate choice in killer whales is also likely guided by signals that promote outbreeding, such as vocal dialects.

Female killer whales may also exert control over which males sire their offspring through the evolution of modified genitalia. Vaginal folds seem to allow female cetaceans to physically obstruct the depth of penile penetration and thus lower the likelihood of fertilization. Consequently, a female could cause an undesirable male's sperm to be deposited farther from the ovum into blind end vaginal recesses by changing her body orientation during copulation, in a type of cryptic mate choice (Orbach et al. 2017). This tactic may be less costly to females than direct resistance of mating attempts by lower-quality males (Orbach et al. 2017). Antagonistic coevolution of penis morphology in male cetaceans probably arose in response to the evolving complexity of the female genital tract (Orbach et al. 2017). In killer whales, the penis has a thin elongated tip, with a conspicuous curl or bend (Fig. 16.4) that likely assists males in overcoming the barriers to fertilization posed by vaginal folds. It is also possible that the exaggerated size of male pectoral flippers (Fig. 16.2) may assist males in holding onto females during copulation, thus countering evasive movements.

Fig. 16.4 Male southern Resident killer whales engaging in sociosexual play behavior; the individual in the foreground is swimming on its side, with the pectoral fin and penis visible above the water's surface. The thin, elongated tip of the penis with its characteristic curl is also evident. A ten-year-old subadult male (J45) is visible swimming alongside. Photograph by Sara Tavares, taken under research permit issued by Fisheries and Oceans Canada

16.5.2 Male Intrasexual Aggression

While observations of aggressive interactions between male killer whales have not been reported, this may be partly due to the difficulty of detecting underwater behaviors. Such interactions may also escape notice if they are infrequent or of short duration, and because they are likely to occur during dynamic superpod encounters when large numbers of individuals are present, social groups are constantly mixing, and whales are engaging in other surface-active, percussive, or body contact behaviors. Aggression between males may fail to leave visible scars, for instance, if combatants strike one another with their flukes or use their rostrums as battering rams (Connor et al. 2000). However, tooth rake scars are reported in many odontocetes worldwide (McCann 1974; MacLeod 1998), including killer whales, and can be used to estimate the level of aggression between conspecifics (Scott et al. 2005; Robeck et al. 2019; Ham et al. 2021; Grimes et al. 2022). Tooth rake marks are common on the skin of both Resident and Bigg's killer whales of the eastern North Pacific and occur across all sex and age classes, indicating that at least mild aggressive behavior is a routine means of social communication (Robeck et al. 2019; Grimes et al. 2022). Since killer whales are apex predators, and since ecotypes actively avoid associating with one another (Bigg et al. 1990), tooth rakes are

assumed to arise from interactions between individuals belonging to the same population.

In northern Residents, rake mark frequency and density are significantly higher in adult males than in females or juveniles and also increase with male age (Robeck et al. 2019). This suggests that male northern Residents may engage in physical aggression as a means of competing for sexual partners or to establish dominance hierarchies related to reproduction. Aggressive interactions could function either to physically exclude other males from accessing females in estrus (i.e., contest competition) or could be ritualized displays meant to influence female mate choice (i.e., display competition). The latter is more likely, as previously discussed. Females might observe these interactions and allow the victor to mate or may select mates with more scarring as an indication of male quality (MacLeod 1998; Orbach 2019). Males may also use existing scars to evaluate the relative fighting ability or dominance rank of competitors and thus avoid costly aggressive interactions that they are unlikely to win (MacLeod 1998, Orbach 2019). The frequency of severe rake marks (covering >50% of the observable body area) was eight times greater in male northern Residents over 30 years of age than in males belonging to the next youngest age class (25–29 years) (Robeck et al. 2019). As the primary breeders, older males are the most likely to engage in aggressive contests with one another for access to females and thus would be expected to receive more rake marks than other demographic categories (Robeck et al. 2019). It is also possible that the higher incidence of rake marks and scarring evident on mature male northern Residents actually arises from adult females attempting to fend off unwanted mating attempts. Unless they are very deep, rake marks on killer whale skin heal over time and are generally thought to persist for <2 years (Bigg 1982; Robeck et al. 2019). Thus, the greater incidence of scarring on the oldest males reflects higher frequencies of recent aggressive interactions, rather than a lifetime accumulation of marks. Male-male aggressive interactions likely occur when multiple groups of Resident killer whales from different maternal groups aggregate temporarily for socializing and mating, given that males remain philopatric and mating is exogamous (Barrett-Lennard 2000).

Male Bigg's killer whales show a similar increase in rake mark acquisition with age when compared to male northern Residents (Robeck et al. 2019). Male Bigg's could receive these rake marks during intrasexual competition as well, although under slightly different circumstances given the more fluid social structure of this ecotype. There is evidence that lone (or "roving") males occasionally disperse from their natal groups at sexual maturity (Baird and Dill 1996), a behavior that may be related to searching for mating opportunities. However, adult female Bigg's killer whales also show a similar degree of rake mark injuries to that of adult males. Tooth rake marks in this ecotype may therefore result from dominance interactions that occur whenever dispersing individuals attempt to integrate themselves into new groups, whether for breeding or other purposes (Robeck et al. 2019). As in northern Residents and Bigg's, rake marks are common in all demographic categories of the southern Resident population, and males exhibit higher densities and frequencies of scarring than females (Grimes et al. 2022). However, older adult male Southern

residents (>20 years) have fewer rake marks than younger individuals (Grimes et al. 2022), the opposite pattern to northern Residents, implying that little aggression occurs among males of breeding age in this population. This could be due to the smaller size of the southern Resident population, which currently (as of 2022) contains only nine males >20 years and of these only three are >30 years (Center for Whale Research 2019). Intrasexual competition between males may therefore be less prevalent in southern Residents if only the oldest and largest males are allowed to mate and there are very few animals in contention for these breeding opportunities. Young adult males that have yet to attain their full body size would be unlikely to initiate aggressive interactions with larger competitors if contests are expected to end in injury or defeat.

Observations of adolescent and adult male killer whales with moderate to severe dorsal fin injuries provide further evidence of potential male-male aggression in this species. These injuries often begin with bite or rake marks on the dorsal fin that are clearly made by the teeth of conspecifics (Fig. 16.5), producing fin disfigurements that can become progressively worse over a span of months or even years (Fig. 16.6). The dorsal fins of male killer whales are almost twice as tall as those of females (Ford 2014) and, as discussed previously, are a secondary sexual trait that likely evolved as a signal of male fitness valued by potential mates (i.e., intersexual selection via female mate choice; Alves et al. 2017). As such, they are undoubtedly physiologically costly to maintain and may be particularly vulnerable to buckling or collapse; even seemingly minor wounds can lead to fairly dramatic fin disfigurements, including significant tissue loss at the fin tip, buckling of the trailing edge (Fig. 16.5), and occasionally partial or complete dorsal fin collapse (Fig. 16.6).

An analysis of photo-identification records from 2007 revealed that about 18% of northern Resident males and 4% of west coast Transient males (>12 years) display evidence of progressive dorsal fin injuries (Fisheries and Oceans Canada, unpublished report). On average, males are first injured at about 20 years of age (coinciding with the approximate onset of physically maturity, when they are more likely to compete with one another for breeding opportunities); however, these injuries do not appear to impact overall life span. Similar to northern Residents, 23% of adult males in a New Zealand fish-eating killer whale population showed evidence of abnormal, wavy, collapsing, or fully collapsed dorsal fins (Visser 1998). Two of the males with abnormal dorsal fins from New Zealand also had prolific tooth rake scars over large portions of their bodies. A more recent study of collapsed dorsal fins indicates that this type of abnormality is present in about 1–6% of photo-identified killer whales, depending on the region and population, and that the vast majority (>90%) of individuals with bent fins are males (Alves et al. 2017). The large size of male dorsal fins likely makes it an easy—and given its immobility, less dangerous—appendage for other whales to grasp with their teeth during aggressive interactions (see rake marks in Fig. 16.5, image *b*, and bite mark in Fig. 16.6, image *a*). For this reason, dorsal fins may be specifically targeted during such altercations if damaging another male's fin inflicts a future signaling (and therefore fitness) disadvantage. Once a male killer whale's dorsal fin has buckled or collapsed, photo-identification data suggest that it will not regain its previous shape. Because dorsal
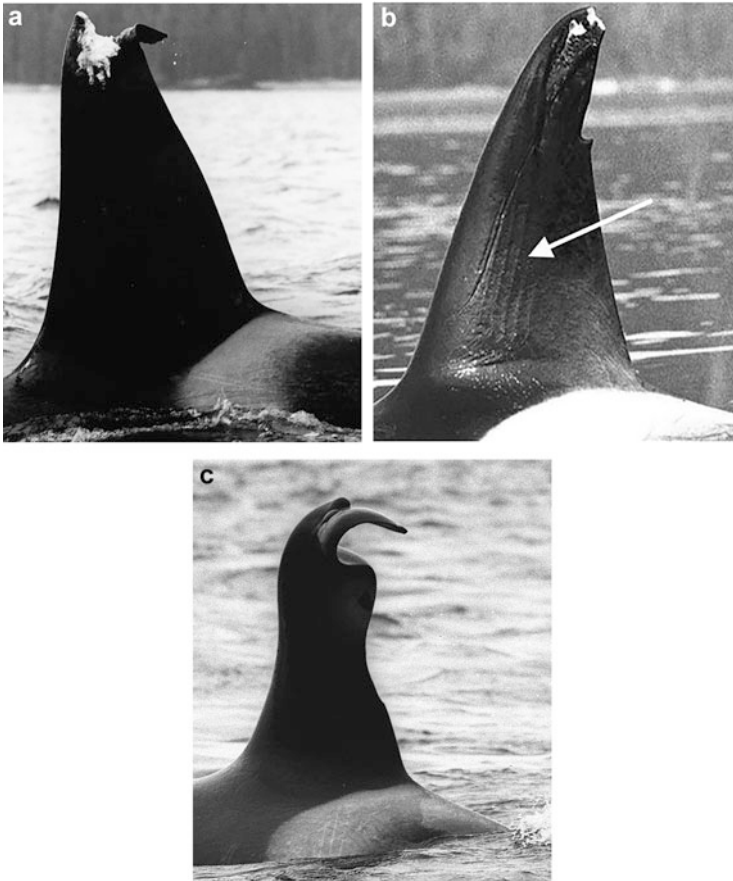
Fig. 16.5 Examples of dorsal fin wounds sustained by adult male northern Resident and Bigg's killer whales of the northeast Pacific, likely as a result of intrasexual aggression. Injuries include significant tissue loss (northern Resident killer whale H07 at 25 years old, photographed by Graeme Ellis, *a*), tooth rake marks (west coast Transient killer whale T74 at 24 years old, photographed by Dena Matkin, *b*), and buckling of the trailing edge (northern Resident H04 at 24 years old, photographed by John Ford, *c*). Photographs *a* and *c* were taken under research permit issued by Fisheries and Oceans Canada, and photograph *b* was taken under research permit issued to the North Gulf Oceanic Society by the National Oceanic and Atmospheric Administration (NOAA) and National Park Service (Glacier Bay National Park and Preserve)

fin injuries and associated cases of fin collapse are somewhat uncommon, we suspect that aggressive competition between males plays a minor role compared to female mate choice in killer whale mating systems. However, in populations where body scarring is more prevalent among mature males than other demographic classes (e.g., northern Residents) and where dorsal fin injuries appear to be inflicted by conspecifics, contest competition or ritualized displays of aggression may be occurring to some extent.
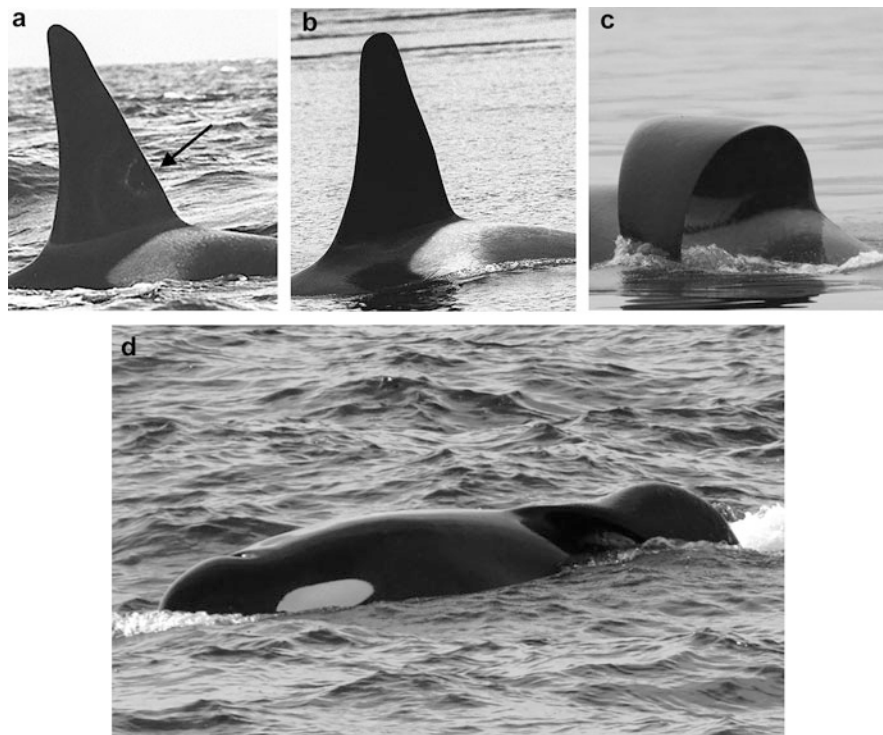
Fig. 16.6 Progression of dorsal fin collapse in the adult male northern Resident B13, beginning with a bite mark visible along the trailing edge (indicated with arrow), probably sustained from male-male intrasexual aggression. The first wound appeared when this individual was 16 years old (*a*) and the fin tip displayed evidence of curling by the following year (*b*, both photographs by Graeme Ellis). The collapse of the dorsal fin progressed until it was folded over to the left side of the whale's body about three years after the original wound occurred (*c*, photograph by Jared Towers), and it had completely collapsed by the time the whale was 20 years old (*d*, photograph by Mark Malleson); after which no further changes were observed. All photographs taken under research permit issued by Fisheries and Oceans Canada

16.5.3 Male-Male Sociosexual Play

In addition to potentially interacting aggressively, male northern Resident killer whales also frequently form male-only "play" groups in which males of all but the youngest age class (calves <3 years) engage in sociosexual behaviors (Rose 1992). These are temporary groupings, lasting from several minutes to hours. Groups typically consist of pairs, although groups of three or four killer whales occur in about a third of such events, and group membership is often fluid (Rose 1992). Adolescent males (12–25 years) participate more often than juveniles (<12 years) or adults (>25 years), and unrelated individuals are typically favored as partners over matrilineal kin (Rose 1992). Males in these groups exhibit active, at-surface behaviors including chasing, rubbing, head-butting, beak-to-urogenital slit body

orientations, percussive fluke slaps, aerial breaches, and penile displays (Fig. 16.4) (Jacobsen 1990; Rose 1992). On occasion, individuals attempt to insert their penises into the genital slits of other males in the group (Rose 1992). Physical contact is usually reciprocal rather than unilateral and declines in frequency with age (Jacobsen 1990; Rose 1992). Sociosexual play groups are an important component of male behavior in northern Residents, with individuals spending an average of >10% of their total activity budget in this manner (Rose 1992). As adolescents participate four times more often than adults, and because behaviors are typically reciprocal, it has been proposed that male-only social groupings in Resident killer whales represent affiliative play interactions, rather than functioning to establish or maintain dominance hierarchies (Rose 1992). These groupings likely allow young males that are sexually but not yet socially mature to practice their courtship skills and may provide an outlet for the libidos of adolescent males that are not yet old enough to successfully breed. While direct observations of mating behavior in killer whales are extremely rare (Barrett-Lennard 2000), adult male northern Residents have been observed interacting with females using stereotyped behaviors that mirror those performed in male-only play groups (e.g., reciprocal beak-genital body orientations) (Jacobsen 1990). This supports the hypothesis that play groups serve as practice opportunities for males to become proficient in courtship and mating behaviors (da Silva and Spinelli 2023, this book; Ham et al. 2023, this book). The purpose of reciprocal beak-genital body orientations in killer whale courtship behavior is currently unknown; however, similar contact behaviors have been observed in other delphinid species during sociosexual activity states (Bearzi and Politi 1999; Markowitz et al. 2023, this book). This behavior is unlikely to be related to olfactory or pheromone cues, as odontocetes lack the vomeronasal (Jacobsen's) organ and associated receptor genes used by terrestrial mammals for detecting reproductive pheromones, and unlike mysticetes, anatomical and genetic evidence suggests that odontocetes have little to no sense of smell (Kishida et al. 2007; Berta et al. 2014; Suzuki et al. 2018).

16.5.4 Coercive Mating, Male Breeding Alliances, and Infanticide

Coercive or forced mating by individual males seems unlikely in killer whales (or cetaceans in general), as herding or restraining females in an underwater, three-dimensional environment would prove difficult for a single male (Whitehead and Mann 2000). Adult female killer whales are also more maneuverable than mature males, given their smaller body and appendage sizes, and presumably this allows them to avoid unwanted mating attempts. In addition to greater maneuverability, females may also use physical aggression to defend themselves from unwanted copulations, possibly contributing to adult male body scarring (as described in previous section). Groups of males may employ social alliances to herd or gain reproductive access to females, a strategy that is rare in mammals but occurs in other

delphinids such as bottlenose dolphins (*Tursiops* sp.) (Wells et al. 1987; Connor et al. 2001; Möller et al. 2001; Parsons et al. 2003), Atlantic spotted dolphins (*Stenella frontalis*) (Elliser and Herzing 2014), and possibly Risso's dolphins (*Grampus griseus*) (Hartman et al. 2008). However, there is no evidence that this behavior occurs in killer whales. Alliance formation appears to be less prevalent in those bottlenose dolphin populations with more pronounced sexual size dimorphism (Connor et al. 2000), likely because selective pressure is acting on traits relevant to male contest competition, rather than on formation of male social bonds (Brightwell and Gibson 2023, this book). Consequently, male alliances are also unlikely to arise as a sexual strategy in killer whales, as they are the most sexually dimorphic of any dolphin species and display evidence of potential intrasexual aggression (tooth rake marks and dorsal fin injuries). Given the scarcity of observations of killer whale mating behavior in the wild, however, and the expected direct and inclusive fitness benefits (Krützen et al. 2003; Parsons et al. 2003) if brothers were to form mating coalitions within their maternal groups, it is still possible that male reproductive alliances could exist in this species. But it is much more probable that female killer whales have a large degree of control over which males they allow to mate, and their matrilineal social structure (resulting in strong bonds between female relatives) may also confer some protection if females band together to prevent forced copulations (Gowans et al. 2007).

Infanticide is a type of delayed sexual coercion in which adult males kill young that they are unlikely to have sired; this behavior may increase a male's reproductive success by causing postpartum females to return to estrus more quickly (Connor et al. 2000; Lukas and Huchard 2014). Although observed in other delphinid species (McEntee et al. 2023, this book), only one observation of infanticide has been reported in killer whales; a mature male Bigg's killer whale and his post-reproductive mother killed the neonate of a maternally unrelated female from the same population (Towers et al. 2018). With no other observations of infanticidal behavior, it is unclear whether infanticide is an aberrant behavior in killer whales or whether it serves an adaptive function by increasing a male killer whale's mating opportunities. Killer whales conform to some of the life history characteristics that promote the evolution of infanticide, namely, they are continuous breeders and relatively few males may monopolize the majority of reproduction (Lukas and Huchard 2014). However, it seems unlikely that infanticide constitutes a widespread sexual strategy if paternity is tenuous, because a male might kill his own offspring rather than a rival's. This is probably the case for many killer whale populations given their apparent lack of paternal kin recognition, the ephemeral nature of associations between mating pairs, and the likelihood that females mate with multiple males each estrous cycle. Mating with multiple males may constitute a sexual counterstrategy by which females confuse paternity to avoid infanticide (McEntee et al. 2023, this book), initiating an evolutionary arms race of male strategies related to sperm competition, such as increased relative testes size (Lukas and Huchard 2014), a trait which killer whales also exhibit. Species with large testes often experience secondary loss of infanticide (Lukas and Huchard 2014), so it is possible

that male killer whales engaged in infanticide more frequently in their evolutionary past but are currently transitioning away from this sexual strategy.

16.5.5   Sperm Competition and Polygynandrous Mating

The pronounced sexual dimorphism, signs of male-male aggression, and highly skewed male reproductive success evident in killer whales indicate a mating system in which males compete for access to estrus females (Connor et al. 2000). Competition to determine which males successfully sire offspring probably takes the form of displays that influence female mate choice, possibly in combination with occasional aggressive interactions between males. Selection for signals of male quality (e.g., body and appendage size) is therefore high. Additionally, female killer whales may mate with multiple males per estrous cycle, which is expected given their matrilineal social structure. It is likely that killer whales thus have a polygynandrous mating system in which individuals of both sexes mate with multiple partners, and therefore post-copulatory selection in the form of sperm competition may also occur. Sperm competition results when sperm from different males compete to fertilize the same ovum (Parker 1970; Smith 1984; Stockley and Purvis 1993). More sperm per ejaculate, greater ejaculate volume, and the ability to mate more frequently can all improve a male's likelihood of successfully siring offspring, and these traits are thus adaptive under sperm competition. Investment in testes mass as a percentage of body mass is used to infer the extent of sperm competition (and by association, the likelihood of females mating with multiple males) in mammals (Harcourt et al. 1981; Connor et al. 2000). Cetaceans tend to have slightly larger testes compared to similarly sized terrestrial mammals (Kenagy and Trombulak 1986; Aguilar and Monzon 1992), and most delphinids have larger testes than predicted by a regression of testes on body weights across all cetacean families (Aguilar and Monzon 1992). Killer whales are ranked intermediately (13th of 31 species analyzed) in this measurement (MacLeod 2010), suggesting that killer whale mating tactics involve some degree of sperm competition. Killer whales also have long penises relative to their body length (Carl 1946), a trait which occurs in cetacean species that engage in sperm competition, presumably because selection favors males that can deposit their sperm as close to the ovum as possible (Brownell and Ralls 1986; Dines et al. 2014). Furthermore, an elongated penis likely helps overcome the barriers presented by vaginal folds (Orbach et al. 2017) and may also have arisen as a counterstrategy for combating evasive movements by females during unwanted copulation attempts.

For continuous breeders like killer whales, larger males are predicted to achieve more favorable copulation timing, and smaller males should therefore invest more in sperm production to overcome this disadvantage (Stockley and Purvis 1993). Under this scenario, the correlation between testes and body size of individual males is predicted to weaken, which appears to hold true for killer whales (based on measurements from Norwegian and Antarctic populations) and further implies that sperm competition occurs to some extent (Stockley and Purvis 1993). In addition,

the transcription factor GATA4, which is involved in testes development (Kyrönlahti et al. 2011), shows a fixed difference in eastern North Pacific Residents compared to other killer whale ecotypes, a genetic change that could reflect increased sperm competition (Moura et al. 2014). Sperm competition may provide a selective advantage to male Residents, since mating occurs in large but temporary multigroup aggregations and it is presumably difficult for individual males to monopolize or guard access to receptive females. Unless females avoid mating with all but the highest-quality male they encounter, it is likely that they could mate with multiple males in quick succession during these superpod events.

16.5.6 The Role of Acoustic Behavior in Killer Whale Reproduction

Other than the role that acoustic dialects (Ford 1989, 1991) likely play in mate choice and inbreeding avoidance in Resident killer whales (Barrett-Lennard 2000), little is known about how vocalizations are used during courtship and mating in this species. Since killer whales are highly vocal and possess complex acoustic repertoires (Ford 1989, 1991), and given that acoustic signals travel much farther underwater than visual ones, vocal behavior is likely an important component of killer whale mating systems. Vocalizations by male animals can serve as displays of reproductive quality to attract nearby females (e.g., Eriksson and Wallin (1986)), stimulate female solicitation behaviors (e.g., McIntosh et al. (1978), Baker and Baker (1988)), influence female estrous cycles (McComb 1987), or advertise dominance to competing males (e.g., Krebs et al. (1978)). In cetaceans, male vocal behavior has been theoretically linked with mating strategies. Examples include mature male sperm whales using slow clicks (Weilgart and Whitehead 1988) and male Atlantic spotted dolphin alliances using synchronized vocalizations (Herzing 2015) to drive away potential competitors, male bottlenose dolphins using popping vocalizations as a threat signal to compel female consorts to remain close by (Smolker and Connor 1996), and male mysticetes using songs to either influence female mate choice or exclude competitors (Payne and McVay 1971; Glockner 1976; Croll et al. 2002; Schall et al. 2020; Kowarski et al. 2022). Vocalizations linked to reproduction could also be used by female killer whales—either to indicate to males that they are in estrus or conversely females might remain silent to avoid detection and mating attempts by undesirable males. Vocal behaviors are likely an incredibly important component of killer whale mating systems and one that remains to be explored fully.

16.6   Conclusions and Future Directions

This chapter summarizes the current available knowledge about sexual behavior and mating systems in the killer whale, largely based on data from the well-studied Resident ecotype of the eastern North Pacific. Killer whale mating patterns appear to be primarily driven by pre-copulatory intersexual selection, in which female preference for large body and appendage size in males has led to skewed male reproductive success and the evolution of extreme sexual dimorphism in this species. Displays of intrasexual aggression, as evidenced by tooth rake scars and dorsal fin injuries, may play a secondary role in determining which males successfully sire offspring. Females also appear to select mates based on maternal group membership, using acoustic and visual kin recognition to determine which males are least closely related to them, presumably as a means of inbreeding avoidance. Mating is thus more prevalent during the late spring through early fall, when large aggregations comprised of multiple maternal groups are more commonly observed. During adolescence, young male Resident killer whales practice courtship behaviors with other males in sociosexual play groups. Killer whales are probably polygynandrous (i.e., both sexes mate with multiple partners), and the coevolution of testes size, penis length, and penis morphology in males with genital tract complexity in females implies that post-copulatory sexual selection (i.e., sperm competition) may also occur in this species.

Additional genetic pedigree studies, particularly for ecotypes other than Residents, are needed to provide information about mating patterns for other populations of killer whales. Paternity analysis of similar-aged calves belonging to the same maternal groups could clarify whether female killer whales engage in mate choice copying, a behavior that could further skew male reproductive success. Focal-follows or other detailed behavioral studies of social interactions during multigroup aggregations (i.e., superpods), including the application of emerging data collection technologies such as unoccupied aerial vehicle (UAV, Ramos et al. 2023, this book) and underwater video footage, could provide the first descriptions of courtship and copulation behavior in wild killer whales. Acoustic recordings made in conjunction with these visual observation techniques would help clarify the role of vocal behaviors in killer whale mating systems. These approaches could also be used to confirm the existence of male intrasexual aggression and elucidate its potential role in breeding success.

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Chapter 17
Beaked Whale Sexual Dimorphism, Mating Strategies, and Diversification

Filipe Alves, Sarah L. Mesnick, Massimiliano Rosso, and Robert L. Pitman

Abstract Beaked whales (Ziphiidae), with 24 currently recognized species, are arguably the least known large animals on the planet, despite being widespread and at times abundant. *Mesoplodon*, with 16 currently recognized species, is by far the most speciose cetacean genus. Recent technological and taxonomic advances, long-term photographic-identification studies, and historical whaling data have allowed new insights into their social and mating strategies and how these may have driven diversification within the family. In most beaked whales, only adult males have exposed teeth—a single "tusk" erupts from each lower jaw and is used in contests to determine access to breeding females. How forcefully males of different species engage conspecifics varies widely based mainly on differences in tooth size/ placement and jaw structure. We compiled data on key dimorphic traits including beak modification, tooth size and location, and prevalence of scarring in adults, for all beaked whales. More detailed information is given for the four best-studied species—northern bottlenose whale and Baird's, Cuvier's, and Blainville's beaked whales. We then compared these traits with what is known about their social organization and reproductive anatomy to make inferences about mating strategies. More aggressive species tend to occur in small groups with only one dominant adult male present and have small testes relative to body size, suggesting that male reproductive success is largely determined by precopulatory contest competition

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and female defense polygyny. Less aggressive species tend to occur (at least at times) in larger, mixed-sex groups with multiple adult males present, and females may mate with multiple males, which favors postcopulatory sperm competition and polygynandry. We further discuss how conflicting pressures arising from males using their beaks for both feeding and fighting could have sparked an adaptive radiation in tooth development and beak morphology among beaked whales, especially within *Mesoplodon*, which would have had implications for male-male competition, social structure, sexual strategies, and, perhaps ultimately, evolutionary divergence and speciation within this group.

Keywords Breeding · Color patterning · Life history · Male aggressiveness · Reproductive anatomy · Scarring patterns · Sexual competition · Social organization · Testis size · Tusks · Ziphiidae

17.1 Introduction

Sexual selection is responsible for the evolution of some of nature's most extravagant animal features, endowing males with showy ornaments to attract receptive females and equipping others with an arsenal of weapons to fight for them (Darwin 1871; Emlen 2008). As part of a strategy for acquiring mates in the deep oceans of the world, male beaked whales (Ziphiidae) famously use the combat option, brandishing enlarged tusks or a weaponized melon for their armament and a reinforced beak for armor (Heyning 1984; Gowans and Rendell 1999; MacLeod 2002; Lambert et al. 2010). These whales comprise the second most diverse cetacean family (after Delphinidae), and although the evolutionary drivers behind this diversification are unknown, sexual selection, in which males battle over reproductive access to females, likely plays an important role (Dalebout et al. 2008; Steeman et al. 2009; Lambert et al. 2011). In this chapter, we review morphological diversity among extant beaked whales and discuss possible socio-ecological drivers of this diversification.

17.2 Background

Beaked whales first appeared in the early Miocene, and by the middle Miocene, a major diversification had occurred, related to sexually selected modifications to the beak and teeth for mandibular tusk development in adult males (Lambert et al. 2010; Bianucci et al. 2016; Ramassamy 2016). Today, there are 24 known species in 6 genera: *Berardius*, *Hyperoodon*, *Indopacetus*, *Tasmacetus*, and *Ziphius* include 8 species, while *Mesoplodon* is by far the most speciose cetacean genus, with 16 currently recognized species. All extant beaked whales are deep divers that prey mainly on meso- and benthopelagic fish and squids (MacLeod and D'Amico

2006). They show a remarkable range of sexual dimorphism, most of which pertains to modification to male feeding and fighting apparatus—teeth and beaks.

Beaked whales are thought to feed primarily by suction feeding, which has resulted in a significant reduction in the number of functional teeth (Heyning and Mead 1996; Werth 2006). The females and young in most species do not have erupted teeth, while adult males retain one or two pairs of enlarged mandibular teeth as tusks for fighting with other males, most likely used to establish dominance and determine access to breeding females (Heyning 1989; MacLeod 2002). Interestingly, despite the prevalence and severity of scarring among males of various species, there are no reported observations of males using their tusks in actual battles. There is a wide and diagnostic array of variations in the number, shape, size, and location of teeth in beaked whales (Table 17.1; Mead 1989; Dalebout et al. 2008). In adult males of most species, a single, enlarged tooth erupts from each lower jaw. The exceptions are from the two most basal genera (Bianucci et al. 2016; McGowen et al. 2020); in *Berardius* spp., both sexes have a pair of teeth in the tip of each lower jaw, and in Shepherd's beaked whale *Tasmacetus shepherdi*, both sexes have a full set of functional teeth, with an enlarged tooth at the tip of each mandible that erupts only in adult males. In the four remaining genera (*Hyperoodon, Ziphius*, *Indopacetus*, *Mesoplodon*), males retain a single pair of functional teeth. Given the prevalence of contest competition among living ziphiids, they show surprisingly little sexual size dimorphism (Box 17.1): except for the northern bottlenose whale *H. ampullatus* in which males are considerably larger than females (Gowans et al. 2000). Overall, for species in which there are data, there is little dimorphism in body size, although females may be slightly larger in some species (Table 17.1; MacLeod 2006, 2018).

Box 17.1 Size Relationships Between Sexes

When males engage in direct combat for females, males are usually larger than females (Clutton-Brock 1989; e.g., sperm whales *Physeter macrocephalus*, Amazon river dolphins *Inia geoffrensis*; Dines et al. 2015). When males are much larger than females, they are not the optimal size for foraging and traveling with groups of females and young (Weiss et al. 2021) and may spatially or socially segregate (Whitehead 2003; Martin and da Silva 2004; Foster et al. 2012). Most beaked whales are monomorphic with respect to body size (MacLeod 2006)—is it because males generally occupy the same range and habitats year-round as females? Agility could aid in contests between males, or males might form alliances to increase their "size" (Tolley et al. 1995).

Based on an analysis of group sizes, MacLeod and D'Amico (2006) suggested that there may be two different social structures among beaked whale species. Longman's *I. pacificus* and Baird's beaked whales *B. bairdii* occur in large groups (up to 100 individuals, mean group size of 19 and 8 individuals, respectively). In contrast, Cuvier's beaked whale *Z. cavirostris*, bottlenose whales *Hyperoodon* spp.,

Table 17.1 Aggression in male beaked whales

Species	Body length, median (maximum), m[a]	Tusk size[b]	Beak reinforcement[c]	Tooth rake scarring[d]	Rostrum aspect ratio[e]	Male associations[f]	Group size[g]	Testes weight, g[h]
Aggression: high								
Northern bottlenose whale[i] *Hyperoodon ampullatus*	6.4 (10)	Small	Major	Light	Medium	Male alliances; male groups; mixed groups	Small	2600
Southern bottlenose whale *Hyperoodon planifrons*	6.4 (6.9)	Small	Major	Heavy	Medium	?	Small	?
Andrew's beaked whale *Mesoplodon bowdoini*	4.2 (4.4)	Large	Major	Heavy	High	?	Small	?
Hubbs' beaked whale *Mesoplodon carlhubbsi*	4.7 (5.3)	Large	Minor	Heavy	High	?	Small	500
Blainville's beaked whale *Mesoplodon densirostris*	4.1 (4.6)	Large	Major	Heavy	High	None	Small	?
Pygmy beaked whale *Mesoplodon peruvianus*	(3.9)	Small?	Major	Heavy	High?	?	Small	?
Stejneger's beaked whale *Mesoplodon stejnegeri*	4.8 (5.7)	Large	Major	Heavy	High	?	Small	?
Cuvier's beaked whale *Ziphius cavirostris*	5.5 (6.9)	Large	Major	Heavy	Low	Male alliances; male groups; mixed groups	Small	8300
Aggression: Low to moderate								
Arnoux's beaked whale[j] *Berardius arnuxii*	(9.3)	Large	Minor	Heavy (both sexes)	Medium	Mixed groups	Large	?
Baird's beaked whale[j] *Berardius bairdii*	9.6 (11.1)	Large	Minor	Heavy (both sexes)	Medium	Male alliances; male groups; mixed groups	Large	17,400

Sato's beaked whale[j] *Berardius minimus*	6.6 (6.9)	Large?	Minor	Light? (both sexes?)	Medium	Mixed groups	Small?	?
Longman's beaked whale *Indopacetus pacificus*	(6.5)	Small	Minor	Light	High	Mixed groups	Large	?
Sowerby's beaked whale *Mesoplodon bidens*	4.5 (5.5)	Small	Minor	Light	High	Male groups	Small	?
Ramari's beaked whale *Mesoplodon eueu*	5.3	Small	Minor?	?	High	?	Small	?
Gervais' beaked whale *Mesoplodon europaeus*	4.1 (5.6)	Small	Minor	Light	High	?	Small	320
Ginkgo-toothed whale *Mesoplodon ginkgodens*	4.9 (5.1)	Large	Major	Light	High	?	Small	280
Gray's beaked whale *Mesoplodon grayi*	4.5 (5.6)	Small	Minor	Light	High	Male groups Mixed groups	Small	199
Hector's beaked whale *Mesoplodon hectori*	3.7 (4.3)	Small	Minor	?	High	?	Small	?
Deraniyagala's beaked whale *Mesoplodon hotaula*	(4.3)	Large	Minor	?	High	?	Small	?
Strap-toothed beaked whale *Mesoplodon layardii*	5.1 (5.8)	Large	Minor	Light	High	Male groups	Small	?
True's beaked whale *Mesoplodon mirus*	4.6 (5.3)	Small	Minor	Light	High	?	Small	327
Perrin's beaked whale *Mesoplodon perrini*	(3.9)	Large?	Minor	?	High	?	Small	200
Spade-toothed beaked whale *Mesoplodon traversii*	(5.3)	Large	Minor	?	High	?	Small	?

(continued)

Table 17.1 (continued)

Species	Body length, median (maximum), m[a]	Tusk size[b]	Beak reinforcement[c]	Tooth rake scarring[d]	Rostrum aspect ratio[e]	Male associations[f]	Group size[g]	Testes weight, g[h]
Shepherd's beaked whale *Tasmacetus shepherdi*	(7)	Small	Minor	Light	Medium	?	Medium?	?

Species are listed according to the Committee on Taxonomy (2022), in two categories: "high" or "moderate/low" aggression based on a subjective ranking of the size of the tusk and degree of beak reinforcement to support combat and prevalence and severity of conspecific tooth rake scarring. Also indicated are body length, rostrum length/width ratio, male associations, group size, and testis weight

[a] Median (and maximum) body length in meters for males from Table 17.1 in MacLeod (2006), Dalebout et al. (2012), Thompson et al. (2012), Yamada et al. (2019), and Carroll et al. (2021). When males were not available, lengths are from females or individuals of unknown sex

[b] Relative total tooth size (not just exposed portion); from illustrations in Mead (1989), measurements in Ellis and Mead (2017), and subjective scoring by the authors

[c] Modifications to the beak to support combat, including meso-rostral ossification, development of maxillary crests, and additional bone deposition on the mandibles; from Mead (1989), Ellis and Mead (2017), descriptions in Jefferson et al. (2015), and subjective scoring by the authors

[d] Prevalence and severity of conspecific scarring; from descriptions in Jefferson et al. (2015) and subjective scoring by the authors

[e] Rostrum length/width ratio: high, longer and thinner, and low, shorter and broader; from photos and illustrations of skulls in Mead (1989), van Helden et al. (2002), Dalebout et al. (2002, 2014), Jefferson et al. (2015), and subjectively scored by the authors

[f] Adult male social associations: Males observed together in long-term affiliations ("male alliances"); in groups (groups of adult males or groups of males of mixed ages, "male groups"); and/or observed with groups of females ("mixed groups"). Descriptions from the literature, including Benjaminsen and Christensen (1979), Lien et al. (1990), Hooker and Baird (1999a, b), Gowans et al. (2001), Pitman and Lynn (2001), Urbán et al. (2007), Falcone et al. (2009), Fedutin et al. (2015), Jefferson et al. (2015), Baird (2019), and Pitman et al. (2019)

[g] Group size; from MacLeod and D'Amico (2006), Donnelly et al. (2018), Fedutin et al. (2015), and authors' personal observations

[h] Maximum testes weight (total weight in grams of both testes, without the epididymides, when possible; from Benjaminsen and Christensen (1979), Delhon et al. (1987), and Dines et al. (2015)

[i] Unlike other beaked whales, northern bottlenose whales are known for headbutting rather than using their tusks in combat with rivals

[j] Unlike other beaked whales, teeth erupt in both adult male and female *Berardius* and tooth rake marks are common on individuals of both sexes

and mesoplodonts *Mesoplodon* spp. occur in small groups (averages ranging from 2 to 4 individuals, maximum group size ~20). Among these, large groups usually comprise multiple adult males with females and immatures, while small groups typically include one or two adult males together with females and immatures (MacLeod and D'Amico 2006; MacLeod 2018).

17.3   Four Species of Beaked Whales

Detailed information about the biology and social organization for the four best-known beaked whale species is summarized below, highlighting what is known about their mating strategies.

17.3.1   *Northern Bottlenose Whale*

The northern bottlenose whale is endemic to the North Atlantic, where it inhabits temperate to arctic waters, with an apparent preference for deep continental slope areas (> 500 m; Moors-Murphy 2018). Large-scale migratory movements are unresolved, as some suggest that the whales undertake seasonal north/south migrations (Gray and Flower 1882; Benjaminsen and Christensen 1979; MacLeod et al. 2004) while others suggest inshore/offshore movements because sightings are observed in part of their range year-round (Whitehead and Hooker 2012).

Life history information comes largely from whaling and stranding data (Benjaminsen 1972; Christensen 1973; Benjaminsen and Christensen 1979; Mead 1989). After a gestation of about 12 months, calves are born at a length of ~3.5 m. Lactation was estimated to last 1 year with a calving interval of 2–3 years, but recent work using stable isotopes from dentine suggests that calves do not wean until 3–4 years of age (Feyrer et al. 2020). Females reach sexual maturity at a shorter mean length than males (6.9 vs. 7.5 m, respectively) but at an older mean age (11 vs. 7–11 years, respectively, based on dental layers). At physical maturity, males are approximately 1 m longer than females and live approximately ten years longer (maximum length and longevity based on dental layers: males, 9.8 m, 37 years, and females, 8.7 m, 27 years). The mean testes weight for mature males was 1.2 kg/pair with a maximum of 2.6 kg.

Northern bottlenose whales appear to be unique among beaked whales in that they apparently use their prominent maxillary crests and enlarged melons (Box 17.2, Fig. 17.1) in head-butting contests (Gowans and Rendell 1999). Southern bottlenose whales *H. planifrons* have only moderately developed maxillary crests; flattened melons have not been reported, and head-butting has not been documented. The high degree of synchronicity in diving and circling behavior observed during at least four instances of head-butting suggests some degree of ritualization, perhaps similar to the "parallel" walks of red deer stags *Cervus elaphus* (Gowans and Rendell 1999).

Fig. 17.1 Top: An adult male southern bottlenose whale in the Southern Ocean; the tooth rake marks on the body appear to be random squiggles. Photo: Stephen E. Gast. Bottom: The head and beak of an adult male northern bottlenose whale in the Gully, Nova Scotia. As is often the case, there are no visibly erupted teeth. Photo: Whitehead Lab, Dalhousie University

Groups are generally small (mean 3.6, range 1–22), and there is some evidence of sexual segregation at sea (MacLeod and D'Amico 2006). Females show fission/fusion associations, while males sometimes form longer term (1–2 years) alliances—a situation more like the common bottlenose dolphin *Tursiops truncatus* (Brightwell and Gibson 2023, this book) than the ecologically similar sperm whale (Gowans et al. 2001). Geographical segregation of the sexes was noted by early whalers (Gray and Flower 1882); old males sometimes form groups of 4–5 animals, and females with calves sometimes form separate groups, especially in June (Ohlin 1893). The

small testes (relative to body size) are consistent with a large investment in precopulatory contest competition, and it is possible that large males or male alliances prevent other males from accessing estrous females.

Box 17.2 Bottlenose Whales: Butting Heads

Compared to northern bottlenose whales, adult male southern bottlenose whales have a moderately developed melon and a single pair of teeth that erupts from the tip of the lower jaw; like most beaked whales, they are often heavily scarred with rake marks from other males. By contrast, adult male northern bottlenose whales have apical teeth which are rarely visible and their rake marks are inconspicuous. Instead, older males have a massively developed melon that sometimes bulges out over the tip of the relatively short beak; it is so imposing that it appears to restrict the male's ability to make contact with their teeth during aggressive encounters. They have been observed to headbutt (Gowans and Rendell 1999), possibly to resolve their disputes, and this probably explains their conspicuously flattened foreheads (Fig. 17.1). The skull of the adult male northern bottlenose whales has a pair of massive boney (maxillary) crests that rise up from the rostrum; these are not found in females (or any other beaked whales) and are presumably used to buttress its weaponized melon.

17.3.2   Baird's Beaked Whale

Largely because it has been targeted by (mostly Japanese) whalers, Baird's beaked whale is one of the best-known ziphiids. It is distributed mostly over deep (1000–3000 m), continental slope waters around the temperate North Pacific, including the Sea of Japan, Sea of Okhotsk, and Bering Sea (Jefferson et al. 2015; Kasuya 2017). Off the Pacific coast of Japan, it occurs along continental shelf margins during the summer (May–November) and then moves to unknown wintering grounds (Kasuya and Miyashita 1997; Kasuya 2017). School size is generally large for a beaked whale, usually ranging from 3 to 20 individuals (mean 7.9, range 1–100; MacLeod and D'Amico 2006; Kasuya 2017); groups at the surface are typically tightly bunched, often seemingly in contact with each other (Fig. 17.2; Balcomb 1989).

Life history information for Baird's beaked whale was recently summarized by Kasuya (2017). After a gestation of approximately 17 months, a single calf is born at a length of about 4.5 m; fully mature individuals reach 11 m with females slightly longer than males (40 cm). Compared to males, females attain sexual maturity at an older age (10–15 vs. 6–11 years), at a longer body length (9.8–11.1 vs. 9.1–10.7 m). Based on tooth layer counts, males live longer than females by ~30 years (maximum 84 and 54 years., respectively). The mean testis weight (i.e., mean of both testes) of mature males ranged from 1.4 to 8.7 kg with an asymptote of 5.3 kg at age 40 years.

Fig. 17.2 Baird's beaked whale is the largest beaked whale (to 11 m); it occurs in some of the largest groups (to 100 animals), but at the surface, it forms tight groups, perhaps as a defense against killer whales *Orcinus orca*. Older individuals, of both sexes, are heavily raked from the teeth of conspecifics as shown in this group off Southern California. Photo: Delaney Trowbridge

While histological data can detect the onset of sexual maturity, the testes continue to grow until the whale is 30–40 years old, and it is possible that only these old males participate in reproduction.

Berardius spp. are unique among extant beaked whales as both sexes have erupted teeth and extensive tooth rake marks. Adult males are often more heavily scarred than females but probably only because they live longer than females (Kasuya 2017). This suggests that within this genus, teeth are not used to establish breeding hierarchies among mature males but instead have been retained for mediating social interactions among individuals of both sexes. There is also evidence of sexual segregation at sea, including a stranding of ten mature males in Mexico (Urbán et al. 2007); schooling is probably adaptive for evading predators such as killer whales, but pregnant or lactating females may also want to avoid the attentions of aggressive males, which could lead to segregation (Weiss et al. 2021). Fedutin et al. (2015) presented evidence of a fission/fusion society but with some stable alliances among older animals, possibly males. *Berardius* is the least sexually dimorphic beaked whale, and testes are larger relative to body size than in most other beaked whales (MacLeod 2010; Dines et al. 2015), indicating that males are less likely to be able to monopolize access to females through contest competition, that females may mate with multiple males, and that postcopulatory sperm competition likely occurs. Kasuya (2017) noted the unusual life history characteristics of

Baird's beaked whale (lower male mortality resulting in an excess of mature males) and speculated that older males, perhaps relatives, may help in rearing young.

17.3.3   Cuvier's Beaked Whale

Cuvier's beaked whale has the most extensive range of any beaked whale species (Heyning 2002), being widely distributed in offshore waters of all oceans, in both hemispheres, excluding only polar waters (Heyning and Mead 2009). Populations often occur in restricted ranges (Cioffi et al. 2021); photographic identification and telemetry data have found a high degree of individual residency (Baird et al. 2008; Foley et al. 2021; Tenan et al. 2023), which can lead to genetic structuring, especially in the presence of biogeographical barriers (Onoufriou et al. 2022). One effect of genetic structuring is the morphological variation with regional differences in osteological cranial characters (Heyning 1989).

The average length at sexual maturity is 5.8 m for females (min 5.27 m) and 5.5 m for males (min 5.1 m; Heyning 1989; Santos et al. 2007). The largest reported length was 6.9 m (Heyning 1989), but there appears to be no difference in length between the sexes, and the ratio of female-to-male maximum length varies from 96% to 104% (Omura et al. 1955; Nishiwaki and Oguro 1972; MacLeod 2006; Box 17.1). The modal length (all age classes combined) reported from stranding data was 5.5–5.6 m (MacLeod 2006). Gestation period is unknown but probably around 12 months, and the mean length at birth is 2.7 m. Interbirth interval is around 3–4 years and weaning occurs when the calf is 2–3 years (Tenan et al. 2023). There are no detailed studies of longevity, though females have been estimated to live to 30 years and males 36 years based on tooth layer counts (Heyning 1989). The two longest spans for documented individuals were 24 years for a female identified as a probable adult at first identification (Hawai'i; Baird 2019) and 22 years for a female with a calf at first identification (Mediterranean Sea; Tenan et al. 2023).

Median group size ranges between 2 (Hawai'i, Canary Islands, Mediterranean Sea) and 3 individuals (Cape Hatteras; Baird 2019); the largest group recorded was 11 individuals (Moulins et al. 2007). Groups may separate while foraging at depth and then rejoin during ascent (Alcázar-Treviño et al. 2021). Mixed age/sex class groups with multiple adult males are common (Falcone et al. 2009). Preliminary data from Hawai'i suggest that females with small calves may associate with other adults (Baird 2019). In the Mediterranean Sea, females with calves are more likely to associate with one or two adult males, while juvenile individuals are more likely to associate with other juveniles (Rosso et al. 2007). Using satellite-linked depth-recording tags, Cioffi et al. (2021) found that adult male-male pairs showed extended periods (weeks) of synchrony in diving behavior while all pairs that included an adult male with an individual of another age/sex class dove synchronously for less than one day.

The few photographic identification studies of Cuvier's beaked whales suggest a fission/fusion social structure without stable groups (Rosso et al. 2007; Falcone et al.

2009; Baird 2019), and although multi-male groups occur (McSweeney et al. 2007), heavy scarring on males (e.g., Rosso et al. (2011)) suggests that contest competition is the most likely mating strategy. However, in situations where males cannot monopolize access to females, theory predicts that selection will favor males that locate and inseminate females using both pre- and postcopulatory traits (Parker et al. 2013; Lüpold et al. 2014). Consistent with this theory, Cuvier's beaked whale has relatively larger testes relative to their body size than other ziphiids (MacLeod 2010; Dines et al. 2015), and postcopulatory sperm competition could also occur (Cioffi et al. 2021).

17.3.4   Blainville's Beaked Whale

The Blainville's beaked whale *M. densirostris* is the most widely distributed mesoplodont, with a circumglobal distribution in tropical and warm temperate waters, preferentially over deep and slope waters (MacLeod et al. 2006; Abecassis et al. 2015; Fernandez et al. 2021). Studies near oceanic islands in the Atlantic and Pacific have identified resident populations (reviewed in Hooker et al. (2019)).

Analysis of longitudinal datasets on associated individuals of known age class, sex, kinship, residency status, and spatiotemporal patterns reveals a social structure driven by available access to females (McSweeney et al. 2007; Badenas et al. 2022). Female defense polygyny by males has been suggested for populations in Hawai'i (McSweeney et al. 2007), the Bahamas (Claridge 2006), and Canary Islands (Suárez 2018); this hypothesis was also supported, along with high residency levels among adult females, at Madeira Island (Badenas et al. 2022). Associations are stronger between adult females and immatures than between either class and males. In Madeira, adult females associated with immatures for at least 3.5 years (Badenas et al. 2022), while in Hawai'i the maximum period has been about 2.5 years. This suggests that calves disperse between two and three years of age (Baird 2019), as supported by the lactation period that may last 2–3 years (MacLeod and D'Amico 2006). Blainville's beaked whales exhibit a general pattern of one adult male traveling with a small group of females for hours to months, and females have higher site fidelity and longer-term associations than males (Badenas et al. 2022), indicating a social structure driven by female philopatry and defense polygyny. Throughout their range, their social structure is stratified by age/sex class, with group sizes relatively small (mean 3–4 individuals, range 1–11; MacLeod and D'Amico 2006; Alves et al. 2018; Baird 2019).

Gestation period is unknown for Blainville's beaked whales but is probably about 12 months, and females give birth to a single calf, as inferred for most beaked whales (MacLeod 2018; Baird 2019). Based on a tooth layer count, a female that had recently become sexually mature was estimated to be nine years old, so it likely takes a decade to reach sexual maturity and give birth to the first calf (Claridge 2013; MacLeod 2018). Due to the males' large tusks, raised like horns above the top of the head, and extensive mandible reinforcement, Blainville's beaked whales incur the

Fig. 17.3 Top: A battle-scarred adult male Blainville's beaked whale with a broken right tooth in the Bahamas; beginning just behind the blowhole and running along the back are numerous longitudinal tooth rake furrows from other males. Photo: A. Friedlaender. Bottom: Adult males often show a conspicuous hump on the back, as in this animal photographed in the Canary Islands, which may be to blunt the impact of the gouging tusks. Photo: Crístel Reyes, University of La Laguna, with permit from Spanish Government

heaviest tooth rake damage among beaked whales (Box 17.3, Fig. 17.3). This along with small testes (relative to body size) is further evidence of contest competition as the dominant male mating strategy. Most groups are small, with only one male present (Badenas et al. 2022), so it is likely that roving males search and fight for receptive females and spend little time with them other than to mate, although some males may mate guard long enough to increase assurance of paternity.

> **Box 17.3 Jousting Beaked Whales?**
> The tooth rake marks on adult male Blainville's beaked whales tend to be concentrated on the top of the head and run down along the back (Fig. 17.3), which may only occur if two males pass by each other dorsum to dorsum (MacLeod 2002). For this maneuver to work, opponents would have to face each other, both turn 90° either left or right in the same direction, and charge at each other, similar to the jousting of knights on horseback. In addition to the deep furrows that they give each other, the occasional broken tooth (presumably from hitting the tooth of another whale) is testament to the violence inflicted. Male Blainville's also show a hump on their back just behind the blowhole—perhaps some extra padding to absorb impact, like the chest shield on male elephant seals *Mirounga* spp. Other mesoplodonts (e.g., pygmy and Hubbs' beaked whales) show tooth rake scarring more prevalent on the ventrum (Heyning 1984; Pitman and Lynn 2001), and it is possible that males of some species deliberately target the genital area.

17.4 Sexual Competition in Beaked Whales

Beaked whales appear to show marked variation in level of aggression during male-male contests (Heyning 1984; Dalebout et al. 2008), with the results of this ranging from the disfiguring furrows of Blainville's beaked whales (Fig. 17.3), to the often barely perceptible scratches of ginkgo-toothed beaked whales *M. ginkgodens* (Table 17.1). In this section, we review the sexually dimorphic characters of beaked

whales, including scarring patterns, and how they might relate to overall mating strategies.

17.4.1 Teeth and Beak Morphology

How forcefully males of different species can strike conspecifics depends on the relative size and location of the teeth and on the amount of buttressing teeth received from additional bone and gum tissue around them (Heyning 1984; MacLeod and Herman 2004; Table 17.1). Tooth location in beaked whales varies from the tip of the lower mandible (Cuvier's, Shepherd's, Longman's, Ramari's *M. eueu*, and True's *M. mirus* beaked whales, bottlenose whales) to various locations caudally (Mead 1989; Jefferson et al. 2015). Apical teeth are oval in cross section, while postapical teeth are laterally flattened along the long axis of the lower jaw (Heyning 1984). Tooth size of adult males ranges from 5 cm in True's beaked whale to approximately 33 cm in strap-toothed beaked whale *M. layardii* (Box 17.4, Fig. 17.4). The two species with the largest amount of exposed tooth—Stejneger's

Fig. 17.4 Top: Overhead view of the lower jaw of an adult male strap-toothed beaked whale showing how teeth would have wrapped around the rostrum and overlapped each other. Photo: collected 2004, Te Kaha near Mouriuri stream, New Zealand. CC BY 4.0. Te Papa (MM002655). Bottom: Different skull close-up of top of teeth showing the tiny denticles that do raking during tussles with other males. Photo: T. Sim, https://en.wikipedia.org/wiki/Strap-toothed_whale, accessed 11 May 2023 (Creative Commons CC-BY-SA)

M. stejnegeri and strap-toothed beaked whales—show conspicuous wear on the front and inner surfaces of the teeth (Yamada 1998; Pitman et al. 2019), which may be attributed to prey abrasion during suction feeding (Ramassamy 2016). In other species with large teeth (e.g., Blainville's, Hubbs' *M. carlhubbsi*, and Andrew's *M. bowdoini* beaked whales), most of the teeth is sheathed in bone or gum tissue, perhaps to prevent abrasion. At the opposite end of the exposed tooth-size spectrum, adult male northern bottlenose whales have small teeth that do not always erupt and are barely visible when they do (Moors-Murphy 2018); perhaps because males apparently butt heads to settle contests (Gowans and Rendell 1999), they may not require teeth (Fig. 17.1). The male ginkgo-toothed beaked whale has a relatively large tooth (6.5 × 11.5 cm), but only the tiniest tip is exposed above the bone and gum tissue so that tooth rake scars are almost nonexistent (Nishiwaki et al. 1972); Heyning (1984) viewed this as evidence that this species had a different social structure than other mesoplodonts.

Box 17.4 Strap-Toothed Beaked Whale

The strap-toothed beaked whale has some of the most bizarre teeth in the animal kingdom. Among the 16 currently known species of *Mesoplodon*, tooth size, shape, and placement among adult males vary according to species (Sect. 17.4.1). Teeth positioned further back on the lower jaw can be used more forcefully, but they need to be elevated above the rostrum, which can be done by raising the tooth up on a boney arch or growing a longer tooth. Male strap-toothed beaked whales grow the longest teeth of any beaked whale: a single tooth, at least 33 cm long, erupts from the middle of each lower jaw; it is flat (strap-shaped) and armed with a small, sharp denticle on the tip (Fig. 17.4). Normally among beaked whales, the bigger the tooth, the more vigorous the combat; but it appears that the only reason for this massive tooth is to provide support for the tiny cutting edge. Overlong teeth, however, are vulnerable to breaking or loss during forceful contact between males; to guard against this, the teeth grow up and back, and wrap around the upper jaw, where they can be supported by the underlying flesh and bone. The teeth can grow long enough that they overlap each other on top of the beak, and they can wrap so tightly around the upper jaw that movement is severely restricted: a mature, 5.4 m male could open its jaws only 4.0 cm at the tip (Sekiguchi et al. 1996). Although this might appear to constrain feeding ability, adult males clearly feed normally, and a reduced mouth opening may allow for more powerful and directed suction.

The amount of reinforcement that males' teeth receive in the mandible ranges from almost none (e.g., Gervais' *M. europaeus*, Hector's *M. hectori*, and True's beaked whales; Heyning 1984) to the massive boney arch in Blainville's beaked whale, which raises each tooth above the level of the head (MacLeod 2002; Fig. 17.3). In addition to strengthening the mandible, adult males (and some females)

of extant and extinct species also show various degrees of mesorostral ossification (increased swelling and density of various rostral bones that fills in the mesorostral canal) forming, in some cases, the densest bone recorded in the animal kingdom (Heyning 1984; Lambert et al. 2011); this modification may allow combative males to make forceful contact with their teeth while reducing the possibility of damaging their own rostrum (Heyning 1984). Alternative explanations for mesorostral ossification (e.g., ballast for diving, acoustic reflector for sound production) fail to account for the sexually dimorphic aspect of this trait (MacLeod 2002; Lambert et al. 2011). Gol'din (2014) suggested that beaked whales might use "echoic imaging" of the species-specific bony structures in male skulls for individual or species recognition. Acoustic studies, however, have shown that beaked whales in the North Pacific have species-specific vocalizations (Baumann-Pickering et al. 2013) such that passive acoustics would be more effective and less costly. Furthermore, the dimorphic skull structure of beaked whales could generate an "acoustic signature" that identifies individuals as adult males (Cranford et al. 2008).

Beak length in extant ziphiids ranges from extremely long and narrow Gray's *M. grayi* and Sowerby's *M. bidens* beaked whales to the short stout in Cuvier's (Table 17.1). Blunt heads and wide jaws have been identified as important adaptations for suction feeding in odontocetes (Werth 2006); furthermore, it has also been suggested for a beaked whale with a long set of jaws, "suction pressures are weakest anteriorly and decline precipitously as gape increases" (Ramassamy 2016). Neither of these arguments address that beaked whales are likely obligate suction feeders and that many extant and extinct taxa have extremely long rostra (Mead 1989; Bianucci et al. 2013, 2016). It is clear that "feeding through a straw" has some yet undetermined advantage for some deep divers.

17.4.2 Color Patterning

Most beaked whales have a subtle, often ontogenetically developed, color patterning, which along with an accumulation of persistent scarring means that the sex and maturity of individual whales become more evident with age and perhaps a useful social signal. Color pattern variation among different ziphiid species comes mainly from two different sources: (1) externally acquired markings and (2) genetically controlled, species-specific pigmentation patterning. Externally acquired markings are derived from several sources, but the most important are bite wounds from cookie-cutter sharks *Isistius* spp. and tooth rake marks from conspecific males. Cookie-cutter sharks are small (to 50 cm), mesopelagic, and feed by taking single bites of flesh out of large animals and retreating (Pitman et al. 2019). The wounds can form white scars that are visible for many years (Baird 2016), and although relatively small (5–7 cm), they are often numerous so that older beaked whales of both sexes are usually easily distinguished. How prominent tooth rake scars are from adult male conspecifics depends on the relative size and placement of the teeth and how aggressively males of different species wield them (Heyning 1984; Table 17.1).

Fig. 17.5 Right flank photos of the same Cuvier's beaked whale male in the Mediterranean. The two pictures on the left were taken when the animal was still a toothless subadult, while the two pictures on the right were taken 13 years later, when the animal was a toothed adult. During the juvenile age, this male acquired intraspecific scarring along the lumbar area only; during the adult age, the scarring accumulated also along the cape and the antero-dorsal body part. Photos: Marco Ballardini and Massimiliano Rosso

Although females and young animals are sometimes raked, adult males are often readily distinguishable by their conspicuous scarring—forming an acquired sexually dimorphic trait. Some species have long, longitudinal scars while others have random patterns; for some species, rake marks appear to be concentrated dorsally between the blowhole and the dorsal fin and on the sides and ventral area for others (Box 17.5, Fig. 17.5). Although it has been suggested that extensive rake marks might be a signal of male quality in aggressive interactions (MacLeod 1998), it is not clear how prominent scarring would distinguish winning combatants from losers. Much remains unknown about tooth rake patterns on beaked whales and what they can reveal about the fighting tactics of different species.

> **Box 17.5 Scarring in Beaked Whales**
> In beaked whales, adult males are generally more heavily scarred by tooth raking than are adult females—up to seven times more in Cuvier's beaked whales. Also in Cuvier's, the prevalence of scarring on different body parts also appears to be age/sex related where adult males have more scarring along the cape; the dorsal area behind the blowhole, and lumbar flanks, while scarring on adult females, juveniles, and subadult males occurs mainly around the lumbar flanks (Coomber et al. 2016, 2022). Generally, as males mature, they acquire more scarring along the cape and the antero-dorsal part of the body (Fig. 17.5), likely caused by ritualized charging (jousting, Box 17.3) and that might indicate experience/dominance that can be evaluated by rivals before escalating the fight (MacLeod, 1998). The reason for intraspecific scarring along the ventrum is unknown but may be the result of harassment or sexual coercion.

Fig. 17.6 An adult female (presumably the mother) and calf Blainville's beaked whale off Madeira Island. Photo: Annalisa Sambolino, MARE-Madeira/ARDITI

Beaked whale calves are generally counter-shaded (darker above and paler below; Jefferson et al. 2015; Carwardine 2020), perhaps associated with being left at or near the surface during the foraging dives of their mothers (Box 17.6, Fig. 17.6). The juveniles of most beaked whales have very similar, largely nondescript, color patterns (Mead 1989). Adults of most beaked whales also have largely nondescript color patterns, which often makes field identification of this group problematic. Most species appear black, slate gray, or sometimes brownish, tan, or white, with little or no obvious patterning. In most species, the adult color pattern of both sexes is monomorphic (e.g., *Berardius* spp., Gervais', True's, Shepherd's, strap-toothed, and Blainville's beaked whales; Jefferson et al. 2015; Carwardine 2020). In pygmy beaked whales *M. peruvianus*, the adult male develops a conspicuous broad white swathe over its back that passes down and back between the blowhole and the dorsal fin (Pitman and Lynn 2001), making it the most sexually dimorphic ziphiid with respect to color patterning. Strap-toothed beaked whales are unique among extant ziphiids in having a bold black, white, and gray color pattern; Shepherd's beaked whale also has a distinctive pattern and is unique among ziphiids in that juveniles and adults have the same color pattern (Pitman et al. 2006; Donnelly et al. 2018). In several species, adults of both sexes have a prominent white beak (e.g., Gray's, Hector's, Hubbs', strap-toothed, and Andrew's beaked whales), which may be useful for social signaling in lowlight conditions (Pitman 2018).

Box 17.6 Do Foraging Mothers Leave Their Calves Alone at the Surface?

Beaked whales dive deep (1000–3000 m) during long periods (1–3 hours) to forage. Their infants (Fig. 17.6) have not likely yet developed such extraordinary diving capabilities. There are no records of calves alone at the surface and little evidence of alloparental care (MacLeod and D'Amico 2006; Dunn et al. 2017; pers. obs.). This is especially relevant in species of beaked whales with small groups of 2–4 individuals (Sect. 17.2) and highly coordinated foraging dives (Aguilar de Soto et al. 2020; Alcázar-Treviño et al. 2021). In deep diving and matrilineal sperm whales and pilot whales *Globicephala* spp., calves stay with other members of the group or alone at the surface (Gero et al. 2009; Augusto et al. 2017; pers. obs.). While their mothers forage in synchrony with other members of the group, do beaked whale calves stay at the surface? Do they remain alone, a couple of hundred meters below the surface, perhaps to avoid predators like killer whales? Do they dive in synchrony with their mothers, even as neonates (Dunn et al. 2017)?

It seems unlikely that beaked whales use color pattern for species recognition—adults spend much of their time in total darkness, either at depth or at the surface at night, situations where acoustic signaling for species recognition is probably much more reliable. Instead, we suggest that beaked whale pigmentation patterning serves primarily to distinguish adults from juveniles and in many cases males from females. Furthermore, a lack of scarring and adult color patterning on juveniles may help prevent unwanted social interactions by identifying them as either females not yet ready to breed or males not yet ready for combat.

17.4.3 Reproductive Anatomy

Testes size (relative to body size) is positively correlated with the intensity of sperm competition across a diversity of taxa and can provide insights into beaked whale mating strategies and the relative strength of pre- vs. postcopulatory sexual selection (Kenagy and Trombulak 1986; Dines et al. 2015). For example, males in species that display conspicuous weaponry (several mesoplodonts, northern bottlenose whales) exhibit smaller testes relative to their body size, which suggests that their reproductive success is largely dependent on precopulatory competition (reviewed in Dines et al. (2015)). On the other hand, one species that does not appear to engage in combat or display dimorphic weaponry—Baird's beaked whale—has larger testes relative to body size compared to the other beaked whales; individuals may mate with multiple partners and males apparently invest more heavily in postcopulatory traits that provide advantages in sperm competition (Dines et al. 2015). Currently, we lack testes data for most beaked whale species that would allow more rigorous

testing of these predictions. Interestingly, some beaked whales with less conspicuous teeth and scarring (e.g., ginkgo-toothed and True's beaked whales) also show very small relative testes size (Dines et al. 2015).

The unique vaginal foldings of female cetaceans can also provide insights into mating strategies, as they are thought to be under sexual selection and may provide some clues into postcopulatory cryptic female choice (Orbach et al. 2017, 2023, this book). Orbach et al. (2017) examined four species of *Mesoplodon* (Sowerby's, Stejneger's, Gervais', and pygmy beaked whales). All four had only very thin, "leaflike" cranial vaginal folding, less than observed in any other cetacean species; an observation consistent with the relatively small testes sizes observed in male mesoplodonts and low levels of sperm competition (Dines et al. 2015).

17.5 Social Segregation

In cetaceans, differences between the sexes (e.g., energetic needs, predation risk, disease risk, male harassment) result in fundamentally different pressures, often leading to spatial or social sexual segregation (Wells et al. 1987; Martin and da Silva 2004; Galezo et al. 2018; Weiss et al. 2021). The best evidence for sexual segregation among beaked whales comes from mass strandings (e.g., ten adult male Baird's beaked whales (Urbán et al. 2007) and eight adult female Stejneger's beaked whales (Savage et al. 2021)). From a group of six Sowerby's beaked whales swimming nearshore, three that stranded were all males, perhaps indicating a male social group (Lien et al. 1990). Additional evidence for sexual segregation among other species comes from at-sea sightings and whaling data, including Baird's beaked whale (Omura et al. 1955; Nishiwaki and Oguro 1972), northern bottlenose whale (Benjaminsen and Christensen 1979), pygmy beaked whale (Pitman and Lynn 2001), and strap-toothed beaked whale (Pitman et al. 2019). Although sexual segregation at sea appears to be widespread among beaked whales, its adaptive significance is unknown, but it could be that females pregnant or with calves gain an advantage by foraging without males or need to avoid harassment or coercion by adult males (e.g., Würsig and Pearson 2015; Galezo et al. 2018; Markowitz et al. 2023, this book).

17.6 Discussion

Adult males of most beaked whale species likely have few breeding opportunities: females take about a decade to reach sexual maturity, they may come into estrus only once every 3–5 years, most occur in groups of only 2–3 individuals, and in at least some species, females do not live as long as males, resulting in a surfeit of males. A receptive female is a rare resource—one to be fought over.

Interspecific differences in the prevalence and severity of tooth rake scarring on male beaked whales highlight different levels of aggression during male-male interactions. These differences are associated with different social organizations and different mating strategies (Heyning 1984; Ralls and Mesnick 2019). Species with heavily armed, aggressive males (e.g., Cuvier's, Stejneger's, and Blainville's beaked whales) apparently engage in male-male combat to monopolize access to females. These species typically have only a single dominant adult male, or occasionally two (Baird 2019; Cioffi et al. 2021; Badenas et al. 2022), associated with female calf groups. In contrast, species with long beaks and smaller, more apical teeth are known to occur (at least at times) in larger, multi-male groups (Longman's, Sowerby's, Gray's, and strap-toothed beaked whales; Table 17.1).

It is likely difficult or impossible for individual males to control access to females in larger, mixed groups. In these cases, selection may favor male agility and speed (and perhaps smaller body size, Box 17.1), and females may mate with more than one male, which favors larger testes and increased spermatogenesis to win paternity (Mesnick and Ralls 2018). In addition, males of some species may find advantage in numbers by forming alliances as has been suggested for northern bottlenose whale and Cuvier's and Baird's beaked whales (Gowans et al. 2001; Fedutin et al. 2015; Baird 2019; Table 17.1).

Beaked whales have been cited as the only sexually selected mammalian radiation outside of terrestrial ungulates (Dalebout et al. 2008). In both groups, male-male battles over reproductive access to females has apparently led to diversification of weaponry and speciation (Heyning 1984; Emlen 2008). We suggest that diversification among beaked whales may have resulted from a conflict that arose when males began using a relatively fragile beak for both feeding and fighting. Cuvier's beaked whale is a monotypic genus with a worldwide distribution, while *Mesoplodon* species cumulatively occupy essentially the same geographic range but comprise at least 16 different species. Cuvier's beaked whale has a relatively short, stout beak, allowing males to retain their apical teeth and use them with considerable force. *Mesoplodon* spp., on the other hand, have longer, narrower, more vulnerable beaks (Fig. 17.7), and the evolutionary trend in this genus appears to have been toward moving the teeth further back in the jaw and modifying the rostrum, so they can be used more forcefully (Moore 1968; Heyning 1984; Mead 1989). This trend has occurred at different times, to different degrees, and in different geographic locations. It appears to represent a series of localized responses to the problem of maintaining a long, narrow beak for suction feeding at depth while also using it as a weapon in combat, and it could be key to the remarkable radiation within this group.

Fig. 17.7 Dorsal view of the skull of an adult male Gray's beaked whale from New Zealand showing the long, narrow beak at risk during interspecific combat. Photo credit: CC BY 4.0. Te Papa (MM002134)

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Chapter 18
Sexual Behavior and Anatomy in Porpoises

Check for updates

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Abstract Among the taxonomic family of porpoises (Phocoenidae), mating behavior in nature has been described in detail only for the harbor porpoise (*Phocoena phocoena*). We review this species' unusual mating habits based on a study in San Francisco Bay, California, USA, and present new data from across its range in the North Pacific, North Atlantic, Black Sea, and managed care. Results confirm the

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male's unique laterality oriented solely to the female's left side as contact occurred both in nature and managed care. The male's high-energy sexual approach to the female led to splashy aerial behavior at the surface in nature. Drone footage provided observations of subsurface mating behavior, including evidence of male–male sexual interactions and a male calf interacting sexually with its mother. Harbor porpoise reproductive anatomy is also presented, with new comparative information on the vaquita (*Phocoena sinus*). The harbor porpoise's lateralized behavior and anatomy (i.e., long asymmetric penis, large testes size, convoluted asymmetric female reproductive tract) may have coevolved. We note gaps in knowledge, suitable platforms for future investigations (drones, bridges, boats, and coastal cliffs), and what is known about mating behavior in other porpoise species, including hybridization. We conclude with conservation implications for porpoises and encourage researchers to recognize and report mating behavior as baseline data valuable for establishing marine conservation areas.

Keywords Dall's porpoise · Harbor porpoise · Hybridization · Laterality · Mating behavior · Mating strategy · Mating tactics · Narrow-ridged finless porpoise · Social behavior · Sperm competition · Vaquita

18.1   Introduction

The porpoises (Phocoenidae) comprise a modest sized family of seven species that are among the smallest cetaceans. Unique features of porpoise anatomy that appear to play a role in sexual behavior include small, raised epidermal tubercles on the back or dorsal fin.[1] Porpoises in managed care at times rub each other with their tubercles, which may be important in social exchanges, serve a sensory function, and also assist in molts (Amundin and Amundin 1971; Liu et al. 1986; Kasuya 1999; Teilmann and Sveegaard 2019). Another porpoise characteristic is the weak spade-

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[1]Tubercles are a phocoenid feature, and a morphological analogue may exist in the genus *Cephalorynchus*, which can display serrations along the leading edge of the flipper (Baker 1978 referring to "rugose nodules"; Best 1988; Goodall et al. 1988). These are more prevalent in males and have a tactile function in social interactions (Johnson and Moewe 1999).

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shaped teeth that differ from the stout conical teeth of most dolphins, which may be the reason porpoises are not known to use their teeth to rake conspecifics in social and sexual interactions, as is common in many dolphin species (Martony 2020).

Porpoises are widely distributed from subpolar to tropical waters. Despite the coastal presence of nearly all porpoise species, except some populations of harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), and spectacled porpoise (*Phocoena dioptrica*), many remain poorly known (Jefferson et al. 2015; Nielsen et al. 2018). Most porpoises are shy and inconspicuous, routinely altering their behavior and moving away from vessels. Only Dall's porpoises regularly approach boats to travel in the bow wave (Jefferson 1991). Porpoise group sizes are generally small, ranging from solitary animals to small groups (< 10), and rarely to several hundred in the harbor porpoise (Jefferson et al. 2015; Butler et al. 2017). The distribution, behavior, and group composition of porpoises pose a major impediment to researchers seeking to understand the sex lives of porpoises.

Mating behavior has never been described for the southern hemisphere Burmeister's porpoise (*Phocoena spinipinnis*), nor the critically endangered vaquita (*Phocoena sinus*) in the Gulf of California. Burmeister's porpoises exhibit greater length in males than females at sexual maturity (sexual size dimorphism), but whether this difference remains at physical maturity is inconclusive (Reyes and Van Waerebeek 1995). Vaquitas show reverse sexual size dimorphism, in which the female is larger than the male (Torre et al. 2014). Based on limited observations in nature, mate guarding behavior has been suggested for the sexually dimorphic spectacled porpoise and Dall's porpoise (Sekiguchi et al. 2006; Willis and Dill 2007; Frandsen and Galatius 2013). The slightly sexually dimorphic finless porpoises (*Neophocaena*) of Asia have undergone a recent taxonomic split (Jefferson and Wang 2011); narrow-ridged finless porpoise (*N. asiaeorientalis*) reproduction has been relatively well studied, but less is known about the Indo-Pacific finless porpoise (*N. phocaenoides*; Hao et al. 2006). Even the familiar and widespread harbor porpoise, which is reverse sexually dimorphic, in size has not been intensively observed in all its habitats (e.g., the Black Sea, northwest Africa), and behaviors of harbor porpoise hybrids with Dall's porpoise are poorly understood. More specimens of all species are needed to advance studies of reproductive physiology, anatomy, and genetics, which could shed light on life histories, including mating systems. In these efforts, beach-cast carcasses are of value. Several species of porpoises, notably harbor porpoises and narrow-ridged finless porpoises, have been kept in managed care facilities and have been a source of additional information. Although porpoise calves have been born in managed care and some have survived, limited attention has been given to sexual behaviors including their onset in individuals reared in managed care facilities.

This chapter primarily focuses on the harbor porpoise, which based on cetacean species studied so far, demonstrates a unique combination of lateralized and aerial sexual behavior. We review existing information available for the species and present new mating behavior data from the North Atlantic and Black Sea, with additional records from the North Pacific. We include the first photo-documentation

of mating behavior for the Black Sea subspecies, and observations of male–male and mother–calf sexual interactions. Original research on the sexual behavior of animals in managed care facilities increases our understanding of the development of lateralized sexual behavior. New information is also presented on reproductive anatomy in the harbor porpoise and vaquita, along with a discussion of harbor porpoise anatomy that may provide insights on mating behavior patterns. We discuss effective approaches to collecting porpoise behavioral data using drones, bridges, land, small boats, and video cameras (including smartphones), and underwater cameras for animals in managed care.

18.2   Narrow-Ridged Finless Porpoise

The mating habits of the narrow-ridged finless porpoise have been studied in China, where conservation research has focused on the endangered Yangtze River subspecies (*N. a. asiaeorientalis*) either in enclosed oxbow lakes (Wei et al. 2002) or aquaria (Wu et al. 2010). The first birth in an aquarium was reported in 2005 (Wang et al. 2005). Chasing, synchronized swimming, and rubbing of genital slits with dorsal tubercles preceded ventrum-to-ventrum mating (Hua et al. 1994). The mating event lasted 30–60 min, of which copulation was only 2 min. Females sometimes responded to males that chased them with a tail-slap directed at the male (Hua et al. 1994). Sexual activity occurred throughout the year with peaks in April–July and September (Wang 2005). Increased testes size was positively correlated with the frequency of sexual behavior, but may have also been influenced by other factors such as social rank and water temperature (Wu et al. 2010). Socio-sexual (non-conceptive) behavior was prevalent (Zhang et al. 2015), and group hierarchies may influence how animals position themselves during physical contact (Platto et al. 2017). Most (65%) socio-sexual behaviors were cooperative male–male interactions thought to be related to the formation of coalitions (Zhang et al. 2015). Such behaviors begin early in life; a male calf's interaction with adults of both sexes was primarily ventrum-to-ventrum contact (Xian et al. 2010).

Knowledge of the mating behavior of the other subspecies of narrow-ridged finless porpoise, the East Asian finless porpoise (*N. a. sunameri*), is comparatively limited. Mating behavior occurred between March to September in the Inland Sea when group sizes increased; it was common to see mother–calf pairs followed by one or two adults, presumed males attending the female as she approached her estrous cycle (Kasuya and Kureha 1979). This attending behavior was also evident in managed care settings, where dominant males spent significant time with females engaged in pre-copulatory behaviors (mouthing, nudging) and both sexes rubbed their sensitive dorsal tubercules across the body of other porpoises (Liu et al. 1986; Nakahara 2009). During copulation, males positioned themselves ventrum to ventrum below the female. Females sometimes evaded the approach of a dominant male, giving a subordinate male an opportunity to copulate. However,

paternity analyses revealed that only the dominant male sired calves despite having seasonally enlarged testes that suggest sperm competition (Nakahara, 2009).

18.3 Dall's Porpoise: Mate Guarding

Dall's porpoises are sexually dimorphic, displaying male secondary sexual characteristics (Jefferson 1990; Amano and Miyazaki 1993). The only other porpoise species with well-developed male secondary sexual characteristics is the spectacled porpoise that has a greatly enlarged dorsal fin in adult males compared to females (Goodall and Schiavini 1995). The female's reproductive tract is notable for its weakly developed vaginal folds (Morejohn and Baltz 1972). The physical features of male Dall's porpoises (larger than females, secondary sexual characteristics, relatively small testes) suggest they may compete for females through contest competition and polygyny is inferred (Kenagy and Trombulak 1986; Jefferson 1990; Ferrero and Walker 1999). Most females calve each summer and enter estrus a month later (Kasuya and Jones 1984; Ferrero and Walker 1999). Dall's porpoises in the Salish Sea in the Pacific Northwest formed male–female pairs following summer calving, when a mother accompanied by her neonate calf often associated with an adult male (Willis and Dill 2007). This pairing behavior, which may last hours or days, is consistent with mate guarding in which a male remains close to a female during her estrous phase to reduce the chance of copulations by other males. Male–female pairs ($n = 18$) stayed together longer, maintained distances closer to each other, and surfaced in synchrony more than male–male pairs ($n = 24$). On six occasions, males actively chased other males away from females, which sometimes distressed their calves (Willis and Dill 2007); this mate guarding strategy may also be population-specific. In other regions, females with neonate calves occurred alone or with other female–calf pairs (Kasuya and Jones 1984; Jefferson 1987).

18.4 Harbor Porpoise

Harbor porpoises have been described as "living life in the fast lane" because they are one of the most short-lived cetaceans and females have a rapid (often annual) reproductive cycle (Read and Hohn, 1995). In the Gulf of Maine, few adults lived more than 10 years and females spent much of their adulthood pregnant and lactating (Read and Hohn 1995). The average age of sexual maturity is 3.6–4.6 years for females (131–154 cm) and 3–4 years for males (130–143 cm), with adults generally reaching lengths of 145–175 cm and weights of 50–75 kg (Gaskin et al. 1974; Hohn and Brownell 1990; Sørensen and Kinze 1994; ÓlafsdÓttir et al. 2002; Matsui et al. 2021). The species displays reverse sexual dimorphism in size, with females generally larger than males of similar ages. In most areas, females are on average approximately 8–10% longer and 20% heavier than males, and males lack obvious

secondary sexual characteristics (Gaskin et al. 1984; Hohn and Brownell 1990; Read and Tolley 1997; Gol'din 2004; Galatius 2005, Murphy et al. 2020). The harbor porpoise mating system is polygynandrous, in which males and females copulate with multiple conspecifics (Bjørge and Tolley 2018), and reproductive peaks are seasonally synchronized (Lockyer 1995; Read and Hohn 1995). Gestation lasts 10–11 months and calves lactate for 8–12 months (Read 1990; Sørensen and Kinze 1994). Calves are typically born from May to September, depending on the region, followed by females entering estrus (Hohn and Brownell 1990; Read and Hohn 1995; Neimanis et al. 2000; Hasselmeier et al. 2004; Hall 2011; Norman et al. 2018). Hormone levels in female harbor porpoises in a managed care facility in Japan indicated the possibility of seasonal polyestry (Arai et al. 2017). Males undergo marked changes in testes size throughout the year, with maximum testes masses achieved in the summer when females are in estrus. Testes are inactive during the winter months (Neimanis et al. 2000; Kesselring et al. 2019). The very large testes-to-body mass ratio (4%, with combined testes weights of up to 2.7 kg; Gaskin et al. 1984), lack of secondary sexual characteristics, and reverse sexual size dimorphism, suggest a male mating tactic of sperm competition (Fontaine and Barrette 1997). Harbor porpoises ranked highest of 30 cetacean species in inferred level of sperm competition (MacLeod 2010). Noting their "megatestes," Fontaine and Barrette (1997) predicted males would mate with multiple females, attempt to mate many times with the same female, and not fight over access to females. Males grow fast and mature early at a minimum size enabling them to expend much energy into reproduction (Murphy et al. 2020).

18.4.1 Hybridization: Harbor Porpoise × Dall's Porpoise

Intergeneric hybridization of harbor porpoise with Dall's porpoise has been reported where their ranges overlap off the coast of British Columbia, Canada, and in the Salish Sea, Pacific Northwest, USA. Although the two species are sympatric elsewhere in the Eastern and Western North Pacific, no hybrids have been reported there. Multiple records of Salish Sea hybrids have been documented based on photo-identification, behavioral observations, strandings, and molecular analyses (Baird et al. 1998; Willis et al. 2004; Crossman et al. 2014, Morin et al. 2021). Hybrids generally had morphological traits intermediate between the two species, with individual variation that may lead to an underrepresentation of hybrids when using morphology to identify them (Willis et al. 2004; Crossman et al. 2014). It is possible that many abnormally pigmented Dall's porpoises, such as gray or white individuals (Morejohn et al. 1973; Joyce et al. 1982; Miller 1990), may be hybrids (Willis et al. 2004). Genetically identified hybrids (18 of 27) were mistaken for either parent species based on morphological assessment by experienced researchers (Crossman et al. 2014). The maternal parent of harbor porpoise × Dall's porpoise hybrids was consistently the Dall's porpoise (Willis et al. 2004). However, 30% of genetically identified hybrid porpoises had harbor porpoise mitochondrial DNA, indicating that

at least sometimes harbor porpoises are the maternal parent (Crossman et al. 2014). Confirmed female hybrids with neonate calves mean that at least some female hybrids are fertile and can backcross with either species, but are more likely to do so with Dall's porpoises (Willis et al. 2004; Crossman et al. 2014). Given that most hybrids are born to Dall's porpoise mothers, it is likely these hybrids will behave like a Dall's porpoise and therefore would be more likely to mate with another Dall's porpoise rather than a harbor porpoise. This directionality of hybridization (in which the paternal parent is a harbor porpoise) may reflect the differences in the species' mating behaviors. Harbor porpoises may compete for females through sperm competition in contrast to the mate guarding and polygyny of Dall's porpoises, possibly resulting in polygynandrous male harbor porpoises indiscriminately pursuing females of either species (Willis et al. 2004).

18.4.2   San Francisco Bay Behavioral Case Study

Prior to recent work in San Francisco Bay, California, harbor porpoise mating behavior in nature was rarely reported. In the Bay of Fundy/Gulf of Maine, a site of long-term harbor porpoise investigations, copulation was only documented a total of five times over 5 years (Gaskin and Blair 1977) with no behavioral details provided. A brief early account of harbor porpoise mating behavior comes from a 1970 research expedition in the Black Sea in which two adults accompanied by a calf were encountered. The adults were observed for 5 min as they engaged in aerial behavior (repeated leaping) and also swam belly to belly for several seconds (Bel'kovich et al. 1991). During vessel surveys from 1987 to 1989 in Danish inner waters, mating behavior was seen only once. A male approached a mother–calf pair and separated the calf from the female, after which the adults engaged in chasing. Mating was then described near the surface producing "high splashes" (Kinze 1990).

Studies of harbor porpoise behavior in San Francisco Bay led to the systematic description of their mating habits, the first for any phocoenid (Keener et al. 2018). Over an 8 year period (2010–2018) in San Francisco Bay, photographs were obtained of 144 mating events from the Golden Gate Bridge. The males' rapid sexual approaches toward females were characterized by high energy and precision timing as males rushed to contact females. Males approached females with sufficient force and speed to result in male aerial behaviors (69% of copulatory attempts), which were observed exclusively in mating contexts (Keener et al. 2018). Males did not exhibit smooth head-first re-entries and instead made a splash as they contacted the water with their ventrum or flank. Typically, the duration of a mating event was 1–2 s (Keener et al. 2018). Remarkably, males always attempted to copulate by positioning their ventrum on the females' left side, even if the male began an approach while positioned on the female's right side (Keener et al. 2018). This extreme laterality in sexual approach is unique among cetaceans and mammals studied to date (Orbach et al. 2020; Lilley et al. 2022).

The penis was visible in 60% of the 96 mating events where the male's ventrum was visible (Keener et al. 2018). However, intromission was seen rarely (2 events) and was observed as the copulating pair was positioned crosswise at the surface with the male's ventrum pressed against the female's left flank (Keener et al. 2018).[2] Males also engaged in displays without attempting to copulate, consisting of postures in which males rolled their bodies to present their ventrum toward the females (with or without extruding the penis), an activity that could be seen while the animals were below the surface. Males initiated all mating events, based on photographs, videos, and observations, and mostly approached lone females (62.5% of events) or females with a calf (25% of events; Keener et al. 2018). Males generally ignored the presence of calves, and calves swimming on the mothers' left side were temporarily separated from their mothers by the fast-approaching males. In one instance, a male drove away a female's calf before pursuing her. Males did not herd nor coerce females and there was no evidence of mate guarding. Other adults of unknown sex were seen near some mating events, but none of them interfered with a mating male nor sexually approached the female. No male–male competition was observed and males occasionally approached one or more females repeatedly (Keener et al. 2018). These findings validate some predictions made about the behavior of harbor porpoises based on their reproductive biology and anatomy, supporting the hypothesis that males compete primarily by sperm competition (Fontaine and Barrette 1997; MacLeod 2010). In the absence of contest competition, the male's smaller body size than the female's may be useful for maneuverability in rapid sexual approaches (Murphy et al. 2020).

Females were sexually approached by males when at the surface (95% of occurrences; Keener et al. 2018). Males likely timed their approaches to coincide when females were taking a breath, possibly to make it more difficult for the female to maneuver during the brief moment of contact. Females generally appeared to be unaware of a male's presence until he was in immediate proximity, potentially indicating that males did not advertise their presence acoustically. Based on an analysis of 28 events captured on video, females reacted to male sexual approaches with high-intensity evasive behaviors such as fluke lifts ($n = 9$), dives ($n = 20$), and occasionally with passive receptive behaviors including no reaction or listless floating ($n = 5$; Orbach et al. 2019). Females also engaged in behavioral responses with ambiguous functions including dives ($n = 20$), peduncle curls ($n = 15$), body rolls ($n = 20$), and direction changes ($n = 5$; Orbach et al. 2019). Compared to other odontocete species and in contrast to the findings of MacLeod (2010), Orbach et al. (2019) evaluated multiple aspects of harbor porpoise anatomy and sexual behavior and reported that harbor porpoises had an intermediate level of sperm competition.

Despite the synchronized summer estrous cycle and winter regression of testes, mating activity in San Francisco Bay harbor porpoises occurred year-round (Keener et al. 2018). The stock of harbor porpoises studied, a distinct population with an

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[2]Hector's dolphin (*C. hectori*) males sometimes contact the flank of the female with chest or ventrum, referred to as a sexual "pounce" (Slooten 1994).

estimated abundance of <8000 animals (Forney et al. 2020), is non-migratory unlike many other populations across the species' range; it is not clear if stable residency facilitates out-of-season mating attempts. Because this description of harbor porpoise mating behavior was based on the small San Francisco Bay Area stock, we assessed whether the same pattern of high-energy lateralized and aerial mating occurred in other populations and subspecies of harbor porpoises.

18.4.3   Range-Wide Harbor Porpoise Mating Patterns in Nature

Solicitations of harbor porpoise mating behavior data across the species' entire range in the northern hemisphere resulted in a compilation of photo-documented observations from 1999 to 2022 from 23 locations where three reproductively isolated subspecies inhabit major marine basins: the North Pacific (*P. p. vomerina*), North Atlantic (*P. p. phocoena*), and Black Sea (*P. p. relicta*; Table 18.1; Fig. 18.1). Free-swimming harbor porpoise aerial behavior or mating events (sexual approaches or attempts to copulate) were photographed primarily by researchers or naturalists affiliated with organizations engaged in the study of local coastal environments (91% of contributions, $n = 21$). All data (e.g., date, GPS location, platform) were checked by a member of our research team. Of the 138 mating observation events contributed, half ($n = 69$) were on video totaling 19 min 21 sec and half ($n = 69$) were captured in 133 still photographs (Table 18.1). Digital photography platforms included land (46%, $n = 63$), drones (42%, $n = 58$), vessels (12%, $n = 16$), and a bridge ($n = 1$). A consensus-based process was used to evaluate potential mating events ($n = 135$) after analysis by an experienced team. Specifically, behavior was assessed for contact between male and female, the male's position with respect to the female during a sexual approach, male aerial behavior (>1/3 body above water), female response, and occurrence at or below the surface. When the sex of an individual could not be determined by observation of a penis, genital slit, or dependent calf, sex was presumed based on the typical mating behavior described in Keener et al. (2018). Of the 138 mating events, three were reviewed separately for non-reproductive socio-sexual behavior.

A mating event typically lasted 1–2 s ($n = 64$ videos). Mating events occurred in all months of the year, with a range of 2–40 events per month (January = 2, February = 7, March = 4, April = 40, May = 17, June = 5, July = 5, August = 6, September = 7, October = 8, November = 10, December = 6). April was a high outlier due to numerous drone-based videos collected over a 4 day effort in Denmark. The occurrence of mating behavior in all months, also found in San Francisco Bay, California (Keener et al. 2018), was surprising given the seasonal regression of testes and presumably low male hormone levels. It is plausible that constant year-round practice of sexual approach maneuvers could be an important activity for males as their mating behavior is a high-intensity, precisely timed activity.

Table 18.1 Images evaluated for free-swimming harbor porpoise mating behavior. Data were contributed from 23 locations ($n = 138$ events). The map # refers to locations indicated on Fig. 18.1

Map #	Waterbody	Location	Nation	Year	Format	Events	Contributor	Affiliation
1	NE Pacific	San Francisco Bay, CA	USA	2021	Still	1	W Keener	The Marine Mammal Center
2	NE Pacific	Monterey Bay, CA	USA	2015	Still	1	D Bianchetta	Monterey Bay Whale Watch
3	NE Pacific	Burrows Pass, Salish Sea, WA	USA	2014–2022	Still	14	C Elliser, K MacIver	Pacific Mammal Research
4	NE Pacific	Puget Sound, Salish Sea, WA	USA	2018	Still	1	D Anderson	Cascadia Research Collective
5	NE Pacific	Puget Sound, Salish Sea, WA	USA	2022	Video	4	C St. Ours	Pacific Mammal Research
6	NE Pacific	Howe Sound, Salish Sea, BC	Canada	2015, 2019	Still/video	13	A Hall	Porpoise Conservation Society
7	NE Pacific	Morse Basin, Prince Rupert, BC	Canada	2015	Still	1	C Birdsall	Ocean Wise Research
8	NE Pacific	Kachemak Bay, AK	USA	2019, 2022	Still/video	4	M Webber, DD Tobin	The Marine Mammal Center, University of Alaska
9	NW Atlantic	Gulf of Maine, ME	USA	2018	Still	1	K Pielmeier	Allied Whale/College of the Atlantic
10	NE Atlantic	Mount's Bay, Cornwall	England, UK	2013–2015	Still/video	3	D Jones, R Knee	Marine Discovery Penzance
11	NE Atlantic	Bristol Channel, Devon	England, UK	2011	Still	1	D Jenkins	Seawatch Foundation
12	NE Atlantic	Scarborough, Yorkshire	England, UK	2015, 2021	Still	3	S Baines	Seawatch Foundation
13	NE Atlantic	Flamborough, Yorkshire	England, UK	2017	Still	1	J Hood	Flamborough Bird Observatory
14	NE Atlantic	St. George's Channel, Pemb.	Wales, UK	2016–2020	Still	19	H Dunn	Sea Trust Wales

15	NE Atlantic	Gulberwick Bay, Shetland Is	Scotland, UK	2018–2019	Video	16	N McCaffrey	Southspear Media & Surveys
16	NE Atlantic	Inner Sognefjord	Norway	1999	Video	1	F Graner	Sealife Productions
17	NE Atlantic	Nordvika	Norway	2020	Still	1	C Mignot	Photographer
18	NE Atlantic	Kattegat	Sweden	2013	Still	1	T Edenborg	Photographer
19	NE Atlantic	Romsø Sound	Denmark	2018–2022	Video	42	ST Ortiz, H Hamel, D Brennecke	University of Southern Denmark
20	NE Atlantic	Little Belt	Denmark	2020	Video	1	L Kondrup	Natur & Ungdom Fredericia
21	NE Atlantic	Eastern Scheldt	Netherlands	2021	Still	3	F Zanderink	Stichting Rugvin
22	Black Sea	Constanţa, W Black Sea	Romania	2020	Still	5	R-M Paiu	Mare Nostrum NGO
23	Black Sea	Zonguldak, S Black Sea	Türkiye	2019	Video	1	N Uluduz	Zonguldak Bülent Ecevit University
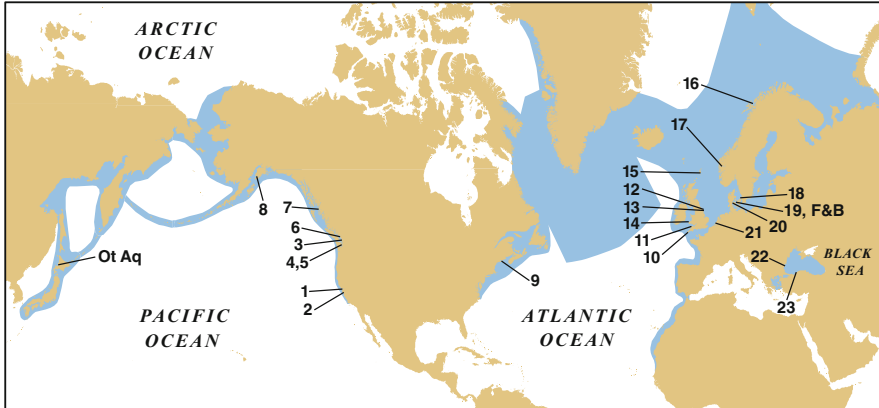
Fig. 18.1 Harbor porpoise global distribution map and locations that contributed mating/aerial behavior images for this species (numbers from Table 18.1). Two managed care facilities are also indicated (Fjord&Bælt, Denmark and Otaru Aquarium, Japan). Porpoise range information from Jefferson et al. (2015) and Nielsen et al. (2018). Map: Nina Lisowski

Photographs from land, bridge, and vessel platforms comprised 80 events with mating behavior exclusively at the surface. In contrast, drone-based videos revealed that 42 mating events occurred underwater. Of the 135 mating events evaluated, aerial behavior that appeared to be unrelated to mating ("high leaps"- single, high arcing, head-first, re-entry leaps) in 18 events was excluded from the mating behavior analysis. High leaps occurred for unknown reasons, possibly functioning in non-sexual social interactions or foraging, and mostly when no other adult porpoise was near the aerial individual (Fig. 18.2a). A similar type of high leap, which did not look like the serial leaping ("porpoising") of traveling dolphins, was observed in Denmark (Amundin and Amundin 1973). An additional 10 events were excluded in evaluating lateralization criteria because the male's position in proximity to the female was blocked by an animal's body or by splashes, or in some instances the male halted his approach well before reaching the female. It was possible to determine the sex of at least one porpoise engaged in mating behavior in 38 events as a penis was visible in 31 events (Fig. 18.2b) and a dependent calf was present in 10 events (Supplemental Video 18.1). The sexes of both adult male and female porpoises were known in three events. The terms *female* and *male* include both confirmed and presumed members of the sex.

Our observations confirm extreme laterality in the male harbor porpoise's mating behavior and are consistent with results in Keener et al. (2018) from San Francisco Bay, in which males attempted to contact the female's left side, and in some instances the penis remained erect immediately following a mating approach (Fig. 18.2c, d). In 100% of range-wide mating events, males attempted to contact the females' left side ($n = 107$). The male made physical contact with the female in 71% of events ($n = 76$), typically touching his ventrum on the female's left flank during his approach from behind angled crosswise to the female's body. The male's
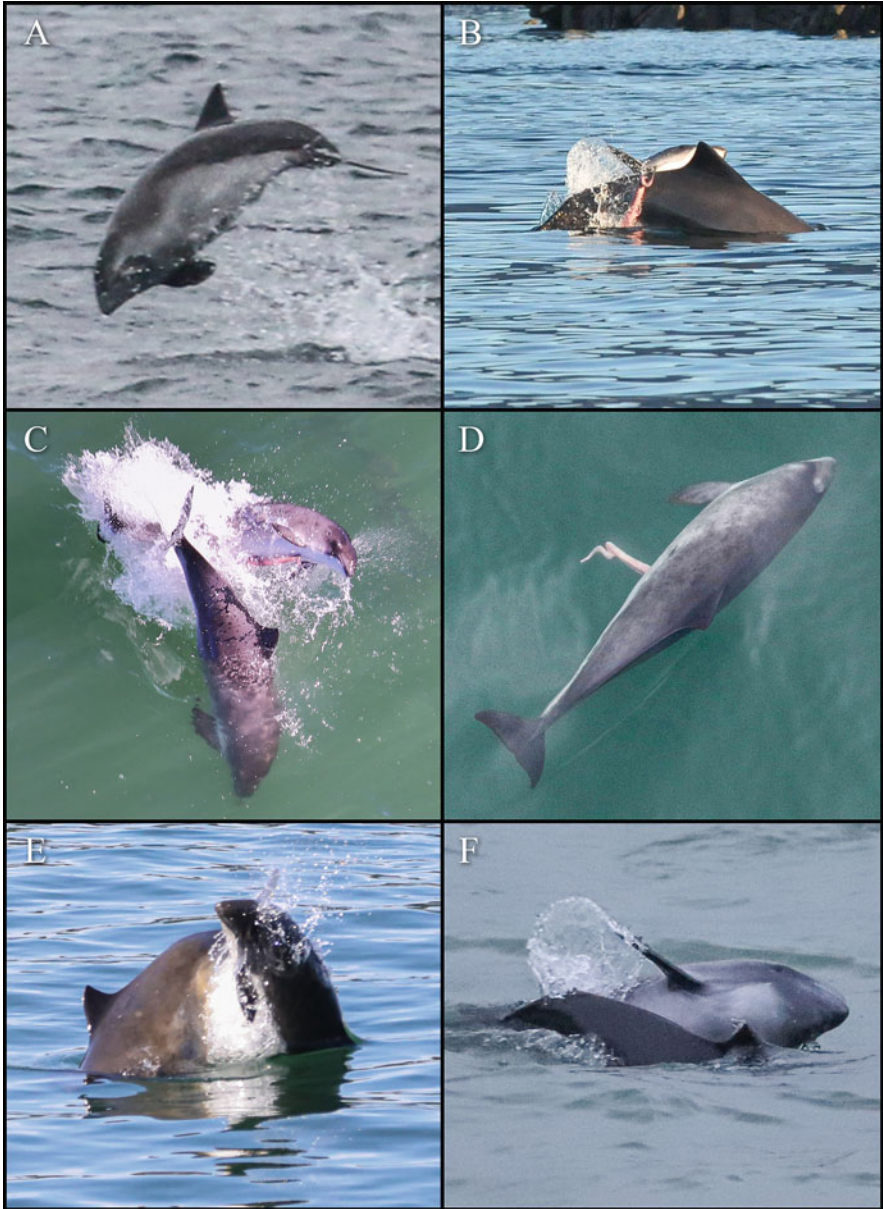
Fig. 18.2 Harbor porpoise behavior in nature. (**a**) High leap, English Channel, UK. (**b**) Male left-sided mating approach with penis on the female's right side, Prince Rupert, Canada. (**c**) Energetic male left-side mating approach, penis erect, female fluke lift and partial body roll, San Francisco Bay, California, USA. (**d**) Male with erect penis immediately after a left-sided mating approach, San Francisco Bay, California, USA. (**e**) Male left-sided approach perpendicular to the female, Salish Sea, Washington, USA. (**f**) Typical male mating approach to left side of the female, Black Sea, Romania. Photos: (**a**) Rebecca Knee/Marine Discovery Penzance; (**b**) Caitlin Birdsall/Ocean Wise Research; (**c**) Joey Meuleman/The Marine Mammal Center; (**d**) Marc A. Webber/The Marine Mammal Center; (**e**) Cindy R. Elliser/Pacific Mammal Research; (**f**) Romulus-Marian Paiu/Mare Nostrum NGO

energetic sexual approach led to his aerial behavior in 52% of 117 events ($n = 61$) (Fig. 18.2e, f). No copulations with confirmed intromission were observed. In 8% of events ($n = 10$), the male was most proximate to the female at the surface, and in 39% of events ($n = 46$) his approach was executed entirely underwater. The subset of surface events photographed only from land, bridge, or vessels ($n = 62$) revealed aerial behavior by the male in 89% of events ($n = 55$; Supplemental Video 18.2). The male's partial or full body breach usually terminated with a conspicuous splash. Of the 38 events in which the sex of an animal was determined, all 31 confirmed males executed left-sided approaches to the presumed females, and included aerial behavior in 74% ($n = 23$) of those events; ten confirmed females were approached from the left by males, and 5 of those males exhibited aerial behavior.

Males appeared to initiate all sexual approaches and predominately (91%, $n = 107$) approached single target porpoises (presumed females). Most mating events occurred when the female was at the surface (66%, $n = 76$). Two events were excluded because the female's position could not be ascertained. Female responses to the male's approach varied across a spectrum from little reaction to tail-slapping. Female behavioral responses most frequently included body rolls (47%, $n = 52$ of 110 events that could be evaluated for this criterion) and fluke lifts (43%, $n = 47$), which could occur simultaneously. Fluke lifts often appeared to function in evading or deterring the male's approach. Females were observed rapidly lifting their flukes, reaching a vertical position with the tailstock straight up in the air, simultaneously rolling on their long axis, occasionally resulting in a slap contacting the male. The females' rapid and energetic fluke lifts generated a considerable splash that slightly preceded the re-entry splash created by the males (Fig. 18.2c, e). Little or no reaction by a female occurred in 25% of events ($n = 28$). Other non-mutually exclusive female behavioral reactions included changes of direction (13%, $n = 14$), acceleration (4%, $n = 5$), or an immediate dive ($n = 1$). The subset of ten confirmed females did fluke lifts in seven events, body rolls in four events, and changed directions/accelerated in two events.

In one instance, a male porpoise made repeated sexual approaches towards a female. A male was photographed in the Black Sea off Romania energetically rushing to contact the same female's left side five times over a period of 9 min. In cases where females were accompanied by calves, males appeared to ignore the calves' presence as they approached females. Socio-sexual (non-conceptive) behavior collected by drone from the Shetland Islands, UK, showed a male–male interaction; a male hooked his fully erect penis around the tailstock of a target porpoise, a confirmed male based on its genital slit (Supplemental Video 18.3). The target male remained relaxed and did not exhibit any of the typical evasive behaviors used by females. He was a distinctly marked individual and was observed in a subsequent video exhibiting typical male behavior as he rushed to the left sides of other individuals. This is the first confirmed instance of male–male sexual behavior in harbor porpoises. While same-sex behavior was never documented in the San Francisco Bay study, it was expected due to its ubiquity among other species, including finless porpoises (Zhang et al. 2015; da Silva and Spinelli 2023, this book; Ham et al. 2023, this book). To date, there is no record of an interaction

where more than one male in a group simultaneously has an erect penis. In Denmark, a dependent male calf, estimated to be aged 9–10 months and therefore not yet weaned, was observed via drone sexually interacting with its mother. He approached the left flank of his mother three times within 2 min, twice with his penis visible. In one contact event that lasted 5 s, he rolled underneath her until they were positioned ventrum-to-ventrum. This type of early sexual activity parallels that seen in other odontocetes, including Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, Mann 2006; Supplemental Video 18.4).

18.4.4   Harbor Porpoise Mating Behavior in Managed Care

Harbor porpoises have been maintained in recent decades in managed care facilities in Denmark, the Netherlands, Japan, and Canada. Successful births have been reported since 2007 (Blanchet et al. 2008b). Information on the sexual behaviors of porpoises has been reported from the Fjord&Bælt (marine research center and aquarium) in Denmark and the Dolfinarium Harderwijk in the Netherlands. Numerous mating events observed in multiple projects at these facilities suggested a seasonal mid-summer peak during which males were the initiators of activity, but a female could determine the outcome of an approach by rolling her body away from the male (Benham et al. 2001; Desportes et al. 2003). Males attempted to mate indiscriminately, did not form male alliances, and did not dominate other males (Delgado-García 2009). We report the first investigation of harbor porpoise mating behavior in managed care facilities focused on lateralized sexual approaches by the male.

At Fjord&Bælt, three harbor porpoises were housed in an outdoor enclosure (30 × 20 m, average depth 3–4 m), with netting allowing for natural water to flow in from the adjacent harbor and Great Belt. The animals are exposed year-round to natural environmental conditions of tidal currents, temperature, and light. "Eskild" (male) and "Saga" (female) were born in nature in 2019, bycaught, and brought to the facility in winter 2020 (aged approximately 1.5 years; Fig. 18.3). "Freja" (female) was born in 1995 and was extremely old at the time of the study; she gave birth twice, unsuccessfully in 2006 (Blanchet et al. 2008a) and successfully in 2007 (Blanchet et al. 2008b). Eskild was first observed exhibiting sexual activity in August 2021 when he was 2 years old and 117 cm in length. During the summer and fall of 2021–2022, mating behavior was recorded using GoPro video cameras (Hero9 Black or Hero7 Silver models equipped with a wide-angle Max lens). For underwater observations, the camera was attached to a pole held 1 m below the surface in proximity to the porpoises. For above-water observations, the camera was suspended 8 m above the pool enclosure.

A total of 47 observational sessions from August 19, 2021 to September 14, 2022 amounted to 11 h 45 min of effort and resulted in 101 mating behavior events recorded. Subadult Eskild sexually approached both females, but showed a preference for subadult Saga (82% of events, *n* = 83). His penis was visible in 71% of
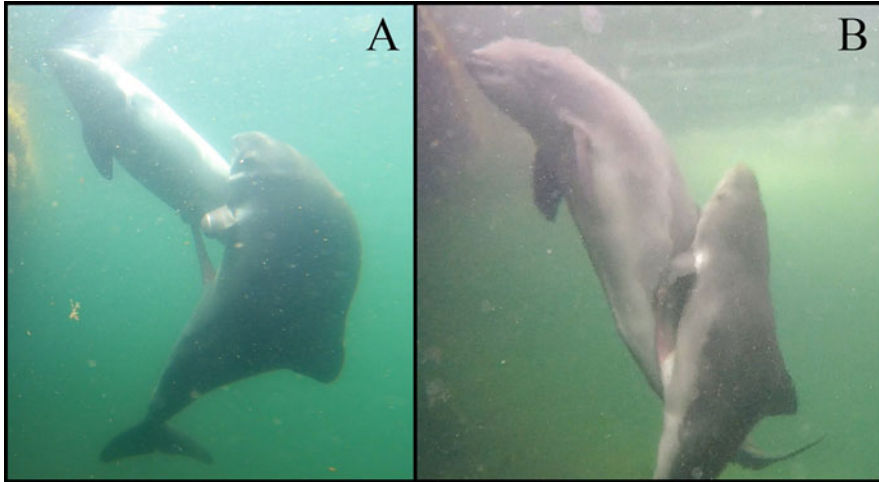
Fig. 18.3 Harbor porpoise mating behavior observed at Fjord&Bælt in Kerteminde, Denmark. Females were stationed at the surface near the edge of the pool enclosure. (**a**) Subadult male "Eskild" copulates with subadult female "Saga." (**b**) Subadult male rubs penis against left flank of adult female "Freja." Photos: Freja Jakobsen/University of Southern Denmark

events ($n = 72$). Eskild's sexual approaches usually resulted in contact with the target female ($n = 82$; Fig. 18.3a, b). His rapid approaches were initiated from the female's left side in 84 events and from below in 11 events. In six events, the angle of approach could not be discerned because of poor water clarity or camera angle. The male was positioned on the left side of the female at the closest point of approach in 100% of events, consistent with findings of free-swimming harbor porpoises in San Francisco Bay (Keener et al. 2018) and range-wide results reported here. Typically, Eskild attempted to copulate by approaching a female while she was stationary at the surface and positioned vertically at the edge of the pool with her attention directed toward a trainer. In nature, males tend to time their sexual approaches when females are swimming horizontally. When approached, the females showed avoidance behavior in 30% of events ($n = 29$); they turned their ventrum away from Eskild by executing a body roll or tilt or swam away. In one instance, Freja tail-slapped Eskild. Most sexual approaches appeared to be attempts to copulate but penetration was difficult to observe because the male's body position often blocked the view. Copulation with intromission was clearly observed only once, with Saga. Although Eskild was young, his frequent sexual behavior supports the hypothesis that males show interest in approaching females before reaching sexual maturity. Although one may speculate that the left-sided mating approach is innate as it was documented in a young male in a managed care facility, Eskild lived his first 9 months in nature where he may have encountered males sexually approaching his mother or nearby females, providing many learning opportunities. Manitzas Hill et al. (2023, this book) provide additional information on odontocete sexual behavior in managed care facilities.

At the Otaru Aquarium in Otaru, Japan, a visitor in an underwater glass-walled viewing room recorded 61 s of video footage in 2017 that captured harbor porpoise mating behavior. The pool housed two adult males, one adult female, and one subadult female, all bycaught in the Western North Pacific. A male with an erection made two sexual approaches to a female, both times targeting her left side at his closest point of contact. The first copulatory attempt may have resulted in intromission. These events were followed by grooming (using his dorsal fin to contact the female) without the penis extruded. The target female then increased her speed as the male with an erect penis followed her.

18.4.5   Harbor Porpoise Sexual Anatomy

Features of the harbor porpoises' reproductive anatomy were described by Meek (1918) from stranded specimens in the UK. The structure of the vagina is complex, characterized by multiple internal folds, spirality, and bilateral asymmetry (Orbach et al. 2020). Out of 20 cetacean species assessed, the harbor porpoise has the most vaginal folds (up to 13; Orbach et al. 2017b, 2023, this book). Orbach et al. (2020) used innovative techniques such as geometric morphometrics to quantify 2D variation in shape and photogrammetry of vaginal lumen endocasts (silicon molds) to quantify 3D directional asymmetry of the vaginal canal in specimens from California; the internal vaginal lumen showed variations between individuals and was highly asymmetric due to complex 3D spirals and deeply recessed vaginal folds (Orbach et al. 2020, 2021). A vagina from a harbor porpoise from the Eastern North Atlantic, reported here for the first time, showed similar extensive vaginal folding to specimens from the Eastern North Pacific (Fig. 18.4). The harbor porpoise penis is long for a small odontocete (~50 cm) and consists of a fibro-elastic shaft and a distal filiform tip (Meek, 1918; Orbach et al. 2017a). Meek (1918) described the shaft, which can be quickly extruded as rigid while the distal part remains pliable, presumably to better pass into the vagina. Based on the shapes of the genitalia, the bodies of the male and female may rotate as they copulate. Three artificially distended harbor porpoise penises were found to be asymmetric, with tips that originated on the left sides of a blunt knob and bent to the left (Fig. 18.5, upper right). The asymmetric shapes of the vagina and penis were both left-canted with similar angular bends that mirrored one another (Orbach et al. 2020).

The asymmetry apparent in female and male harbor porpoise genitals corresponds with the unique lateralized mating approach of the male, the result of an intersexual evolutionary "arms race" to control paternity (Orbach et al. 2019). The similarity in both North Pacific and North Atlantic female reproductive tracts (Fig. 18.4) supports new behavioral data presented here that confirm range-wide lateralized mating approaches by males. Vaginal folds and spirals may inhibit the depth or direction of penile penetration and semen movement, and the asymmetric penis appears to have coevolved to circumvent protruding vaginal barriers (Orbach et al. 2017a). To increase the chances of a successful copulation that achieves fertilization, males use

Fig. 18.4 Similarities in extensive vaginal folding of sexually mature harbor porpoises from the North Pacific (Alaska) on the left and the North Atlantic (Germany) on the right. Vaginal structures show asymmetry as a gauntlet for penis or sperm before reaching the cervix (truncated at top of images). Animals in dorsal recumbency with incision along ventral midline. Photos: Dara N. Orbach/Texas A&M University-Corpus Christi (left); Alexandra Rieger/University of Veterinary Medicine Hannover (right)

a left-sided sexual approach and contact females only with the optimum angle and body orientation. Females may respond by evasive maneuvers (e.g., body rolls, energetic fluke lifts) during copulation that could misalign the angle of penetration and prevent semen from reaching the cervix (Orbach et al. 2019). The harbor porpoise is a striking example of the coevolution of behavior and anatomy in which both sexes adapt and counter-adapt to control paternity.

18.5 Vaquita Sexual Anatomy

Although mating behavior of the vaquita has (to our knowledge) not been documented in nature, the semblance in male genital morphological shape with the harbor porpoise (Fig. 18.5) suggests that similar evolutionary pressures may be acting on genital form. Whether male vaquitas sexually approach females exclusively on the female's left side remains unknown. No insights could be derived from female morphology as a vaquita vagina recently assessed was dissected with a dorsal incision, instead of along the ventral midline, preventing direct comparisons with harbor porpoise reproductive tracts. One study of the vaquita ($n = 56$ specimens)

Fig. 18.5 Penises of post-mortem sexually mature vaquita (lower left) and harbor porpoise (upper right), artificially inflated to simulate erection. Ruler = 15 cm. Photo: Dara N. Orbach/Texas A&M University-Corpus Christi

concluded that lifespan, age at sexual maturation, seasonal reproduction, large testes size, and reverse sexual size dimorphism are all similar to the harbor porpoise (Hohn et al. 1996). Yet, based on residual testes mass, the vaquita ranked 18th of 30 cetacean species in terms of inferred level of sperm competition (MacLeod 2010).

18.6   Conclusions and Recommendations

Our data confirm that the harbor porpoise male's high-energy sexual approach to the female is oriented exclusively to her left side at the moment of contact, both in nature and in managed care facilities. Images from locations across the harbor porpoise's range suggest that this pattern of lateralized behavior is pervasive in all three subspecies. Comparisons of female reproductive tracts from the North Pacific and North Atlantic demonstrate similarities in internal structures, supporting our observed range-wide mating behavior pattern. Drone-based observations revealed underwater mating behavior events without evidence of activity at the surface.

In nature, energetic mating activity at the surface often leads to splashy aerial behavior due to the female's rapid reactive fluke lifts and the male's re-entry to the water at an oblique angle. Although visual observations were not used in our analyses, personal experiences by the authors suggest that because mating events happen suddenly at the surface, more could occur in an area than can be captured by

camera. Researchers should be aware that aerial behavior accompanied by a brief intense splash may be a sign of mating rather than foraging. Resource managers should factor observations of such behaviors into decisions affecting potential mating hotspots. Because breeding is a key life history parameter, recognition of lateralized aerial behavior at the surface and locations where this activity is prevalent could help support the designation of marine protected areas or implementation of conservation measures.

Our new findings were possible because of contributions from investigators across the harbor porpoise's global range, an international collaboration that exemplifies the fruitful working relationships needed for the conservation of widespread porpoise species. Additional avenues of inquiry about porpoise mating behavior should be pursued, such as using acoustic recordings to augment photography. For example, detecting bioacoustic signals during mating attempts may address whether harbor porpoise males ambush oblivious females. Porpoises are less common in managed care facilities than dolphins, but more detailed behavioral work with known age harbor porpoises, including ones born in facilities, could elucidate whether certain sexual behaviors are learned or innate. Morphological studies can fill knowledge gaps for lesser-known species like the Burmeister's porpoise, spectacled porpoise, and vaquita. At the subspecies level, penis shape and reproductive tract structures are still not reported for Black Sea harbor porpoises.

We recommend considering options for observation platforms in field work on porpoise behavior. Harbor porpoises can be wary around boats (particularly powerboats, less so near kayaks and sailboats); therefore, drone, land, and bridge-based observations may reduce the potential for interference with natural behaviors. While aerial platforms (drones, bridges) could capture mating occurring underwater, some surface activity may be missed due to splashes. Regardless of platform, imagery techniques and equipment are important and still photos were more difficult to evaluate than video clips because photographers rarely photographed an entire behavioral sequence from beginning to end, capturing only an instant of the action. Mating events are brief, especially when observed at a low angle from vessels or shore; they happened without warning, which often resulted in images partially obscured by surface splashing. Our collective experience supports the value of high-resolution digital cameras with zoom lenses (100–600 mm) from land, vessel, and bridge platforms.

Drones In Denmark, the mating behavior of harbor porpoises in nature was recorded using a drone from March to October 2018–2022 during annual field surveys around the Island of Funen. Mating attempts were observed in the Romsø Sound, Kerteminde Bay, and the Great Belt. The drone (DJI Phantom 4 Pro V2.0) was launched from the beach or from a small boat in clear weather (wave height <0.1 m and wind <36 km/h) and above shallow waters (depth <10 m) to facilitate the tracking of porpoises underwater. Best results were achieved when the surface was flat calm. Flights lasted less than 25 min at altitudes between 10 and 30 m above sea level, depending on group size and water clarity. No negative reactions to the drones by porpoises or other wildlife (e.g., foraging seabirds) were observed, but

usually the aircraft was flown to the side of the porpoises rather than directly overhead to minimize noise disturbance. Drones not only enabled observations without disturbing the natural behaviors of porpoises at the surface; they also captured action deep (to ~5 m) in the water column. Behavior transpiring below the surface offered new insights on same-sex behavior and the age at which sexuality is expressed. See Torres Ortiz et al. (2021) and Ramos et al. (2023), this book.

Land Because harbor porpoises usually are coastal, land-based observations are feasible where the species is regularly seen. Since 2014, mating attempts have been photographed from 6 m above sea level overlooking a narrow (400–500 m) stretch of water known as Burrows Pass near Anacortes, Washington, USA. The waters are generally calm, providing excellent conditions for viewing harbor porpoises that occur year-round (Elliser et al. 2018). The partial elevation provides a better vantage point compared to being on a small boat, allowing tracking of groups and activity that may occur prior to a mating event. Mating behavior occurred both in isolated instances (with no prior clues) and during heightened activity at the surface (foraging, aggregating in small groups displaying energetic movements and splashing).

Vessels Although harbor porpoises tend to avoid powerboats, researchers have had some success photographing the behaviors of a semi-enclosed, small population (~50) in the Eastern Scheldt (Oosterschelde), the Netherlands. Best practices were to idle or turn off the motors and to turn off all boat electronics (e.g., depth finder/fish finder). Similarly, in Kachemak Bay, Alaska, USA, mating behavior was photographed with digital still cameras from a vessel with engines and electronics turned off, while also tracking porpoises with a wide-angle video camera (even a mobile phone) to continuously capture surface action.

Bridge Bridges with pedestrian walkways that span porpoise habitat may be productive and economical photography platforms. Harbor porpoises have been photographed from the Golden Gate Bridge in San Francisco Bay, USA, since 2008. The bridge crosses a 1.5 km strait, with observation sessions conducted during high tides from the bridge's eastern public sidewalk, 70 m above sea level. The platform's chief limitation was that focal follows of socially active harbor porpoises could not be continued once they swam beneath the deck of the bridge.

All porpoise species face a variety of threats in a world increasingly modified by humans in the Anthropocene. The few remaining vaquita could be killed incidentally by unchecked gillnet fishing in the last small area where they survive in the upper Gulf of California. All species are confronted by habitat degradation from some combination of coastal and nearshore development, resource extraction, marine litter, chemical pollution, noise pollution, vessel traffic, bycatch in fisheries, direct harvests, and overfishing of shared resources (Mesnick et al. 2023, this book). Insufficient attention has been paid to the accelerating coastal habitat alterations associated with climate change and its effect on porpoises. Such challenges underscore the need for more studies on porpoise reproduction and sexual behavior that could inform management decisions affecting the survival, recovery, and long-term health of these small cetaceans.

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Chapter 19
Sperm Whale Reproductive Strategies: Current Knowledge and Future Directions

Ana Eguiguren, Christine M. Konrad Clarke, and Mauricio Cantor

Abstract Sperm whales' reproductive strategies are centered around their extreme sexual dimorphism, both in morphology and behavior. Females are much smaller than males and are highly social. Females live in stable, matrilineally based social units with communal care of calves, including cooperative defense and allonursing. In contrast, male sperm whales are large nearly solitary nomads. Males disperse from their natal social unit and move toward the poles, where they eat and grow almost three times larger than females. Males' great ranges span across and between ocean basins, allowing global genetic connectivity. As they rove the warm waters where females concentrate, mature males avoid each other; physical aggression on the breeding grounds is rarely observed. Instead, males may rely on powerful acoustic displays to establish dominance over potential competitors and provide females with an honest quality signal. Associations between sexually mature males and groups of females tend to be transitory. Disproportionate mating success of some males is suggested by evidence of paternal relatedness within female social units. Sperm whale mothers provide a substantial investment of time and energy to calves, resulting in the slowest reproductive rate among cetaceans. The peculiar characteristics of sperm whale mating systems reflect the evolutionary interplay between habitat structure, predation risk, sociality, and reproduction. A convergence of reproductive biology between sperm whales and African elephants likely results from similarities in these ecological pressures. Despite sperm whales being one of the most studied cetaceans, much remains unknown about their reproductive

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strategies. Most of what we know comes from whaling data and long-term observational and modeling studies. The rapid advances in technology for behavioral and physiological studies at sea can refine our understanding of these elusive deep-diving animals' social, mating, and caring systems and the extent to which these vary across oceans.

Keywords Alloparental care · Convergent evolution · Intra-sexual competition · Mate choice · Sexual dimorphism

19.1 Introduction

The sperm whale (*Physeter macrocephalus*) is a unique creature shaped by the deep ocean—a dark desert where these whales live highly social lives (Whitehead 2003). Their distinctiveness is showcased in their morphology; sperm whales are the largest toothed predators, their massive heads contain the world's biggest brains in absolute size, and they possess the most powerful biological sonar. Sperm whales use these extreme characteristics for hunting deep-sea creatures, communicating with conspecifics, and sustaining a rich social and cultural life (reviewed by Cantor et al. 2019). Sperm whales are the most sexually dimorphic of all cetaceans (Fig. 19.1)—mature males can be 40% larger than females and three times as heavy (Rice 1989). The

Fig. 19.1 Female and immature sperm whales gathered around a large mature male off Dominica, West Indies, showing their distinct body size dimorphism (credit: Marina Milligan, Dominica Sperm Whale Project)
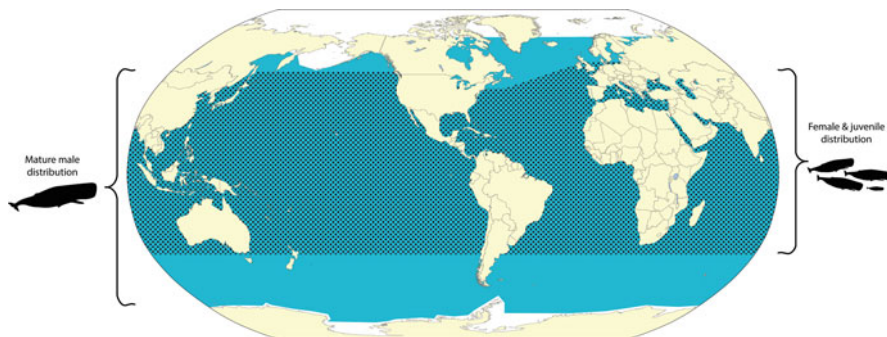
Fig. 19.2 Approximate representation of the global sperm whale distribution. The range of mature males is in blue, and the range of females is in the dotted pattern (modified from Whitehead 2009)

magnitude of such morphological differences between sperm whale sexes parallels sex-based distinctions in social behaviors, distribution, movements, and ecology, all of which have consequences for their reproductive strategies (Whitehead 2003).

Female sperm whales are highly social, whereas males are solitary nomads. The complex sociality of females is reflected in their multilevel societies (Whitehead et al. 2012; Cantor et al. 2015). At the lowest level, individual female sperm whales spend their lives in close contact with few other individuals (Christal et al. 1998; Gero et al. 2014) to whom they are often matrilineally related (Lyrholm and Gyllensten 1998; Mesnick 2001; Gero et al. 2008; Konrad et al. 2018b). These long-term associations are called *social units* (Whitehead 2003). Members of different social units interact with other social units over a few hours to a few days, forming *groups* (Christal and Whitehead 2001). These temporary groups are exclusively formed among members of social units that share a considerable portion of their vocal repertoire of "codas" (acoustic communication signals used in social contexts). These social preferences give rise to the uppermost social level, the *clan*, comprising 100s–1000s of individuals with shared vocal repertoires (Rendell and Whitehead 2003). In contrast, male sperm whales leave their maternal social unit at a young age (6–16 years; Best, 1979), heading toward high-latitude waters where they eat, grow, and sexually mature. These bachelor males can form occasional associations with other males (Christal and Whitehead 1997; Kobayashi et al. 2020) but ultimately spend most of their adult lives solitarily (Whitehead 2003).

Females prefer warm waters, while males are distributed circumglobally. The multilevel societies of females inhabit warm tropical and subtropical waters within a 0–40°N/S latitudinal range; males can occupy waters from the equator to the polar regions (Best 1979; Whitehead 2003; Fig. 19.2). Females can travel hundreds of kilometers a year but are philopatric at the ocean basin scale, as demonstrated by the significant differences in the maternally inherited mitochondrial DNA between oceans (Lyrholm and Gyllensten 1998; Engelhaupt et al. 2009). Males can travel much further than females; mature male sperm whales travel 5000 km a year on average (Mizroch and Rice 2013). Males leave polar waters to visit tropical waters

and interact with females in search of mating opportunities (Rice 1989; Mizroch and Rice 2013). Homogeneity in nuclear DNA around the globe suggests that males reproduce with females across ocean basins (Lyrholm et al. 1999; Engelhaupt et al. 2009). These spatial differences between the sexes and morphological and behavioral ones are associated with distinct trophic niches between females and males.

The sperm whale diet mainly comprises deep-sea squids (Kawakami 1980). Female sperm whales are effective hunters of their chosen prey, whereas males tend to have a more generalist diet which may include fish and crustaceans (Clarke et al. 1988; Best 1999; Mendes et al. 2007). These trophic differences result partly from the large-scale differences in the geographical distribution of males and females, yet small-scale habitat preferences also matter. For instance, in the Mediterranean Sea population, where male and female sperm whales are confined to the same ocean basin, sex-based trophic niche distinctions remain (Pirotta et al. 2020b) and mirror the distinct small-scale habitat preferences between the sexes (Pirotta et al. 2020a). In other areas where males and females co-occur, males usually have lower feeding success rates suggesting that females can outcompete them (Whitehead 2003).

Why and how did these extreme differences in morphology, behavior, distribution, and ecology arise? The origin of the extreme sexual dimorphism in sperm whales is most likely rooted in different sexual selection pressures on each sex (Whitehead 2003). Thus, the extraordinary sexual dimorphism in sperm whales highlights the interplay between mating strategies and all other aspects of behavior and ecology in a species' evolution (Whitehead 1993). Here, we review the current knowledge of the sperm whales' reproductive biology, mating system, and care system and how these strategies have contributed to shaping their lives through evolutionary time and in recent years. We consider how emerging field techniques can advance our understanding of these elusive social animals' reproductive biology, mating tactics, and care systems.

19.2 Reproductive Biology

Most of what we know about sperm whale reproductive biology comes from research on whaling operations from the late 1900s, during which researchers collected data on reproductive parameters by inspecting the reproductive organs and body measurements of thousands of hunted whales, as well as the composition of groups observed in the field (e.g., Ohsumi 1965; Gaskin 1970; Best 1979; Best et al. 1984; Clarke et al. 2012). As a result, while the reproductive physiology of sperm whales is well established, their reproductive behaviors remain largely unknown and may only be revealed by studying live individuals.

Sperm whales are referred to as the quintessential K-selected species because of their slow reproductive rates and high investment in their offspring (Whitehead 2009). Females typically reach sexual maturity—indicated by the age of first ovulation—at 9 years (Rice 1989) and can conceive shortly after (10 years; Best

et al. 1984). However, there is significant variation in female age of sexual maturity across regions (6–13 years; Rice 1989; Clarke et al. 2012). After sexual maturation, females continue to grow until they achieve physical maturity when they are 25–45 years old (Rice 1989). Individuals produce a single calf every 4–6 years with a 14–16-month gestation period (Ohsumi 1965; Best et al. 1984; Rice 1989).

Throughout their lifetime, female sperm whales experience a steady decrease in fecundity after they are 10–14 years old, which plummets after they are 40 (Ohsumi 1965; Best et al. 1984; Whitehead 2009). This pattern inspired the hypothesis that sperm whales may be one of the rare species—along with killer whales (*Orcinus orca*), short-finned pilot whales (*Globicephala macrorhynchus*), chimpanzees (*Pan troglodytes*), and humans (Croft et al. 2015; Betty et al. 2023, this book; Wright et al. 2023, this book)—to display menopause (Whitehead 2003). However, although reproductive rates drastically decrease over time, there is no support for a prolonged post-reproductive lifespan in sperm whales (Ellis et al. 2018). Old and less fertile females may increase their reproductive success by caring for their kin, as observed in pilot whales (Betty et al. 2023, this book; Würsig et al. 2023, this book). There is also evidence of geographic variation in pregnancy rates, which may be related to the effects of whaling directed on large males.

Like females, male sperm whales achieve sexual maturity at around age ten, as indicated by the presence of spermatozoa in their testes (Best 1979). Stable isotope analyses suggest males leave close to the onset of sexual maturity at 9–10 years of age and then move toward high latitudes in their 20s (Mendes et al. 2007). Males in their 20s experience a brief growth spurt followed by a decaying growth rate that can last until they are 60 (Rice 1989). Although males achieve *sexual* maturity at a similar age as females, it seems that males may not begin mating (i.e., reach *sociosexual* maturity) until they are 20 years old (Best et al. 1984). Throughout the text, when we refer to mature males, we refer to sociosexually mature males.

19.2.1 Copulation

Several events have been described as copulation among sperm whales (Dudley 1725; Best et al. 1984). Some describe the presence of large males among a group of females and juveniles displaying intense surface activity. In contrast, others describe belly-to-belly contact (in horizontal or vertical orientation) between a large whale assumed to be a male and a smaller one believed to be a female. However, these descriptions are inconsistent, and direct intromission has yet to be observed (Whitehead, 2003), so we caution against the interpretation of these interactions as copulation.

19.2.2 Seasonality of reproduction

Sperm whales breed most of the year (Rice 1989). In the Northern hemisphere, sperm whales breed between January and August, with a peak between March and June (Rice 1989). In the Southern hemisphere, sperm whales breed between July and March, with a peak between September and December (Rice 1989; Clarke et al. 2012). Not much is known about the seasonality of breeding in tropical waters. No discrete migration patterns associated with breeding have been described for sperm whales. Coinciding with this prolonged breeding season, female sperm whales have a prolonged estrous period, which lasts throughout the breeding season. Females enter estrus every 3–5 years, spending the interim time either gestating, lactating, or resting (Rice 1989; Clarke et al. 2012).

The factors influencing ovulation timing are unknown. Ovulation may be spontaneous or induced by mating or the presence of a mature male (Best et al. 1984). There is some evidence of synchronized ovulation among groups of females (Best et al. 1984). However, it is uncertain whether synchrony of estrus is achieved by induction between females, food availability, or the presence of males. While there is no evidence of seasonality in male fertility, the abundance of mature males in female-dominated areas may vary within a year (Whitehead 1993). However, there is no evidence of a direct link between this seasonality pattern and female reproductive availability.

19.3 Mating Strategies and Tactics

> The male was the focus of intense attention from all group members, who crowded in on him, rolling themselves along his huge body. They just seemed delighted that he was there. For his part, the male was all calm serenity and gentleness.
> Gordon (1998, 22–25).

Historically, descriptions of the sperm whale mating system centered on male–male competition for control over groups of females. Mature males were called "schoolmasters" that controlled access to "harems" (groups of females; e.g., Beale 1835). Accounts from open-boat whaling years (late nineteenth century) of intense fights between males involving head-butting, jaw-locking, and tooth-shattering (Clarke and Paliza 1988) may have influenced such portrayals. It was later found that associations between males and groups of females are ephemeral (Best 1979). Moreover, the association between groups of females and individual males seems to be determined by female choice rather than male aggression (Whitehead 1993). Here, we describe the mating strategies and tactics of male and female sperm whales.

19.3.1 Male Roving

Mature males visit the warm waters inhabited by groups of females and stay in a given region for a short period within a year (Whitehead 1993; Gero et al. 2014), but exactly how long they stay until heading poleward remains unknown. In warm water, males rove between groups of females and associate with specific females over a few days to weeks (Whitehead 1993; Coakes and Whitehead 2004; Gero et al. 2014).

The same males are rarely re-sighted with the same group of females or in the same breeding ground over different years (Whitehead 1993; Jaquet and Gendron 2009; Gero et al. 2014). Yet, some degree of male philopatry exists; studies in various ocean basins have documented mature males returning to the same areas over the years (Christal 1998; Gero et al. 2014; van der Linde and Eriksson 2020; Girardet et al. 2022). For example, an 8-year study around the Azores found that, while the majority of males were sighted only during 1 or 2 years, one individual was re-sighted every year (Van der Linde and Eriksson, 2020). It is unclear whether the scarcity of re-sightings of mature males across years results from the challenge of finding them because of their low abundance on breeding grounds (<5%; Whitehead 1993; Gero et al. 2014) and fleeting presence in a given area or from a lack of male geographic or social philopatry. Additionally, there may be individual variations in the movement patterns of mature males among breeding grounds.

When males cannot defend territories or females, roving among groups of females is a better mating strategy than staying with a group if the benefits of encountering new females outweigh the benefits of staying (Whitehead 1990). A model predicted that roving would be favored over residency when the time to find a new female group is shorter than a female's typical estrous cycle and that roving would be more favorable in species with variation in the competitive ability of males (Whitehead 1990). Non-territorial species with high sexual dimorphism often have a roving strategy, suggesting that this behavior is linked with some form of size-dependent male–male competition, which may lead to delayed sexual maturity (Whitehead 1994). Males would thus benefit from delaying reproduction until they are large enough to be competitive (Whitehead 1994). However, it is not apparent how male size is involved in male–male competition in sperm whales despite the remarkable sexual dimorphism.

19.3.2 Male Contest Competition

In species with pronounced sexual dimorphism, aggression between males is frequent. However, observations of aggression between male sperm whales within breeding grounds are rare (Whitehead 2003; Gero et al. 2014). In 11 years across four decades of study around the Galápagos Islands, only one instance of aggression between males was documented (Whitehead 1993). Similar work off Dominica,

spanning nearly 20 years, reported no aggression among males (Gero et al. 2014). However, males sometimes have parallel tooth scars, presumably acquired during fights with other individuals (Kato 1984). Because these scars are more frequent among larger males than younger ones, they may happen during intra-sexual contest competition (Best 1979; Kato 1984). As these tooth rake scars are most often acquired at higher latitudes, in male-only feeding grounds (Kato 1984; Whitehead 2003), scarring in male sperm whales, as in other odontocetes, is hypothesized to have evolved as a signal of male quality, rather than resulting from direct competition for individual females (MacLeod 1998). Sperm whales do not develop teeth until sexual maturity (and until then use suction to feed without teeth), which supports the hypothesis that sperm whale teeth evolved in the context of intra-sexual competition (MacLeod 1998). Indirect evidence of male–male combats is occasional missing or broken teeth (Clarke and Paliza 1988). However, the frequency of broken teeth is similar among sexes and age classes, providing weak evidence of intra-sexual fighting as the primary cause (Whitehead 2003).

The anatomy of the male sperm whale's head may also support male contest competition. Open-boat whaling records described males using their heads as a "battering ram" against other males and whaling vessels (Berzin 1972; Carrier et al. 2002). Mechanical models indicate that the organs within the sperm whale nose could act as shock absorbers during male–male head-butting (Carrier et al. 2002; Panagiotopoulou et al. 2016). Mature males have disproportionally larger heads than females, which protrude up to 1.5 m from their lower mandible (Cranford 1999). Most of this difference is accounted for by the hypertrophy of two underlying organs, the *spermaceti* and the *junk* (homologous to the odontocete melon), which facilitate sound production and processing (Fig. 19.3; Cranford 1999). The spermaceti organ accounts for most of the relative size dimorphism between the sexes and can account for up to 30% of male body weight compared to 20% in females (Whitehead 2003). Among odontocetes, the relative size of the melon and the degree of sexual dimorphism are positively correlated, suggesting that enlarged melons may aid male–male competition (Carrier et al. 2002), but for sperm whales, this competition may be acoustic rather than physical.

There is considerable criticism against the hypothesis that the enlarged male sperm whale head functions primarily as a weapon for intrasexual contest competition. First, the scarcity of documented fights involving head-ramming between males mentioned above raises whether this behavior is typical enough to result in strong sexual selection (Whitehead 2003). However, it could be that fights between males are rarely observed because they take place very quickly or below the surface (Clarke and Paliza 1988). Secondly, the sound production organs involved in echolocation and communication are in the proposed collision area, making head-butting potentially dangerous (Huggenberger et al. 2016).
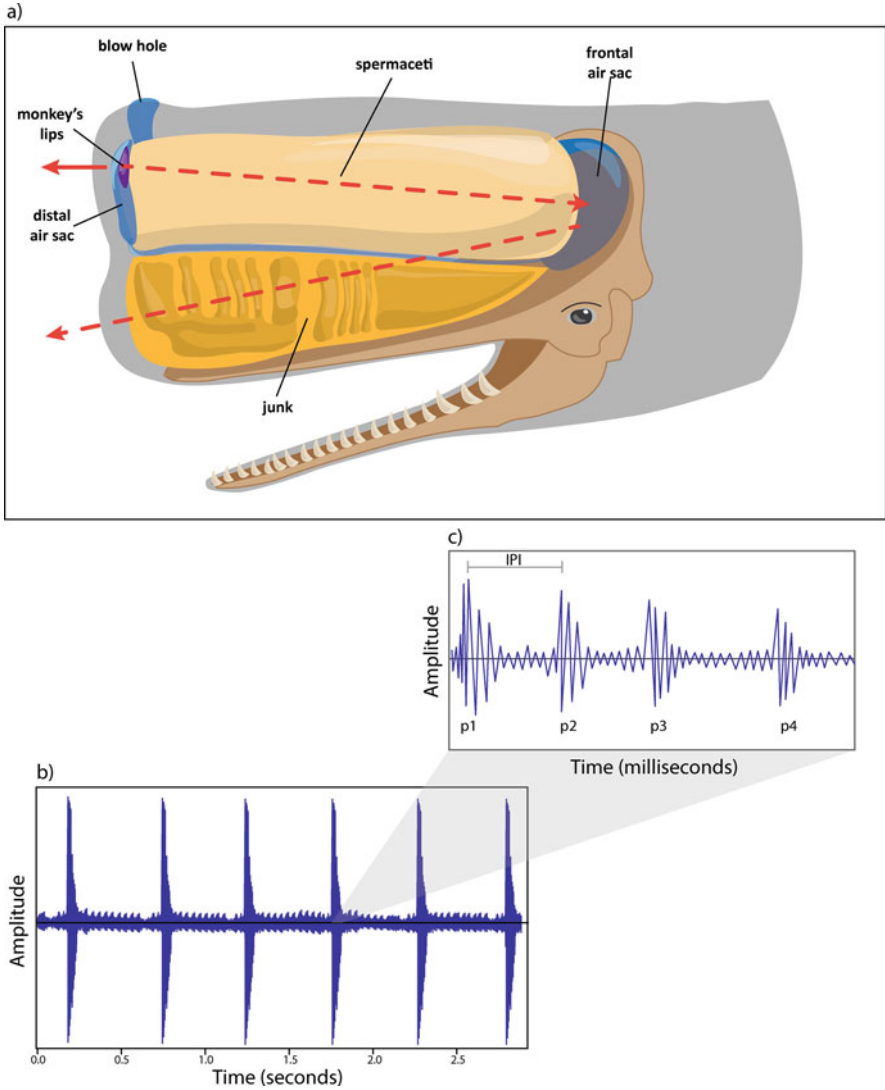
Fig. 19.3 Illustration of the sperm whale's nose anatomy (**a**). Red arrows show the trajectory of sound produced in the "monkey's lips." The solid arrow indicates the trajectory of the first pulse in a click, while the dashed line shows the trajectory followed by subsequent pulses (modified from Norris and Harvey 1972; Huggenberger et al. 2016). Waveforms of the multipulse structure of a sperm whale click: (**b**) the waveform of a sequence of clicks and (**c**) a single click are shown. Individual pulses within a click are indicated as p1–p4, and the inter-pulse interval (IPI) is shown in the inset (**c**) (modified from Norris and Harvey 1972). The IPI is thus proportional to the size of the sperm whale's nose

19.3.3 Male Signal Competition

Alternatively, sperm whale head sexual dimorphism may be used for acoustically signaling male quality. Physiologically constrained acoustic signals can act as indicators of male quality (Fitch and Hauser 2003; Wyman et al. 2012; Orbach 2019). Females may use acoustic displays to assess the quality of potential mates and males to gauge each other's competitive potential (Fitch and Hauser 2003). Through their sound production mechanism, sperm whale vocalizations carry accurate information on the size of their producer. Sperm whale clicks contain multiple evenly spaced pulses (Backus and Schevill 1966), which result from the reverberations of a single click first produced at the front of the sperm whale head in the *monkey lips* and then bounce against the air sacs surrounding the spermaceti organ (Norris and Harvey 1972). The inter-pulse interval (IPI) of sperm whale clicks is therefore proportional to the size of the spermaceti organ (Gordon 1991). Thus, the male sperm whale head may advertise size and quality (Cranford 1999).

In the ocean, where sound travels long distances, acoustic displays can be an energetically effective way for males to advertise their size and assess potential competitors' dominance while avoiding costly confrontations and minimizing travel (Orbach 2019). Sperm whale clicks may be audible to other whales in a 60 km radius, making these vocalizations an effective means to advertise the male's presence to competing males and interested females (Madsen et al. 2002). Given that male sperm whales are very rarely observed together (<100 m) in breeding grounds, it seems likely that they use acoustic signals to avoid each other (Whitehead 1993; Christal and Whitehead 1997). Male sperm whales produce "clangs," also referred to as "slow clicks," which have longer inter-click intervals (6–8 s), lower directionality, and higher energy in low-frequency ranges than regular echolocation clicks (Weilgart and Whitehead 1988; Madsen et al. 2002). Males produce slow clicks most of their time on breeding grounds (75%) (Whitehead 1993), but they also make them at high latitudes (Madsen et al. 2002; Oliveira et al. 2013), suggesting slow clicks do not function exclusively in sexual competition but could also serve for communication with other males in the context of cooperation or competition for prey (Whitehead 2009; Cantor et al. 2019).

19.3.4 Female Mate Choice

In sperm whales, observations of interactions between females and mature males suggest that female mate choice plays a key role in mating (Whitehead 1993). Female groups' reaction to a visiting male varies from actively traveling toward him and displaying a highly excited state to diving away from him (Whitehead 1993). Overall, females tend to aggregate around males (Gero et al. 2014, Girardet et al. 2022), with some males being especially well received. The breadth of reactions of groups of females toward males and a perceived lack of aggression

from males directed toward females and other males within breeding grounds (Whitehead 1993) indicates that female mate choice plays a central role in sperm whale reproduction. How exactly this female choice operates remains poorly understood.

Sperm whales likely can distinguish social membership (at the social unit and clan level) based on vocal repertoires (Hersh et al. 2022). Modeling efforts suggest there may be a greater affinity of certain mature males to certain clans or vice versa, but it remains inconclusive whether such association is between males and their natal clan or other clans (Rendell et al. 2005). Males sometimes mate with females from multiple vocal clans, as shown by second-degree relationships among vocal clans (Konrad et al. 2018a) and no nuclear DNA differences among vocal clans (Whitehead 2003). Most genetic analyses assessing regional and global population structure have not included clan identity (Mesnick et al. 2011; Alexander et al. 2016; Day et al. 2021; Girardet et al. 2022; Palmer et al. 2022) or only examined maternally inherited mitochondrial DNA (mtDNA; Rendell et al. 2012). Thus, while clan membership could play a role in female mate choice, it remains unknown whether females prefer males from specific clans (Rendell and Whitehead 2005; Rendell et al. 2005).

Another possible female mating tactic is copying the mate choices of other females (Westneat et al. 2000; Laland 2004; Orbach 2019). This tactic is consistent with evidence of shared paternity within and between sympatric social units (e.g., Konrad et al. 2018b; Girardet et al. 2022). However, this is not definitive because some shared paternity would be expected if females in a social unit are simultaneously receptive in the presence of an acceptable male (Westneat et al. 2000). Likewise, high levels of shared paternity could also be explained by some males having attractive characteristics or traits that enable outcompeting rival males, such as large body size.

Females may choose to mate with the same male in multiple years. This has been suggested by a few possible full sibling relationships (Pinela et al. 2009; Konrad et al. 2018b; Girardet et al. 2022). However, more robust genetic analyses are required to rule out other potential relationships for these cases. Additionally, research in the Indian Ocean indicates that past mates may be well received in subsequent visits. Girardet et al. (2022) described a gathering of approximately 60 individuals from multiple social units that coincided with the arrival of a mature male, which was genetically identified as the likely father of a calf born the same year in that area. If females tend to mate again with past mates, this could induce males to return to the same areas.

19.4   Care System

The care of their young is very remarkable, they not only carrying them on their tails and suckling them, but often rising with them for the benefit of the air; and however they are

chased or wounded, yet as long as they have sense, and perceive life in their young, they will never leave them (...).

Paul Dudley (1725)

19.4.1 Maternal Care of Offspring

Compared to other cetaceans, sperm whale females invest heavily in their offspring through prolonged gestation and post-partum calf care. These traits contribute to their slow reproductive rate.

Weaning occurs over a prolonged period, with substantial variation in the age of calves. In the Eastern Caribbean, calves appear to nurse from a minimum of 3 years up to 8 years (Gero et al. 2014). Whalers found milk in the stomach of a 13-year-old juvenile and solid food in the stomach of 1-year-old calves (Best et al. 1984). The latter observation could indicate that calves forage independently or receive food from older members of their social unit. While first-year calves seem to suckle 20–47% of the time based on tagging data, their echolocation and diving abilities (up to 662 m and 44 min) suggest that they may supplement their diet with foraging (Tønnesen et al. 2018). Thus, the transition from nursing to independent foraging likely occurs over several years. Maternal investment is likely greatest when calves are young, as females are less socially connected when their calf is less than a year old, presumably because they dedicate time to nursing and foraging to meet the energetic demands of lactating (Gero et al. 2013).

Sperm whale maternal investment may also include teaching their young, as in other odontocetes (Atlantic spotted dolphins, *Stenella frontalis*, Bender et al. 2009; killer whales, Guinet and Bouvier 1995). For a female's behavior to qualify as teaching, she must modify her behavior in the presence of her calf in a way that does not directly benefit herself while enabling the calf to more efficiently acquire skills or knowledge (Caro and Hauser 1992). Although there is no evidence of sperm whale females teaching their calves, the sperm whale social system provides an opportunity for this behavior. Teaching can evolve in a species when appropriate mechanisms for social learning exist, and the teacher benefits from the learner's learning (Hoppitt et al. 2008). Sperm whales meet these criteria, given their social learning ability (evidenced by their culture; Whitehead and Rendell 2014) and the potential benefits to the mother of both inclusive fitness and direct benefits by reducing the duration of calf dependency. Even if teaching does not occur, sperm whale calves have ample opportunities for social learning (Cantor et al. 2019; Rendell et al. 2019).

19.4.2   Alloparental Care

Communal care of calves is a key aspect of sperm whale reproductive strategies. Calf care, particularly for protection against predators, is a hypothesized driving factor of sperm whale social structure (Best 1979; Whitehead 1996; Gero et al. 2013). Unlike the infants of other cetacean species with close maternal attendance (Rendell et al. 2019), sperm whale calves spend time without their mother while she forages. Thus, alloparenting, defined as the behavior of a non-parent that benefits the calf and differs from what the caregiver would do if the calf were absent, is likely important for sperm whales (Woodroffe and Vincent 1994; Whitehead 1996). Sperm whales accompany each other's calves, referred to as babysitting, and collectively defend against predators by gathering in defensive formations, such as the "rosette" (Fig. 19.4), with calves in the middle of the circle (Weller et al. 1996).

There is evidence that female sperm whales provide milk to calves that are not their own, i.e., allonurse. Calves attempting to suckle from multiple females in their social unit (Gordon 1987; Gero et al. 2009; Konrad et al. 2019) make short, shallow dives beside females (Fig. 19.5) and perform mammary bumps assumed to stimulate the milk let-down reflex (Gero and Whitehead 2007; Johnson et al. 2010). Suckling behavior may not result in milk intake (Cameron 1998), and it is uncertain whether calves receive any milk from other females. Yet, in the absence of receiving milk or

Fig. 19.4 Illustration of a cooperative defense formation, referred to as a Rosette or Marguerite formation, based on the description by Weller et al. (1996)

Fig. 19.5 A young calf (> 1 year old) performing dives associated with nursing next to an allonurse from his social unit (credit: Dominica Sperm Whale Project, 2016)

other benefits (e.g., social or emotional; Lee 1987; Cameron 1998), it is unlikely a calf would invest energy attempting to suckle from allonurses. Further supporting the hypothesis of allonursing, lactating females consistently outnumbered calves within groups of sperm whales killed by whalers (Best et al. 1984).

Although mature females and juveniles of both sexes provide allocare (Gero et al. 2009; Konrad et al. 2019), some individuals do so disproportionately. In the Eastern Caribbean, allonurses are often close maternal kin (Konrad et al. 2019). However, this may be context dependent. For example, in one Eastern Caribbean social unit all observed allonursing was performed by first-degree relatives of the mother, yet in social units where mothers had no close kin, unrelated female members provided allocare (Fig. 19.6; Konrad et al. 2019; Sarano et al. 2021). Reciprocation of alloparental behavior has also been observed in some cases (Gero et al. 2009, 2013) but not in others (Konrad et al. 2019). Additionally, young females may provide a disproportionate amount of calf care, suggesting that they benefit from opportunities to gain maternal experience (Konrad et al. 2019). Older females may also be valuable sources of allocare within their social units, given the prevalence of lactating females over the age of 40 despite females of this age rarely having young calves (Best et al. 1984). Finally, the age of the calf appears to affect the amount of allocare it receives, with allonursing and babysitting prevalent for calves less than a year old (Konrad et al. 2019).

Some differences may occur in alloparenting among clans and regions. For example, differences in diving synchrony have been documented between two vocal clans in the Pacific Ocean, which may have implications for the patterns of calf care between clans (Cantor and Whitehead 2015). Additionally, a study of calf
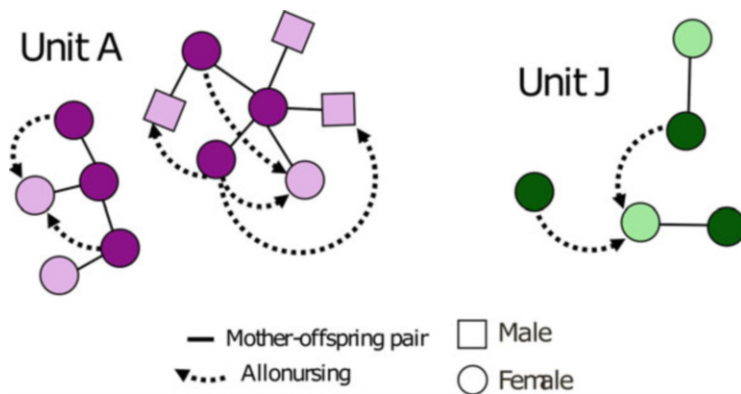
Fig. 19.6 Differing patterns of allonursing in different social units from the Eastern Caribbean. Nodes represent individual whales from Unit A (purple) and Unit J (green), with darker shading indicating mature or juvenile individuals and light shading indicating calves. Solid edges between individuals denote mother–offspring relationships. Arrows point from mature or juvenile female to the calf observed attempting to nurse from her (figure based on results from Konrad et al. 2019)

care within social units from the Sargasso Sea and the Eastern Caribbean noted differences in the patterns of allocare (Gero et al. 2009).

19.5   (An Odd) Convergent Evolution of Reproductive Strategies

The morphological, reproductive, and behavioral traits that make sperm whales unique among marine mammals reveal surprising similarities with the African elephant (*Loxodonta africana*; Weilgart et al. 1996; Whitehead 2003). Like sperm whales, African elephants have large bodies and brains and are the most sexually dimorphic terrestrial mammal, with mature males up to two times heavier than females (Sukumar, 2003). Females of both species form long-term matrilineal social units in which they cooperatively care for the young (Moss, 1983). Males of both species disperse from their natal units when juvenile, at 9–18 years of age, and either form bachelor groups or lead solitary lives (Whitehead 1994, 2003). Mating is delayed well beyond puberty when male elephants are over 29 years old (Sukumar 2003). Elephant males also rove between groups of receptive females with marked preferences for older males, resulting in biased paternal patterns (Moss 1983). Mature male elephants also have distinct foraging strategies and home ranges that differ from groups of females and juveniles (Shannon et al. 2006). The remarkable parallels in the life histories and mating strategies of sperm whales and African elephants are coupled with similarly large home ranges, ecological success, and cognitive abilities, and likely reflect convergent evolution (Whitehead 2003).

Mating system evolution reflects predation pressure, habitat structure, resource availability, and sociality (Bowyer et al. 2020). The different reproductive strategies adopted by males and females within a species reflect different costs and benefits incurred by each sex (Orbach 2019). In sperm whales, there are significant differences in the energy budgets of males and females; while females dedicate considerable resources to the long-term care of their offspring, males invest in slow and continued growth to increase their chances of mating (Whitehead 2003). Thus, the female-centric societies in sperm whales and elephants likely emerged as a means of communal calf care against predation (Lee 1987; Sukumar 2003; Whitehead 2003; Rendell et al. 2019). The home ranges over which females of these species roam favor the development of longer-lasting social bonds in female social units compared with those of other social species that face similar predation pressures but have restricted home ranges (Whitehead 2003). The female investment in offspring is associated with a high incentive to choose a high-quality male (Whitehead 2003). Among sperm whales and African elephants, high-quality males are large and old (Moss 1983; Whitehead 1994, 2003; Sukumar 2003). Males grow to outcompete rivals and rove between groups of receptive females to maximize mating opportunities (Whitehead 1990, 1994). Thus, the distinct mating strategies of both sexes of sperm whales and elephants produce differences in morphology, sociality, and ecology (Sukumar 2003; Whitehead 2003).

19.6   Effects of Whaling on Sperm Whale Reproduction

Whaling operations have yielded insights into sperm whale reproductive biology. Sperm whales were the main target of the whaling industry between the eighteenth and nineteenth centuries and the 1950s–1980s (Whitehead 2002; Whitehead and Shin 2022). The global sperm whale population declined by approximately 57% over the past 300 years (Whitehead and Shin 2022). Although commercial whaling was banned in 1986, recovery has been slow or non-existent among sperm whale populations (Whitehead and Shin 2022). This results from the intrinsically low reproductive potential of sperm whales and the lingering effect of whaling on the sex ratio and the transmission of social information (Whitehead 2003).

While open-boat whaling targeted male and female sperm whales indiscriminately, modern whaling operations in some regions primarily targeted mature males (Hope and Whitehead 1991; Whitehead 2003). The proportion of mature males caught off Perú and Chile declined drastically, from 35% between 1958 and 1961 to 2% between 1979 and 1982 (Ramirez 1989; Whitehead et al. 1997). The removal of mature males from the Eastern Tropical Pacific Ocean was associated with a decrease of ∼ 15% in pregnancy rates (Ramirez 1989). The effects of whaling on sperm whale reproductive potential lingered long after the whaling moratorium took effect. Between 1985 and 1995, the ratio of mature males to females around the Galápagos Islands remained significantly lower than expected (Cantor et al. 2017). Likewise, indicators of female fecundity were considerably less than those reported

in regions where mature males were not as aggressively targeted in recent decades (Whitehead et al. 1997). In the 2010s, the proportion of males and calves off the Galápagos had slightly increased, suggesting a slow recovery of mature males that visit Eastern Tropical Pacific waters, corresponding with higher calving rates (Cantor et al. 2017). The population of Antarctic sperm whales—exclusively composed of mature males—has had the highest estimated rate of increase in recent decades (Whitehead and Shin 2022). While promising, it may take up to two decades after the cessation of whaling for the reproductive potential of sperm whale populations to be restored to inherent levels (Whitehead and Shin 2022).

The reproductive success of sperm whales may have also been affected by whaling through social disruption (Whitehead and Shin 2022). Female sperm whales acquire much of their behavior through social learning, including foraging strategies, movement patterns, and social behaviors (Whitehead and Rendell 2004; Marcoux et al. 2007a, b; Cantor and Whitehead 2015; Eguiguren et al. 2019). Whalers may have removed individuals who were vital knowledge holders, which can have lasting effects across generations (Whitehead 2003; Whitehead and Shin 2022), as seen among African elephants. The impact of poaching on elephant social structure and reproductive rates was detected up to 15 years after the end of poaching for ivory (Gobush et al. 2008). Accounting for the effects of social disruption in population models of sperm whales has helped explain why the recovery of their populations has not been as fast as expected (Whitehead and Shin 2022).

19.7 Conclusions and Future Directions

Until recently, sperm whales were among the most hunted species of large mammal. Today, sperm whales are recognized for their ecological role, strong familial ties, rich learned cultures, and complex societies. Still, much remains to be discovered about their reproductive strategies, mating systems, and care systems. We suspect that most answers will come from accumulating long-term observational data and non-invasive technological advances, which record behavior, acoustics, and at-sea movements with unprecedented detail.

One gap in our understanding of sperm whales' lives is the long-distance movements of mature males between feeding and breeding grounds. Photo-identification from scientific expeditions and citizen science (Levenson et al. 2015) may reveal the movement patterns of individual males. In addition, telemetry can provide insights into individual movements across the vast three-dimensional oceanic realm (Palacios et al. 2022). Although more invasive and logistically demanding, tracking individuals with tags can provide data on long-distance displacement within and across ocean basins (Lefort et al. 2022), as well as body orientation and fine-scale movements in the water column (Palacios et al. 2022), which could reveal inter-individual interactions. Moreover, attaching recording devices to whales can also provide information on acoustic communication (Johnson and Tyack 2003; Andreas et al.

2022) and long-term social interactions (Ortega-Ortiz et al. 2012). This high-resolution communication and social information can shed light on another poorly understood aspect of sperm whale reproductive strategies: mate selection.

Understanding mating choices will require an improved understanding of male–female interactions, likely using a multi-platform approach (Andreas et al. 2022; King and Jensen 2022). For instance, underwater imaging can reveal interactions between females and males as they approach social units (Girardet et al. 2022) and aerial drones can quantify behavioral interactions at the surface (Weiss et al. 2021). Behavioral data will be best interpreted in the context of mate choice if knowledge of reproductive status is available (e.g., via hormonal analyses, Dunstan et al. 2012; Hunt et al. 2013). Understanding mate choice also requires an understanding of traits that are attractive to the opposite sex. To investigate whether size affects mate choice, genetic analyses can be coupled with body size estimates obtained by passive acoustic monitoring using inter-pulse intervals of male echolocation clicks (Beslin et al. 2018) or morphometrics from drones (Dickson et al. 2021; Glarou et al. 2022).

Combining multiple sampling platforms will also advance our understanding of sperm whale calf care. In addition to nursing and defending calves, maternal and alloparental behaviors could include provisioning with solid food and teaching. Studies on how calves acquire coda dialects and foraging behavior may illuminate how they learn these skills. Additionally, extending studies across ocean basins will help provide a fuller picture of sperm whale calf care. As we improve the ability to record and understand multiple behavioral and physiological data types, we will gain insights into how sperm whales mate, reproduce, and care for the next generation as they slowly recover in the post-whaling era.

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Chapter 20
Reproductive Tactics in Baleen Whales

Franca Eichenberger, Ellen C. Garland, and Emma L. Carroll

Abstract While a variety of reproductive tactics are readily witnessed in odontocetes, such behaviors can be far more elusive in baleen whales and in some cases are yet to be observed. This leads researchers to study the reproductive behaviors in mysticetes using a variety of research methods which have improved greatly in recent years. Genetics and genomics tools can provide valuable information on maternity, paternity, age, diversity, and kinship, while acoustic tools can provide new insights into the function of sexual displays such as song. In this chapter, we explore what is known about reproductive strategies and tactics of baleen whales, with a particular focus on the comparatively well-studied right whales (*Eubalaena* spp.) and humpback whale (*Megaptera novaeangliae*). Finally, we showcase that by integrating multiple data types, we can explore the interactions between anatomy, physiology, reproductive success, age, population dynamics, and acoustic displays to better understand the mating systems of baleen whales.

Keywords Age · Baleen whale · Genomics · Molecular ecology · Reproductive strategy · Reproductive success · Sexual selection · Song · Tactics

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20.1 Mating Systems and Reproductive Strategies of Baleen Whales

There are many gaps in our understanding of mating systems and strategies of marine mammals, in particular for many of the mysticete suborder (baleen whales). The species are often rare, endangered, or otherwise difficult to observe; few observations may have therefore been made of their mating behavior, especially at the temporal scale necessary to evaluate lifetime reproductive success. When mating behaviors are observed, understanding the full behavioral repertoire and its context is challenging due to the elusive nature of mammals that spend most of their time submerged.

Most baleen whales undertake seasonal migrations to feed, mate, and give birth. The distances of these migrations and the extent to which breeding and feeding areas are separated from each other vary greatly across species, sometimes even across populations (e.g., non-migratory Arabian sea humpback whales, *Megaptera novaeangliae*: Mikhalev 1997). While some of the largest lunge feeders (rorquals), blue and fin whales (*Balaenoptera musculus* and *B. physalus*), appear to breed dispersed across unobserved offshore areas (Simon et al. 2010; Sears et al. 2013), other baleen whales aggregate on distinct breeding grounds (e.g., humpback whale; gray whale, *Eschrichtius robustus*; southern right whales, *Eubalaena australis*). The reproductive behaviors of most baleen whales indicate a polygynous mating system (successful males mate with multiple females), yet variance in male reproductive success is relatively low in comparison to polygynous mammals on land (Cerchio et al. 2005; Frasier et al. 2007; Carroll et al. 2012). Parentage analyses have further revealed that females mate with different males across years (e.g., Clapham and Palsboll 1997; Frasier et al. 2007), thus hinting toward a polygynandrous mating system (both males and females mate with multiple partners). However, direct observations of females mating with multiple males within the breeding season have, so far, only been reported in bowhead whales (*Balaena mysticetus*, Tarpley et al. 2021), gray whales (Swartz 1986), and North Atlantic right whales (*Eubalaena glacialis*, Mate et al. 2005). Despite the similarities in reproductive strategies (i.e., polygynandry, polygyny) across species, the behaviors that individuals engage in within their species' mating system can vary considerably (Table 20.1).

Much of what we know about mysticete reproductive behavior comes from humpback, right, and gray whales. There are similarities in the reproductive behaviors between these species: males typically aggregate in groups of a few to a few dozen individuals, where they physically compete to be closest to a single female at the center of the group (Tyack and Whitehead 1982; Norris et al. 1983; Kraus and Hatch 2001; Parks et al. 2007). However, while male humpback whales produce one of the most complex acoustic and culturally transmitted displays in the animal kingdom (Payne and McVay 1971; Payne and Payne 1985; Noad et al. 2000; Garland et al. 2011), the acoustic displays of right and gray whales are much simpler (Crance et al. 2019; Matthews and Parks 2021; Parks 2022). Right whales have the largest testes to body mass ratio of any baleen whale, indicating the important role of

Table 20.1 Overview of the male reproductive tactics and the potential for female choice in baleen whales. "Distribution" refers to the distribution of individuals in space during the breeding season. "Pre-copulatory trait investment" was based on the presence of elaborate vocal displays (i.e., song) with higher investment for more complex songs (see Table 20.2). "Post-copulatory trait investment" was based on whether the phylogenetically controlled residuals of maximum testes mass regressed onto maximum body length were lower than expected (low), as expected (medium), or higher than expected (high), based on Dines et al. (2015). "Potential for female choice" indicates the hypothetical possibility for female choice to occur based on the species' mating system and the observed or inferred male reproductive tactics, and whether female choice likely takes place before and/or after copulation

Family	Species	Distribution	Pre-copulatory trait investment	Post-copulatory trait investment	Male reproductive tactics	Potential for female choice	Source
Balaenopteridae	Bryde's whale, *Balaenoptera edeni*	(dsp)	(Low)	Medium	(Sc, Sp)	u	1–3
	Omura's whale, *B. omurai*	(dsp)	Low–medium	u	(Sc, S)	u	1–4
	Sei whale, *B. borealis*	(dsp)	(Low)	Medium	(Sc, Sp)	u	1–3
	Blue whale, *B. musculus*	disp	High	Medium	Sc, S	preC(+postC)	1–3, 5
	Fin whale, *B. physalus*	disp	High	Medium	Sc, S	preC(+postC)	1–3, 10
	Humpback whale, *Megaptera novaeangliae*	aggr	High	Low	C, S, Sc, E	preC	1–3, 6–11
	Antarctic minke whale, *B. bonaerensis*	(dsp)	(Low)	u	(Sc)	u	
	Common minke whale, *B. acutorostrata*	dsp	Medium	Medium	Sc, S	(preC+postC)	1–3
Eschrichtiidae	Gray whale, *E. robustus*	aggr	Low	High	Sp, Sc	postC	1–3, 12
Balaenidae	Pygmy right whale, *Caperea marginata*	(dsp)	(Low)	(Medium)	(Sc)	u	3
	NA right whale, *Eubalaena glacialis*	aggr	Low	(High)	Sp, Sc, E	postC	13–16
	NP right whale, *E. japonica*	(aggr)	Low–medium	High	Sp, Sc, S	postC(+preC)	1–3
	S right whale, *E. australis*	aggr	Low	(High)	Sp, Sc	postC	17–19

(continued)

Table 20.1 (continued)

Family	Species	Distribution	Pre-copulatory trait investment	Post-copulatory trait investment	Male reproductive tactics	Potential for female choice	Source
	Bowhead whale, *Balaena mysticetus*	aggr	High	High	Sp, S, Sc	preC+postC	1–3, 20, 21

Abbreviations: aggr, breeding aggregations; dsp, dispersed; C, contest competition; Sc, scramble competition; E, endurance competition; Sp, sperm competition; S, singing; preC, pre-copulatory; postC, post-copulatory; u, unknown or unclear; ( ) for inferred or hypothesized

References: (1) Ralls and Mesnick (2019); (2) Dines et al. (2015); (3) Brownell and Ralls (1986); (4) Cerchio (2022); (5) Sears et al. (2013); (6) Tyack and Whitehead (1982); (7) Clapham and Palsbøll (1997); (8) Cerchio et al. (2005); (9) Pack et al. (2012); (10) Simon et al. (2010); (11) Herman (2017); (12) Swartz (1986); (13) Kraus and Hatch (2001); (14) Mate (2005); (15, 16) Frasier et al. (2007, 2013); (17) Carroll et al. (2012); (18) Burnell (2001); (19) Rowntree et al. (2001); (20) Würsig and Clark (1993); (21) Tarpley et al. (2021)

Table 20.2 Overview of baleen whale song from species that have been suggested to sing. Seasonality refers to the act of singing within a given year. Estimates of song complexity levels (simple, low complexity, high complexity) are based on the general song structure and sound repertoire (as given in "Song description") and the temporal and spatial variation of song. Temporal and spatial variation refer to changes in song (e.g., structure, composition, frequency). Audio examples of each species are provided online (https://doi.org/10.1007/978-3-031-35651-3_20).

Family	Species	Song description	Seasonality	Frequency (Hz)	Song complexity	Temporal variation	Spatial variation	Sex of singer	Reproductive function	Source
Balaenopteridae (rorquals)	Omura's whale, Balaenoptera omurai	Amplitude-modulated vocalizations, rhythmically repeated	u	15–20	Simple but not much known	u	u	u	Suggested	1
	Blue whale, B. musculus	Low-frequency songs that consist of a series of phrases each comprised of 1–5 sounds units	(Year-round)	16–100	Relatively low	Worldwide decline in frequency	Geographically distinct	Male	Suggested, further hypothesized to indicate male body size	2–4
	Fin whale, B. physalus	Low-frequency pulses arranged into stereotypic sequences at regular intervals (i.e., inter-pulse intervals, IPIs)	20 Hz calls produced mainly during the breeding season	15–40	Relatively low	Increase in IPIs, decrease in peak frequency	Geographically distinct	Male	Suggested, further hypothesized to attract females to aggregations of prey	5–12
	Humpback whale, Megaptera novaeangliae	Highly stereotyped and hierarchically structured: a sequence of sounds ("units"), creates a "phrase," repeated phrases form a "theme," and several different themes in a particular order make a "song"	Mainly during breeding season, and migration, and to a lesser extent on feeding grounds	50–4000	High	Changes in song structure and complexity during cultural evolutions and revolutions	Geographically distinct, high population conformity	Male	Suggested, further hypothesized to serve as a multi-message display and to indicate male quality	13–21
	Common minke whale, B. acutorostrata	Low-frequency pulse trains with variable IPI structure and peak frequencies	Seasonal but unclear if due to changes in vocal behavior or	55–150	Relatively low	Limited variability between years	Geographical variability in pulse train duration	(Male)	Suggested	22–24

(continued)

Table 20.2 (continued)

Family	Species	Song description	Seasonality	Frequency (Hz)	Song complexity	Temporal variation	Spatial variation	Sex of singer	Reproductive function	Source
Balaenidae	NP right whale, *Eubalaena japonica*	Stereotypic sequence of gunshot sounds	absence of whales at recording sites (Seasonal)	50–1500	Simple	u	Multiple song types within each region	Male	Suggested, further hypothesized to encode information on resource availability	25
	NA right whale, *E. glacialis*	Long patterned sequences of gunshots (unclear if song due to data deficiency)	(Seasonal)	50–1500	(Simple)	u	u	(Male)	Suggested to function as female advertisement or male–male agonistic signal	26–28
	Bowhead whale, *Balaena mysticetus*	High diversity of song types comprised of highly modulated sounds and biphonation	(Mainly during breeding season)	50–4000	High	Complete renewal of singing repertoire	Multiple song types within each region but shared among smaller clusters of animals	u	Suggested, further hypothesized to indicate male quality	29–32

Abbreviations: u, unknown or unclear; () for inferred or hypothesized

References: (1) Cerchio et al. (2017); (2) Cummings and Thompson (1971); (3, 4) McDonald et al. (2006, 2009); (5) Watkins et al. (1987); (6) Croll et al. (2002); (7) Delarue et al. (2009); (8) Simon et al. (2010); (9) Morano et al. (2012); (10) Oleson et al. (2014); (11) Širović et al. (2017); (12) Weirathmueller et al. (2017); (13) Payne and McVay (1971); (14) Winn and Winn (1978); (15) Payne and Guinee (1983); (16) Noad et al. (2000); (17, 18) Garland et al. (2011, 2013); (19) Herman (2017); (20) Allen et al. (2018); (21) Murray et al. (2018); (22, 23) Risch et al. (2013, 2014); (24) Risch (2022); (25) Crance et al. (2019); (26) Parks et al. (2005); (27) Matthews and Parks (2021); (28) Parks (2022); (29, 30) Tervo et al. (2011a, b); (31) Stafford et al. (2018); (32) Erbs et al. (2021)

sperm competition as their reproductive tactic (Brownell and Ralls 1986). Despite being in the same taxon and exposed to similar environmental pressures, baleen whales seem to have evolved different reproductive strategies and tactics. This raises the question of what behavioral strategies the lesser-studied baleen whales have evolved and what are the underlying ecological and social drivers that led to the variation in reproductive behaviors across baleen whales. The unique evolutionary history of the transition from land to sea, well-resolved phylogeny, and trait variation of cetaceans offer a great opportunity to test hypotheses on the evolution of mating systems and reproductive behaviors.

20.2 Ecological and Social Factors Shaping Reproductive Tactics in Baleen Whales

Baleen whales share many of the life history characteristics of their phylogenetic terrestrial relatives, yet their locomotion and sensory systems are strikingly different. Over more than 50 million years of evolution (Uhen 2010), the anatomy and physiology of marine mammals became specialized for the marine environment. It is reasonable to assume that the reproductive tactics of baleen whales too are adapted for a life in the ocean.

Baleen whales are highly mobile and undertake some of the longest migrations in any mammal. For example, Oceania (South Pacific) humpback whales travel more than 7000 km between their breeding grounds and Antarctic feeding grounds (Riekkola et al. 2019). While some species show clearly defined migration strategies and large-scale seasonal movements from their polar feeding grounds to clearly distinct breeding grounds closer to the equator (e.g., humpback, blue, and gray whales), others undertake shorter migrations, do not breed near the equator (e.g., fin and right whales), and/or remain at similar latitude year-round (e.g., Bryde's whale, *Balaenoptera edeni*; bowhead whale; pygmy right whale, *Caperea marginata*; Bannister 2018). These migration strategies may even vary across populations (e.g., Bering-Chukchi-Beaufort Sea bowhead whales: Insley et al. 2021). While seasonal migration to warmer waters with fewer predators could represent a female tactic to increase offspring survival (Whitehead and Moore 1982; Corkeron and Connor 1999), the exact reasons why baleen whales travel these sometimes vast distances remain unclear. Considering the diversity of migratory tactics across baleen whale species and populations, the driving forces underlying their movement patterns might vary similarly (Horton et al. 2022).

Many baleen whales are capital breeders; after migrating from productive feeding grounds, individuals at the breeding ground generally go through an elongated fasting period (Costa and Maresh 2018). Females provision themselves and their offspring by feeding on seasonally abundant food sources, often thousands of miles from where they give birth. The long migration and elongated fasting period further increase the costs of reproduction for female baleen whales as female body condition

Fig. 20.1 Southern right whale cow–calf pair, photo taken in the Auckland Islands Maungahuka in the Aotearoa New Zealand subantarctic by the University of Auckland Waipapa Taumata Rau southern right whale research team, under New Zealand Department of Conservation permit 84845-MAR

affects fetal and calf growth (Christiansen et al. 2014, 2018). The capital breeding strategy also means nursing a calf leads to rapid depletion of a female's fat stores and body condition; in southern right whales, females lose an estimated 25% of their body volume in their calves' first few months of life due to lactation (Christiansen et al. 2018; Fig. 20.1). At this stage of development, the calf grows up to 1 m/month, highlighting the effectiveness and cost of this provisioning (Best 1994; Christiansen et al. 2018). Females may build up energy reserves required for reproduction over multiple feeding seasons, resulting in the need for longer inter-birth intervals. This likely reflects a female reproductive tactic in which the female delays reproduction to build up sufficient energy storage that may ultimately increase the survival of herself and that of her future offspring. Flexibility in reproductive timing may provide females with a buffer for poor prey conditions in a single year (Christiansen et al. 2022b). It may be that many females can become pregnant annually but carry the fetus to term only if conditions allow. The early stages of pregnancy (first and second trimesters) only incur about 5% of the total energetic cost of gestation (Christiansen et al. 2022b). It could therefore be that females can (physiologically) "decide" if the amount of energy resources obtained during the summer feeding period is sufficient to continue with the pregnancy. There is evidence that calving rates of southern right whales relate directly to environmental conditions that impact prey availability at offshore feeding grounds (Leaper et al. 2006; Seyboth et al. 2016). Similarly, the annual pregnancy rates of humpback whales along the Western Antarctic Peninsula may represent a response to favorable ecological conditions at these feeding grounds (Pallin et al. 2018b).

Compared to females, male baleen whales carry little of the reproductive costs, and their mating and reproductive success are mainly limited by distribution of mating partners in space and time. Due to the lack of stable groups in mysticetes and the absence of prey resources at their calving grounds, individuals are typically widely distributed. To combat this, many baleen whale species aggregate on breeding grounds every year (Table 20.1), many show site fidelity to these locations (Baker et al. 2013; Carroll et al. 2013), and produce acoustic displays audible across vast distances to find mates (Sect. 20.2.2). The variable inter-birth intervals of females can produce a male-biased operational sex ratio (ratio of receptive adults at any time in a population) at these breeding grounds, and further increase male competition for breeding opportunities (Boness et al. 2002). The 3D underwater habitat and great dispersion of individuals across the breeding ground, or the absence of distinct breeding grounds in some species, make it challenging for males to monopolize and defend groups of females or territories against other male competitors. Considering that fasting at the breeding ground is typical of baleen whales, food sharing and resource defense are also unlikely tactics. By process of elimination, (1) direct male–male competition over mating access in the form of male contest, endurance, and/or scramble competition, (2) indirect competition by attempting to attract females via elaborate displays (e.g., song), or (3) sperm competition over successful female fertilization are all possible and non-mutually exclusive reproductive tactics. All of these reproductive tactics are inferred or have been observed in baleen whales, and below we discuss each of them.

20.2.1 Direct Male–Male Competition over Mating Access

In some species, direct male–male interactions are readily observed and allow insights into mating tactics. The temporary group formations of three or more adults in right, gray, and humpback whales often peak around the breeding season and offer opportunities for direct competition between males for female mating access despite a commonly scattered distribution and solitary behavior (Norris et al. 1977, 1983; Everitt and Krogman 1979; Tyack and Whitehead 1982; Clark 1983; Clapham et al. 1992; Würsig and Clark 1993; Kraus and Hatch 2001) (Figs. 20.2 and 20.3). The level of aggression and intensity of male–male interactions within such groups vary across species. In humpback whales, males often engage in agonistic fights to gain or maintain the privileged position closest to the female of the group (Tyack and Whitehead 1982; Clapham et al. 1992) and show high levels of surface activity and behavioral displays (e.g., charges and peduncle strikes) that indicate the aggressive nature and intensity of these interactions (Baker and Herman 1984; Fig. 20.3). Males also often escort a single female (with or without her newborn calf) to form a pair. It is unclear whether the male's defense and the escorting of the female result in copulation or reflect mate guarding following earlier copulation (Clapham 1996). In right, gray, and bowhead whales, male–male interactions within these temporary group formations appear to be much less aggressive than in humpback whales.

Fig. 20.2 A group of ten socializing southern right whales photographed by drone in the Auckland Islands Maungahuka in the Aotearoa New Zealand subantarctic by the University of Auckland Waipapa Taumata Rau southern right whale research team, under New Zealand Department of Conservation permit 84845-MAR

Although aggregations of several males within temporary group formations are most likely driven by intra-sexual selection among males, they may also offer females the possibility to assess multiple potential mates. In North Atlantic right whales and humpback whales, females may facilitate the formation or increase the size of male aggregations to incite competition among males by surface-active displays (Clapham 2000) or vocalizations (Kraus and Hatch 2001; Parks 2003; Parks and Tyack 2005; Parks et al. 2007). Females may thus use aggregations of competing males to secure the highest quality male by mating with (or being fertilized by, see Sect. 20.2.3) the winner of the competition or through active mate choice.

The traits that allow a male to outcompete rivals underwater are likely different from the traits determining the outcome of male–male competition on land. While large body size is often correlated with increased strength on land and a clear advantage in fighting, a large size might come at the cost of reduced maneuverability underwater (Le Boeuf 1991; Segre et al. 2022). Better agility due to small size may be more advantageous in male–male competition in baleen whales considering the 3D underwater habitat, in contrast to terrestrially mating mammals (Mesnick and Ralls 2018a). However, large body size could increase the duration a male remains on breeding grounds, which are devoid of food (Craig et al. 2003), therefore increasing mating opportunities. Apart from maneuverability, male endurance and stamina likely also play an important role in determining a successful competitor,

Fig. 20.3 Humpback whale competitive group on their breeding grounds off the coast of New Caledonia in the South Pacific. The photo was taken by Opération Cétacéas, under a permit issued by the Province Sud

considering the hours-long duration of competitive group formations. Interestingly, mature-sized females at times have a preference for large males (Pack et al. 2012), suggesting that sexual selection could still favor large body size in males through female mate choice. Large male body size may convey other advantages, such as large offspring size, which has been correlated with low mortality in the first year of life in southern right whales (Best and Rüther 1992). Considering the atypical mammalian sexual dimorphism in mysticetes, where females tend to be slightly larger than males, selective pressures for large body size in females resulting from their higher energetic demands for reproduction likely outweigh sexual selection pressures for large body size in males (Ralls 1976).

20.2.2   Indirect Competition to Attract Females via Male Song

Baleen whales have a high variety of sounds and acoustic displays ranging from the low-frequency sounds of fin and blue whales, some sounds of which are below human hearing, to the star-wars-like vocalization of dwarf minke whales (*Balaenoptera acutorostrata*), to the more complex and hierarchically structured songs of humpback whales (Clark and Garland 2022). While all baleen whales vocalize, some also produce male-only breeding vocalizations termed "songs"
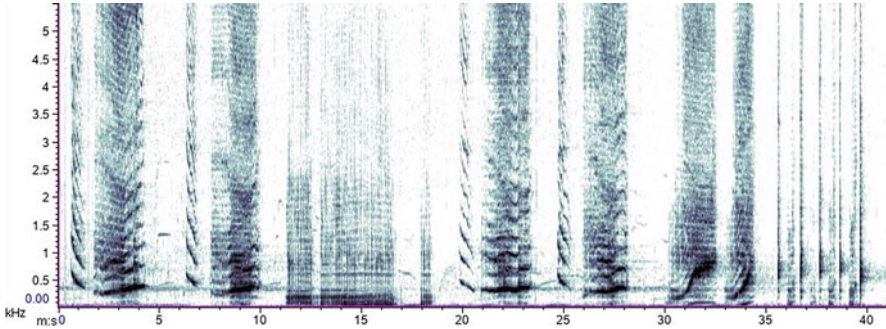
Fig. 20.4 Spectrogram of a small, continuous section of humpback whale song showing a variety of units recorded from a lone male on the breeding ground off the coast of New Caledonia in the South Pacific in 2018. Corresponding audio is provided online. The *x*-axis indicates time in seconds; the *y*-axis shows frequency in kHz. Spectrogram was generated in RavenPro 1.6 (Hann window, 75% overlap, 2048 point FFT, 16-bit)

(Table 20.2); these range in complexity from simple songs (comprised of a few sound types) of North Pacific right whales (*Eubalaena japonica*) to the highly complex songs of bowhead and humpback whales (Garland and McGregor 2020).

The highly stereotyped and hierarchically structured song of humpback whales is one of the most elaborate and complex vocal displays in the animal kingdom (Fig. 20.4). Songs typically last from 5 to 35 min; however, males may sing for many hours (Payne and McVay 1971; Winn and Winn 1978; Garland et al. 2013). Although songs change progressively each year through cultural evolution, all males within a population conform to the same song type at any given time (Winn and Winn 1978; Payne and Guinee 1983). In the South Pacific, a population's current song can be rapidly replaced by a novel song during so-called cultural revolutions (Noad et al. 2000; Garland et al. 2011). This indicates that despite the song's high complexity, males are able to learn entirely novel songs very quickly (i.e., within one season).

Humpback whale song has received considerable attention over the past 50 years, yet the underlying function(s) of song and its role within the mating system remain debated. There is clear evidence that singing is displayed solely by males which sing during the breeding season (including on migration and occasionally on the feeding grounds), and consequently singing is recognized as a male mating behavior (Glockner 1983; Baker and Herman 1984; Darling et al. 2006; Smith et al. 2008). Most studies have investigated the function of humpback whale song in the context of intra-sexual selection: (1) mediator of male–male interactions or male dominance relationships (Darling and Berube 2001; Cholewiak et al. 2018), (2) a spacing mechanism (Tyack 1981, 1983; Frankel et al. 1995), and (3) an index of association (Darling et al. 2006). Others suggest it is directed at females (inter-sexual selection): (4) female attraction to individual males (Winn and Winn 1978; Tyack 1981; Frankel et al. 1995) and (5) female attraction to an aggregation of communally singing males within the postulated lek mating system (Herman and Tavolga 1980;

Herman 2017). Although most studies on song function have focused on either intra-sexual or inter-sexual drivers, many conclude that both selective pressures are likely at play (Frankel et al. 1995; Clapham 2000; Darling and Berube 2001; Craig et al. 2002; Herman 2017; Cholewiak et al. 2018; Murray et al. 2018); song may thus serve more than a single function.

Humpback whale song contains both simple and complex phrase types, suggesting it might act as a multi-message display (Murray et al. 2018). Simple phrase types typically contain low-frequency sounds suitable for transmitting a signal across long distances and may thus facilitate a female's and/or male's ability to locate a singer over large distances (Bradbury and Vehrencamp 1998; Murray et al. 2018). The high-frequency sounds typical of complex phrase types convey information over a shorter range; thus, these shorter-range signals may be directed at females akin to how courtship usually occurs once potential mates are within close proximity (Bradbury and Vehrencamp 1998). Further, the high structural variability found in complex phrase variants appears ideal for conveying information on male quality, thus allowing the possibility of female mate choice to be the driver of song complexity (Hebets and Papaj 2005; Murray et al. 2018). However, female preference for any humpback whale song characteristic has yet to be investigated.

Compared to humpback whales, much less is known about the songs of other baleen whales, but several commonalities and differences across mysticete song are becoming apparent. The extraordinary diversity and variability of bowhead whale songs (Stafford et al. 2018; Erbs et al. 2021) suggest a complexity not dissimilar to the better-known humpback whale song. The songs of blue whales, fin whales, minke whales, North Pacific right whales, and Omura's whales are structurally simple, especially in the case of the latter two (Table 20.2). Although the songs of mysticetes show diverse levels of complexity and variability, they share several commonalities: (1) songs contain elements that aid long-distance communication across the ocean (e.g., contain low-frequency sounds and/or high redundancy; Payne and Webb 1971; Bradbury and Vehrencamp 1998; Clark and Ellison 2004; Risch 2022); (2) songs show some level of change across time (Noad et al. 2000; McDonald et al. 2009; Garland et al. 2011; Širović et al. 2017; Weirathmueller et al. 2017; Helble et al. 2020); (3) in at least rorquals, songs show some level of conformity within geographically distinct groups (Payne and Guinee 1983; McDonald et al. 2006; Garland et al. 2011, 2013; Darling et al. 2014; Risch et al. 2014; Širović et al. 2017; Weirathmueller et al. 2017); (4) song has been proposed to serve a reproductive function (Croll et al. 2002; Tervo et al. 2011b; Risch et al. 2013; Cerchio et al. 2017; Tyack 2022); and (5) for several species, song may convey individual-specific information and/or serve as a potential indicator of male quality (McDonald et al. 2006; Tervo et al. 2011b; Herman 2017; Clark et al. 2019; Crance et al. 2019; Erbs et al. 2021). For more detailed information by species, we direct readers to a recent review of baleen whale songs (see Clark and Garland 2022).

For species where the sex of the individual was determined, all singers were male (humpback whales: Payne and McVay 1971; fin whales: Croll et al. 2002; blue whales: McDonald et al. 2006; North Pacific right whales: Crance et al. 2019), and song mainly occurred during the breeding season (e.g., Smith et al. 2008), thus

indicating that mysticete song likely serves a reproductive function and may therefore be under sexual selection. However, several species sing on the feeding grounds and during migratory stopovers (e.g., Owen et al. 2019). Singing outside the main breeding season might be driven by elevated testosterone levels during the spring or fall season while individuals are still on their high-latitude feeding grounds, as reproductive conditioning likely starts months before the peak breeding time (Vu et al. 2015). Such singing may represent a low-cost opportunistic advertisement by males to court females that failed to conceive, and/or possibly an intra-sexual display (Clark and Clapham 2004).

The 3D underwater habitat, the slightly larger body size of females relative to males (Ralls 1976), and the absence of organs to grab and force females into mating all promote female behavioral freedom and thus allow for a relatively strong influence of female mate choice compared to most other mammals. Male–male competition and female mate choice are possible and non-exclusive drivers for the function of whale song. More research is needed to better understand whether song signals the singer's quality and whether males and/or females adapt their reproductive choices or behaviors upon receiving that signal.

20.2.3 Sperm Competition for Successful Female Fertilization

Except for bowhead, right, and gray whales, few matings have been observed by humans, and it is not known whether females mate with multiple males. Relative testes size and penis length serve as a proxy for the role of sperm competition (Würsig et al. 2023, this book) and can shed light on the reproductive tactics of baleen whales. The relative testes size and penis length of right, bowhead, and gray whales are larger than those of all other baleen whales, and larger than expected based on their body mass, indicating the importance of sperm competition as their main reproductive tactic (Brownell and Ralls 1986; Dines et al. 2015). As mentioned in Sect. 20.2.1, interactions among males in these species are relatively unaggressive and females mate with multiple males during the breeding season (Swartz 1986), sometimes even simultaneously (Mate et al. 2005), suggesting that males are unlikely to monopolize access to females (Swartz et al. 2023, this book). Further, the higher-than-expected microsatellite heterozygosity in offspring of North Atlantic right whales indicates post-copulatory competition among males (Frasier et al. 2013). As relatedness of mating pairs was not lower than expected under random mating, this excess of heterozygous offspring does not appear to result from pre-copulatory mate choice for dissimilar mates (Frasier et al. 2013). Instead, the observed patterns indicate the presence of post-copulatory selection for dissimilar gametes. However, it remains unclear whether these patterns are due to biased fertilization (e.g., cryptic female choice for dissimilar sperm) or biased mortality of zygotes (Frasier et al. 2013).

In comparison, the relative testes size of male humpback whales is lower than expected based on their body mass (Dines et al. 2015). Male humpback whales appear to engage in direct contest competition (Sect. 20.2.1), which suggests that males attempt to monopolize and defend access to females, thus reducing opportunities for sperm competition (Lüpold et al. 2014). Together with their elaborate acoustic displays (Sect. 20.2.2), this indicates their investment in and reliance on precopulatory reproductive tactics. In most other rorquals (blue whale, fin whale, minke whale, Bryde's whale, and sei whale), relative testes size is within the range expected based on their body mass (Dines et al. 2015), and males are unlikely to be able to monopolize access to females due to their dispersed distribution (Table 20.1). Thus, sperm competition remains a possible male reproductive tactic in most rorquals.

20.3   Toolkit for Studying Reproductive Tactics

Considering the long lifespan of baleen whales, long-term data collection is crucial to cover a wide range of the species' life history and to make inferences on sexual maturity and how reproductive tactics may change with age, experience, and/or condition. Many long-term studies on baleen whales are focused on the assessment of the population, rather than focal follows of individual whales. However, the identification of individual whales enables researchers to follow them long-term to learn more about their life history patterns, and to ground truth and calibrate tools to study mating systems, reproductive tactics, and other factors such as population dynamics (e.g., epigenetic aging, photogrammetry).

An example of a study that has shed light on changes in reproductive patterns is the extensive long-term monitoring program on Oceania humpback whales that has allowed for reconstruction of recapture histories and modeling of reproductive parameters in females (Chero et al. 2020). The relatively high calving rates of females at their breeding ground in New Caledonia are consistent with high pregnancy rates inferred by blubber progesterone levels on their migratory corridors (Riekkola et al. 2018) and feeding grounds (Pallin et al. 2018b), and may partially be driven by an increased reproductive capacity of this population (Chero et al. 2020). Epigenetic aging of individuals at this breeding ground could reveal whether this increased reproductive capacity is related to the age structure of the population, and/or if the anthropogenic pressures caused by commercial whaling led to the modification of breeding parameters (i.e., age at maturity or birth interval) (Chero et al. 2020).

The combining of long-term behavioral observations with molecular data is also a powerful approach. For example, paternity analysis using a long-term dataset of photo-identification and molecular data of endangered North Atlantic right whales revealed low variation in male reproductive success (Frasier et al. 2007). Combining the paternity data with measures of neutral and functional genetic diversity further indicated the presence of post-copulatory selection for dissimilar gametes that may represent cryptic female choice (Frasier et al. 2013). This integration of genetic

parentage and genetic diversity also unveiled a possible mechanism to mitigate the loss of genetic diversity after population exploitation (Frasier et al. 2013).

Research methods and technologies have greatly improved in recent decades, resulting in a variety of tools for data collection and analysis offering new and deeper insights into the life of mysticetes. The examples above integrated long-term observational datasets, genetics, and hormonal (physiology) datasets. Building on these multidisciplinary approaches will allow us to explore interactions among anatomy, physiology, reproductive success, age, and vocal displays, to better understand the reproductive tactics of baleen whales. In Table 20.3, we highlight tools that can increase our understanding of the reproductive strategies and tactics of baleen whales.

20.4   Conclusions and Future Directions

While the *Balaenidae* and *Eschrichtiidae* species appear to rely heavily on post-copulatory reproductive tactics by competing for successful fertilization rather than mating access, the morphology, behavior, and distribution of many species within the *Balaenopteridae* (rorquals) suggest their reliance on pre-copulatory tactics. The often aggressive interactions among males within competitive groups suggest that male humpback whales compete primarily via direct contest competition by attempting to prevent matings by other males. The more widely dispersed distribution and lack of breeding aggregations of blue and fin whales could indicate scramble competition, where males directly compete in their efforts and efficiency of searching for and locating receptive females as their reproductive tactic, and highlights the importance of acoustic cues to find mates. Based on the trade-off between pre- and post-copulatory trait investment, the lack of prominent pre-copulatory traits of many baleen whales (Dines et al. 2015), except for a few species with elaborate male songs (see Sect. 20.2.2), and the apparent lack of direct contest competition in most baleen whales (apart from humpback whales; Sect. 20.2.1) suggests that polygynandry (often mediated by sperm competition) may be more common within mysticetes than the lack of direct observational evidence to date suggests, outside of the *Balaenidae* and *Eschrichtiidae* families. Thus, irrespective of the reproductive tactics males employ, the elaborate acoustic displays and large testes size observed in several mysticete species suggest that female baleen whales may be able to exert a certain level of choice before and/or after copulation.

Much can be learned when taking a comparative perspective across marine mammals to understand reproductive tactics. While some species of pinnipeds and odontocetes show extreme levels of male-biased dimorphism in body size (e.g., elephant seals, *Mirounga* spp.; killer whales, *Orcinus orca*) and weaponry (e.g., walrus, *Odobenus rosmarus*; narwhals, *Monodon monoceros*) (Mesnick and Ralls 2018b), sexual size dimorphism in baleen whales is relatively moderate and female-biased, and further characterized by an absence of any dangerous male-specific weaponry. The temporal and spatial distribution and social structure of females

Table 20.3 Tools that can be used to delve deeper into the reproductive tactics of baleen whales

Tool	Description	Examples in baleen whales
Individual identification	Baleen whales can be individually identified by photo-identification of unique markings (e.g., ventral fluke patterns of humpback whales: Katona and Whitehead 1981; callosity patterns in right whales: Payne et al. 1983; Kraus et al. 1986; flank pigmentation patterns in blue whales: Sears et al. 1990) and/or genetic identification (e.g., microsatellite genotyping: Garrigue et al. 2004; Olavarría et al. 2007; Wade et al. 2011; Wiig et al. 2011; Baker et al. 2013; Carroll et al. 2013)	Reproductive histories of female humpback whales (Baker et al. 1987) Reproductive capacity of an endangered and recovering population of humpback whales (Chero et al. 2020)
Sex identification	Identifying the sex of individuals can be difficult in wild marine mammals; this can be done using behavioral observations and genetic markers	Identifying the sex of focal animals in southern right whale social groups (Best et al. 2003)
Genetic parentage analyses	Using Mendelian inheritance patterns of genetic markers to infer maternity and paternity patterns (see Chap. 4)	Patterns of maternity and paternity can provide information on the reproductive skew, and variation in reproductive success (Cerchio et al. 2005; Frasier et al. 2007), the strength of sexual selection, as well as reproductive interchange among populations (Garrigue et al. 2004; Carroll et al. 2012)
Genetic diversity	Genetic diversity not only offers valuable insights into the demography and gene flow across populations; it further can be used to identify genes under selection and to assess the role of female choice within a species' mating system (e.g., genetic compatibility: Mays and Hill 2004; Puurtinen et al. 2005). Untangling molecular patterns of non-random fertilization in the context of post-copulatory sexual selection can shed light on the role of female choice and the resulting impacts on population biology and evolutionary genetics (gamete compatibility: Springate and Frasier 2017)	Diversity and duplication of MHC genes in several mysticetes suggest that these genes are under positive selection (Baker et al. 2006; Moreno-Santillán et al. 2016) Linking parentage with genetic diversity revealed the post-copulatory reproductive strategy in North Atlantic right whales which might indicate cryptic female choice (Frasier et al. 2013)
Molecular age biomarker	Measurable changes in DNA or RNA abundance or sequence that change over the lifespan of an animal can be used to estimate age (Jarman et al. 2015) Epigenetic clocks make use of	Epigenetic age estimation has been applied to several baleen whale species (Polanowski et al. 2014; Goto et al. 2020; Tanabe et al. 2020; García-Vernet et al. 2021), and other cetaceans (Bors et al. 2021; Robeck

<div align="right">(continued)</div>

Table 20.3 (continued)

Tool	Description	Examples in baleen whales
	age-related changes in DNA methylation levels to estimate the age of living whales using skin biopsy samples. Such epigenetic clocks need to be calibrated using individuals of known age, thus highlighting the crucial role of long-term data collection for the assessment and ground-truthing of such methods	et al. 2021). If related to other factors such as behavior, body size, hormone levels, and reproductive success, an individual's estimated chronological age can offer new insights into the reproductive strategies and life history parameters that, considering the lifespan of these animals, are out of reach of most datasets
Endocrinology	Estimating hormone levels in individuals can tell us more about their sexual maturity or reproductive state (see Hunt et al. 2017). Hormone concentrations can be measured using multiple matrices: blubber, respiratory vapor ("blow"), and fecal samples (Rolland et al. 2005; Hunt et al. 2013), and for the retrospective and longitudinal assessment of reproductive hormones: baleen plates (Hunt et al. 2014, 2016)	*Progesterone*: inference of pregnancy status and rates (e.g., Kellar et al. 2013; Hunt et al. 2016; Pallin et al. 2018a, b; Kershaw et al. 2021) *Testosterone*: can be used to infer reproductive maturity and status of individuals or seasonal changes in reproductive state (e.g., Kellar et al. 2009; Vu et al. 2015; Cates et al. 2019; Mingramm et al. 2020; Melica et al. 2021) *Estradiol*: can provide information on female reproductive maturity and receptivity (e.g., Mingramm et al. 2020; Lowe et al. 2022)
Bioacoustics	Baleen whale vocalizations can be recorded using handheld equipment taken at the individual whale through to passive acoustic monitoring using autonomously deployed recorders that are anchored to the seafloor. Sound units are typically quantified for multiple acoustic parameters to ensure consistent classification of sound types (Dunlop et al. 2007; Garland et al. 2017; see also Clark and Garland 2022)	A quantitative comparison of the similarity in arrangement, structure, and complexity in humpback whale song (Garland et al. 2012, 2013, 2017; Allen et al. 2018) can uncover song dynamics at large spatial scales such as the unidirectional cultural revolutions (discussed in Sect. 20.2; Garland et al. 2011), through to intricate intra- and inter-individual differences (Allen et al. 2018; Murray et al. 2018). By uncovering song differences, whether large-scale or extremely subtle, we may be able to tease apart aspects of the song that signal male quality and thus may serve in female mate choice
Animal-borne tags	There are a wide variety of tag types ranging from high-resolution behavior loggers to satellite tags that provide tracking data over large spatial and temporal scales (Goldbogen et al. 2013). Biologgers are tags equipped with additional sensors (e.g., accelerometer, hydrophones, video cameras,	Satellite tracking can tell us about the migratory routes and spatial usage of species and individuals and can reveal migratory and reproductive strategies (e.g., Garrigue et al. 2015; Derville et al. 2018; Mackay et al. 2020) Biologgers, regularly used to study the foraging ecology and diving

Table 20.3 (continued)

Tool	Description	Examples in baleen whales
	magnetometers) making them a powerful tool to simultaneously track the behavior and environment of individuals (Watanabe and Goldbogen 2021). Such tools are extremely valuable for species that are more located offshore, deep diving, or live in environments that are otherwise hard to reach (e.g., ice shelf)	behavior of marine mammals, could reveal further insights into the cost of reproduction and vocal communication of marine mammals
Drone technology	Drones, or unoccupied aerial vehicles (UAVs), provide a cost-effective option for monitoring, photogrammetry, and behavioral observations of free-ranging marine species. Aerial photogrammetry can be used to estimate the body size and condition of individuals (e.g., Dawson et al. 2017; Burnett et al. 2019; Christiansen et al. 2019; Aoki et al. 2021). UAVs can be used to obtain acoustic measurements close to the whales (Lloyd et al. 2016; Frouin-Mouy et al. 2020) and respiratory blow samples for genetic, endocrine, and microbiological analyses (Atkinson et al. 2021)	As capital breeders, baleen whale body condition and reproductive costs likely play an important role in their reproductive strategies. UAV photogrammetry and long-term sighting histories can be used to establish growth patterns to estimate age based on body mass, explore the energetic costs of female reproduction (e.g., Christiansen et al. 2014, 2022a, b), or the relationship between migratory timing and body condition (Russell et al. 2022) Paring acoustic recordings and overhead visual observations could shed light on the behavioral context and function of acoustic displays (e.g., song)

increase the potential for single males to monopolize groups of females in land-breeding pinnipeds, and led to the evolution of male alliances and temporary courtships in several odontocetes (Mesnick and Ralls 2018b; Brightwell and Gibson 2023, this book; Chivers and Danil 2023, this book). Reproductive strategies and tactics across pinnipeds, odontocetes, and mysticetes are highly variable, yet the reproductive tactics within each suborder vary similarly. Understanding how the diversity of ecological and social factors across and within each suborder shape the reproductive behaviors of individuals will shed light on the evolution of reproductive strategies and tactics of baleen whales.

The emergence of new technologies has greatly enhanced the detail and scope of investigations that are now possible. Future directions include the employment of animal-borne tags and drone technology to study the behaviors of species and individuals that are difficult to observe or approach. The use of genomics, epigenomics, and endocrinology offers insights into the genetic quality, reproductive maturity and status, and physiological condition, providing a comprehensive picture at the level of the individual needed to untangle the multifaceted factors shaping their reproductive tactics and the role and mechanisms of female choice. Understanding the function(s) of baleen whale song is a largely unanswered question that is ripe for

exploration through a multidisciplinary approach that offers insights into the proximate and ultimate causes of singing. This could then be expanded into a comparative perspective to investigate the evolution of song and complex communication in multiple taxa, both marine and terrestrial. By understanding reproductive tactics employed by large whales, we provide invaluable contributions to the wider understanding of mating behavior across taxa.

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Chapter 21
Gray Whale Sex, Reproductive Behavior, and Social Strategies

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Abstract Gray whale sexual behavior and copulation are observed throughout their range. The most prominent period for reproductive behavior is during the southward migration from summer feeding areas to wintering areas where some breeding occurs and calves of the year are reared. The seasonal migrations of gray whales are believed to function, in part, to bring together individuals that are otherwise widely distributed during the period of estrus to facilitate mating and reproduction.

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Sexual behaviors and sexual strategies for this species appear to align closely with those of balaenid (not rorqual) whales, although such comparisons need further investigation. Gray whales are polygynandrous (multi-mate) breeders. There does not appear to be female choice of mates, as groups of numerous females and males aggregate, and multiple copulations occur. Female estrus begins in mid-November and continues to early December; females may undergo a second estrus, extending into February, if they fail to conceive during their first cycle. Male gray whales have large testes and concomitantly produce large volumes of sperm, so they are believed to be sperm competitors; that is, they rely on multiple copulations (and sperm volume) to produce offspring. Multiple copulations with different males during the female estrus period may increase the likelihood that the timing of conception results in the birth of a calf approximately 13 months later near or in the wintering area(s). Mating bouts can last for minutes to hours, interspersed with surface-active-social-sexual behavior. Some all-male groups have been observed with erect penises engaged in social-sexual behavior in the absence of any females. Instances of male aggression toward postpartum females with calves of the year, sometimes resulting in injury or death, have been reported. As a result of dedicated long-term research in the past several decades, the state of knowledge on gray whale reproduction has greatly expanded and updated information on this topic is summarized in this chapter.

Keywords Acoustics · Eastern North Pacific population · Gray whales · Male aggression · Migration · Polygynandrous (multi-mate) breeding · Scramble competition · Sexual strategies · Social-sexual behavior · Sperm competition · Western North Pacific population

21.1 Migration and the Reproductive Cycle

Gray whales occur along the margins of the eastern North Pacific (ENP) and western North Pacific (WNP), migrating annually from northern feeding areas to southern wintering areas that represent a round trip journey of 15,000–20,000 km that spans up to 55° latitude (Swartz 2018). Seasonally predictable sources of food have helped shape the life history of gray whales into two general periods that are linked by the annual migration: (a) summer feeding in the higher latitude waters where food is abundant and whales are widely dispersed across a large territory and (b) overwintering in lower latitude waters, where whales are more closely aggregated. The seasonal occurrence in southern wintering areas serves several hypothesized functions, including (a) escape from inhospitable environmental conditions (e.g., sea ice, water temperature) in northern areas, (b) reduction of risk from killer whale predation during the period when calves are born (Corkeron and Connor 1999; Sumich 2014; Weller et al. 2018; Black et al. 2023), and (c) the successful rearing and survival of calves (Jones and Swartz 2009). The gray whale reproductive cycle is tightly synchronized with this migration and this relation is described below.

21.1.1 Migration and Reproductive Timing

The southward migration helps to concentrate whales spatially and temporally, thereby facilitating mating. By late November, most gray whales are moving south from summer feeding areas to wintering areas. This southern migration is segregated by age, sex, and reproductive condition. The first pulse of migrants is led by (a) near-term pregnant females, followed by (b) estrus females and mature males and then (c) immature animals of both sexes (Rice and Wolman 1971). The northward migration begins about mid-February and is also segregated according to age, sex, and reproductive condition. The first phase of this northward migration includes (a) newly pregnant females followed later by (b) adult males and anestrus females and then (c) immature whales of both sexes. The second phase of the northward migration consists mostly of mothers with calves. These pairs are observed on the migration route between March and May and they generally arrive to the summer feeding grounds between May and June (Jones and Swartz 1984).

During summer and fall, most whales in the ENP feed in the Chukchi, Beaufort, and northwestern Bering Seas. An exception to this generality is a relatively small number (roughly 200) of "Pacific Coast Feeding Group" (PCFG) whales that routinely return each summer and feed along the Pacific coast between southeast Alaska and northern California (Darling 1984; Calambokidis et al. 2002; Moore et al. 2007). Three primary wintering aggregation areas and lagoons in Baja California Sur, Mexico, are utilized, and some females are known to make repeated returns to specific lagoons (Jones 1990; Martínez-Aguilar et al. 2023). In the WNP, gray whales feed off Far East Russia during summer and fall in the western Okhotsk Sea and southeastern Bering Sea (Weller et al. 1999, 2002; Tyurneva et al. 2010). Historical accounts (Andrews 1914; Nishiwaki and Kasuya 1970; Wang 1984) and contemporary data (Weller et al. 2008, 2016; Nakamura et al. 2021) indicate that coastal waters off Asia were, and continue to be, part of a WNP migratory route and portions of the South China Sea are reputed wintering areas (Weller et al. 2002, 2013). Until about the mid-2000s, whales in the WNP were thought to be geographically isolated from whales in the ENP; however, satellite-tagging, photo-identification, and genetic research has documented some whales identified during the summer in the WNP migrating to the ENP in the winter, including coastal waters off Canada, the USA, and Mexico (Weller et al. 2012, 2016; Mate et al. 2015; Martínez-Aguilar et al. 2022). These findings suggest that some whales summering in the WNP migrate to the ENP west coast of North America in winter, while others migrate south to waters off Japan and China (Weller et al. 2008, 2013, 2016).

Studies of gray whales summering in areas off the Pacific Northwest between southeastern Alaska and Northern California and off Sakhalin Island in Far East Russia have found intra- and inter-annual fidelity for many of the whales observed (Darling 1984; Weller et al. 1999; Calambokidis et al. 2002, 2017; Bröker et al. 2020). While this same pattern of seasonal site fidelity may exist in various parts of the Arctic feeding grounds, data from those areas do not exist at the level necessary to determine such.

21.1.2 Implications of Summer Feeding Location on Mating

With the above in mind, the location(s) where whales feed in the summer has possible implications for mating. For instance, some information on the timing of migration has been gleaned from three whales satellite-tagged during 2010 and 2011 on the Sakhalin Island summer feeding area in the WNP. All three whales migrated east, with one (a 13-year-old male) remaining off Sakhalin until 10 December while the other two (both females, ages six and nine) remained there until 24 November before migrating to areas occupied by ENP gray whales (Mate et al. 2015). These data indicate that at least some, and perhaps all, animals making the winter migration from the WNP to the ENP are still far to the west, and therefore only in proximity to other whales migrating from the WNP, during the primary conception period that occurs between late November and early December (Rice and Wolman 1971). The plausibility of this possibility is consistent with the results of genetic analyses, in which significant nuclear genetic differences have been found between the whales that feed off Sakhalin Island in the WNP and gray whales in the ENP (Brüniche-Olsen et al. 2018; Lang et al. 2022). These differences indicate that whales feeding off Sakhalin Island are not mating at random with ENP gray whales, a finding that suggests assortative mating may be occurring as a result of location (i.e., summer area) and migratory timing (Lang et al. 2022).

Similarly, the above scenario for whales summering in the WNP may also apply to PCFG gray whales and other similar seasonal aggregations that may exist in the ENP. Over 50% of PCFG individuals have been sighted in areas off the Pacific Northwest in November and December despite a limited amount of effort. Satellite-tagging research on PCFG gray whales revealed that 18 whales started their southward migrations between 3 December to 13 February (Lagerquist et al. 2019), a period of time that is later than the estimated period of conception between mid-November to early December (Rice and Wolman 1971). Although these factors could result in a higher likelihood of assortative mating among PCFG whales, genetic analyses do not support such a hypothesis; research has yet to detect significant nuclear DNA differences when PCFG whales are compared with ENP whales that feed in Arctic waters or those using the wintering aggregation areas and lagoons in the Baja California peninsula, Mexico (D'Intino et al. 2013; Lang et al. 2014).

21.2 Reproductive Life History

21.2.1 Estrus and Conception

Most gray whale conceptions occur each year during a 3-week period, overlapping the early portion of the southward migration, from mid-November to early December (Rice and Wolman 1971). In the ENP, studies have shown that sexual

activity and copulatory behavior occur during migration (Norris et al. 1983; Swartz 1986) and continue once the whales have reached their wintering areas off Mexico. These observations seemingly support the suggestion that females that failed to conceive after their first ovulation may experience a second estrus cycle that is later, possibly extending into February, in the same breeding season (Rice and Wolman 1971). Newly pregnant females are the first to leave the Baja California peninsula wintering areas in the spring, migrating to summer feeding areas to begin replenishing their metabolic "energy stores" that had been greatly depleted during the previous southward migration in combination with the nutritional demands related to the growth of their fetuses (Sumich 2014).

21.2.2 Age, Sexual Maturity, and Sex Ratio

The oldest female gray whale killed during scientific whaling operations between 1959 and 1969 in the ENP was estimated to be 75 years old and was pregnant (Rice and Wolman 1971). Minimum age estimates for individual living gray whales photo-identified in the Mexican wintering areas range from 45 to 53 years (Martínez-Aguilar et al. 2023). Males and females attain sexual maturity between 5 and 11 years (average is 8 years for both sexes; Rice and Wolman 1971; Bradford et al. 2010). Females generally produce one calf every 2 years, although longer inter-birth intervals of 3 or more years may occur (Rice and Wolman, 1971; Jones, 1990; Weller et al. 2008; Martínez-Aguilar et al. 2023). Gray whale calves are born singly and the sex ratio has been reported to be 1:1 in the ENP (Rice and Wolman 1971). A recent study using genetic analysis found that 66.1% of whales first identified as calves on the WNP feeding area in the Okhotsk Sea were males (Weller et al. 2009; Lang 2010). It is not known what factors influence the proportion of male calves born per year, and the male bias found in the aforementioned study may simply reflect stochastic variation (Cooke et al. 2016).

21.2.3 Gestation, Size at Birth, Weaning

The gestation period for gray whales is estimated to be 11–13 months with births occurring from late December to early March (Jones and Swartz 1984; Sumich 2014). The median birth date is 27 January when near-term pregnant females are migrating southward and in or near their wintering areas. At birth, calves are 4.5–5.0 m in length and weigh approximately 1000 kg. Females have a close and protective bond with their calves and fight fiercely to defend them when threatened (Scammon 1874). Weaning occurs at 6–8 months, primarily in summer feeding areas, when calves are 7.6–8.5 m in length (Rice and Wolman 1971; Weller et al. 1999; Sychenko 2011). Post-weaning survival (survival from their first feeding

season as calves to the following season) is estimated at 0.65–0.70 and varies annually (Bradford et al. 2006; Cooke et al. 2019).

21.2.4 Lactation and Female Resting Period

To nurse, a female gray whale swims slowly or rests motionless at the surface while her calf approaches from below and nudges the abdominal area of its mother as a cue, whereupon milk is pumped from the female's teat into the mouth of the calf. Calves consume about 189 l of milk daily, which is 53% fat and 6% protein (Sumich 2014). Mothers and calves remain in the wintering areas off Mexico until April or May, allowing calves sufficient time to strengthen and rapidly increase in size before their first northward migration. After weaning their calves in July and August on the summer grounds, females then have a 3–4 month resting period to focus on feeding to fatten and replenish their "energy stores" in advance of their next estrus cycle that begins anew around November to December, thus completing the 2-year reproductive cycle (Rice and Wolman 1971; Swartz 1986; Jones 1990).

Studies in the WNP show that lactating females are commonly in poorer body condition than other whales (Bradford et al. 2012). Although their body condition typically improves somewhat through the feeding season, the probability that lactating females would have complete within-season recovery is generally low, indicating that post-parturient females are typically not able to fully replenish their energy stores before their next opportunity to breed. Calves are in consistently good body condition, resulting from high maternal investment during lactation, even after weaning.

21.3 Gray Whale Reproductive Strategy

Female gray whales enter their first seasonal estrus at the onset of the southward migration and along the migratory route. The compressed breeding season of gray whales combined with the segregated and phased nature of the migration appears to have helped shape their mating system by precluding the monopolization of available females by males.

21.3.1 Polygynandrous Mating System

The mating system of gray whales is polygynandrous (multi-male and multi-female). Male defense of mates in "harems" or other similar aggregations that give dominant males exclusive access to females, as seen in other polygynous mammals with compressed breeding seasons, does not appear to be the case with gray whales.

Fig. 21.1 A group of three sexually aroused male gray whales. No female was identified in this group. While this "all male" behavior is observed throughout the gray whales' range, it's utility or significance remains unclear. Photo credit: Fabian Missael Rodríguez-González

When in estrus, females copulate with multiple mates to enhance the likelihood of conception. There does not appear to be female-based pre-copulatory choice of mates, as mating groups vary in size, often with numerous females and males aggregated together. In these groups, multi-mate and multiple copulations occur. Social-sexual behavior is not limited solely to the wintering areas. Video capable suction cup tags have revealed that gray whales feeding off the Pacific Northwest coast in the spring engage in close physical contact both underwater and at the surface, rubbing against each other with their bodies and flippers, which is sometimes accompanied by males with erect penises (JC, pers. comm.). Sexually active all-male groups are also seen during migration as well as winter and summer areas (Darling 1977; Jones and Swartz 1984, 2009; Youngson and Darling 2016; Fig. 21.1).

21.3.2 Operational Sex Ratio and Scramble Competition

The 2-year breeding cycle reported for gray whales (Rice and Wolman 1971) means that at the start of each breeding season, 50% of the mature females are available (or unavailable) for mating. This proportion of available females skews the operational sex ratio to a 2:1 male bias. Thus, competition between males for mating opportunities would be expected (Emlen and Oring 1977). Evidence for overt aggressive male–male competition for available females, however, has not been reported. Instead, gray whales appear to have evolved a more cooperative "scramble

competition" mating strategy where males jostle to be in position next to an estrus female without being directly aggressive to each other (Clutton-Brock 2016). Such mating can occur in what are termed "explosive breeding assemblages," where both sexes converge (e.g., during migration) for a relatively short-lived, highly synchronized mating period. Sexual activity occurs during their migration and while the whales occupy the wintering aggregation areas and lagoons in the ENP (Gilmore 1960; Rice and Wolman 1971; Norris et al. 1983; Jones et al. 1984), suggesting that rather than mating in one specific portion of their range or location, the timing of reproduction is more important. That is to say, a "core time" rather than "core area" is the factor that assures gray whales conceive within a limited period and, in turn, best ensures that calves will be born 11–13 months later in an optimal wintering location: one that increases their potential for growth, development, and survival (Jones and Swartz 2009). This line of reasoning suggests that the long-time use of "breeding area" to describe the lagoons of Mexico in the ENP, and similar regions in the WNP, is not accurate and should be properly termed "wintering aggregation areas," where some mating occurs.

21.3.3 Testes-to-Body Weight Ratio and the Multi-mate Breeding System

The lack of direct evidence for male–male competition in gray whales, such as pronounced sexual dimorphism, male territorial defense, and communal displays, suggests that competition and sexual selection may occur at some level other than that of the individual. The testes-to-body weight ratio in gray whales predicts a multi-male breeding system, which is consistent with the breeding behavior observed in this species. Brownell and Ralls (1986) reviewed the literature on baleen whale testes size, penis length, and mating system. They reasoned that in species with sperm competition, large testes that produce large amounts of sperm per ejaculation would serve to dilute and displace the sperm of rival males and that longer penises would deliver the sperm closer to the ova. Gray, right (*Eubalaena glacialis*), and bowhead (*Balaena mysticetus*) whales are species without obvious male–male competitive behavior and possess both large testes-to-body weights and penis-to-body lengths. Conversely, the humpback whale (*Megaptera novaeangliae*) with smaller testes, a shorter penis, and conspicuous interactions between breeding males has been selected to compete to a greater extent by preventing rival males from mating rather than by sperm competition (Brownell and Ralls 1986; Eichenberger et al. 2023, this book; Würsig et al. 2023, this book).

21.4 Reproductive Behavior in the Eastern North Pacific Wintering Lagoons

The scientific understanding of gray whale reproductive behavior during the winter, when calves of the year are nursing and breeding among single whales continues, comes almost strictly from studies conducted in the coastal lagoons along the Pacific coast of the Baja California peninsula, Mexico.

21.4.1 Surface-Active Behavior

Early reports of gray whale mating behavior that described "trios" consisting of a mating pair and a third individual or "helper" were oversimplifications (Samaras 1974; Miller 1975; Gilmore 1976). More recent observations have confirmed that mating groups range in size from pairs to several individuals of mixed age/sex (except calves) and may stay engaged in mating bouts that last for two or more
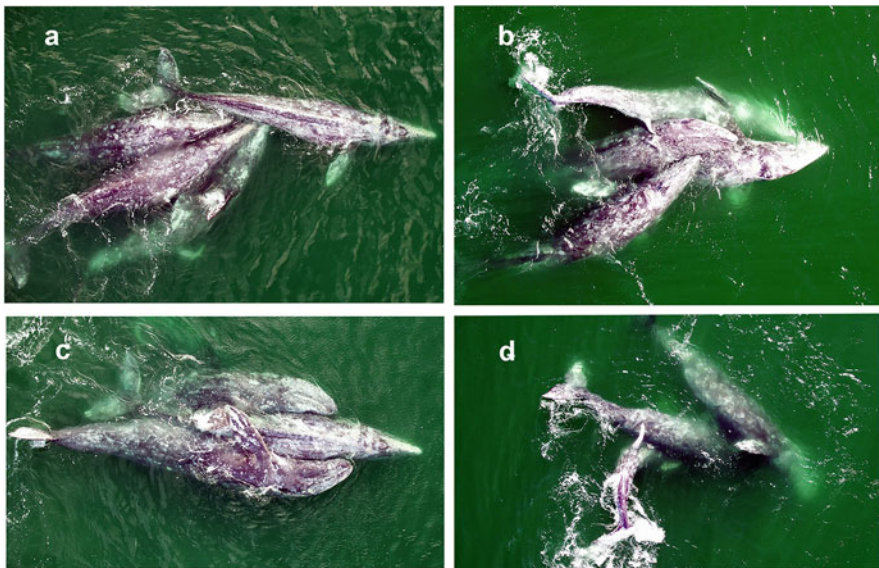
Fig. 21.2 A typical gray whale courting/mating group sequence photographed by drone in Laguna San Ignacio. (**a**) Three gray whales (presumed males) investigating and stimulating an estrus female in advance of initiating a mating bout and copulation. (**b**) Courting/mating bouts typically begin with male gray whales gathering and positioning themselves around the estrus female for attempts at copulation. (**c**) Typical "hugging" position of male gray whales when attempting copulation with an estrus female. (**d**) While one male copulates with the estrus female, other males remain with the courting group and stand by for additional mating opportunities. Photo credit: Fabian Missael Rodríguez-González

hours with additional whales joining in the bouts as if stimulated by the sexual activity of the core group (Jones and Swartz 1984; Fig. 21.2a–d). Mating bouts may also include high-speed chases, termed "freight train races," where group members (presumably males) appear to pursue a lead animal (presumably a female in estrus), with multiple individuals lunging through the water, creating spectacular bow-waves, and sometimes cover 3–4 km before resuming a mating bout. As the winter season progresses and the northward migration begins, the occurrence of sexual activity becomes less frequent as the numbers of single adult whales in and near the lagoons decline.

21.4.2 Acoustic Behavior

While gray whales are acoustically active throughout their range, including during their migration (e.g., Guazzo et al. 2017; Burnham et al. 2018), and while feeding (e.g., Moore and Ljungblad 1984), they appear to be most acoustically active in their wintering areas (Dahlheim et al. 1984; Ollervides 2001), both in terms of the variety
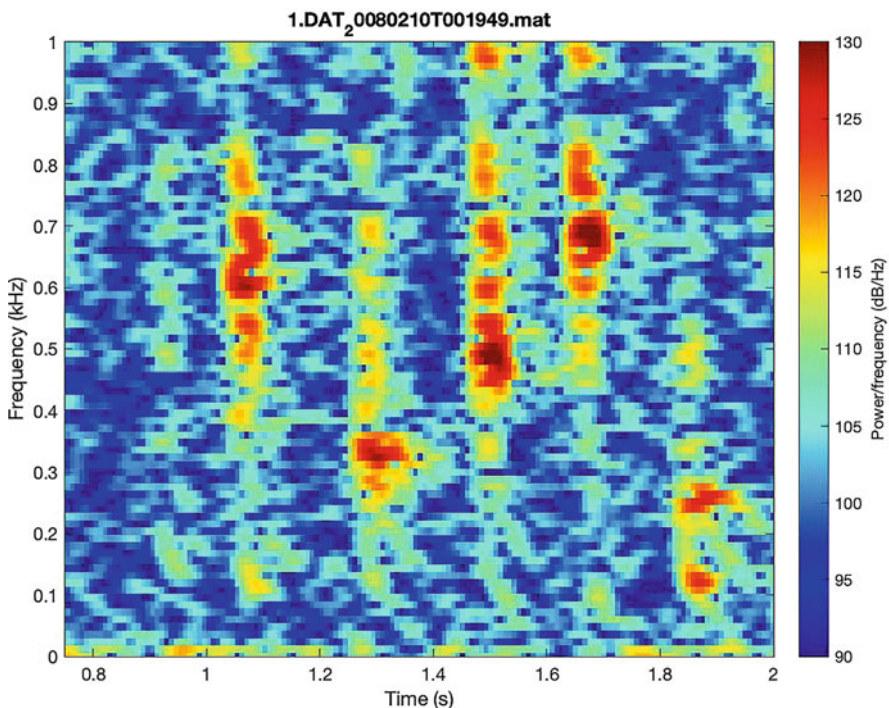
Fig. 21.3 Spectrogram of a gray whale S1 call recorded on bottom mounted acoustic recorders in Laguna San Ignacio, Baja California Sur, Mexico: February 10, 2008, at 00:19:49 local time. Note the varying peak frequencies in each pulse, or "note." Photo credit: Aaron Thode

of sounds produced and the frequency of vocalizations. Acoustic calls attributed to gray whales in the wintering lagoons include "low-frequency rumbles," "pulses, moans, and whistles," "chirps," "clicks," "bongs," "knocks," "pulses," "snorts," "slamming," and "bubble bursts." There are over 14 distinct, mostly low-frequency, sound types produced by gray whales reported in the scientific literature.

While gray whales have been reported to produce a variety of different calls, the "S1" call is common in the wintering lagoons (Dahlheim et al. 1984; Ollervides 2001; Charles 2011), but relatively rare during fall and spring migrations (Guazzo et al. 2017). The S1 is characterized by a sequence of knocks with the tonal texture of conga drums (Dahlheim, 1987; Fig. 21.3) and has a high source level, or volume, which makes it detectable over greater distances than other types of calls (Dahlheim 1987). The S1 call is thought to serve a communication function, with animals producing their own S1 call in response to hearing another animal's S1 call (Ponce et al. 2012). Field observations of gray whales found associations between the occurrence of the S1 call and social-sexual reproductive behavior (Charles 2011). The S1 call has also been reported during social-sexual interactions by feeding gray whales off British Columbia, Canada (Youngson and Darling 2016). In summary, the S1 call is a loud, common call that is used for two-way communication between individual whales of all demographics but is particularly common among individuals engaged in mating or social-sexual behavior.

21.4.3   Spatial Segregation and Behavioral Incompatibility

In January and February, females with calves and adult courting whales occupy the lagoons, and although female–calf pairs routinely travel the entire length of a lagoon, they actively avoid passing through areas with concentrations of courting adult whales. In broad terms, gray whales in the wintering lagoons behave as two separate segments: (a) social-sexual mating groups of single adult males and females in estrus and (b) post-parturient females with their newborn calves. Single breeding adults of both sexes engage primarily in social-sexual behavior, while females with new calves generally remain solitary, devoting their energies to nursing and nurturing their offspring (Jones and Swartz 1984).

In one of the wintering lagoons (Laguna San Ignacio) courting groups composed of adult whales (males and females without calves) occur at highest densities in the "lower" one-third of the lagoon nearest the lagoon entrance and their density decreases with increasing distance from the entrance. In contrast, most females with newborn calves are concentrated in the inner two-thirds of the lagoon furthest from the entrance. These inner waters are often referred to as "nurseries," where mothers and their calves are mostly resting and nursing (Figs. 21.4 and 21.5). Few single whales visit these nursery areas, providing relative solitude for females following parturition and during early development of their calves (Jones and Swartz 1984, 2009).

Fig. 21.4 Female gray whale and her newborn calf in Laguna San Ignacio, Baja California Sur, Mexico. Female gray whales will often support their newborn calves by swimming underneath the calf and keeping it near to the water surface until the calf develops a regular swimming rhythm for surfacing to breathe. Photo credit: Sergio Martínez-Aguilar

The average minimum length of stay for single adult whales (adult males and females without calves) in the wintering lagoons is short (7.5 days) in comparison to the average length of stay for females with calves (32.2 days). These residency times reflect a high rate of turnover for single whales in the lagoons (Martínez-Aguilar et al. 2023). Further, photo-identification studies show that during the winter, single adult whales circulate among the three primary wintering lagoons and the nearshore bay waters, presumably looking for mating opportunities, while females with calves

Fig. 21.5 When traveling the gray whale calf often positions itself close to and just behind the head of its mother where the "slipstreaming" effect of water passing around the mother's body assists the calf's swimming by pulling it along. Photo credit: Steven L. Swartz

spend longer periods within the lagoons (Martínez-Aguilar et al. 2023). Harassment by courting whales is a major factor driving female–calf pair avoidance of courting whales (Jones and Swartz 1984). Members of courting groups (presumably males) pursue females with calves and attempt to mate with the females. Mating bouts are highly disruptive events and involve groups of multiple individuals thrashing at the surface, throwing their flukes and flippers, as they maneuver for mating position (Norris et al. 1983; Jones and Swartz 1984; Swartz 1986; Figs. 21.6 and 21.7). Calves may become separated from their mothers and/or can sustain injuries or even be killed in these circumstances. In one instance, a well-known female with her calf was relentlessly pursued and harassed by courting single adult whales, and the mother was separated from the calf. A few days later, this female was found dead, likely as a result of her injuries. The fate of her calf was never determined (S. Martínez-Aguilar. Pers. Comm).

21.4.4 Acoustic Crypsis

The levels of ambient biological noise in the inner lagoon areas, where females with young calves segregate themselves, can be high and thereby provide acoustic "crypsis," or the ability of mother–calf pairs to avoid observation or detection by other animals through the exploitation of sound. This ambient noise arises from

Fig. 21.6 A gray whale surface-active social-sexual courting/mating group of mixed sexes of individual adult whales in Laguna San Ignacio, Baja California Sur, Mexico. Photo credit Steven L. Swartz

snapping shrimp sounds, tidal flow across the ocean bottom, wind-generated waves on the surface, and to a lesser extent panga (small vessel) transits and fish chorusing (Seger et al. 2015). Sounds recorded from mainly mother–calf pairs suggest a larger repertoire than previously reported, possibly due to faint calls recorded only at close range (Frouin-Mouy et al. 2020). Thus, in the wintering lagoons, mothers and calves may take advantage of acoustic cryptic communication strategies (low-level sounds in high-noise areas) for maintaining contact in a low-visibility environment while simultaneously reducing a potential risk of eavesdropping by predators or courting whales. Acoustic crypsis strategies have also been proposed in North Atlantic right whales (Parks et al. 2019), southern right whales (Nielsen et al. 2019), and humpback whales (Videsen et al. 2017).

21.5 Future Directions for Studying Gray Whale Reproduction

21.5.1 Paternity Research

Although valuable information on female reproductive success can be obtained through visual observations of mothers associated with their calves, evaluating
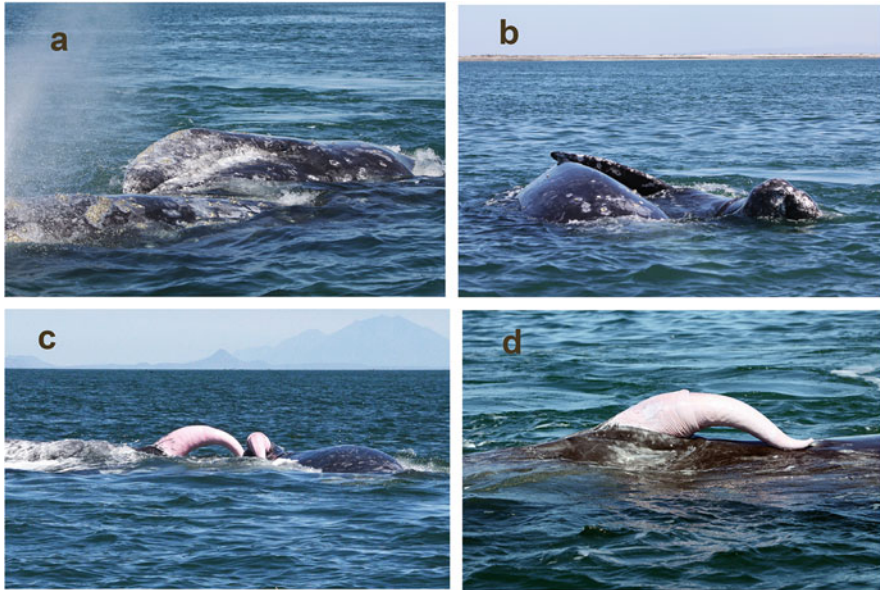
Fig. 21.7 Gray whales courting/mating. (**a**) A gray whale male approaching and positioning itself at the side of a presumed female for a mating opportunity. (**b**) A gray whale male (right) approaching and "hugging" a presumed female (left) with its flippers. (**c**) Gray whale males in a courting/mating group approaching a presumed estrus female and positioning themselves for a mating opportunity. (**d**) The erect penis of a male gray whale in Laguna San Ignacio, Baja California Sur, Mexico. The gray whale penis with its bifurcated tip appears to be "prehensile" and this capability may serve to assist the male in locating the entrance of the estrus female's vagina for intromission of semen. All photos taken in Laguna San Ignacio, Baja California Sur, Mexico. Photo credit: Steven L. Swartz

factors that influence male reproductive success is only feasible through genetic analyses of paternity (Gerber and Krützen 2023, this book). Such analyses provide the most information when a high proportion of animals in the population have been sampled, and the genetic results can be integrated with long-term sighting histories of individual whales. For example, in North Atlantic right whales, where ~63% of identified individuals were sampled, the combination of genetic analysis of paternity with 20 years of photo-identification records revealed that the age distribution of assigned fathers was biased toward older males, with the youngest assigned father being approximately twice the average age of first fertilization in females (Frasier et al. 2007). These results suggested that mate competition may prevent younger male right whales from reproducing. A similar approach in areas where a high proportion of whales have been genetically sampled (e.g., WNP, PCFG) and those samples are linked to long-term sighting histories of individuals could provide insights into factors influencing male reproductive success in gray whales.

Another method that may increase understanding of gray whale reproduction is assessment of reproductive hormones. In other baleen whale species, reproductive

hormone assays of blubber biopsies and fecal samples have been used to determine pregnancy rates (e.g., Atkinson et al. 2020), better understand the physiological stress levels associated with different reproductive states (e.g., Valenzuela-Molina et al. 2018), and infer patterns of male reproductive seasonality based on trends in testosterone levels over time (e.g., Vu et al. 2015; Carone et al. 2019). Reproductive hormones have also been measured in whale blow samples (e.g., Burgess et al. 2018). In addition, analysis of reproductive hormones in baleen, while only attainable from dead whales, provides the opportunity to track the recent reproductive histories of individuals, increasing understanding of calving intervals, age of sexual maturity, and timing of the breeding season (Hunt et al. 2016, 2022; Lowe et al. 2021). In gray whales, analysis of reproductive hormone concentrations in fecal samples and blubber biopsies have focused on evaluating how reproductive hormones vary with age, reproductive status, season, and life history stage (Lemos et al. 2020, Melica et al. 2021). Although analysis thus far has been limited to a single sample, Hunt et al. (2017) demonstrated that reproductive hormones can be detected in gray whale baleen. These studies highlight the potential utility of reproductive hormone assessments to provide insight into gray whale reproduction.

21.5.2   *Linking Reproductive and Acoustic Behavior*

Bioacoustic tags, capable of collecting acoustic data as well as information on acceleration and depth, and unoccupied aerial vehicles (UAVs or drones) equipped with video, photographic, and other sensors (e.g., thermal) are examples of rapidly developing technologies that can further expand the understanding of reproductive behavior in gray whales (Ramos et al. 2023, this book). When paired together, underwater calls of gray whales that are linked to their behavior at the surface can be collected simultaneously, including data from breeding and other social-sexual groups. Alternatively, a recent study using two drones, one capable of landing on the water near whales to collect acoustic recordings and the other for obtaining aerial imagery of whale behavior, demonstrated the feasibility and utility of this research approach (Frouin-Mouy et al. 2020).

Acoustic communication plays a vital role in the social interactions of many marine mammal species, but gray whale acoustic behavior and vocalizations are just beginning to be evaluated. While the S1 call described in Sect. 21.4.2 above seems associated with gray whale reproduction, its specific role has yet to be determined. The statistical approach taken by Ponce et al. (2012) could be designed to count the number of S1 calls detected, not only in relation to the total number of whales but to the two demographic classes: single whales and female–calf pairs. If the S1 call is indeed a social contact call used mostly by single whales that are actively trying to breed, its presence should be correlated with the presence of single whales but uncorrelated with the presence of female–calf pairs, when observed across multiple seasons.

21.5.3 Role of Wintering Lagoon Entrance Aggregations in Reproduction

Whalers in the nineteenth century first reported aggregations of gray whales at the wintering lagoon entrances off the Pacific coast of the Baja California peninsula, Mexico, leading to the eventual discovery and exploitation of the high concentrations of whales inside of the lagoons proper. In recent decades, reports from scientists and observations of local fishers and eco-tourism operators confirm that gray whales actively enter and leave the winter lagoon interiors and form aggregations at the entrance points (Jones and Swartz 1984; Jones 1990). These entrance point aggregations of whales are difficult to observe due to their distance from the shore and high surf where they occur, precluding detailed study and evaluation of the importance of these areas to gray whale reproductive behavior in the winter. A new generation of affordable "fixed-wing" and "hovering" drones have good potential to serve as effective and safe platforms to observe gray whale sexual and mating behavior in these portions of their winter range.

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Chapter 22
Bowhead Whale Reproductive Strategies

William R. Koski, J. Craig George, and Bernd Würsig

Abstract Bowhead whales (*Balaena mysticetus*) have adopted growth and reproductive strategies to survive in a challenging environment where no other mysticete whales reside. They grow slowly, become sexually mature at around 25 years (later than other mammals), and do not give birth until they have sufficient energy reserves for the best possible chance of survival of the calf to weaning and long-term survival of the mother. To compensate for late maturity and long inter-birth intervals, some seem to have the capability to live to 200+ years of age, making them the longest-lived mammal known to date. Bowhead whale males have large testes per body size, and it is hypothesized that the basic polygynandrous system of females and males mating with multiple partners per estrous cycle allows for males to not compete violently against each other. Instead, they use sperm competition by volume of sperm for enhanced capability to father as many offspring as possible. Also, as in right whales (*Eubalaena* spp.), the length of the penis is proportionally longer than those of balaenopterids. Details of sperm volume, potential variabilities of sperm viabilities, and actual paternities are unknown, but some patterns can be inferred from the closely related right whales with similar morphologies.

Keywords Birthing period · Calf dependency · Calving · Calving intervals · Gestation · Growth rates · Mating behavior · Sexual maturity · Sperm competition · Surface-active groups

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22.1   Introduction

Living entities have evolved to maximize their long-term survival including selecting and specializing in niches where they can effectively compete with other species in their habitats. Bowhead whales (*Balaena mysticetus*) have taken this specialization to an extreme level by living year-round in a challenging geographic region where no other closely related species reside. To ensure survival of individuals in this isolated and unpredictable environment, bowhead whales have adopted conservative reproductive and growth strategies. They can live to be 200+ years old, and sexual and physical maturity is delayed compared to other species. They delay raising a calf for decades, producing young only when their energy reserves are sufficient to maximize survival of a calf and its mother (George et al. 2021b). Growth in young whales emphasizes the head and feeding apparatus at the expense of postcranial skeletal structures. The size of the head relative to the body and the length of baleen plates is greater than most other mysticetes so that they can efficiently feed on small low-density invertebrates. This chapter describes what we currently know about the above strategies with respect to reproduction in this slow-growing and long-lived mammal.

22.2   Age and Length at Sexual Maturity

Bowhead whale growth is slow compared to other cetaceans (Koski et al. 1993; George et al. 2011). They appear to forgo growth in favor of storing energy reserves that allow them to survive long periods with a negative energy balance (i.e., during periods when they use more energy for normal activities than they obtain from feeding) (George et al. 2021a, b). Male bowhead whales mature at a length of 12–13 m when they are about 25 years old (O'Hara et al. 2002; Tarpley et al. 2016). Female bowhead whales become sexually mature at 14.2 m when they are estimated to be about 25 years old (Koski et al. 1992) based on samples from harvested whales collected up to 1992 (Tarpley et al. 2016). More recent harvest data, however, have identified sexually mature females 12.6–13.9 m, suggesting that there may be a trend toward sexual maturity at a younger age in recent years (Tarpley et al. 2021). The appearance of smaller sexually mature females in the harvest at Utqiaġvik (formerly Barrow), Alaska, was thought to be due to more favorable feeding conditions that have resulted from increases in productivity with longer and more extensive areas of open water each year. However, young female bowhead whales migrate past Utqiaġvik later than older females (Koski et al. 1993). Thus, the appearance of small sexually mature female bowhead whales in the harvest in recent years may be due to the migration being earlier. Koski et al. (1993) identified bowhead whales as small as 12.3 m with calves in the Eastern Beaufort Sea during summer in the early to mid-1980s when the smallest pregnant females harvested at Utqiaġvik were 14.2 m (Tarpley et al. 2016). For comparison with bowhead whales,

North Atlantic right whales *(Eubalaena glacialis)* become sexually mature much earlier at about 10 years (Knowlton et al. 1994; Rolland et al. 2005; NMFS 2022), blue whales (*Balaenoptera musculus*) at 10 years for females and 12 years for males (Sears 2002; NAMMCO 2020a), fin whales (*Balaenoptera physalis*) at 7–12 years for females and 6–10 for males (Aguilar 2002; NAMMCO 2022a), humpback whales (*Megaptera novaeangliae)* at 5–15 years (Clapham 2002, 2018; Gabriele et al. 2007; Best 2011), sei whales (*Balaenoptera borealis*) at 8–10 years (Horwood 2002; NAMMCO 2020b), and gray whales (*Eschrichtius robustus*) at 6–12 years (Jones and Swartz 2002; Swartz et al. 2023, this book).

George et al. (2011) examined the question of whether corpora accumulation is, on average, the same for left and right ovaries. They found no significant difference in the number of corpora in each ovary; however, they did find large variation where the number of corpora could vary by up to 12 scars. Ohsumi (1964) examined corpora-accumulation curves and noted baleen whales were "Type 1" ovulators where right and left ovaries attained maturity at the same time and overall accumulation rates were similar. Bowheads appear to be consistent with Ohsumi's characterization of baleen whales. George et al. (2021b) examined sex differences in the maximum body lengths of bowhead whales. They noted that among several hundred whales harvested since 1972, the 10 longest were females. The maximum reliable lengths for females were about 19 m while the maximum lengths for males were 16–17 m. However, maximum lengths of whales measured photogrammetrically are about 8.2% shorter than those of hunter-harvested whales, as there appears to be some "stretching" when whales are hauled onto shore (George et al. 2004). The longest whale measured in photographs was 17.57 m (Koski et al. 2006).

Reproductive senescence is poorly understood for bowhead whales, mainly because relatively few whales over 100 years have been aged. The current method of aging old bowhead whales relies on aspartic acid racemization (AAR; Wetzel et al. 2017), with exact age estimates insecure. There is no evidence for reproductive senescence in males. A large male bowhead estimated to be 159 years old had seminal fluid extruding from its penis (George et al. 1999). There is, however, information on possible senescence in female bowhead whales based on examination of reproductive tracts and age estimates using AAR (Wetzel et al. 2017). The oldest female that has been harvested with a fetus was estimated to be 121 years old. The three oldest female bowhead whales that were harvested had AAR age estimates of 133, 139, and 149. They all had small, regressed corpora albicantia and no corpora lutea, suggesting that they were reproductively quiescent or senescent (George et al. 2021b). Although these age estimates are not precise, they suggest that at least some female bowhead whales might be able to produce calves over a period of about 100 years.

22.2.1 Mating Period and Location

Bowhead whale behaviors associated with mating have been seen throughout the year, but a recent study (Fortune et al. 2017) found that some of this behavior is associated with stimulation of the epidermis during the molt, and therefore is not a reproductive activity (Würsig and Koski 2021). In particular, close physical presence and rubbing with pectoral appendages seem to assist with removal of dead skin and stimulation of new skin. Most calves are born over a very short period from late April to late May (Koski et al. 1993, 2008), suggesting that most successful mating occurs over a short time as well. On April 13 and 14, 2005, hundreds to perhaps one thousand or more bowhead whales were seen and photographed mating in the Bering Sea north of St. Lawrence Island (Figs. 22.1 and 22.2; Koski et al. 2005). Activities associated with mating have also been reported in autumn (Koski et al. 1993; Würsig and Clark 1993), but it is unknown how much of this behavior might be non-procreative. This behavior may have been rubbing relative to sloughing skin stimulation or it may have been non-reproductive mating attempts (Würsig and Koski 2021; Ham et al. 2023, this book; Würsig et al. 2023, this book). Several

Fig. 22.1 Mating behavior in a group of bowhead whales photographed on April 13 and 14, 2005, ~50 km north of St Lawrence Island, Bering Sea. The female (upside down at the top of image) is being aggressively pursued by several males. The resting whales on the lower right are probably males "catching their breath." From Koski et al. (2005)
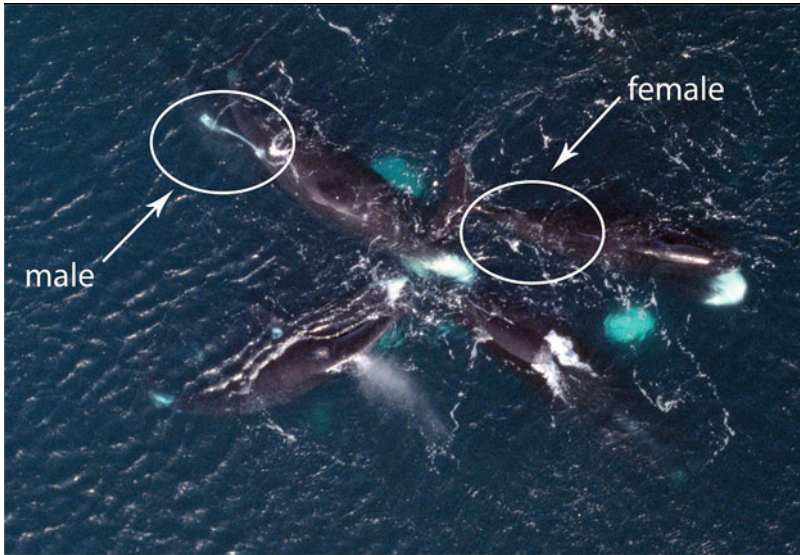
Fig. 22.2 Five male bowhead whales chasing a female (diving). with the penis of one of the males clearly visible

observations of presumed sexual activity in autumn were clearly sexual in nature, with extruded penises visible (Würsig et al. 1993). However, integration of variable lines of observational information and information below on gestation suggests that the main mating period is in late March to mid-April when most Bering, Chukchi, and Beaufort seas (BCB) bowhead whales are in the Bering Sea (Reese et al. 2001; Koski et al. 2005). Data from examination of ovaries suggest that female bowhead whales may ovulate up to three times during a reproductive cycle if the first and second ovulations do not result in a pregnancy (Tarpley et al. 2016). This likely explains observations of smaller numbers of whales engaged in mating activities during mid-April to late May than in early-to-mid April.

In addition to an overall decline in the number of whales seen engaged in mating activities later in the spring, the group sizes of whales engaged in mating behaviors have declined from early April to late May. Carroll and Smithhistler (1980) described mating behavior during May near Utqiaġvik and typical group sizes have been 4–6 animals. Similarly, during the many years of ice-based whale census observations west of Utqiaġvik, mating behavior was described by observers on several occasions and group size has been 4–6 animals as seen from the ice edge. The smaller group sizes seen during May (4–6 animals) than during April (up to 24+; Koski et al. 2005) could be due to waning sexual behavior because most ovulating sexually mature female bowhead whales have become pregnant during their first ovulation, which appears to be in early-to-mid April.

22.2.2   Mate Selection

A hypothesis advanced by Kenagy and Trombulak (1986) and summarized for mammals in general by Clutton-Brock (2016) relates large testis size (generally by weight) to body size/weight in polygynous/polygynandrous (multi-mate) mating systems. This hypothesis is likely operating in bowhead whales. Males need a large volume of sperm to mate with as many females as possible during a proscribed mating season. In multi-mate systems, where the females are inseminated by more than one sexual partner, a higher volume of sperm also enhances the likelihood of paternity (Lüpold 2013). This relationship of sperm competition by volume was further advanced for gray whales, right whales, and bowhead whales by Brownell and Ralls (1986; see Gerber and Krützen 2023; Würsig et al. 2023, this book, for a summary for cetaceans); all of these species have large testes relative to their body size. Tarpley et al. (2021) mention that the largest single testis measured so far for a bowhead whale weighed 211 kg and was 1.5 m long. The estimated body mass of that whale was about 54,000 kg, making the testes/body weight 0.0078 (combined testis weight 422/per body weight 54,000). A relatively small number of harvested male bowhead whales had a combined testicular weight over 150 kg ($n = 9$) and only 5 had combined testes weights over 200 kg. The largest combined weight was 422 kg in a 14.6 m whale. A sexually mature male bowhead whale from the Eastern Canada-West Greenland (EC-WG) stock that was 14.1 m long had a single testis size of 42 kg (Heide-Jørgensen et al. 2012). Spermatozoa volume is massive due to the large size of the epididymis that can rival the testis (Haldiman and Tarpley 1993). Sperm competition can also be at sperm viability level; that is, some sperm will survive longer in the uterus making them more likely to impregnate their mate (Lüpold 2013); this has not been explored in bowhead whales, to our knowledge. In the closely related North Pacific right whale (*Eubalaena japonica*) the largest combined testes weight of 972 kg was in a 16.3 m whale and the next largest combined weight was 955 kg in a 17.0 m whale. Both whales were from the western North Pacific (Omura et al. 1969).

Very little has been published of the penis of the bowhead, but it is fibroelastic type like that found in most artiodactyls. From our field observations of a few large males, the penis is long (to 3.0 m) and slender (see also Fig. 22.2). As in right whales, penis length in bowheads, as a percentage of total body length, appears to be greater than that of balaenopterids. Little information is available on the morphology of spermatozoa in baleen whales. Tarpley et al. (2021) provide a photograph of spermatozoa from a 16.6 m adult male bowhead whale, but the morphology and size are not provided. The apparently strong physical sperm competition by volume may mean that male bowhead whales are rather indiscriminate in their choice of mates, but aspects of mate selection for both sexes are unknown. We explore mate selection further in the following section on mating behavior.

22.2.3 Mating Behavior

Bowhead whale sexual behavior entails much scramble competition, with males maneuvering to gain access to females, possibly almost always near the surface (Würsig and Clark 1993). In the Bering Sea and near Utqiaġvik, where the water is clear, we saw chasing well below the surface (perhaps to 20–30 m), but we do not know how much farther below the surface it may occur. Similar to observations of right, gray, and humpback whale sexual interactions, there can be many whales involved (mostly males; Figs. 22.1 and 22.2) with at least one female, and much white water being created, making observations by humans as to specifics particularly difficult (Würsig et al. 1993). These interactions are generally termed surface-active groups (SAGs), following a definition for humpback whales (Clapham 1996). However, in humpback whales, testes to body size ratios are much smaller than in the apparent sperm competing bowhead whales, and in humpbacks there are very aggressive male–male interactions, termed contest competition Clapham 1996, 2018). In the apparent sperm competitors, while there is swift action, males appear to attempt to outmaneuver each other without much overt aggression (Dines et al. 2015). There is even the (unproven) provocative suggestion that males at times help each other to gain access to females, by one male pushing down on a ventrum (belly)-up female and another attempting to insert his penis (as shown for southern right whales, *Eubalaena australis*, Payne 1995). If true, this also makes sense for apparent strong sperm competitors; if only by helping each other, each male receives a better chance at inseminating the female.

While males are jostling for position, females tend to hold their breath while ventrum-up, making it difficult for males to mate with them (Würsig et al. 1993). That female inverted behavior is likely to represent a form of female choice, where perhaps the most adroit, experienced, largest, longer-lasting male has a better chance to inseminate the female. When the female needs to breathe, she rolls dorsum-up while rapidly surging ahead and diving, again appearing to evade the males. Würsig et al. (1993) provide several sequential line drawings of SAG activities; also see Figs. 22.1 and 22.2). It is not clear how often female bowhead whales mate with different males, but in southern right whales, the same female has been seen multiple times in different SAGs (Payne 1995; Brown and Sironi 2023, this book); it is unknown whether she is physiologically reproductively active throughout this time. At any rate, sperm competition does not negate the probability of polygynandry in these animals with super-large testes and can presently be hypothesized for bowhead whales. SAGs may also consist at times of bowhead whale male homosexual activity (Finley 1990), as in other whales (Darling 1977 for gray whales; Kraus and Hatch 2001 for northern right whales (*Eubalaena glacialis*); and Sironi 2004 for southern right whales; see also Brown and Sironi 2023, this book).

Surface-active groups (SAGs) of many males and one to several females (Würsig and Clark 1993; Koski et al. 2005) are "commonly" seen in spring in the Beaufort Sea, but also occur at other times of the year (e.g., Everitt and Krogman 1979; Würsig et al. 1993). It is not known for what reason extra-seasonal apparent matings
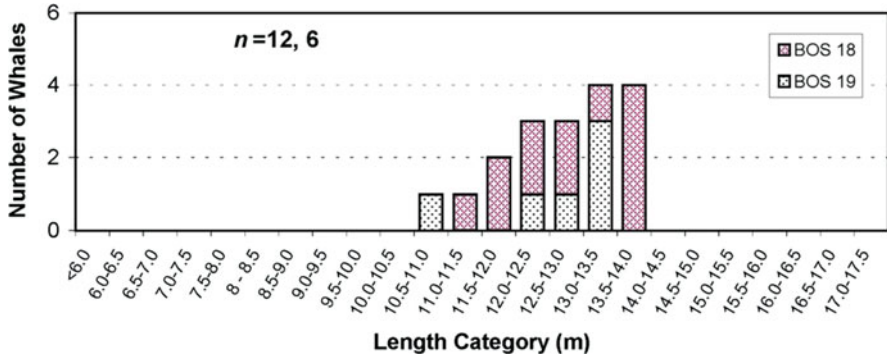
Fig. 22.3 Sizes of bowhead whales observed engaged in presumed sexual activity during behavior studies conducted in the Central Beaufort Sea on September 20, 1998. Lengths were determined by aerial photogrammetry conducted using the methods of Koski et al. (1993). Figure prepared by William R. Koski, and used here with permission

or mating attempts occur, but it has been hypothesized that while some of it is homosexual, it may also represent especially young animals learning mating patterns and physical maneuvering needs (Würsig et al. 2023, this book; Fig. 22.3). Not all apparent mating attempts occur in SAGs, and at times (and reported infrequently, probably as it is difficult for humans to witness), apparent mating has been reported for only two or three animals in much more leisurely rolling and touching activities than in SAGs (Würsig et al. 1985). While it is very likely that female bowhead whales mate with multiple males during estrus, this has been confirmed for right whales (Brown and Sironi 2023, this book). In right whales, two males with penises inside one female at the same time have even been reported (Mate et al. 2005 for northern right whales; Würsig 2000 for southern right whales), with strong evidence for competition being at sperm volume level, and perhaps with other physiological advantages. In Würsig (2000), the larger male seemed to be preferred by the female, as she tilted toward the larger male and thereby pulled the smaller male's penis out of her; the larger male went to apparent orgasm, with clear muscular contractions from base toward tip of penis. The gentle-seeming interactions, including caressing by flippers after the mating event, indicate that at least at times female choice may not be simply among several males in large aggregations, but may be more of a one-on-one interaction of choice. While the above vignettes are of right whales, the similar large testes and apparent polygynandrous system of bowhead whales allow us to predict—with caution—that multiple mating strategies may also be involved in bowhead whales.

While detailed analyses of bowhead whale sounds and song have not been unequivocally linked with sexual behavior, it is likely that this link exists (Würsig and Clark 1993). Stafford et al. (2012) analyzed bowhead whale song recorded in Fram Strait between Greenland and Svalbard. Song-type calls were initiated in late October, with near-constant singing from late November until early March. Singing occurred somewhat intermittently through March-early April and ended abruptly in

late April. While the number of new songs had decreased by March, the highest diversity of different song types occurred in March. It has been speculated that bowhead whale song is a male reproductive display similar to that of humpback whales (Stafford 2022; Eichenberger et al. 2023, this book). Peak singing coincides with the peak breeding/conception period in late March and April (see above) for BCB bowhead whales.

22.2.4 Gestation

The bowhead whale gestation period appears to be slightly more than 1 year based on the main mating period in late March to mid-April and the peak of calving in late April to late May (Koski et al. 1993). This assertion is supported by small embryos (3 cm) and near-term fetuses (366–455 cm) having been found in harvested whales during the spring hunt at Utqiaġvik, Alaska (Tarpley et al. 2016, 2021). Reese et al. (2001) proposed a ~14-month gestation period like the 13.5-month gestation in gray whales (Dale Rice). However, bowhead and gray whale gestation is slightly longer than of blue (10–12 months; Sears 2002; NAMMCO 2020a), fin (11 months; Aguilar 2002; NAMMCO 2022a), and humpback whales (11–12 months; Clapham 2002; NAMMCO 2022b), and considerably longer than sei whales (7 months; Horwood 2002, 2018; NAMMCO 2020b).

22.2.5 Birthing Period and Location

Bowhead whale calves are born in spring during the northward migration from the southwestern Bering Sea to the Eastern Beaufort Sea and mother and calf pass northern Alaska during the latter part of the migration in water with extensive ice cover that is <0 °C (Angliss et al. 1995; Koski et al. 2004, 2008). Although it seems like a stressful time to calve, bowhead whales avoid encounters with their main natural predator, the killer whale (*Orcinus orca*), and calving occurs a short time before the mothers arrive at prime feeding areas in the Eastern Beaufort Sea (Citta et al. 2015).

The question of how neonates withstand parturition into <0 °C sea water has not been investigated but does not appear to result in mortality of the calf. Based on between-day sightings of recently born calves in mother–calf pairs near Utqiaġvik, it appears that mothers interrupt their migration for a few days after they calve to recover from the stress of calving and to permit calves to become strong enough to migrate (Koski et al. 2004; Arnold Brower, Sr, pers comm to JCG). When mothers and newborn calves begin their journey toward summer feeding areas, the calf has at times been seen to ride on the back of the mother (Würsig et al. 1999). The calf sits on the lower back of the mother and appears to be able to maintain this position passively due at least in part to the Bernoulli effect. The riding behavior by very

young calves is probably a method to reduce the energetic requirements of the calf during migration and hence to reduce the stress of migration on the young calf.

Most calves appear to be born in the Chukchi and Western Beaufort seas based on few sightings of calves in the Bering Sea, the relatively high occurrence of mature females 11/64 (17%) harvested at Utqiaġvik in spring carrying a full-term fetus (NSB unpublished data), and only one sighting of a young calf in the eastern Beaufort Sea during summer (Koski et al. 1988). However, some calves are born in the Bering Sea. Noongwook et al. (2007) reported that Saint Lawrence Island whale hunters have reported seeing migrating mother/calf pairs in April and May, but the frequency of such sightings was not quantified: "*Mothers with calves travel as part of the large-whale group and are seen as early as April, but with greatest frequency in mid-May. Calves may be born as late as June. Hunters say they are harvesting pregnant females more frequently now than years ago, which is consistent with observations of increasing numbers of whales and particularly small whales*" (Noongwook et al. 2007). In addition, Koski et al. (1993) estimated that 14% of calves were born before 1 April, when most whales are still in the Bering Sea, and 11% were born after 1 June, when most whales have passed Utqiaġvik. Some sexually mature females harvested at Utqiaġvik in May had near-term fetuses and these ranged in total length from 366 to 455 cm (Tarpley et al. 2016, 2021). It appears that first-time mothers calve late in the spring after they pass Utqiaġvik, based on a comparison of the sizes of mothers seen during the summer with those passing Utqiaġvik in late April to early June during the 1980s to early 1990s (Koski et al. 1993).

22.2.6   *Calf Size at Birth*

There are limited data on the lengths of newborn calves, but the estimated near-term fetal lengths ranged from 400 to 450 cm in Nerini et al. (1984). Koski et al. (1993) suggested a mean size at birth of 430 cm based on the estimate of Nerini et al. (1984) and photogrammetric measurements of young calves photographed near Utqiaġvik. More recent data from near-term fetuses harvested from 29 April to 15 June had a mean size of 413 cm (George, field observations). Twelve of the 16 near-term fetuses were >400 cm (Tarpley et al. 2021) and the largest fetus was 455 cm. Based on photographic data from late spring and early summer, calves with their mothers had total lengths of around 4.4 m; however, most of these calves were more than a few days old so this overestimates the size of a newborn calf. The mean 4.4 m calf size is about 30% of the 14.7 m mean length of all photogrammetrically measured mothers (Fig. 22.4a; W Koski, unpubl data). Agbayani et al. (2020) reported that average size at birth of gray whales was 4.6 m, or 39% of the mean size of mature females (11.7 m; Rice and Wolman 1971).
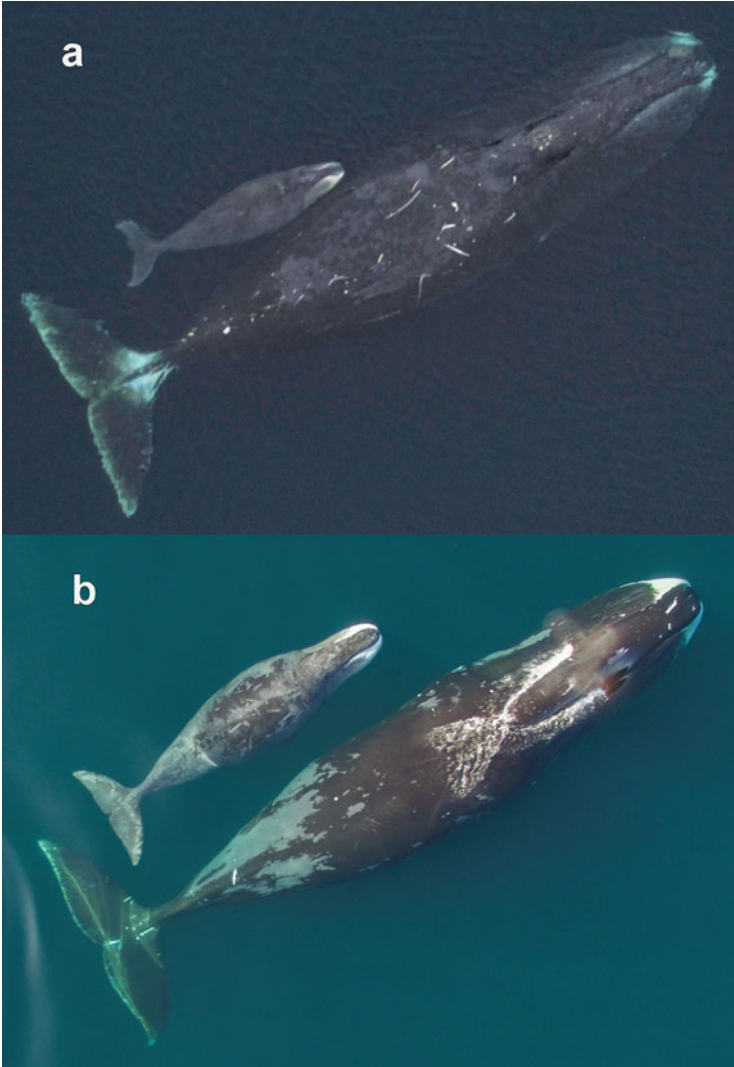
Fig. 22.4 (**a**) A bowhead whale mother and newborn calf photographed near Utqiaġvik AK in spring 2004. Photo taken by W. Koski; (**b**) A bowhead whale mother with a 4–5-month-old calf photographed in Cumberland Sound during August 2019. Photo taken by Ricky Kilabuk

22.2.7   Calf Dependency

Bowhead whale calves remain with their mothers for about 10–11 months (Koski et al. 1993, 2004, 2008). Calves are primarily born during April to early June, and only a few yearlings have been seen with their mothers near Utqiaġvik in spring (Koski et al. 2012). The vast majority of yearlings are solitary when they pass

Utqiaġvik toward the end of the spring migration, well after other immature whales (Koski et al. 2012). While few calves born the previous year are still with their mothers in spring, milk in the stomach of one yearling harvested in spring (it was probably born late in the previous year) indicates that it was still nursing (George and Suydam 2014; Tarpley et al. 2021). Stomach analyses of 12 calves of the year that were harvested in autumn found that nine had only milk in the stomach, two of them also had invertebrates, and one was empty. This indicates that calves begin to feed on invertebrates when 5–7 months old, but their main source of nourishment is milk (George and Suydam 2014; Sheffield and George 2021). Calf dependency is quite similar in related southern right whales, where females and their 1-year-old young return to the general winter-time mating area just before females and young separate (Taber and Thomas 1982). Other species of baleen whales are weaned at an earlier age than bowhead whales and after they arrive on their feeding grounds with their mothers (6–8 months for blue, fin, sei, gray, and humpback whales; Aguilar 2002; Clapham 2002; Horwood 2002, 2018; Jones and Swartz 2002; Sears 2002; NAMMCO 2020a, b, 2022a, b). Despite a longer period of dependency on their mothers, bowhead whale calves are generally less than half the length of their mother when weaned (Koski et al. 1993), while the other species of mysticetes are generally about two-third to three-quarter the length of their mothers at weaning (NAMMCO 2020a, b, 2022a, b). Gray whales, for instance, are weaned at about 8.7 m (Jones and Swartz 2002), which is about 74% of the average length of a mature female gray whale (Rice and Wolman 1971).

22.2.8 Calving Intervals

Early photographic studies suggested that bowhead whale calving intervals were mostly 3 and 4 years (Miller et al. 1992; Rugh et al. 1992; Koski et al. 1993). Consistent with the calving intervals during those years were reproductive cycles of 2 years with very low calf production followed by 1 year with moderate calf production and 1 year with high calf production (Koski et al. 1993). Tarpley et al. (2021) summarized the considerable literature on bowhead whale calving intervals and calving rates for bowhead whales of the Bering–Chukchi–Beaufort (BCB) stock that was collected during post-mortem examination of harvested whales, aerial surveys, and progesterone spikes in baleen of mature females (Rolland et al. 2018). Tarpley et al. (2021) included data from more recent years (1993–2013) than Tarpley et al. (2016) and concluded that the average inter-birth interval is just over 3 years with an average pregnancy rate of about 0.32 calves/year. George et al. (2018) reported a positive and statistically significant trend in pregnancy rate during their study period; however, these findings are being reanalyzed. Right whale calving intervals are similar to bowhead whales (Davidson et al. 2018; Watson et al. 2021), but calving intervals for North Atlantic right whales have increased since the 1980s to about 5 years (Kraus et al. 2001, 2007). In comparison to bowhead and right whales, calving intervals of other baleen whales are generally 2 years (gray

whales—Jones 1990; Jones and Swartz 2002; humpback whales—Clapham 2002; Baker et al. 1987; fin whales—Aguilar 2002) and are 2–3 years for blue whales (Sears 2002).

It is worthwhile to compare lactating bowhead whales with other migratory baleen species. Lactating gray whales in Mexican overwintering lagoons were in better body condition than other gray whales (Christiansen et al. 2021); however, it is not known whether the better body condition was maintained to weaning of the calf, which is several months later and after they leave the wintering lagoons. It is also not known whether females that had calves the previous year were more likely to die than other sexually mature gray whales during mass mortality events that periodically have occurred recently (Perryman et al. 2002, 2021). Survival of sexually mature bowhead whales is extremely high (98.4–99.6%, Zeh et al. 2002; Givens et al. 2017), so few bowhead whale mothers are likely to have died as a result of giving birth to a calf and raising it to weaning.

22.2.9   Growth Rates

During the nursing period, bowhead whale calves grow rapidly (Fig. 22.4a, b; Koski et al. 1993), but between weaning and approximately year 5, bowhead whales display sustained baleen and head growth and an almost unprecedented pattern of limited growth in the rest of their bodies (i.e., the postcranial portions). Large autumn calves and small yearlings or even 2+-year-old bowhead whales can overlap in body length (Koski et al. 2012; George and Suydam 2014). During this period, they withdraw resources from the skeleton, in particular the ribs, which may lose 40% of bone mass (George et al. 2016). The body lengths of whales 2–5+ years old overlap, with little annual increase in body length (Lubetkin et al. 2008; Koski et al. 2012). This emphasis on baleen and head growth is unique among baleen whales and prepares the young whales for efficient feeding on tiny invertebrates in an environment with low densities and unpredictable presence of their primary prey. Following this hiatus in growth, bowhead whale growth becomes more rapid (Koski et al. 1992; Lubetkin et al. 2012) but is still slow compared to cetaceans inhabiting warmer waters (George et al. 2021b). Once growth resumes in year 6, it takes 13–20 years to grow to the age of sexual maturity (i.e., at about 25 years old) and another 30 years or more to attain physical maturity at an age of 50–60 (Koski et al. 1992; Lubetkin et al. 2012).

In other baleen whales, growth is rapid until they are weaned and then slows down or stops after they depart their feeding grounds. The second growth phase starts when they return to their feeding ground at about 1.5–2.5 years old, whereas in bowheads, the slow growth extends until they are 5+ years old. Sexual maturity in right whales is around 9 years (Hamilton et al. 1998), blue whales 8–10 years (Sears 2002), fin whales 6–8 years (Aguilar 2002), sei whales about 10 years (Horwood 2002), humpback whales about 5 years (Clapham 2002), and gray whales 6–12 years (Jones and Swartz 2002).

Bowhead whales store energy reserves in their blubber to ensure survival during periods of low food abundance rather than applying these reserves more immediately to growth as do other cetaceans (Burns 1993; George 2009). George et al. (2021a, b) speculated that these apparently conservative growth and reproductive strategies appear to be possible only for geographically isolated species such as the bowhead whale.

22.3   Conclusions and Future Directions

Most of the information summarized above has come from harvest and photographic data collected from the BCB stock of bowhead whale. These data have been used for management of the EC-WG stock and should be validated by studies conducted on that latter stock. Estimates of growth rates and reproductive parameters rely heavily on accurate estimates of age. Calves and yearlings can be accurately identified in photographs based on their morphology (Koski et al. 1993, 2012), and whales up to about age 10 can be reliably aged based on the length of their baleen (Lubetkin et al. 2008). The latter information can only be obtained from harvested whales, which results in much smaller sample sizes for analyses and makes analyses impossible for stocks other than the BCB stock. Approximate age estimates for whales older than about 10 years come from AAR analyses (Wetzel et al. 2017). DNA methylation has been used to estimate the ages of a few EC-WG bowhead whales (Li et al. 2021; Parsons et al. 2023), and this method appears to provide more precise age estimates than AAR based on data from known age animals of other species in captivity. We recommend that tissues already aged using AAR and tissues from recently harvested whales be aged using DNA methylation. This will permit us to obtain better estimates of growth and reproduction parameters.

Biopsy samples from bowhead whales can be used to determine the age of sampled whales using DNA methylation (Parsons et al. 2023), the sex of sampled whales (Linsky et al. 2022), pregnancy rates for sexually mature whales (Pallin et al. 2018), and their diet (Marcoux et al. 2012; Pomerleau et al. 2018). From combinations of these data and with samples from a large number of whales, the ages at sexual maturity and senescence of female bowhead whales can more accurately be determined, and the population structure can be determined as well. Bowhead whales segregate by size class in the summer feeding areas (Koski et al. 1988) and so the diets of different size classes are expected to be different. Analysis of stable isotopes from biopsy samples will provide information on the differences in diet and energetics of different size classes of bowhead whales.

Genetic analyses of biopsy samples to determine the parents of bowhead whales will provide information on reproduction history of the parents. For example, if the age of a young animal is obtained and there is information for its mother about the years when she had calves, the information for the young animal could contribute to the sequence of years when the mother had or did not have calves. If a male bowhead is found to be the father of many animals, it would provide information on the

existence of "super males" or males that father a disproportionately high proportion of the recruits to the population (Gerber and Krützen 2023, this book).

Drones have become a valuable tool for observing the behavior of animals while minimizing disturbance (Fortune et al. 2017; Ramos et al. 2023, this book). Recent studies of bowhead whales in eastern Canada have provided more detailed information on behavior than earlier studies from fixed wing aircraft because camera resolution has improved, and whales do not appear to be disturbed by battery-powered drones flying at low altitudes above them (W Koski, pers obs). During the same studies, accurate information on whale sizes and body condition can be obtained from still photographs.

Also, as noted by Brownell and Ralls (1986) there is still a need to collect additional anatomical data on harvested bowhead whales. Special attention should be given to the following: (1) size of testes and weights, (2) epididymides, (3) sperm morphology, (4) total length and girth of the penis, and (5) the size of the vagina and the number of vaginal folds (see also Orbach et al. 2023, this book). In addition, details are lacking on the morphology and viability of the sperm.

Bowhead whales have adopted many growth and reproductive strategies that have enabled them to survive in a challenging environment where no other mysticetes co-occur throughout their principal range. It appears that these strategies permit bowhead whales to survive long periods with negative energy balances by storing energy reserves in a thick layer of blubber. To obtain this energy in an environment with overall low annual productivity, they have developed an efficient feeding apparatus that can filter tiny organisms from the water column, as right whales of the related genus *Eubalaena* do. To ensure that they have adequate energy reserves to survive periods with low productivity, they delay reproduction until energy reserves are sufficient to successfully wean their young and at the same time enhance the survival of the mother. As a direct result of this cautious approach to using food resources for growth and raising a calf, females do not become sexually mature until they are in their mid-twenties, in comparison to other baleen whales which become sexually mature at 5–12 years (Hamilton et al. 1998; Aguilar 2002; Clapham 2002, 2018; Horwood 2002; Jones and Swartz 2002; Sears 2002). They counterbalance late sexual maturity and long periods between giving birth to calves with their extraordinary longevity. Bowhead whales are the longest living mammal discovered to date, apparently living to ages of 200 years or more and female bowheads may be capable of producing calves for 100 years, which is longer than other mysticetes are thought to live. Blue and fin whales, for instance, are believed to live to 80–90 (Aguilar 2002; Sears 2002; NAMMCO 2020a, 2022a), humpback and right whales to 70 (Hamilton et al. 1998; Clapham 2002, 2018), and sei whales to 50–70 years (Horwood 2002; NAMMCO 2020b).

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Chapter 23
Right Whale Sexual Strategies and Behavior

Moira Wilding Brown and Mariano Sironi

Abstract North Atlantic and southern right whale social interactions and sexual behavior have been studied for decades. Understanding whale mating systems can inform about many aspects of their biology and even their anatomy. Right whales have a polygynandrous mating strategy where females and males mate with multiple partners within a breeding season. It is hypothesized that this promotes sperm competition among males and likely explains the large testis-to-body-size ratio in *Eubalaenids*. Surface active groups (SAGs) characterize mating behavior in North Atlantic and southern right whales, where two or more animals are at the surface with frequent physical contact. Observations of copulation in SAGs have led to the hypothesis that conception is the primary function, with females practicing a mating strategy where the chance of conception with the largest and likely healthiest male would be maximized. Right whales produce their entire acoustic repertoire of known calls while in SAGs and sounds are thought to serve a social communication function. In the North Atlantic, surface active behavior is seen in all habitat areas and in all months of the year in which right whales are sighted. SAGs tend to increase in size and vigor as the mating season approaches, resulting in spectacular and highly energetic courtship activity with group sizes numbering 30 animals and more; however, the whereabouts of any breeding ground is unknown. On southern right whale calving grounds, mother-calf pairs use relatively shallow waters along the coastline, and SAGs tend to occur farther from shore: calving and mating occur in winter in largely the same habitat areas. Analyses of seasonal timing and group composition of individually identified animals within SAGs suggest that they may serve multiple other roles, since conceptive and non-conceptive groups have been

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revealed. SAGs often include pregnant females, juveniles, and occasionally calves. Some groups consist of exclusively same sex individuals. It has been hypothesized that, in addition to conception, SAGs may also provide opportunities for right whales to socialize, play, learn, practice mating, and identify potential future mates.

Keywords Juvenile sexual behavior · Mating behaviors · Non-conceptive behavior · North Atlantic right whale · Polygynandrous mating · Sexual behavior · Southern right whale · Surface active groups

23.1   Introduction

After one day at sea with North Atlantic right whales, colleague Malcolm Hunter wrote in his journal "Half a century of witnessing wildlife spectacles on every continent, including dozens featuring lions, tigers, and bears, but nothing can compare with August 8, 1995 on the Bay of Fundy Canada, watching male North Atlantic right whales thrashing about to position themselves next to a lone female."

When the editors invited us to contribute a chapter to this text, our thoughts went to the many hours of many days spent watching and puzzling over groups of so-called thrashing right whales in the North Atlantic (*Eubalaena glacialis*) and Southern Hemisphere (*E. australis*). Not all assemblages are equally energetic, some are relatively calm unions of two or three animals. Larger gatherings can be seen from a distance of one mile or more, the air above heavy with fountains of mist. As we approach, we notice the sounds of explosive blows and the churning of their surprisingly agile bodies – at times their tails were almost touching their heads. Meanwhile, the inverted focal female, with her genital slit in the air, apparently incites competition among attendant males who jockey for position beside her for an opportunity to mate when she rolls upright to breathe. This is the social behavior named courtship in right whales.

Garnering insights about whale behavior is challenging, with observations often confined to a few moments when the whales surface to breathe. But there are those times when researchers come across a pair or more, sometimes many more, whales remaining at the surface for minutes to hours. At times the whales are engaged in seemingly calm interactions (Fig. 23.1a). At other times, there is a confusing, at least to the observer, melee of heads, bodies, and tails maneuvering around each other at the surface (Fig. 23.1b).

We present a synthesis of what is known and hypothesized about social interactions and sexual behavior of right whales in the North Atlantic and southern hemisphere species. This chapter is illustrated with previously unpublished images and video clips from boats, airplanes, drones and shore. The status of North Pacific right whales (*E. japonica*) remains precarious, robust life history data are lacking, calving grounds remain a mystery, and the poor understanding of even broad scale movements despite visual and acoustic surveys over the past 20 years (Harcourt et al. 2019) precludes including this species.

Fig. 23.1 (**a**) Three North Atlantic right whales in a small surface active group (SAG) unusually close to shore in the Bay of Fundy; (**b**) a high-energy SAG in the Grand Manan Basin, North Atlantic right whale critical habitat, lower Bay of Fundy, Canada. The white-bellied animal is the focal female belly-up and surrounded by several males. One of the males to the left of the female is about to lay his flipper on her belly. Moira Brown, Canadian Whale Institute

North Atlantic and southern right whales are tracked over time using photo and video images of natural markings called callosities, unique patterns of keratin-structured raised skin tissue on the top and sides of their heads, lips and chins, and lip crenulations and by pigmentation patterns that are used to distinguish individuals over time (Payne et al. 1983; Kraus et al. 1986, Hamilton et al. 2007). Scarring from their encounters with human activities including fishing gear entanglement and to a lesser extent vessel strike (Knowlton and Kraus 2001; Knowlton et al. 2012; Sironi et al. 2021) and in southern right whales from Argentina kelp gull (*Larus dominicanus*) wounding (Marón et al. 2015a) provide additional marks to differentiate individuals that in some cases may be temporary. The ability to tell individuals apart is important for describing all behaviors. Modern drone technology (Ramos et al. 2023, this book) has allowed for rapid and rather inexpensive photo and video imagining of right whales, providing images of unprecedented levels of detail to understand who is who and who does what in the midst of the surface active groups (SAGs).

Cetacean social behavior is typically derived from observations of whales at or just below the surface (Sironi 2004; Brown et al. 2007). Behaviors are described by distance between individuals (usually in body lengths) and the relative positioning of animals in the association (i.e., head-to-head, belly-to-belly) (Kraus and Hatch 2001). Images and video footage of right whale movements (Azizeh et al. 2021), associations, and unique identifiers have permitted researchers to hypothesize individual strategies of social behavior (Lonati et al. 2022). Data on age, sex, reproductive state, and relatedness of individuals from genetic profiles derived from skin biopsy samples can be integrated to interpret social interactions and speculate on roles and strategies (i.e., Frasier et al. 2007, 2013). This is more feasible in relatively small populations, such as with the North Atlantic right whale, while in the larger southern right whale populations, less is known about each individual, but there are more individuals to learn from. Detailed right whale life history data make it possible

to learn about why right whales display such elaborate sexual behavior to maximize their individual fitness.

23.2   Mating Behavior, Gestation, and Parturition

Donnelly (1967) provided the first account of mating behavior in southern right whales from observations during a month-long period in late August and September 1965, in Algoa Bay, South Africa. He adopted the term *courting pairs* of whales for a social grouping of two whales rolling and splashing together, detectable from a great distance with "*flukes and flippers waving above the surface*," engaged in apparent mating behavior albeit with apparent tenderness and grace (Donnelly 1967). The courtship events were divided into pre-copulatory (female horizontal, male caressing), copulatory approach (female horizontal and dorsum up, male rolls under and positions belly-to-belly), and post coitus behavior (female returns to dorsal side up posture which was assumed to be the normal responsive behavior; Donnelly 1969). The admittedly difficult-to-detect sequences of behaviors were described as a female horizontal at the surface with head and "forequarters" exposed while the male actively dove, circled, and caressed the female for at least 4 h, often resting his chin on her hindquarters (Donnelly 1967). Group size was usually two whales, although polygamous events of three and four whales were seen. The term "polygamous" was used by Donnelly (1967) to indicate a mating system where a single male is able to obtain reproductive access to a number of females either simultaneously or serially. Males were identified as such when they surfaced and rolled on their back after a horizontal belly-to-belly position with the female; coitus was estimated to be rapid, taking no longer than one-half minute, occurring about every one-half hour and likely not always successful (Donnelly 1967). Body positioning was head-to-head and side-to-side. In some events, an unresponsive female lay on her side away from the male and occasionally on her back with the male attempting to turn her over (Donnelly 1969). Donnelly (1967) estimated the measure of male coital success by a "*flurry of fluke movements*" after which the male surfaced and rolled belly-up for about 20 s.

   Donnelly (1969) reviewed the seasonality of southern right whale arrival in coastal calving areas and courtship behaviors for a first approximation of ten-month gestation with calving occurring at least in alternate years. Early efforts to calculate the gestation period of southern right whales based on mating behavior seen in coastal waters roughly coincided with the winter calving period were not substantiated, at least in Argentine waters because calving females were rarely seen in the year preceding a calving (Donnelly 1969; Payne et al. 1983). Three explanations were proposed: (1) gestation may be longer, up to two years, (2) there is delayed implantation occurring, and (3) female occupancy in coastal waters the year before calving is brief (Payne 1986).

   Reproduction and gestation were investigated in southern right whales in South Africa. Using records of stranding neonates, length of fetuses, estimates of

fetal growth rates, and mean size at birth, the gestation period was estimated at 357–396 days or roughly 12–13 months (Best 1994). A similar rarity of females seen in the prior year giving birth was attributed to short coastal residency or conceptions occurring outside coastal waters (Best 1994). Burnell and Bryden (1997) suggested a gestation duration of 355 days for right whales in the Head of the Bight, Australia, based on mating and calving activities. The latter two estimates suggest a 12-month gestation for southern right whales. The most likely of Payne's (1986) explanations is that mating can take place not only in coastal waters but also further offshore as there has been no support for a two-year gestation period (Best 1994) or delayed implantation, which is unknown for cetaceans (Boness et al. 2002).

Here we define the area where calves are born as the calving ground; the nursery ground is where mothers provide neonatal care (i.e., suckling, protection from predators), and the breeding ground is where courtship and copulation occur. More than one of these activities can take place in the same ground. For instance, southern right whales use the Atlantic coast of South America for different purposes, with most pregnant females concentrating in calving grounds such as Península Valdés in Argentina (Payne 1986; Payne et al. 1990) and southern Brazil (Groch et al. 2005), where mating also occurs. In other areas, such as the Uruguayan coast (Costa et al. 2007; Jorge et al. 2010) and Golfo San Matías in Argentina (Arias et al. 2018), mostly reproductively active individuals gather to breed and socialize while the areas are also used by some mothers with calves. In recent years, as population size and density increase in the Península Valdés calving ground in Argentina, mother-calf pairs use the optimum areas along the coast of the gulfs and displace solitary individuals and breeding groups to suboptimal zones that are farther from shore and in deeper waters (Sueyro et al. 2018); in this case, the mothers with calves are still well within the known breeding ground.

In southern right whales, behavioral observations are primarily confined to wintering calving areas. In these areas, the most common social unit is the mother-calf pair, with a strong bond between the two for the first year of the young whale's life. Permanent separation from the mother occurs when calves are 12–15 months old (Taber and Thomas 1982; Burnell 2001). Female right whales typically calve once every three years, and stay in nursery grounds such as Península Valdés and South Africa with their calves for the first 2–3-month postpartum (Payne 1986; Payne et al. 1990; Best and Rüther 1992; Cooke et al. 2003). During this time, the playful calves, which measure up to 5 m at birth, grow 2–3 m in length (Whitehead and Payne 1981; Best and Rüther 1992; Christiansen et al. 2022) and develop locomotor and social skills (Taber and Thomas 1982; Thomas and Taber 1984).

Cow-calf pairs then migrate to their feeding grounds (Best et al. 1993; Zerbini et al. 2016, 2018), and some return when the calves are almost one year old (Thomas and Taber 1984; Rowntree et al. 2001). The yearlings are weaned and begin their lives as independent whales (Sironi 2004). Mature females in their calving years show significantly higher fidelity to the nursery grounds than males, and they return repeatedly to calve and to wean calves at particular locations (Burnell 2001; Rowntree et al. 2001). Adult females that neither forage abundantly nor mate in the nursery grounds migrate to calving grounds with their one-year-old calves

Fig. 23.2 In this large SAG of North Atlantic right whales in the Bay of Fundy, the focal female is in the center of the image. There is one male attempting to copulate with her while she is belly-up. His light gray penis is moving across the female's genital area. Moira Brown, Canadian Whale Institute

probably to wean them there (Thomas and Taber 1984; Rowntree et al. 2001). This suggests that there may be important advantages for yearlings to be weaned in areas where they can socialize with conspecifics (Sironi 2004).

In the North Atlantic, right whales are studied year-round in various habitat areas from the calving ground in the southeast coast of Florida through the mid-Atlantic to well-known spring, summer, and autumn feeding grounds in the Gulf of Maine and more recently in the Gulf of Saint Lawrence. One of the mysteries of the North Atlantic right whale is that they appear to engage in SAGs that are sexual in nature in all the habitat areas year-round (Winn et al. 1986; Parks et al. 2007). Thus, SAGs are the most common social behavior observed for North Atlantic right whales and are thought to be related to reproduction (Fig. 23.2). The assemblage of right whales in a SAG was intentionally described simply as a temporary association of two or more animals (30+ individuals) in close proximity (<1 body length) engaged in frequent physical contact (Kraus and Hatch 2001). This basic definition, derived from hours of observations over decades, was chosen to avoid assigning functional attributes to social groups and avoid potentially masking discrete behavioral functions (Kraus and Hatch 2001). Although similar social groups and behaviors have been described for southern right whales off Argentina (Payne 1986), South Africa (Donnelly 1967; Best et al. 2003), Chile (Galletti Vernazzani et al. 2014), Australia (Burnell et al. 1990), and New Zealand (Patenaude 2000; Carroll et al. 2022), observations are confined to the nearshore southern hemisphere calving/breeding grounds. It is unknown if southern right whales participate in SAGs year-round. Satellite telemetry of southern right whales tagged in their calving grounds could help to discover the location of potential mating grounds further offshore (e.g., Argentina, Zerbini et al. (2016, 2018); Siguiendo Ballenas (2022); South Africa, Mammal Research Institute (2022); New Zealand, Tohora Voyages (2021)).

The discovery of an annual mating ground for North Atlantic right whales has remained elusive. It has long been speculated that the species' gestation period is similar to the 12–13 months estimated for southern right whales (Best 1994). Calves are born off the southeastern USA, sightings of neonates peak from December to February, and conception is speculated to occur between November and February (Kraus et al. 1993; Hamilton and Cooper 2010). There is one documented exception to the seasonal timing of a calf born in the late spring in northeastern US waters (Patrician et al. 2009) and a second geographical exception of a newborn observed in January 2013 in Cape Cod Bay (Hamilton PK pers. comm.).

There was some indication of a potential mating ground based on surveys over a seven-year period in the Gulf of Maine. Cole et al. (2013) compared proportions of females calving the following year (conceptive females) and the proportion of genetically identified fathers within each geographic region that the whales inhabit throughout the year. Based on documentation of about one-half of the cataloged population from November–January 2002–2008, Cole et al. (2013) found significantly higher proportions of known fathers and conceptive females present in the central Gulf of Maine during the estimated conception period when compared to most other areas seasonally inhabited by right whales. The discovery of reproductively successful males and females in the central Gulf of Maine during the boreal winter led the authors to suggest this area as the species' mating ground for some conceptions (Cole et al. 2013). However, the annual use of this region by right whales has not persisted (Cole TVN pers. comm.) and the concept of a single mating ground for North Atlantic right whales remains to be addressed. Some individuals stay in northern feeding areas in the Gulf of Maine and along the Scotian Shelf during the winter (Cole et al. 2013; Durette-Morin et al. 2022). North Atlantic right whale females migrate to a calving ground in the southeast USA to give birth but not to mate (Kraus and Rolland 2007; Cole et al. 2013). There are, however, some right whales including juveniles, adult males, and non-calving females that have been documented in the southeast US calving area during winter (Hamilton et al. 2007; Hamilton and Cooper 2010). Gowan et al. (2019) modeled decades of sighting data from the calving ground and found differences in migratory probabilities depending on an animal's reproductive state and age class, indicating that right whales have the potential to migrate to the southeast USA each winter but that this migration is condition-dependent. The model indicated that males were more likely to use the southeast US habitat area than non-calving females and that females in the year before and following calving may overwinter in feeding areas to increase blubber reserves for future reproduction (Gowan et al. 2019). This migratory behavior of females not migrating in a nonreproductive year is called skipped breeding partial migration (Gowan et al. 2019). For comparison in migratory differences, a southern right whale female was tagged with satellite monitored transmitters in Península Valdés, Argentina, in 2015 when she had no calf and in 2021 when she was accompanied by a calf (Siguiendo Ballenas 2022). The tracks showed that she used different areas of the southwest Atlantic in two years, possibly preferring different feeding destinations based on her reproductive status.

23.3 The Sexual Behavior of Right Whales: A Group Strategy

Sex and hunger are the two primary animal instincts: hunger propels animals to migrate in search of food and sex compels them to come together and mate. There are a bewildering number of mammalian mating systems for sexual reproduction, but it is all governed by one underlying instinct or drive to maximize individual reproductive success, as every animal tries to put as many copies of its genes into future generations. The distribution of males is largely governed by the distribution of females (Eichenberger et al. 2023, this book; Würsig et al. 2023, this book).

Arguments about which sex benefits the most from dispersal to avoid potential inbreeding in polygynous mammals were summarized by Greenwood (1980). Females, who invest heavily in offspring, are the limiting sex while males invest relatively little and compete for access to females. Greater benefits accrue to males gaining access to a large number of females than vice versa (Greenwood 1980). However, since intra-sexual competition is more intense among males than females, a large proportion of males may be denied access to females (Greenwood 1980; Payne and Dorsey 1983).

Right whales have a polygynandrous mating system, where a female may mate with multiple males within a breeding season and a male with multiple females (Brownell and Ralls 1986; Kraus and Hatch 2001; Kraus et al. 2007). In the North Atlantic, some SAGs involve a single focal female that emits calls to attract males, presumably inciting competition among males who compete for access to the focal female at the surface in a belly-up posture (Kraus and Hatch 2001; Kraus et al. 2007; Eichenberger et al. 2023, this book). Right whales produce their entire acoustic repertoire of known calls while in SAGs, that is, a stereotypical contact call, the upcall, and a loud broadband impulsive sound, the gunshot, which is described for all right whale species (Parks et al. 2007; Parks 2022; Eichenberger et al. 2023, this book). These sounds are considered to serve a social communication function (Parks et al. 2007). The focal female in a SAG, located roughly in the center of a group, typically spends most of the time on her back with her genital slit out of the water (Donnelly 1967; Kraus and Hatch 2001). The belly-up posture has been interpreted as an attempt by the female to avoid unwanted copulation, but Kraus and Hatch (2001) suggested it might be more of an assessment of the nearby male and if he is considered the most suitable partner. Males move actively to position themselves next to the female; they appear to follow her orientation (belly-up in avoidance or head-up for a breath) with their flipper(s) and wait until she turns over to breathe (Fig. 23.3), and then copulation can occur (Figs. 23.4. a and b) (Payne 1986; Kraus and Hatch 2001).

SAGs in the North Atlantic and southern hemisphere are undoubtedly sexual in nature as confirmed by frequent observations of erect penises and intromission that are indicative of mating (Donnelly 1967, 1969; Patenaude 2000; Kraus and Hatch 2001; Best et al. 2003; Sironi 2004; Mate et al. 2005; Parks et al. 2007). Males compete for access to the scarce females not through aggression but rather with

Fig. 23.3 An aerial image of at least four southern right whales in a SAG in Península Valdés. The female is belly-up and the closest whale to her left is keeping track of her movements with his left flipper placed on her belly. Mariano Sironi, Instituto de Conservación de Ballenas, Argentina
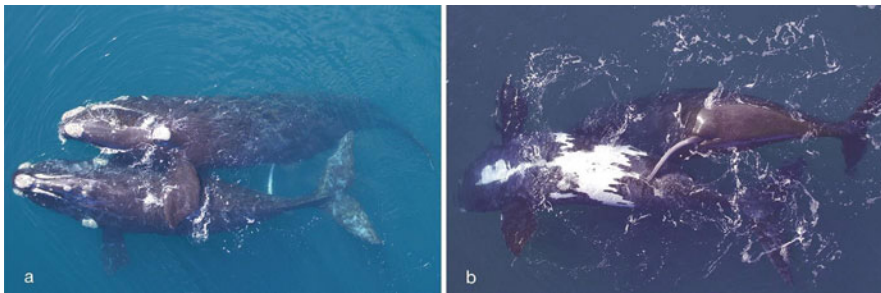
Fig. 23.4 Drone images of two southern right whales copulating in Península Valdés: (**a**) female is head-up and male on his side and slightly underneath the female; and (**b**) the female is inverted in the belly-up position and the male is on his right side. Nicolás Lewin, Instituto de Conservación de Ballenas, Argentina

physical stamina and ability to position themselves close to the focal females in a group and wait for a mating opportunity (Fig. 23.4).

Males have a fibroelastic penis that is a flexible and mobile organ and the actual act of intromission is quite passive. Competition among males can take two forms. First, males compete behaviorally during courtship when they swim, push, turn, and move within a SAG to increase their chances to copulate with a receptive female. This would likely be a learned skill with success related to body size and maturity (Frasier et al. 2007). Mating side-to-side or belly-to-belly, their fusiform body shape allows for few alternatives for copulatory positions. Second, the most decisive male competition likely occurs inside the female's body, through the production of huge

volumes of sperm to increase each male's chances of fertilizing the female's only available ovum. The male that produces the most sperm outcompetes, possibly "diluting" or "washing out" that of other males who recently copulated with the female. Sperm competition likely explains the large testis-to-body-size ratio in this genus, the largest testes in the animal kingdom weighing 500 kg each, a ton in total (Brownell and Ralls 1986).

An additional behavioral indication for sperm competition and female choice in right whales has been collected from observations of multiple males achieving intromission simultaneously. Two males were observed copulating at the same time with the same female in a SAG in the North Atlantic (Mate et al. 2005), while similar observations were made of southern right whales off Argentina (Würsig 2000; D'Agostino et al. 2017) and among the critically endangered Chile-Peru southern right whale population where sightings are scarce (Galletti Vernazzani et al. 2014). Reproductive behavior has been observed off the north-western coast of Isla de Chiloé, Chile, showing the extended penises of two males entering the genital slit of a female, highlighting the importance of these coastal waters as a mating ground for this population (Galletti Vernazzani et al. 2014). The observation of intromission during the peak of the breeding season suggests that this group was exhibiting reproductive behavior (Galletti Vernazzani et al. 2014).

SAGs in the North Atlantic are seen year-round including on the feeding habitats in the summer and early autumn. SAGs do not always occur at the right time for fertilization to happen; most conceptions should occur from October through December, a season with few observations (Kraus and Hatch 2001). Kraus et al. (2007) asked why North Atlantic right whales spend time and energy in SAGs during the high-priority feeding season if that activity does not result in conceptions (Supplementary Video 23.1). Kraus and Hatch (2001) and Kraus et al. (2007) suggested two possibilities: (1) Females may keep track of the performance of different males, make a choice, and mate with the selected male at a later time. (2) Females may require repeated practice to learn how to assess and select males in SAGs, and it may be lower risk to assess them during the feeding season before the stakes become high during ovulation. SAGs observed outside the breeding season in the North Atlantic contained an average of 4.6 animals, but the range was much greater in the North Atlantic than the southern hemisphere during the breeding season: 2–35 whales per group (Kraus and Hatch 2001) versus 2–10 in South Africa (Best et al. 2003). Group size of SAGs in other mating areas has not been published. During a SAG, female whales can mate sequentially with different males.

Frasier et al. (2007) found that fatherhood in North Atlantic right whales was significantly biased to older males, with successful paternity occurring only from age 15 onward, almost twice the age of females. Both the physical competition between mates and the internal competition between sperm may prevent younger males from securing conceptions, thus resulting in a lower effective population size (Frasier et al. 2007). A second factor that has been suggested to favor the reproductive success of older males is testicular development. Although it is unknown when male testes reach adult size, much higher levels of androgen hormones were found in

adults than in juvenile males (Rolland et al. 2005). There may be two factors favoring reproductive success among older males – experience and sperm quantity. If only older males are successful at fertilizing females, then there are even fewer males contributing genes into the next generation. Other male adaptations such as seminal fluid proteins, copulatory plugs, prolonged copulations, and post-ejaculatory guarding behavior that reduce female remating probability have yet to be investigated for right whales (Parker 2020).

23.4 Behavioral Aspects and Differences in Behavior Patterns on Calving Versus Other Grounds

The normal reproductive cycle of northern and southern right whale females lasts for three years. Females give birth to a single calf every three years and lactate for approximately one year, with calves usually leaving their mothers at the end of their natal year (Thomas and Taber 1984; Hamilton et al. 1995; Burnell 2001; Sironi 2004), although genetic profiling of North Atlantic right whale calves revealed unexpected variations in some mother–calf associations and weaning times of 7.5 to 8.0 months (Hamilton et al. 2022). The female then rests for a year to rebuild blubber reserves for the following pregnancy (Marón et al. 2015b). The mean age at first parturition is nine in Argentina (Payne 1986; Cooke et al. 2003, 2015) and Australia (Charlton et al. 2022) and eight in South Africa (Best et al. 2001). The youngest recorded age of females at first calving is five for two individuals in South Africa (Vermeulen E pers. comm.) and six in Argentina, with five cases reported for Península Valdés. The mean age of sexual maturity for North Atlantic females and males is eight years old (Hamilton et al. 1998). There is one case of a minimum age of first parturition of age five (Knowlton et al. 1994). The gestation period is estimated to be the same for northern and southern right whales, 12–13 months (Best 1994).

With equal sex ratios, the above implies that for every potentially receptive female, there is an excess of mature males. With females investing much energy in gestating and lactating a calf (Christiansen et al. 2022), this scenario should promote strong competition among males, with females exercising mate choice in SAGs (Reeb et al. 2003). However, in recent years, changes in calving intervals have been detected for the Argentine and South African southern right whale populations, with intervals of four and five years becoming more frequent (Marón et al. 2015b; Thavar et al. 2021). Consequently, the recovery of the populations may be affected by a reduction in the rate of increase. While the potential reproductive cycle for North Atlantic females is similar, the observed cycle is not. There is a longer average calving interval that increased from 4.0 in 2009 to 9.2 in 2021 (Pettis et al. 2022), a male biased sex ratio (Pace et al. 2017), and an increase in the frequency of high calving intervals (6+ years, Bishop et al. 2022) that suggest there is an excess of mature males and that few nonbreeding females transition into the breeding pool

(Reed et al. 2022). To investigate low birth rates of North Atlantic right whales, Stewart et al. (2022) compared age-corrected body lengths with age at first reproduction, average inter-birth interval, and the number of calves produced per potential reproductive year. Body lengths have been declining over the past 40 years, and although body length was significantly related to birth interval and calves produced per reproductive year, age at first reproduction was not (Stewart et al. 2021). Stewart et al. (2021) found that larger whales had shorter inter-birth intervals, produced more calves per potential reproductive year, and had higher lifetime calf production, although this was a result of longer potential reproductive spans. Declining body sizes are a potential contributor to low birth rates over the past decade for North Atlantic right whales (Stewart et al. 2021). In southern right whales, by combining historical whaling records and drone photogrammetry data, Christiansen et al. (2022) calculated fetal growth rates and birth and found that larger females produce calves that are larger at birth and that have higher fetal growth rates than those born to smaller females.

Southern right whales show site fidelity (Valenzuela et al. 2009) but also flexibility in habitat use on their wintering grounds (Rowntree et al. 2001). For instance, males and females of all ages move frequently between the major regions of concentration on the Península Valdés nursery ground in Argentina and can change their distribution, abandon some areas, and colonize others along the coastline with time (Rowntree et al. 2001). Females also use different calving grounds in different years, as 124 females were recorded calving in Santa Catarina, Brazil, in some years and in Península Valdés, Argentina, in others (Rowntree et al. 2020). The two areas are separated by nearly 2100 km.

Most southern right whale populations are growing (e.g., Argentina, Crespo et al. (2019); Australia, Bannister (2017); New Zealand, Carroll et al. (2022); South Africa, Brandão et al. (2018)). It has been suggested that with growth, populations in some nursing and breeding areas may be experiencing density-dependent processes: when a threshold in density is reached, this elicits a response in habitat use, with mother-calf pairs remaining in the area, while other groups are displaced to new areas (Sueyro et al. 2018). This would be expected to affect habitat use and therefore mating strategies, particularly among males. This is possibly the case in Península Valdés; mothers with calves may displace solitary animals and breeding groups that move to (and likely are recolonizing) peripheral areas with lower density, such as Golfo San Matías to the north (Arias et al. 2018). As a consequence, these areas are used mostly by solitary juveniles and adults for socializing, courtship, and mating and are becoming more important for the reproductive cycle of the species.

Similar spatial and temporal changes and preferences in habitat use, driven by a number of factors, have been described in other well-known wintering grounds such as Southern Brazil (Danilewicz et al. 2016), where mother-calf pairs remained closer to the coast compared to unaccompanied whales (Renault-Braga et al. 2018, 2021). Mating activity was observed in most of the social groups recorded around the Auckland Islands as evidenced by abundant white water, erect penises, and females exposing their bellies to the surface (Patenaude 2000, see also photos in

Eichenberger et al. 2023). Two-thirds of the animals present in groups engaged in social/sexual activity were males ($n = 86$), although the sex ratio of animals biopsied was 1:1 (Patenaude 2000). In the 1990s, mother-calf pairs were about one-quarter of the whales present, with clear evidence that whales gave birth in the area (Patenaude 2000). However, groups containing cow-calf represented 50% of the animals surveyed in 2020/2021 in the Auckland Islands, a clear signal that the New Zealand population is growing and is not limited by food resources (Carroll et al. 2022). Although the high latitude of the Auckland Islands is more consistent with known summer feeding grounds worldwide, they are clearly both an important calving and breeding ground for southern right whales. Also, southern right whales off New Zealand are recolonizing the mainland presumably from a remnant population from the Auckland and Campbell Islands that survived whaling (Carroll et al. 2014). Recent surveys to the remote Campbell Island found an increase in abundance of mostly sub-adult animals; there have been no sightings of calves, but nine photo-identification matches were made with animals previously seen elsewhere in New Zealand (Torres et al. 2017).

Carroll et al. (2012) examined the reproductive autonomy of southern right whales on their New Zealand calving grounds by using paternity assignment and "gametic recapture." Results suggest that individuals returning to the calving ground are reproductively autonomous on a generational timescale and isolated by maternal fidelity on an evolutionary timescale from others in the Indo-Pacific region, indicating that whales using the same calving ground are mating together (Carroll et al. 2012). This is consistent with other southern hemisphere calving grounds such as Península Valdés in Argentina, where adult right whales are frequently seen copulating amidst mothers and calves (Figs. 23.3 and 23.4). In the western south Atlantic, the genetic differentiation between southern right whales sampled in Brazil and Argentina is subtle and likely reflects differences in the demographic aggregation of whales using each region (Carroll et al. 2020). This, coupled with likely immigration from Argentina into Brazil (Groch et al. 2005) and the observation of known individuals in both calving grounds (Rowntree et al. 2020), indicates that whales show plasticity in philopatric behavior and may mate in different years in different calving grounds within the same population.

23.5 Parturition and Parental Care

Right whales give birth during the winter when they gather in their calving grounds. These are located in coastal waters, and in many sites in the southern hemisphere the whales are the focus of intense whale watching activity. In many cases, big, fat females are observed pregnant, and days later, they are resighted with a calf (Christiansen et al. 2022). Despite the many human eyes watching, observations of right whale births are exceedingly rare. In the North Atlantic, the first account of the birth of a right whale calf occurred in the calving ground in the coastal waters of southeast USA (Zani et al. 2008). Researchers on a survey aircraft described seeing a

Fig. 23.5 A southern right whale named *Tehuelche* photographed while in the midst of birthing a calf at Península Valdés, Argentina. The tail of the white calf is visible emerging from the genital slit of the female. Luis Pettite

known adult female thrashing at the surface and that the waters around her were red, and a few minutes later, a small calf emerged from subsurface (Zani et al. 2008). In South Africa, a southern right whale female was seen giving birth to a gray morph calf (Best 1981). Coincidentally, the only reported right whale birth at the Península Valdés, Argentina calving ground was also of a gray morph calf (Sironi et al. 2019). The mother was observed from a whale watch boat right before sunset, when the crew noticed unusual behavior and approached her, photographing the moment of birth (Fig. 23.5). Observations were ended before actual delivery occurred because the local whale watch regulations prohibit navigation after sunset (Sironi et al. 2019).

The rarity of the observations of right whale births suggests that they may occur at night, and the case of *Tehuelche* (Sironi et al. 2019) suggests that this could be the case, although how right whales would benefit from bringing their young to life during the night is a matter of speculation. Frasier et al. (2010) reported on a rare case of two North Atlantic right whale calves that switched mothers and remained with their adoptive mother until weaned. They speculated that the calves must have been in close associations before the biological mother-calf offspring recognition developed and noted that the births may have taken place during an intense storm but did not speculate on a nighttime birth (Frasier et al. 2010).

Fetal growth rate in baleen whales is among the fastest in the animal kingdom. During the last month of gestation, southern right whale fetuses grow between 3 and 4 cm per day (Christiansen et al. 2022). Calves can measure between 4.5 and 5 m in length at birth. The biggest calves are born to the biggest mothers, being nearly 35% of the mother's length (Christiansen et al. 2022). Producing such large offspring is energetically very costly to the females. The main energetic cost for a pregnant female is to produce the heat necessary for gestation (74%), followed by fetal growth (21%), and the energetic cost of the placenta (5%). The energetic cost increases

during the 12 months of gestation and is highest during the last 4 months (Christiansen et al. 2022). With such high investment, it is not surprising that lactating females maintain proximity and display maternal behavior patterns to prevent their calves from spending too much precious energy and to protect them from potential predators including killer whales (*Orcinus orca*) that are present on nursing grounds such as Península Valdés, where at least 12 attacks have been reported (Sironi et al. 2008).

23.6 Non-conceptive Sexual Behavior in Calves and Juveniles

Non-conceptive sexual behavior refers to those animals that participate in SAGs without any possibility of conception taking place (Ham et al. 2023, this book). Conception is not possible if (1) the sexual activity takes place outside of the conceptive season (in the North Atlantic, SAGs have been seen during all months, whereas calving occurs primarily from December through February (Kraus and Hatch 2001)), (2) the focal female is already pregnant (Kraus and Hatch 2001), (3) the sexual interactions are among individuals that are sexually immature, or (4) the individuals in the SAG are of the same sex.

What functions could non-conceptive SAGs have? In North Atlantic right whales, almost all known aged right whales were first sighted in SAGs as juveniles and more than half of the SAGs examined had at least one juvenile (Parks et al. 2007). SAGs with a juvenile focal female were on average smaller than SAGs with mature focal females (Kraus and Hatch 2001). The behavior and social interactions of juvenile male and female southern right whales were studied at their nursery ground in Península Valdés, Argentina, including sexual behaviors (Sironi 2004). Sexual behavior was considered to occur in groups where the penis of one or more males was visible (erections), or body postures involving potential physical contact between the genital slits of two or more whales were repeated during the interactions. The posture belly-to-belly was considered separately from other surface activities to assess the time females and males were in a position where potential genital stimulation (and potential mating) could have occurred, although actual copulations in this posture are not usually possible to see from shore. Females could practice this posture that appears to be relevant to avoid unwanted copulations when they engage in surface active groups as adults. There is only one record from 1974 of a shore-based observation of copulation where a classic belly-up female with two attendant males appeared to choose one male: the pair spent a couple of minutes in close contact with the male's penis partially inserted (Würsig 2000). The penile contractions observed were interpreted to be a male orgasm and deposition of sperm with the penis softening and contracting into the genital slit followed by about 20 s of close contact before leisurely swimming away together until out of sight (Würsig 2000).

Juvenility begins when a young individual can survive the death of its mother and ends when sexual maturity is reached (Janson and van Schaik 1993). Environmental feedback, including social learning and practice, is thought to play an important role in juvenile development (Pereira 1993). Sironi (2004) described sex differences in juvenile southern right whale behavior at Península Valdés. Juvenile females actively maintain interactions with mother-calf pairs while males spend more time with other juveniles. During social interactions, females spend significantly more time belly-up than males, probably to avoid unwanted copulations, and end encounters more frequently by turning away from other whales (Sironi 2004). Juvenile right whales may use the nursery grounds as places to practice locomotory behavior and to socialize with conspecifics. Males may establish relationships with age peers that could be important during their adult lives, especially in SAGs. Females actively seek to interact with mothers and calves, possibly to learn maternal behavior by observing them. Sex differences in social interactions that are part of adult whale behavior begin to be established during the juvenile stage in southern right whales (Sironi 2004).

Juvenile right whale females spend substantial time in the vicinity of and interacting with mothers and their calves as well as more time than males in body postures that are typical of adult females. Juvenile males engage in locomotory behavior patterns that resemble adult mating behavior with partners of similar developmental state (Sironi 2004). Testing the social learning hypotheses in right whales can be difficult without experimentation. However, behavioral data show that the opportunities juveniles have at Península Valdés to learn and to practice skills when they engage in social activities are frequent and might be relevant for their future. Juveniles may also spend time at Valdés to become familiar with the environment where a significant amount of sexual and maternal behavior, and therefore essential behavior for their reproductive success, will take place during their adult lives (Sironi 2004).

There are a few records of non-conceptive sexual behavior between a calf and an adult male. In one instance, a calf was separated from its mother by an adult male, which positioned itself in a belly-up posture underneath the calf, holding it between its flippers (D'Agostino et al. 2017). An underwater video camera captured footage of the male inserting its penis into the calf genital slit (D'Agostino et al. 2017). Similarly, there are two cases of a North Atlantic adult male seen belly-up that held the calf belly-to-belly with its flippers on either side of the calf. One event was filmed using a drone and the male appeared to probe the calf's genital region with his extended penis underwater while the calf rolled, thrashed, and arched (Fig. 23.6) (Lonati et al. 2022). Non-conceptive sexual behavior between a calf and an adult male could be adaptive as it could be important for immature animals to learn successful mating behaviors (Kraus and Hatch 2001; Sironi 2004). Play behaviors of southern right whale calves (e.g., rolling, turning, and touching) with their mothers are thought to help calves develop motor skills and coordination for future socializing, mating, and feeding (Thomas and Taber 1984). Participation in SAGs, a common behavior for juveniles, may function in play, social bonding, dominance sorting, or simply practicing mating behavior (Ham et al. 2023, this book). Juvenile

Fig. 23.6   An adult North Atlantic right whale male on his back, belly-up, holding a calf between his flippers during copulation in the Gulf of St. Lawrence, July 2021. Gina Lonati, University of New Brunswick

males were observed displaying erections in SAGs, but contrary to adults, they were never seen copulating with a female, possibly because they do not yet have the skills nor strength to displace adult males from the best positions to mate (Kraus and Hatch 2001).

Most homosexual behavior in right whales, as in other baleen whales, was observed (or was more evident) among males than among females at Península Valdés (Sironi 2004). No evidence of kin selection or reciprocal altruism in mating strategies exists yet for male right whales. The main function of male-only SAGs involving sexual behavior may be to develop and assess their ability in courtship activity by practicing upon one another, and it could simply be a form of juvenile play behavior (Kraus and Hatch 2001; da Silva and Spinelli 2023, this book; Ham et al. 2023, this book).

23.7   Conclusions and Future Directions

Detailed modern right whale identification catalogues and the use of new technology allow researchers to track life history data – calving events, growth rates, age, sexual maturity, longevity, deaths, sex ratio, and trends in scar acquisition over time. Location and demographic data contribute information on seasonal movements, geographic range, and distribution, as well as reproductive success, associations, abundance, and body condition. Genetic profiling adds to the reproductive story with parentage assignments when possible. These data are critical to undertake population-wide assessments and to develop and monitor recovery strategies.

Perhaps more importantly, these data help track the effects of a changing ocean climate that are resulting in habitat shifts and affecting whale population dynamics (Mesnick et al. 2023, this book).

The critically endangered North Atlantic right whale faces substantial hurdles. Population-wide decline in reproductive output, as characterized by low number of calves born and increase in calving intervals, documented in the late 1990s, were attributed to limited prey availability (Caswell et al. 1999; Fujiwara and Caswell 2002; Meyer-Gutbrod et al. 2015) and a combination of fewer actively reproducing females and lower reproductive rates of some females (Brown et al. 1994).

Although the population decline in the 1990s was followed by a decade of reproductive resurgence until 2010, population decline since has been attributed to a shift in feeding habitat from the Gulf of Maine to the Gulf of St. Lawrence, longer calving intervals for some females recovering from nonfatal entanglements, a greater number of longer calving intervals, and fewer pre-breeding females transitioning to the breeding pool (Meyer-Gutbrod et al. 2021; Stewart et al. 2021; Pettis et al. 2022; Reed et al. 2022). Pregnancy and lactation have high energetic demands (Christiansen et al. 2022) and have been linked to variations in reproduction in North Atlantic right whales (Fortune et al. 2013). Miller et al. (2011) concluded that many females were unable to build a sufficient blubber layer to sustain successful reproduction, thus delaying reproduction until enough food could be consumed. Reed et al. (2022) speculated that sublethal effects of entanglement leading to stunting of North Atlantic right whales (Stewart et al. 2021) affect the transition from pre-breeding to breeding females as small individuals have less energy stores to invest in reproduction.

There have yet to be analyses to assess if shifts in prey availability are affecting the frequency and intensity of SAGs. Knowledge of the location of a mating ground for right whales in the North Atlantic eludes us. Bishop et al. (2022) reported that sexually mature females who have used the feeding habitat of the Gulf of St. Lawrence, Canada, since 2015 were significantly more likely to give birth over this time compared to individuals who were not seen there; juvenile males and females were significantly more likely to use the Gulf of St. Lawrence if their mothers did, although this declined as the youngsters aged. An earlier example of site fidelity from mother to offspring was found for animals using the Bay of Fundy from the 1980s to the late 1990s (Malik et al. 1999), but that was before the climate-induced changes in prey availability affected whale movements and distribution which have become much less predictable than in the late twentieth century.

In the North Atlantic, fewer than one-half of cataloged whales have been recorded in the Gulf of St. Lawrence, Canada (Crowe et al. 2021). A portion of the population is using a yet undiscovered summer feeding area(s), and about one-half of the calves born over the past few years were attributed to mothers who do not use the Gulf of St. Lawrence and are older, on average, than Gulf of St. Lawrence mothers (Hamilton PK pers. comm.). High mortality and injury rates associated with right whales using the Gulf of St. Lawrence pose a significant threat to the species because calf fecundity is associated with the mother's and the pattern of habitat use is learned from the mother. Mother-offspring fecundity and calf-learned distribution patterns

seen previously in the Bay of Fundy emphasize the need to locate other feeding areas (Malik et al. 1999). Future population growth may hinge on our ability to provide adequate protection from anthropogenic stressors on all their feeding, calving, nursing, and breeding grounds. The lethal and sublethal effects and reproductive failure from entanglements in fishing gear can be ameliorated through targeted fishery management, and mitigation is critical for the recruitment of breeding females (Reed et al. 2022).

Combining genetic and isotopic data, researchers have shown that southern right whale calves learn the locations of the feeding grounds from their mothers and that this culturally inherited site fidelity to feeding grounds has a timescale of at least several generations (Valenzuela et al. 2009, Carroll et al. 2015, 2016). This cultural transmission can benefit the young animals in their first migrations, but in turn it could limit the exploration of new feeding areas and opportunities. This could be the reason why adult females at Península Valdés show increased rates of reproductive failure in years following elevated sea surface temperature anomalies in their feeding grounds in the South Atlantic (Leaper et al. 2006, Valenzuela et al. 2009).

A rapidly changing ocean environment is also affecting the southern species. For instance, five decades of photo-identification data on 1380 southern right whale females of Península Valdés, Argentina, have shown that the mortality of adult females increases after strong El Niño events, which could impede population recovery and could cause the population to decline (Agrelo et al. 2021). The South African southern right whales have changed their foraging strategy, with a significant northward shift from South Georgia/Islas Georgias del Sur in the 1990s to the waters of the Subtropical Convergence, Polar Front, and Marion Island, South Africa, in the 2010s, and have a more diverse diet too (van den Berg et al. 2021). These shifts are an indication that right whales are flexible in their prey and habitat preferences, but the recorded decline in reproductive success is a warning sign that in fact the shifts could be a suboptimal strategy (van den Berg et al. 2021).

Since the late 1990s, there have been extensive efforts throughout the range of the North Atlantic right whale to reduce the impacts of human activities, vessel strikes, and entanglement in commercial fishing gear (Kraus and Rolland 2007). Ocean conditions can change quickly, and the human adaptations to protect right whales in a new habitat area need to respond. Since 2009, an unprecedented climate-associated change in prey availability in the Gulf of Maine affected the distribution and reproductive dynamics of right whales (Meyer-Gutbrod et al. 2015, 2022). Right whales adapted temporally and spatially to the decline in prey in their traditional foraging habitat in the Gulf of Maine by finding food in the Gulf of St. Lawrence (Meyer-Gutbrod et al. 2022). Although the whales redefined their distribution to find food in the decade after 2010, the absence of protective measures from human-induced serious injury and mortality in the new habitat had catastrophic effects (Davies and Brillant 2019). The mortalities from vessel strikes and fatal entanglements and serious injury from live entanglements galvanized the Canadian government, in consultation with right whale researchers and industry, to proactively adapt human activities in the Gulf of St. Lawrence. Mandatory measures were implemented to reduce vessel speed and close fisheries where there was a high

Fig. 23.7 Researchers observe two right whales mating next to a boat in Península Valdés, Argentina, 11 September 2022. Claudio Nicolini

risk of overlap (Davies and Brillant 2019). Where there was a disaster for a highly endangered whale, humans found a way to develop, implement, monitor, and enforce protection measures.

It is unknown how the anthropogenic stressors that cause poor body condition and stunting in North Atlantic right whales (Christiansen et al. 2020; Stewart et al. 2021) affect offspring survival and a female's capacity to reproduce nor how they will affect the frequency and timing of social behavior and sexual strategies. In general terms, the distribution of females is determined by resources. If resources are widely scattered, females and males will also be. Different habitat conditions and situations produce different mating strategies for both sexes. Of concern is how prey availability and habitat shifts in response to changes in foraging success will affect male access to adult females. Southern right whales have a circumpolar distribution, and rates of recovery for various populations have ranged from near maximum growth rates (Southwest Australia, South Africa, Eastern South America, and sub-Antarctic New Zealand) to poor or not measurable in others (Harcourt et al. 2019). The Auckland Islands population is an example of a population that is in excellent condition and has high and increasing reproductive rates indicative of being able to find sufficient prey (Carroll et al. 2022) (Fig. 23.7).

Will right whales adapt their lives, including sexual strategies and behavior, to the new ocean conditions? Or will humans change the conditions to make the ocean again a home instead of a threat to right whales? Peaceful coexistence and mutual enrichment could be the basis for human-cetacean relations (Barstow 2008). It is possible (Supplementary Video 23.2).

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Chapter 24
Cetacean Sociality, Reproduction, and Conservation

Sarah L. Mesnick, Randall R. Reeves, Paul R. Wade, Philippa Brakes, and Taylor A. Hersh

Abstract The world's cetaceans (like most of biodiversity) are in crisis, and the need for well-informed conservation action has never been greater. Scientific advancements over the last few decades have provided much insight on the reproductive anatomy, physiology, and behavior of whales, dolphins, and porpoises. Our goal in this chapter is to link scientific findings to practical actions that will improve resilience and conservation prospects of cetaceans. We provide an overview of human activities and their impacts on cetacean reproduction and review the progress (or lack thereof) toward conserving species, with a particular focus on those for which sociality and culture may be important to population recovery. For all cetaceans, it is important to preserve or, where necessary and feasible, reestablish the ecological, demographic, and social conditions that allow the animals to reproduce successfully in their natural environment. The better we understand and integrate knowledge concerning cetacean reproductive health into conservation strategies, the better the chances of achieving species recovery, protecting biodiversity, and preventing future extinctions.

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24.1   Introduction

Like most of biodiversity, the world's cetaceans are in crisis and the need for well-informed conservation action has never been greater. Scientific advancements over the last few decades have improved our knowledge of reproductive anatomy and physiology, mating behavior, and parental care of many species of whales, dolphins, and porpoises. Our goal in this chapter is to link these scientific findings to practical actions that will improve conservation prospects for cetaceans.

Human impacts on, attitudes toward, and relationships with cetaceans have changed over time (Notarbartolo di Sciara and Würsig 2022). Commercial whaling, essentially ended since the mid-1980s, killed millions of baleen whales (mysticetes) and sperm whales (*Physeter macrocephalus*, an odontocete) (Rocha et al. 2014) and sparked global conservation efforts (Fig. 24.1). Drive hunts of small- and medium-sized cetaceans continue in a few regions (e.g., Japan, Faroe Islands, Solomon Islands), but the most serious known obstacle to conserving small cetaceans is incidental mortality in fishing gear (i.e., bycatch) (Read et al. 2006; Brownell et al. 2019). Non-deliberate killing and injuring have also hindered or prevented the recovery of some species and populations of large whales (Johnson 2005; Knowlton et al. 2016). In addition to mortality in fishing gear, the energetic cost of nonfatal entanglement—due to drag from towing gear—can influence a pregnant or lactating whale's energy budget, increase the time needed for her to replenish her energy stores, and ultimately lengthen the birth interval by months or years (van der Hoop et al. 2017; Stewart et al. 2022). There are numerous other sublethal threats, that cetaceans face including habitat loss and degradation, depletion of prey, anthropogenic noise and disturbance, biotoxins, and pathogens. Climate change heightens the threats facing cetaceans through direct, indirect, and cascading effects on habitat, prey, predators, and human activityies in our oceans, rivers, and lakes (Gulland et al. 2022).

The reproductive health of some populations of mysticetes is apparently quite good as they are recovering from the impacts of commercial whaling (Thomas et al. 2016; Fig. 24.2). However, some species of toothed cetaceans (odontocetes) appear less capable than mysticetes of recovering from the severe depletion caused primarily by direct removals through whaling, hunting, and fishery bycatch (Wade et al. 2012; Whitehead and Shin 2022). Wade et al. (2012) suggested that this apparent difference in resilience is at least partly due to the effects of exploitation on highly social odontocetes, including, for example, social disruption, fragmentation of social units, and loss of key individuals. In this chapter, we revisit, update, and expand on these ideas. We do not assume that humans can improve upon what the cetaceans have evolved to do themselves with regard to reproduction. Rather, we consider an important role of conservation biologists is to find ways to preserve, or reestablish,

Fig. 24.1 A large male sperm whale socializing with a group of females and young in waters off the island of Dominica in the Caribbean Sea. Sperm whales are the most sexually dimorphic cetacean in body size. The male's gigantic nose, which is the largest sexually selected organ on the planet (Cranford 1999), contains the spermaceti organ complex, the world's most powerful natural sonar system. The valuable spermaceti oil was part of the impetus for two massive waves of commercial whaling that targeted sperm whales (along with large baleen whales). Post-whaling, population trajectories are varied. Sperm whale populations facing minimal human impact are recovering slowly, but the lingering impacts of whaling may be impeding recovery in some areas by affecting the sex ratio and/or the social cohesion of females. In populations currently experiencing anthropogenic impacts, calving rates are declining (Whitehead and Shin 2022). Photo: ©Flip Nicklin/Minden Pictures; 1994. All rights reserved

the environmental, demographic, and social conditions that would enable cetaceans to reproduce successfully.

As noted by van der Hoop et al. (2017, p 103), "Historically, whale conservation measures have focused on reducing mortality; a shift is required to also address morbidity and the sublethal impacts on individuals and their reproductive rates."

Fig. 24.2 A singing male humpback whale, Maui, Hawaii. Many humpback whale populations have recovered from commercial whaling and some populations are increasing at maximal rates of about 7% per year (Calambokidis et al. 2008; Calambokidis and Barlow 2020). Humpback whale songs are once again reverberating through the ocean soundscape on traditional mating grounds and migratory routes where males sing complex, evolving songs (Darling et al. 2019). While their function and relationship to other aspects of male reproductive behavior remain largely unknown, songs indicate some degree of association between individuals and are generally thought to play a role in breeding (Darling et al. 2019). As human activities in the oceans increase, ambient noise levels are rising too, with potential impacts on communication space for humpback whale song. Photo: ©Flip Nicklin/Minden Pictures (NOAA Fisheries permit #19225); 2020.

Many approaches to the management of human-caused mortality involve calculation of reference points, which are considered "best practice" for managing bycatch and other human-induced mortality (Wade et al. 2021). The "potential biological removal" (PBR) level is one specific reference point used in the United States to meet the objectives of the Marine Mammal Protection Act (Wade 1998). PBR input values are designed to account for population differences in reproduction (see Box 24.1), which theoretically allows for the PBR approach to accommodate cases where a population's reproductive rate has been decreased by sublethal human-caused factors.

Our specific objectives are to (1) define resilience in the context of cetacean reproductive health and conservation, (2) review progress on understanding the social conditions necessary for maximizing cetacean reproductive success, (3) summarize the accumulating evidence showing that aspects of cetacean "reproductive health" (fecundity, mating, survival of young) can be impacted by human activities, and (4) suggest ways of using knowledge about cetacean reproductive health to improve management models and strengthen conservation actions and outcomes.

24.2 Resilience

Wade et al. (2012) defined resilience as the ability of a cetacean population to recover from extreme depletion (very low numbers), the condition that some of the large baleen whales had reached by the time commercial whaling was either brought under strict control or otherwise banned. Such use of the term comports with that of psychologists, who regard resilience as a construct with two distinct dimensions, namely, significant adversity (e.g., whaling) and positive adaptation (e.g., ability to recover) (Fleming and Ledogar 2008; see also Hodgson et al. 2015).

Wade et al. (2012) evaluated species or population differences in resilience to extreme depletion. Moore and Reeves (2018) applied the concept of resilience to the ability of cetaceans to adapt to the effects of climate change. Here, we extend this thinking to examine the resilience of cetaceans to disruption of, or damage to, their reproductive health and how behavioral and physiological plasticity, and sociality, may play a role in aspects of reproductive success. Reproductive health can be impaired by some of the same factors that determine an organism's survival (e.g., bycatch, ship strike, acute disease, toxicity), but there are several additional forms of "significant adversity" that affect reproduction itself (e.g., decreased fertility due to high pollutant burden, sublethal injury, or chronic disease, inadequate nutrition, social disruption). Although survival has generally been viewed as the most pertinent parameter for long-lived animals, it is likely that reproduction is just as (or even more) important and relevant in some cases (Manlik 2019).

24.3 The Social Context of Reproduction

Social living can enhance resilience in an increasingly human-dominated ocean (Brakes and Rendell 2022). Here we briefly review our understanding of sociality and its importance to cetacean reproductive health but also how it can increase vulnerability to disruption by human activities. Perrin et al. (1984) and numerous chapters in this book provide examples of how cetaceans may adapt their reproductive strategies depending on body condition, age, and dominance status (Chivers and Danil 2023, this book; Manitzas Hill et al. 2023, this book). Much has also been written about density-dependent changes in female reproduction following commercial exploitation or high levels of incidental mortality in fisheries (reviewed in Hohn et al. 2007). Density-compensatory changes in reproductive parameters, such as decreased age at sexual maturation and increased rates of ovulation and calving following intense harvest or fisheries bycatch, are generally attributed to changes in prey resources (Fowler 1981, 1984; Hohn et al. 2007). Less focus has been given to the impacts of sublethal anthropogenic impacts on reproductive rates, which may result in delayed age of first reproduction, longer interbirth intervals, and/or extended lactation (e.g., Cramer et al. 2008; Ward et al. 2009; McGuire et al. 2020; Stewart et al. 2022).

Despite the attention that social behavior garnered in the early years of conservation biology (Allee 1931; Ehrenfeld 1970) and recently renewed attention (Brakes et al. 2021; Brakes and Rendell 2022), consideration of animal sociality is complex and not easily integrated into conservation actions. Reduction of a local population to a very small size can exacerbate Allee effects ("undercrowding" or density-decompensation; reviewed in Stephens and Sutherland 1999) and even lead to population collapse (Gilpin and Soulé 1986). When population size is greatly reduced, individuals can have difficulty finding one another for mating (Gascoigne et al. 2009). Antoniou et al. (2018) suggested that a high observed incidence of introgressive hybridization in the Gulf of Corinth, Greece, between an extremely depleted, geographically isolated population of common dolphins (*Delphinus delphis*) and a less depleted and comparatively large local population of striped dolphins (*Stenella coeruleoalba*) was due to the scarcity of conspecific mates, a situation referred to as the Hubbs principle, also known as the "desperation hypothesis" (Hubbs 1955). For some species, returning regularly to a specific location could be a mechanism for ensuring that mates can be found. This may be the case for humpback whales (*Megaptera novaeangliae*), which congregate around tropical and sub-tropical islands in winter, although humpbacks may in fact mate during migration as well (Darling et al. 2019). Reductions to extremely low population sizes can also lead to inbreeding, which has been identified as a factor potentially impeding the recovery of one population of eastern North Pacific salmon-eating killer whales (*Orcinus orca*) (Lacy et al. 2017; Ford et al. 2018; Kardos et al. 2023).

Group living has numerous benefits (Gowans 2019). For mating and reproduction, these include the ease of finding and assessing a suitable mate, such as in dusky dolphins (*Lagenorhynchus obscurus*) that engage in scramble competition (Orbach et al. 2014) and in Amazon river dolphins (*Inia geoffrensis*) that gather in lek-like aggregations (Martin et al. 2008; da Silva and Spinelli 2023, this book). The formation of dominance hierarchies among males presumably confers preferential access to mates and enables females to mate with fit and dominant males (e.g., beaked whales, Alves et al. 2023, this book; narwhals (*Monodon monoceros*), Graham et al. 2020; Fig. 24.3). Alliance formation, such as in male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), provides advantages over rivals and facilitates control of females (Connor 2007), and male "squads" of offshore pantropical spotted dolphins (*Stenella attenuata attenuata*) may play a role in social ordering and reproduction (Pryor and Shallenberger 1991; Mesnick et al. 2019; Fig. 24.4). Communal calf care and defense against predators are some of the many benefits females may derive from group living; these groups may be temporary or long-lasting associations (Wells 2003; Whitehead 2003; Konrad 2019; Mesnick et al. 2019).

When sociality is disrupted, mating, fecundity, and the ability to raise young can be compromised. Populations of highly social species may take longer than expected to recover from depletion if individuals that enhance reproductive success, such as dominant males and female matriarchs, have been lost. Some populations of sperm whales, for example, have not recovered since the end of commercial whaling, perhaps due to the lingering demographic effects of the removal of large males on

Fig. 24.3 "Tusking" male narwhals, Baffin Island, Nunavut, Canada (1985). The tusk of the narwhal, which is actually a greatly enlarged left-spiraling upper left tooth, usually erupts only in males and can exceed 3 m in length. The tusk likely functions as a signal and a weapon during aggressive disputes between rivals (Graham et al. 2020). Narwhals are hunted for their tusks, which are in demand from distant markets, and for their skin which is valued by Inuit as a nutritious delicacy (Heide-Jørgensen 2018). Some populations are still overexploited even though quotas are now established for nearly all areas where narwhals are hunted. A host of other threats are increasing. Noise from vessel traffic, seismic surveys, ice-breaking, fishing, and other sound sources may disturb and stress the whales and decrease their fecundity (NAMMCO 2021). Photo: ©Flip Nicklin/Minden Pictures. All rights reserved

reproduction, while other populations face present-day threats to female social cohesion and pregnancy rates (Whitehead et al. 1997; Gero and Whitehead 2016; Whitehead and Shin 2022). In the eastern tropical Pacific, repeated chase, encircle-ment, and release of dolphins in the tuna purse seine fishery can cause separation of mothers and calves and decrease weaning and pregnancy rates (Archer et al. 2004) and have negative effects on female reproductive rates (Cramer et al. 2008, Kellar et al. 2013). In one of the populations impacted by the fishery, eastern spinner dolphins (*Stenella longirostris orientalis*), only a tiny fraction of males examined reached fully active testes weights and were thus likely capable of successful mating, a situation that suggests a polygynous mating system that could be susceptible to perturbation by the fishery (Perrin and Mesnick 2003).

Although the degree to which mating and rearing strategies in cetaceans are socially learned is unknown, there are hints that some aspects are socially transmit-ted, such as the socio-sexual "dances" within the lek-like aggregations of Amazon river dolphins, where males wave objects in the air, possibly to attract or impress females (Martin et al. 2008; Fig. 24.5). Baleen whales are dispersed over vast areas, which could make locating a suitable mate challenging. Social learning of the timing

Fig. 24.4 Adult male subgroup of offshore pantropical spotted dolphins in the eastern tropical Pacific Ocean. An individual from another adult male subgroup rising from below gapes his jaws in an apparent threat gesture at the group passing over him. Dominant adult male "squads," all with prominent post-anal keels, heavily spotted bodies, and striking facial coloration, swim in precision while other individuals move aside. We know little about the function of these squads, but observations suggest they have a role in social ordering and reproduction (Pryor and Shallenberger 1991). Chase, encirclement, and release from tuna purse seines likely disrupts these and other subgroups in the (Wade et al. 2012; Mesnick et al. 2019). Photo: Karen Pryor; 1979

and routes of migration between feeding and breeding habitat (Carroll et al. 2015), as well as horizontally transmitted song patterns (Garland and Carroll 2022), may have evolved in part to ameliorate the problems associated with long-distance dispersal, although the role of song in male-male interactions, mate selection, and assortative grouping remains enigmatic (Darling et al. 2019; Garland and McGregor 2020; Fig. 24.2). Remarkably, male humpbacks in a population sing fundamentally the same song at any one time, and the song progressively evolves over the course of a season, and over years (Darling et al. 2019). How this is accomplished is not clear, but apparently it involves mutual melding or adoption, which are forms of cultural transmission (Noad 2011; Darling et al. 2019). Similar mechanisms of vocal learning may occur in blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (McDonald et al. 2006; Archer et al. 2020), in which males typically sing the same song within a region, and in other baleen whale species that sing (Cerchio 2022; Risch 2022), although there is variation in the degree of social conformity and individual innovation among species (Stafford 2022). The importance of social learning is also evident in the evolution of post-reproductive lifespans in killer

Fig. 24.5 Displaying Amazon river dolphin or boto. Surrounded by other adult males and females, an adult male boto waves vegetation, or sometimes a lump of clay, above the surface of the water in a ritualized "dance", which has been interpreted as being part of a socio-sexual display within a lek-like mating system (Martin et al. 2008; da Silva and Spinella 2023, this book). In the folklore and culture of some Amazonian people, botos were feared and accorded supernatural powers and, as a result, were rarely hunted. Today, however, botos face many threats, including bycatch in fishing gear, directed hunts, and hydroelectric dams that fragment populations and increase the risk of local extirpations (da Silva et al. 2023). A reduction in the number of individuals in the population could impact the frequency and social context of display. Photo: Projeto Boto, Mamirauá Sustainable Development Reserve, Amazonas, Brazil

whales and short-finned pilot whales (*Globicephala macrorhynchus*) (Croft et al. 2015). The fitness benefits are revealed by higher offspring survival rates when post-reproductive mothers or grandmothers are still alive (Nattrass et al. 2019). In killer whales, socially inherited ecological niches and cultural traditions can influence mating patterns, which in turn can drive evolutionary divergence of ecotypes (Riesch et al. 2012; Foote et al. 2016; Ford 2019).

The costs of disrupting the transmission of socially learned behavior associated with reproduction can have both short-term and lasting consequences. For example, anthropogenic noise can decrease communication space and mask male song for baleen whales (Clark et al. 2009) or displace singers (Cerchio et al. 2014), while the loss of older individuals with knowledge of traditional feeding and breeding grounds and migratory routes could explain why some formerly important habitat of sperm whales and right whales remains deserted despite the cessation of commercial whaling (Kraus and Rolland 2009; Whitehead 2010).

As climate anomalies such as marine heatwaves become more common, our understanding of how such events affect cetacean reproductive health needs to keep pace. In some cases, social learning can provide opportunities for increased ecological resilience, by providing a behavioral buffer to ecological change (Brakes and Rendell 2022). This is evident when looking at socially transmitted foraging strategies, which ultimately translate to individual fitness and reproductive potential. For example, in Indo-Pacific bottlenose dolphins in Western Australia, diverse foraging strategies for some social groups appeared to buffer against the cascading effects of a marine heatwave on the food web (Wild et al. 2019).

24.4 Human Activities and Their Impact on Cetacean Sociality and Reproduction

It is difficult to identify and quantify all the ways by which human activities disrupt cetacean reproductive health. One major mechanism is by killing or otherwise removing animals from the population, which means that key individuals disappear suddenly; any social structure that exists, in terms of group size or composition, is changed abruptly (Williams and Lusseau 2006). Sublethal impacts are more difficult to identify and subtle in their effects on fecundity, behavior, and sociality. Human activities can cause, either directly or indirectly, the fragmentation of social groups, disruption of social behavior, and the loss of key individuals (Lusseau and Newman 2004; Williams and Lusseau 2006; Wade et al. 2012). The effects on reproductive health can be long-lasting, nonlinear, and unpredictable (Wade et al. 2012).

Table 24.1 summarizes some examples of how human activities disrupt aspects of cetacean reproductive health. Disruptive processes rarely take place in isolation. For example, in the eastern North Pacific, the multiplicity of anthropogenic impacts (e.g., Chinook salmon (*Oncorhynchus tshawytscha*) depletion, high levels of contaminants, vessel noise and disturbance, history of live-capture removals) and intrinsic processes (e.g., inbreeding, cultural isolation) confound efforts to understand the root causes of one salmon-eating killer whale population's failure to recover (Lacy et al. 2017; Murray et al. 2021; Kardos et al. 2023). The following case studies illustrate the cumulative impacts of multiple disruptive processes affecting two endangered cetacean populations.

24.4.1 Beluga Whales

Beluga whales in Cook Inlet, Alaska, USA, comprise a small, genetically distinct (O'Corry-Crowe et al. 1997) and geographically isolated population with year-round site fidelity to the inlet (Laidre et al. 2000; Fig. 24.6). The population declined dramatically in the 1990s, primarily due to overhunting (Mahoney and Shelden

Table 24.1 Evidence demonstrating or suggesting human impacts on cetacean reproductive health, some examples

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Whaling				
Insemination	Sperm whales, eastern tropical Pacific	Whaling (selective removal of large males)	Whalers almost eliminated large breeding males from the entire region, reducing pregnancy rates for many years; population decline, together with low calf counts and few large males off the Galapagos Islands, Ecuador, in the years following the end of whaling indicate the scale—around 5% per year—and duration—perhaps 15 years—of such effects	Whitehead et al. (1997); Whitehead and Shin (2022)
Pregnancy rate, calf production	Narwhals, East Greenland, Scoresby Sound region population(s)	Hunting (selective removal of young females)	Decline in observations of fetuses reported by hunters; decline in calves observed in aerial surveys; disproportionate hunt of young females has led to fewer and older females in the population (older females that may tend to have a lower average pregnancy rate)	NAMMCO (2021)
Fishing				
Pregnancy rate	Offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Pregnant females were exposed to significantly less fishery activity than non-pregnant ones, suggesting that the fishery may have an inhibitive effect on pregnancy	Kellar et al. (2013)

Table 24.1 (continued)

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Calf production, age of weaning	Eastern spinner and offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Decline in proportion of adult females with calves; for offshore pantropical spotted dolphins, number of sets on dolphins was a predictor of both proportion with calves and length of disassociation (proxy for age at weaning); decline in reproductive output may be the proximate cause, or one of the proximate causes, of the failure of dolphin populations to recover at rates expected after reduction of high bycatch levels	Cramer et al. (2008)
Mother-calf bond	Offshore pantropical spotted dolphins, eastern tropical Pacific	Tuna purse seining ("setting on" dolphins)	Physical separation of cow/calf pairs caused by chase and encirclement, leading to calf mortality	Archer et al. (2004)
Prey availability				
Fecundity (birth rate)	Killer whales, eastern north Pacific fish-eating populations	Combination of habitat alteration, fishing, and natural variability (likely influenced by climate change) affecting prey populations (particularly of Chinook salmon)	The probability of a female calving differed by 50% between years of low and high salmon abundance. In times of low prey abundance, increased search time and less social cohesion may also affect reproduction. Nutritional stress on females associated with poor body condition and unsuccessful pregnancies	Ward et al. (2009); Wasser et al. (2017); Fearnbach et al. (2018)

Pollutants

Fetus or neonate survival	Harbor porpoises, U.K.	Release of chemical compounds (organochlorines, mainly PCBs) into the environment	Resting mature females had significantly higher mean ∑PCBs than both lactating and pregnant females. Where data were available, these non-offloading [of PCBs] females were previously gravid, which suggests fetal or newborn mortality. Results suggest that reproductive failure could have occurred in up to 39% or more of mature females sampled	Murphy et al. (2015)
Neonate survival	Common bottlenose dolphins, southeastern U.S.	*Release of chemical compounds (organochlorines, mainly PCBs) into the environment*	Significantly higher mortality of calves born to primiparous females	Wells et al. (2005); Schwacke et al. (2002)
Testes weight	Harbor porpoise, U.K.	*Release of chemical compounds (organochlorines, mainly PCBs) into the environment*	Testes of adults in good nutritional condition were negatively associated with PCB concentrations; testes weight is a strong indicator of male fertility in seasonally breeding mammals	Williams et al. (2021)
Pregnancy rate	Common bottlenose dolphins, Gulf of Mexico	Petroleum exposure after *Deepwater Horizon* drilling rig explosion	Pregnant females were tracked for one year after the oil spill; the resulting estimated pregnancy rate was less than a third of those previously reported in unaffected areas (19.4% vs 64.7% respectively)	Kellar et al. (2017)

Table 24.1 (continued)

Aspect of reproductive health affected	Species/population and location	Human activity	Evidence	Reference(s)
Live-capture				
Reproductive potential	Killer whales, eastern North Pacific fish-eating populations	Selective removal ("cropping") of young females	Temporary skew in sex ratio and deficit of reproductively capable females	Olesiuk et al. (1990)
Noise				
Number of singers	Humpback whales, Angola	Noise from seismic survey activity	Number of singers significantly decreased with increasing received level of seismic survey pulses	Cerchio et al. (2014)
Climate anomalies/change				
Number of calves born	Indo-Pacific bottlenose dolphins, Shark Bay, Western Australia	Marine heatwave	Number of calves detected was significantly higher before the marine heatwave. Survival of "spongers" declined less (5.9%) compared with non-spongers (12.2%)	Wild et al. (2019)
Reproductive rates	Humpback whales, Hawaii	Marine heatwave	Reproductive rates declined by 76.5%, coincident with marine heatwave	Cartwright et al. (2019)

Fig. 24.6 Cook Inlet beluga whaless. Beluga whales are highly social animals. Shown here are an adult whale (white; front-most whale), two young adults or subadults (light gray), and a young calf (small, dark gray). Beluga whales are facultative induced ovulators and while mating is difficult to observe in the wild, courtship in captive settings apparently follows ritualized sequences and it is possible that male mating displays help to induce ovulation (Steinman et al. 2012; Richard et al. 2021). Disturbance and disruption of beluga whale behavior and social structure may be a contributing factor to the lack of recovery by this and other beluga whale populations. Photo: NOAA Fisheries / Paul Wade (NOAA Fisheries permit #20465); August 2017

2000), and is classified as Critically Endangered on the IUCN (International Union for Conservation of Nature) Red List and as Endangered under the US Endangered Species Act (ESA). The population continued declining until about 2005 (when hunting stopped), increased somewhat until about 2010, began declining again, and reached its lowest point in 2018 (Wade et al. 2019).

Overhunting apparently caused all or most of the initial declines, but why has the population declined since 2010? Recent studies have shed light on what appear to be the proximal causes of the lack of recovery. First, age of first parturition (birth) appears to be substantially delayed in the Cook Inlet beluga whale population. In other beluga whale populations, age of sexual maturation in females occurs by age seven, with the age of first parturition occurring by age eight (e.g., Burns and Seaman 1986; Heide-Jørgensen and Teilmann 1994; Suydam 2009). In contrast, McGuire et al. (2020) found that the recent age of first parturition in Cook Inlet is considerably greater (at least 10 and probably as old as 13). Second, the birth rate also appears to be reduced. Suydam (2009) reported a birth rate of 0.41 in the eastern Chukchi Sea, where the calving interval was between two and three years. In contrast, mean fecundity in the Cook Inlet population for the period 2005–2017

was estimated to be 0.27, which suggests a calving interval of about 4.6 years (Himes Boor et al. 2022; Warlick et al. 2022). Warlick et al. (2022) concluded that survival of breeding females and young calves is relatively high, but survival of nonbreeders (which includes juveniles) and fecundity may be depressed in the Cook Inlet beluga whale population.

Warlick et al. (2022) extended their analysis to examine annual changes in life history parameters. Fecundity had the strongest correlation with annual population rate of change, followed by adult survival. Among a wide range of environmental covariates, an index of prey biomass (including several species of salmon as well as eulachon (*Thaleichthys pacificus*)) was positively correlated with fecundity and older calf survival. Fecundity and older calf survival were also positively correlated with the returning run size of Chinook salmon in the Susitna River, an important foraging habitat for the Cook Inlet whales (Castellote et al. 2021). Most of the life history parameters were at their lowest value in 2011, at the start of the recent decline in beluga whale abundance, with 2011 and 2012 representing the two lowest years for fecundity.

In the Gulf of Alaska, salmon and forage fish production has been severely impacted by climate change. In Cook Inlet, adult returns of Chinook salmon were low from 2008 to 2012, with one study concluding that this was caused by adverse freshwater conditions the previous five years, including above-optimal spawning and rearing temperatures in the rivers (Jones et al. 2020). Following that, from 2014 to 2016, the eastern North Pacific experienced an extreme marine heat wave that caused declines in forage fish species in the northern Gulf of Alaska, restricting energy transfer to upper-trophic-level species and leading to large-scale mortality events and declines in abundance and breeding success of forage-fish-dependent salmon, groundfish, birds, and mammals (Arimitsu et al. 2021; Suryan et al. 2021). While more research is needed, it is possible that climate effects have contributed to the lack of recovery of the Cook Inlet beluga whale population, by decreasing their food supply and consequently causing declines in birth rates and other life history parameters.

Other factors could also be contributing to the lack of recovery. McGuire et al. (2020) noted that contamination by persistent organic pollutants or other contaminants might be affecting beluga whale reproduction. Another concern is congenital defects observed in some dead neonates (Burek-Huntington et al. 2022); although the cause is unknown, this could be reducing successful reproduction. Cumulative effects from disturbance by noise, vessel traffic, and other factors may also be playing a role (Castellote et al. 2018; McHuron et al. 2023). One possible mechanism is that human disturbance disrupts social behaviors that improve mating success, because beluga whales are facultative induced ovulators (Steinman et al. 2012). A recent aquarium study monitoring hormone levels and behavior showed that hormone levels in a captive female rose only after two males had initiated reproductive displays for three weeks, with ovulation following several weeks later (Richard et al. 2021). Breeding beluga whales in most North American aquaria has

Fig. 24.7 Snow Cone with her newborn calf near Cumberland Island, Georgia. The energy deficit caused by sublethal entanglements in fishing gear, as seen in this photo, and likely other factors are stunting the growth of North Atlantic right whales (Stewart et al. 2021). Smaller mothers have longer inter-birth intervals and produce fewer calves per potential reproductive year, which contributes to the low birth rate of these endangered whales (Stewart et al. 2022; Moore 2023). Photo: Florida Fish and Wildlife Conservation Commission (NOAA Fisheries permit #20556); December 2021

been difficult (Steinman et al. 2012); an exception is a facility that had 54 beluga whales in in two pools,[1] which may have allowed for more social interactions. Given that beluga whale courtship appears relatively complex (Hill et al. 2021), these whales may need relatively undisturbed areas for successful mating to occur.

24.4.2 North Atlantic Right Whales

Physical injury to and mortality of North Atlantic right whales (*Eubalaena glacialis*), caused almost entirely by entanglements in fishing gear and ship strikes, have been the focus of conservation efforts in recent decades, but the potentially related problem of poor reproduction is also of great concern (Corkeron et al. 2018; Moore 2023; Fig. 24.7). As noted by Moore (2023), a management strategy focused solely on minimizing right whale mortality, with inadequate attention paid to

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[1] https://media.fisheries.noaa.gov/dam-migration/appendix_16_marineland_assurance.pdf.

reproductive health, is unlikely to be successful in the long term. The reproductive health challenges and other obstacles to recovery faced by North Atlantic right whales are in stark contrast to the situation of southern right whales (*Eubalaena australis*) in the Southern Hemisphere.

Even without the well-documented, recent changes in their phenology and distribution, North Atlantic right whales have for many decades shown signs of being less robust and less healthy than southern right whales (Christiansen et al. 2020). This includes their generally slimmer body profile that rarely exhibits the "fat roll" behind the blowholes—a striking feature of southern right whale morphology (Pettis et al. 2004). Reproduction rates and outcomes (e.g., ovulation, spermatogenesis, fetal development, calf survival) are heavily influenced by anthropogenic and natural environmental factors that control the quality and availability of food (Li Chen et al. 2009; Rolland et al. 2016; Corkeron et al. 2018). Those factors, in particular the availability of very dense aggregations of late-stage calanoid copepods, are increasingly affected by climate change (Fortune et al. 2013; Meyer-Gutbrod et al. 2021). Mother body condition has been linked to calf growth rate, and North Atlantic right whale calving rates are less than half those of southern right whales (Kraus and Hatch 2001; Christiansen et al. 2018, 2020). There is thus a large body of research showing that North Atlantic right whale reproduction has declined due to direct female mortality (Pace et al. 2017), gear entanglements (van der Hoop et al. 2017), and nutritional deficits from climate-related changes in prey quality and availability (Meyer-Gutbrod et al. 2015), but whether and how reproduction has also been impaired by factors related to sociality is uncertain.

Further compounding the factors affecting reproduction is the mating system itself. Right whales are renowned for phenomenally large testes relative to body size, and their mating system is one of the most compelling examples of sperm competition in mammals (Brownell and Ralls 1986). Parentage analysis, however, has found that older males have disproportionally more calves, with males not obtaining their first paternity until about 15 years of age —almost twice the average age of first fertilizations in females (Frasier et al. 2007). Male-male competition may be preventing young males from reproducing. The uneven distribution of paternities results in a lower effective population size in a species that already has one of the lowest reported levels of genetic diversity, which may further inhibit reproductive success (Frasier et al. 2007). The fact that females are declining at a faster rate than the overall population is further diminishing the effective population size (Reed et al. 2022).

It is unknown whether "surface active groups" of right whales (Kraus and Hatch 2001; Brown and Sironi 2023, this book) vary in size, composition, and/or male "quality" between North Atlantic and southern right whales. However, given the drastically different population sizes, plus the fact that participating in surface active groups must be energetically costly, it is possible that certain behavioral or social aspects conducive to successful copulation have been compromised or lost along the way in North Atlantic right whales. This could make them less capable of recovering when compared to some other baleen whales, including southern right whales. Even if a North Atlantic right whale conceives and gives birth to a calf, the inadequacy of

socially transmitted knowledge could be hindering long-term calf survival. As explained by Brown and Sironi (2023, this book), southern right whale calves (and almost certainly calves of other right whale species) learn from their mothers where and when good food can be found. This culturally transmitted knowledge may serve a calf well in its first migration but could limit the extent to which young whales are inclined (or able) to search for new feeding areas and opportunities in the face of declining prey. For North Atlantic right whales, loss of knowledge may explain the fact that large expanses of their historical range (including southern Greenland, Iceland, and much of Western Europe) have not been reoccupied after more than a century of nearly complete protection from whaling (Kraus and Rolland 2009; Mellinger et al. 2011).

24.5 Integrating Cetacean Reproductive Health into Conservation Actions

As threats to cetaceans change, so must our conservation and management approaches (Jefferson 2019). Population dynamics models, such as population viability analysis (PVA), are being used to investigate cumulative human impacts on cetacean population growth, stability, and resilience (Lacy et al. 2017; Murray et al. 2021). More attention is being paid to understanding, linking, and tracking the consequences of short- and long-term behavioral disturbances from noise and other human activities to changes in cetacean health (body condition), reproductive rates, and population dynamics by evaluating mechanistic transfer functions (National Research Council 2005; Pirotta et al. 2018; Pirotta et al. 2019; McHuron et al. 2021, 2023). Knowledge gaps in understanding the reproductive biology and behavior of endangered species are being addressed by leveraging insights grained from more abundant species in managed care facilities (e.g., Integrated Conservation Planning for Cetaceans[2]). New efforts are being made to determine how sociality and culture structure populations. For example, clan-level differences in foraging strategies of eastern tropical Pacific sperm whales have resulted in signatories to the Convention on the Conservation of Migratory Species of Wild Animals committing to a "concerted action" to seek improved understanding of how social learning creates cultural structuring relevant to conservation (Brakes et al. 2019). A variety of tools and lines of evidence are being applied to identify population units in need of conservation ("units to conserve") and specify the threats they face (e.g., IUCN Red List, US Endangered Species Act, US Marine Mammal Protection Act). Geographical differences in behavior conducive to constrictions in gene flow (female site fidelity, mating system, acoustics, dietary specializations) may be used as possible "lines of evidence" for delimiting cetacean subspecies (Taylor et al. 2017) and male song in blue whales and fin whales is being used to characterize population

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[2] https://iucn-csg.org/integrated-conservation-planning-for-cetaceans-icpc/.

differences (McDonald et al. 2006; Delarue et al. 2009; Archer et al. 2020). In addition to these important approaches, we highlight four specific ways to improve conservation outcomes by explicit consideration of cetacean reproductive health: monitoring, modeling, mapping, and data sharing.

24.5.1 Programs and Tools to Monitor Reproductive Health

Foundational to all conservation efforts are effective population assessment and monitoring programs. Most rely on abundance estimation at frequent intervals. Augmenting this, when possible, by tracking calf numbers—temporally (within an impacted population over time) or geographically (comparing impacted populations vs. non-impacted populations)—can give an early indication of whether and how reproduction is being compromised. Today, innovative field technologies and laboratory approaches provide unparalleled access to information on reproductive health (Nowacek et al. 2016; Ramos et al. 2023, this book). Non-invasive techniques, such as aerial photogrammetry, have been used to track body condition of known individuals, which is linked with reproductive output in eastern North Pacific killer whales and North Atlantic right whales (Fearnbach et al. 2018; Stewart et al. 2022). Fecal steroid hormone assays from samples collected with the assistance of feces-sniffing dogs have been used to determine occurrence, stage and health of pregnancy in females, and the onset of sexual maturation and reproductive seasonality in males (Rolland et al. 2007; Wasser et al. 2017). Endocrine evaluations of biopsies from free- ranging cetaceans have been used to show high pregnancy rates consistent with population recovery in Australian humpback whales (Pallin et al. 2018) and to assess reproductive health in bottlenose dolphin stocks in the Gulf of Mexico following the Deepwater Horizon oil spill (Kellar et al. 2017). In addition to monitoring live animals, studying dead ones via stranding and carcass collection programs can provide critical information on sexual maturity and fertility.

24.5.2 Approaches for Explicitly Incorporating Reproductive Health into Conservation Reference Points

Box 24.1: Assessing Human Impacts: The PBR Example
The "potential biological removal" (PBR) level is a specific reference point developed and applied in the United States to meet the objectives of the US Marine Mammal Protection Act (US MMPA) (Wade 1998). PBR is calculated as the product of three values: (1) N_{min} (an estimate of population size that

Box 24.1 (continued)

provides reasonable assurance that the population size is greater than that level), (2) 1/2 R_{max} (where R_{max} is the maximum annual per capita rate of increase in a population resulting from additions due to reproduction, less losses due to natural mortality), and (3) F_r, a recovery factor set between a value of 0.1 and 1.0; thus, PBR = N_{min} * $0.5R_{max}$ * F_r. The concept of R_{max} implicitly includes values of quantifiable population parameters, such as birth rates, survival rates, and the age of sexual maturity. In other words, it is designed to account, at least implicitly, for species and even population differences in reproductive potential and also outcomes. Where data are limited, the United States relies on default values for R_{max} according to taxonomic group (e.g., cetaceans vs. pinnipeds, NMFS 2023), but case-specific adjustments are allowed for populations for which R_{max} is known or suspected to be higher or lower than the default value. This allows, at least theoretically, for the PBR approach to accommodate cases where a population's reproductive rate has been suppressed by human-caused factors, by lowering the value of R_{max}.

Exploring fecundity and birth rates across species and populations may highlight ongoing changes and impacts that require adjustments to the way conservation management reference points are designed or applied. Not only are threats to cetaceans changing, but such changes may also affect individuals of different sex, age, or stage classes differently. So as threats change, so too must management models. Where a decrease in a population's birth rate can be measured, this can be relatively easily accounted for in the PBR equation (see Box 24.1). However, it is often the case that human-caused reductions in birth rate are suspected but not known or known but not quantified. To investigate this (and other considerations), Punt et al. (2021) evaluated how robust the PBR framework is to the sublethal effects of entanglements in fishing gear and the mainly sublethal (but sometimes lethal) effects of noise from human activities. Modeled sublethal effects had relatively small impacts on recovery probability as long as the recovery factor (F_r) was set to 0.5; if F_r was set to 1.0, sublethal effects could prevent a population from recovering. This emphasizes the need for conservative (i.e., precautionary or risk-averse) management approaches when sublethal effects are known or suspected.

Another consideration is that of age or sex selectivity of human-caused mortality. This follows from the concept of reproductive value in population dynamics, where reproductive value is defined as a female's expected reproductive output over her remaining lifetime. The reproductive value changes substantially with age, with newborn females having a low reproductive value (because they have to survive until the age of first reproduction) and females that have just reached the age of first reproduction having the highest reproductive value. Brandon et al. (2017) tested

whether the PBR framework was robust to age- and sex-selective mortality. They found that if human-caused mortality consists predominantly of young animals or of males, PBR is likely more precautionary than necessary to achieve the conservation goal. Conversely, PBR may not be sufficiently precautionary if human-caused mortality consists predominantly of mature females. The same might occur if human-caused mortality consists largely of dominant males or males with high reproductive output, but this has not been examined.

The US guidelines allow for adjustment of the PBR calculation if human-caused mortality consists primarily of females (National Marine Fisheries Service 2023). This issue becomes more important for species with more extreme life histories, with a long delay until age of first reproduction. Curtis and Moore (2013) provided a framework for calculating reference points for mortality of sea turtles, where age selectivity can be extremely important. A similar approach might be necessary for long-lived cetaceans, if their human-caused mortality is particularly sex- or age-skewed.

Population models generally assume that individuals are interchangeable (i.e., one individual is equivalent to any other) even if age and sex are explicitly modeled in some manner. In highly social species, the removal of certain key individuals such as matriarchs in elephant (*Loxodonta africana*) herds and dominant males in Soay (*Ovis aries*) and bighorn (*Ovis canadensis*) sheep and African elephants can affect reproduction and survival well beyond the expected effect of the removal of a single individual (Wade et al. 2012). This has not been addressed adequately in management models, such as PBR, but could be addressed through individual-based models that recognize the effects of removing matriarchs or other particularly important individuals.

24.5.3 Identifying and Mapping Geographic Areas Important to Cetacean Reproductive Health

Protecting habitat essential for cetacean reproduction is challenging, as these locations may be unknown or span wide areas of ocean. Among the available mechanisms for identifying and describing areas that are important for mating, birthing, and nurturing young are Important Marine Mammal Areas (IMMAs)[3] (Tetley et al. 2022) and Biologically Important Areas (BIA's)[4] (Ferguson et al. 2015). Spatially explicit tools are a promising way of implementing successful marine mammal conservation with substantial benefit to associated biodiversity conservation (Hoyt 2022). In addition, there are benefits to incorporating social dyanamics in spatial management (Smith et al. 2016) and to clearly mapping relationships between prey and cetacean fecundity, as evidence has shown that nutrition affects all aspects of

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[3] https://www.marinemammalhabitat.org/.

[4] https://www.dcceew.gov.au/environment/marine/marine-species/bias.

reproduction (e.g., Meyer-Gutbrod et al. 2015; IJsseldijk et al. 2021). When prey preferences are tied to social or cultural group membership, nutritional issues can be exacerbated. Eastern North Pacific salmon-eating killer whales are an exemplar: their culturally inherited and rigid preference for endangered Chinook salmon has been linked to an extremely high failed pregnancy rate (almost 70%) in one population (Wasser et al. 2017). In eastern tropical Pacific sperm whales, clan-specific foraging variation results in clans faring differently during times of environmental change, such as El Niño Southern Oscillation events (Whitehead and Rendell 2004). Whether variation in foraging success during such events is due to the availability of preferred prey or to some other factor remains unknown, but clans with more foraging success may also experience greater reproductive success (Cantor and Whitehead 2015).

24.5.4 Crosstalk, Data Sharing, and Collaboration Across Geographic Boundaries

Many cetacean species are highly mobile and frequently move across arbitrary national or other jurisdictional boundaries. Even within a single species, we find variation in residency and ranging patterns (e.g., sperm whales, Vachon et al. 2022; killer whales, Ford 2019; common bottlenose dolphins (*Tursiops truncatus*), Oudejans et al. 2015). Yet, researchers in different regions of the world often have vastly different levels of access to resources (financial, technical, etc.), which can result in a patchy understanding of a species throughout its full range. As a first step toward ameliorating this inequity, researchers can make processed data, analytical tools, and pipelines open access (e.g., GitHub). There is ample evidence to demonstrate that open-access data and resources (such as this book) improve science (Munafò et al. 2017; Popkin 2019; Gomes et al. 2022), as well as obvious benefits such as encouraging comparability, trust, collaboration, and transparency among researchers. The wide sharing of data, tools, and knowledge will afford us a more complete understanding of behavior, including reproductive behavior, throughout a species' range.

24.6 Summary

Cetacean conservation will benefit from efforts to preserve, or reestablish, the environmental, demographic, and social conditions that enable animals to reproduce successfully in their natural environment. The better we understand and integrate knowledge concerning cetacean reproductive health into conservation strategies, the better our chances of achieving species recovery, protecting biodiversity, and preventing future extinctions. As summarized whimsically by Marah Hardt (2016),

but with much relevance and as a fitting end for this book, to conserve cetacean sex and reproductive strategies, we need to:

- Give them privacy so they can court without disturbance.
- Give them enough food so they have time for sex and are in good condition.
- Keep it quiet so they can hear each other's songs.
- Keep it clean so that pollutants do not impact their sex drive.
- Stop killing them, directly or incidentally, so key individuals are present and groups remain intact.
- Keep it safe—without hunting, chasing or otherwise stressing them—so they can pursue each other.
- Maintain the climate for sex so that we can slow, stop, or reverse the dire warming scenarios and give the oceans, and the biodiversity they support, a chance.

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