# The Behavioural Biology of Zoo Animals

**Edited by Paul Rose**

# Chapter 3

## Behavioural biology, conservation genomics, and population viability (Open Access)

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# 3

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## 3.1 WHY CONSIDER POPULATION VIABILITY IN A BEHAVIOURAL BIOLOGY TEXTBOOK?

A better question might be: "what is the aim of conservation biology?" We can consider the central purpose of conservation efforts to be the maintenance of the evolutionary potential of species and ecosystems. Evolutionary potential is being able to continue evolving, to be viable and to be sustainable. This important concept was highlighted in a landmark work by Sir Otto Frankel in which he argued that protecting the ability of populations to continue to adapt to future challenges should be the key objective for conservationists (Frankel, 1974). This fundamental idea applies to populations both inside and outside of captivity. DNA is the principal molecular mechanism by which information is inherited over generations and we can think of it as a vessel of this evolutionary potential. Inevitably

then, we must consider the genetic diversity carried within the genomes of captive populations if we are to fully realise the benefits, and mitigate the risks, of captive breeding as a conservation tool to maintain evolutionary potential. Indeed, genetic diversity has long been identified as one of the IUCN's three core global conservation priorities along with species and ecosystem diversity (McNeely, Miller, Reid, Mittermeier, & Werner, 1990). In this introductory chapter, it is not possible to provide an exhaustive coverage of conservation genomics, nor is that appropriate. There are excellent texts that delve into this vast subject in the detail and depth it requires (e.g., Allendorf et al., 2021). Instead, the aim here is to discuss some of the broad concepts to provide evolutionary context when considering the management of behavioural biology in zoo populations. Previous chapters have outlined the many ways in which zoo practitioners can and must use evolutionary ecology to better understand the

behaviours of species in their care, and how collection planning can and should accommodate them to maximise conservation outcomes. Here, we start to think about the implications of these topics on an evolutionary scale; about the impact of captive management on species at the genetic level, and the considerations needed in managing species for evolutionary potential.

A logical place to start is by considering the phenotypic traits of species in our care. All traits are the result of complex interactions between heritable factors, such as DNA or epigenetics (biochemical modifications that change gene expression without altering DNA), and environmental factors (Bošković & Rando, 2018; Falconer & Mackay, 1996). Therefore, even behaviours observed in our captive populations are under at least some degree of genetic or epigenetic influence. For example, meerkats (*Suricata suricatta*) exhibit intergenerational transmission of hormone-mediated aggressive behaviours that maintain their despotic cooperative breeding system (Drea et al., 2021). However, for most organisms, the genetic and epigenetic basis for behaviour is not well understood (Plomin, DeFries, & McClearn, 2008). This is largely because most phenotypic traits are the product of complex networks of genes and gene regulators that interact with each other and numerous environmental influences to varying degrees in space and in time (Falconer & Mackay, 1996). Identifying specific trait-associated genes and their effects on traits such as behaviours or disease risk is therefore challenging. Despite this, investigation of complex genetic traits can provide very valuable opportunities for conservation action. The plight of the Tasmanian devil (*Sarcophilus harrisii*) is an excellent example. Devil populations have faced catastrophic decline due to a highly fatal facial tumour disease that spreads through the direct aggressive behaviour of conspecifics. Significant research effort to uncover the evolutionary genomics of this transmissible cancer in both wild and captive populations has provided vital insight into susceptibility, resistance, and genetic rescue opportunities. These data have directly informed conservation action plans for the species (Hamede et al., 2021). However, the resources available for conservation are often very limited and we must also understand the general evolutionary principles of captive population management, to derive maximum benefit. We can, in part, achieve this by considering genome diversity and the factors that influence it at population and species levels.

## 3.2 UNDERSTANDING THE IMPACTS OF CAPTIVITY ON GENOMIC DIVERSITY

A core aim of captive breeding is keeping populations as evolutionarily close to their wild counterparts as possible. This is easier said than done. Captive populations are often held at sizes far smaller than would be observed in the wild, and therefore their response to evolutionary forces is much different, making the task of managing their diversity complex. One such force, genetic drift, is the stochastic change in allele (gene variant) frequencies between generations due to random sampling of gametes and the fact all populations are finite in size. As alleles can be randomly fixed (present at that genetic locus in all individuals) or lost completely from a population, drift erodes diversity over time. Drift is so influential in the evolutionary trajectory of populations that effective population size (Section 3.3) was developed to more accurately describe populations genetically (Wright, 1931) and is a core parameter in conservation biology. In the face of such stochasticity, the initial diversity of a captive population is very important. However, many captive populations experience founder effects, a type of genetic drift caused by using few individuals (founders) to establish a new population from an established larger population. This can lead to both genotypic and phenotypic differences in the subsequent population and loss of genomic diversity (Mayr, 1999). Captive populations may have also experienced population bottlenecks, perhaps from threats in the wild, again leading to the loss of genomic diversity. As heterozygosity (see Section 3.3) of loci across the genome decreases, populations can lose heterozygote advantage, the fitness benefit of possessing diversity at particular genomic loci (Charlesworth & Willis, 2009). Further to this, the probability of inheriting related (identical by descent) copies of an allele from both parents increases. This is more commonly known as inbreeding. The smaller the population, the greater the likelihood of related alleles meeting in an individual and, without intervention small, isolated populations will become increasingly inbred over time. Inbreeding can result in inbreeding depression, the reduction in

the fitness of inbred individuals. It is predominantly caused by the expression of deleterious mutations (Charlesworth & Willis, 2009) and is detrimental to population viability through impacts such as reduced offspring survival or increased disease susceptibility. Captive populations have played an important role in understanding the impacts of inbreeding depression, including both opportunistic observations of zoo populations (e.g., Ballou & Ralls, 1982) and experimental studies (e.g., Lacy, Alaks, & Walsh, 2013). Mitigating effects associated with small population size form the basis of much of captive population genetic management.

Captive populations are also subject to the effects of natural selection. Adaptation to captivity, where populations evolve in response to selection pressures of the captive environment, is well documented in zoo populations (Frankham, 2008). The fitness of individuals in captivity improves as the population adapts, but this is at an overwhelming detriment to fitness in the wild. Adaptation to captivity impacts many diverse physiological and behavioural traits in different species (Frankham, 2008). A study in white-footed mice (*Peromyscus leucopus*) demonstrated rapid adaptation in behavioural and reproductive phenotypes of the mice under different experimental management regimes. Interestingly, it showed evidence of evolution even in management regimes intended to minimise adaptation to captivity and the impacts of drift (Lacy et al., 2013). We can also learn much about adaptation to captivity by studying domestication. Perhaps the most famous domestication experiment has been conducted with foxes (*Vulpes vulpes*). Beginning in the 1950s, foxes were subjected to selection solely for tameness, but developed many other traits also associated with domestic dogs (*Canis lupus familiaris*) including floppy ears, tail-wagging, and coat colour variation. The work importantly demonstrated that the behavioural traits of tameness were genetically linked to many other phenotypes known as 'domestication syndrome' and suggests that wholescale evolutionary changes in the regulatory networks of gene expression must have occurred (Trut, Oskina, & Kharlamova, 2009). This example demonstrates some impacts of extreme selection pressure, but the magnitude of selection differences between captivity and the wild is not the only consideration. How long populations are subject to selection differences is also important. In steelhead

trout (*Oncorhynchus mykiss*), inherited differences in gene expression across hundreds of genes were discovered after just a single generation in captivity (Christie, Marine, Fox, French, & Blouin, 2016). This demonstrates that captive breeding can lead to detectable population changes incredibly quickly.

So, with evolutionary changes poised to rapidly alter captive populations, are they all doomed to fail? It is important to consider that the relationship between diversity and sustainability is not straightforward (Estoup et al., 2016; Frankham, Ballou, & Briscoe, 2002; Mable, 2019). Some species seem to persist with relatively low diversity, such as the Mauritius kestrel (*Falco punctatus*) whose population successfully recovered from just a single breeding pair (Groombridge, Jones, Bruford, & Nichols, 2000). Others, like the cane toad (*Rhinella marina*), can even become hugely successful invasive species despite reduced diversity (Selechnik et al., 2019). Entire evolutionary lineages appear to maintain long-term viability with generally low genomic diversity, such as the rhinoceros (*Rhinocerotidae*) family (Liu et al., 2021). Whilst our understanding of how such cases occur is still developing, they emphasise the importance of considering the evolutionary ecology of the species we manage and provide some welcome optimism for the future of endangered species harbouring low genomic diversity. Encouragingly, populations reintroduced to the wild can also recover fitness, provided they have at least the minimum remaining fitness to successfully establish in the wild and sufficient remaining diversity for wild selection pressures to act upon (Frankham, 2008). However, maintaining existing genomic diversity and fitness remains a core objective for conservationists, as this will generally provide species with the best possible chances of achieving long-term viability.

## 3.3 METRICS OF VIABILITY IN CAPTIVE POPULATIONS

We know that genomic diversity is important for the evolutionary potential of captive populations, but how do we quantify it and decide what is enough to be viable? As science and technology have progressed, many different metrics have been developed to aid captive species management. The thresholding and quantification of diversity has improved as evidence has accrued from an increasing number of species, management plans,

and conservation histories. Examples of some key metrics that are widely utilised and encountered in management plans include:

- Effective population size ($N_e$): the size of an idealised model population that experiences the same amount of drift, or exhibits the same mean inbreeding rate, as the actual census population size ($N_c$) in question. $N_e$ is usually much smaller than $N_c$.
- Gene diversity (expected heterozygosity, $H_E$): the probability that two alleles of a locus randomly sampled from a population do not share a common ancestor, assuming random mating and Hardy-Weinberg equilibrium (a testable model of allele frequency behaviour).
- Founder genome equivalent (FGEs): how many founders (i.e., wild individuals) would equal the same amount of gene diversity as exists in the living captive population.
- Inbreeding coefficient (F): the probability that two alleles at a locus in an individual share a common ancestor (identical by descent).
- Kinship coefficient (K): the probability that an allele in a locus in individual 1 is identical by descent to an allele randomly sampled in that same locus in individual 2.

Metrics like these are often assessed together to create a snapshot of the genetic state of a population. Tools specifically designed for aiding zoo biologists leverage these metrics to manage populations and studbooks are available, including the well-established PMx (Lacy, Ballou, & Pollak, 2012). How best to manage existing diversity in a population will depend on a range of factors such as whether a pedigree exists and is reliable, the current diversity and demography of the population or metapopulation in both captivity and the wild, and predictions of how quickly the existing diversity is expected to be lost.

Best practice in addressing genetic and epigenetic impacts on captive populations has been the subject of decades of research and scientific debate (e.g., Frankham, 1995; Margan et al., 1998; Ralls et al., 2018). Since their development in the late 1980s, many conservation management plans have loosely followed the 'Ark Paradigm'; a benchmark of retaining 90% gene diversity for *ca.* 100–200 years, as a general guide (Seal, Foose, & Ellis, 1994; Soulé, Gilpin, Conway, & Foose, 1986). However, this may not be appropriate for species with long generation

times such as tortoises (Testudinidae) for example, where specifying a number of generations (e.g., 10) may be more biologically relevant. Of course, some captive populations may fall below these preferred diversity thresholds. In such cases, zoos will generally aim to mitigate further damage by implementing management actions aimed at slowing the rate in which the remaining diversity is lost. How much initial gene diversity there may be is dependent upon both the evolutionary history and conservation status of the population or species (Section 3.2). This highlights the importance of a taxon-specific approach to assessment and management and many species indeed benefit from species-specific management plans, actively curated by zoological collections. Global organisations such as the IUCN and governing bodies of zoos and aquaria publish and regularly update best practice guidelines for captive breeding programmes and genetic management in captivity. Additionally, experts in the field also produce comprehensive general management guidelines for small populations (e.g., Ballou et al., 2012). Collectively, this provides a wealth of continually evolving resources for promoting the evolutionary potential of captive populations whilst underlining the central role of evolutionary biology in furthering species conservation.

## 3.4 FUTURE CONSIDERATIONS IN THE VIABILITY OF CAPTIVE POPULATIONS

The challenge for zoo conservationists is mitigating the impacts of captivity on diversity and viability whilst also maximising the health and behavioural welfare of the species being managed. For example, the obligate cooperative breeding system of meerkats is maintained in the wild by aggressive behaviours such as eviction and infanticide. How might we best conserve this complex trait and ensure genomic representation in the captive population for long-term viability, alongside welfare considerations? Much of this book deals with the important task of accommodating behavioural welfare in captive populations, and in this chapter we have discussed why this needs to be accomplished with evolutionary biology insight. A recent innovation in captive population management is the One Plan Approach to conservation (Byers, Lees, Wilcken, & Schwitzer, 2013). This method integrates evidence-based management of captive population genomic

diversity with the broad range of multidisciplinary considerations necessary for successful species conservation, including behavioural welfare, collection planning, and in situ conservation action (see Chapter 2). This evidence-based management approach inherently requires an evolutionary perspective and further highlights the central role evolutionary biology plays in all aspects of species conservation.

The advancement of technology continues to provide novel tools and techniques for conservation biology (Segelbacher et al., 2021). This will inevitably lead to quicker, easier, and cheaper assaying of populations and enclosures, using increasingly non-invasive, more degraded, and smaller samples. The result is a rapidly increasing quantity and quality of data for decision-making processes (see Chapters 2, 4, and 5). Bio-banking and cryopreservation are important examples of the benefits of technology advancement for endangered species conservation. Initiatives around the globe such as the Frozen Ark Consortium, Frozen Zoo (San Diego Zoo Wildlife Alliance), CryoArks and EAZA (European Association of Zoos and Aquaria) BioBank harvest and store samples such as gametes, blood, cell lines, and embryos. Many consortiums operate not just within the zoo community but also involve museums and academic institutions in coordinated efforts to catalogue and conserve diversity. As technology improves, it becomes more viable to make use of these archives. For example, the black-footed ferret (*Mustela nigripes*) is an ex-situ conservation success story. Thought to be extinct, a small relic population was discovered, captive-bred, and successfully reintroduced across North America. However, due to the extreme bottleneck the species endured, it harbours low genomic diversity. Advancement in cloning technology has enabled researchers to clone a female black-footed ferret from DNA samples taken from the original founding population. Importantly, this individual carries genome diversity lost from the current population and so offers an opportunity for the genetic rescue of the population using ancestral diversity (U.S. Fish & Wildlife Service, 2021). This is a fascinating example of the possibilities for species conservation, albeit with important ethical considerations (Sandler, Moses, & Wisely, 2021). Another exciting aspect of technological innovation is that it will make captive populations increasingly valuable resources not only for conservation, but in furthering our understanding of fundamental biology, as new approaches and investigative opportunities emerge. Consider indirect genetic effects, for example. As discussed at the start of this chapter, the phenotype of an organism results from the interaction between inherited and environmental factors. Indirect genetic effects are a type of environmental influence in which the expression of the genotype of one individual influences the phenotype of another individual (Wolf, Brodie-III, Cheverud, Moore, & Wade, 1998). Captive populations, with their intensive and global management plans, could provide ample opportunities to further our understanding of such evolutionary mechanisms. It is easy to imagine how zoo populations would benefit from research into genomic and phenotypic consequences of conspecific interaction and social setting and how this could inform animal welfare in captivity.

## 3.5 CONCLUSIONS

Maintaining evolutionary potential is a core objective of conservation biology. Genomic diversity is important to this long-term viability as it underpins the very mechanisms of evolutionary change. Without diversity, populations experience a range of effects which increase their extinction risk. Our understanding of how best to maintain diversity for species undergoing ex-situ conservation management continues to evolve as the science and technology behind captive management improves. Here, we have briefly discussed how evolution underpins all aspects of the species in our care and how it needs to inform our ideas and methods for supporting the expression of behaviours. A deeper understanding of the often-complex behavioural biology of species managed in captivity is increasingly important. In terms of the evolutionary trajectory and viability of populations undergoing intensive captive management, it is likely of greater significance than we currently appreciate.

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