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Mate Choice as a Potential Tool to Increase Population Sustainability

The Sustainability Problem

The sustainability of populations has become an important consideration for the zoo and aquarium community. In their analysis of 87 zoo mammal populations, Lees & Wilcken (2009) found that 52% were not breeding to replacement and that 67% fell below the threshold of 200 animals recommended by Baker (2007). Conway (2011) pointed out that new policies and practices in zoo collection management, including more specialisation and focused propagation efforts, are needed if zoos are to fulfil their conservation potential. Regional zoo associations are examining possible reasons for the unsustainability of their populations, but one clear factor is the failure of many assigned pairs to reproduce, often due to pair incompatibility. The typical reaction is to assign another breeding partner, often requiring the transfer of an animal to or from another location. This dating game may finally result in a successful match, but meanwhile valuable time and reproductive opportunities are lost.

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Female Choice and Reproductive Success

In nature, many animals are able to choose their mates and the importance of female choice (females choosing their mates) has been documented in many different taxa (Asa *et al.* 2011). The factors affecting mate choice are not always apparent, but allowing animals to choose can increase pregnancy rates, litter sizes and offspring survival. There are many steps in the reproductive process, from courtship through rearing young to independence, and it appears that mate choice can affect most if not all of them. Most obviously, compatible pairs are more likely to copulate. A female that rejects mating attempts from a particular male will not conceive unless forced, but even when forced, females of at least some species can impede or prevent reproduction. Best studied in birds, females that mate with non-preferred males can eject sperm or even influence the ability of sperm to fertilise ova. Females of some species influence embryo survival and litter size by restricting nutrients or differentially allocating hormones. Females can also withhold parental care and affect survival of offspring that result from non-preferred matings.

Enhancing animal wellbeing and promotion of natural behaviours are goals of modern zoos. Allowing animals to select partners can contribute to the wellbeing of those individuals and better simulates their natural mating behaviour, contributing to something we sometimes refer to as the "happy factor". Happy females (i.e. happy with their partners) are more likely to mate, conceive, incubate or carry a pregnancy to term and more likely to be good parents, also improving offspring wellbeing as well as survival.

If mate choice is important to the reproductive success of most species, then preventing choice could be counterproductive to reaching programme objectives. The benefits from mate choice, for example higher birth or hatching rates and higher offspring survival plus enhanced animal wellbeing, are obvious. Higher reproductive success means higher probability of sustainability and faster growth to the population's target size, which helps to slow the loss of genetic diversity. Allowing animals to exhibit natural reproductive behaviours also reduces the unintentional selection for traits that are adaptive to certain captive environments, but not adaptive to more natural environments for the species.

Mate Choice and Population Genetics

However, allowing mate choice is not without risk and may undermine genetic goals if animals choose mates that are genetically over-represented in the population (Asa *et al.* 2011). Numerous studies have shown that females make good genetic mate choices in terms of their own individual fitness and under the conditions in which they are living. Such choices, however, may not result in maximum retention of genetic diversity in the population, balance founder representation or avoid loss of adaptations to wild environments, which are the primary goals of captive breeding programmes (Lacy 1994).

Fig. 1
Male cheetah scent marking on urine collector.
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Fig. 2
Female cheetah investigating male scent dispenser with male urine sample.
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As many population mangers have found, the most genetically valuable animals in the population (i.e. the top priority animals for breeding) are not always the most successful breeders. Concentrating breeding efforts on such animals can reduce population growth and even lead to demographic instability and population decline. However, ignoring genetic factors and concentrating on good breeders only can reduce genetic variability and long-term population health and increase adaptation to captive conditions. Allowing mate choice by offering multiple genetically acceptable mates may be one tool to help balance demographic and genetic needs of a population and ultimately maintain higher levels of genetic diversity by increasing reproductive success while relaxing the necessity for imposing rigid genetic management.

Integrating Mate Choice and Genetic Management

The cues mediating mate preferences have not been determined for many species, but this need not prevent incorporating choice into breeding programmes. The simplest approach is to provide a female with access to several males and observe her reactions. Generally, females approach and spend more time with or near the preferred male; in addition, species-typical behaviours, such as sniffing or performing visual displays, may be apparent. The female can then be paired with that male for breeding. To minimise any negative impact on population genetics, the several males presented to the female could be limited to those considered to be genetically appropriate potential mates, with the hope that merely having a choice will be sufficient to influence her willingness to mate. It is important to note that sequential presentation of potential mates is not equivalent to allowing choice but is actually sequential mate rejection/acceptance. Studies have shown that females have highest reproductive success when they can assess their mate options simultaneously.

Housing and management constraints may limit the number of males that can be physically presented simultaneously; the feasibility and logistics of providing mate options also varies greatly among species. Assessing choice by substituting appropriate cues (proxies) for the potential mate himself (e.g. scent) is a possible alternative that has been successful in animal models ranging from mice to humans. For example, the preference of a female mouse is consistent whether she is presented with an assortment of males or their urine sample. Thus, rather than transfer a potential mate to a new location, his urine or other scent sample could be sent first to assess the female's reaction before investing the resources, time and risk in transferring the male. As a first step in assessing the practicality of using urine as a proxy for the actual male, one of our graduate students confirmed that female cheetahs (*Acinonyx jubatus*) do investigate male urine samples and can use urine to distinguish between males of different genetic relatedness (Figs. 1 and 2; Mossotti 2010).

Managers might also be able to influence female choice by manipulating cues. Females of some species are more likely to mate with familiar males, so the scent of a partner that would fulfil programme goals could be presented before presenting the potential mate himself. In other species, high rates of scent marking stimulate a female, presumably by

representing male vigour and territory ownership, suggesting another approach to influencing choice. In some species, dominant males mark over scent marks of competitors and females prefer the male that marks on top. Managers could use this strategy to create a "winner" by adding scent samples sequentially so that scent from the male best for achieving population goals is added last. Females also can be influenced by the behaviour of other females and may prefer males that other females have chosen. Thus, appropriate social groups may facilitate mate acceptance, even acceptance of males that might not have been selected were the females housed individually.

Given the clear importance of mate choice in so many species, we believe the zoo community should consider incorporating choice in captive breeding programmes. This should be approached, however, in a careful and controlled manner. Not only is the phenomenon of mate choice very complex, but allowing mate choice could be challenging, both the logistics of offering choice and implementing choice so that it augments rather than hinders population management goals.

Recognising the complexity of this topic, a Mate Choice Symposium was held at Saint Louis Zoo in March 2010, where top scientists who study mate choice came together with zoo population managers, including studbook keepers, species coordinators and population management advisors. After a series of research presentations by the scientists summarising the mechanisms and consequences of mate choice across a wide variety of species, taxon-based working groups discussed the implications of mate choice, opportunities for incorporating mate choice in captive management and potential research projects to investigate these issues. Participants identified possible strategies for incorporating mate choice into our current breeding programmes, including: (1) using information on mate choice to increase the reproductive success of genetically valuable animals; (2) providing multiple genetically acceptable mates rather than a single mate; (3) developing methods for assessing mate acceptability (via testing of odour or other cues) before actual animal transfer; and (4) considering alternate breeding strategies such as specialised breeding centres or inter-institutional management that optimises reproductive success combined with periodic exchange of individuals.

The results of this symposium along with two smaller, related workshops led to the identification of three proposed research projects that span a breadth of taxa, breeding systems and captive management to address issues related to incorporating mate choice into zoo-managed programmes. These studies are designed to evaluate the effects of allowing controlled mate choice within the following populations: a multi-zoo breeding programme for a high-profile species (cheetahs), a single-facility breeding centre (tanagers) and a controlled experimental population (mice). Funding is now being sought to support these proposed projects. It is hoped that such studies can serve as models to help guide the effective use of mate choice in zoo populations.

Allowing choice may improve reproductive success and, ultimately, programme effectiveness. A better understanding of mate choice can help population managers reach their goals for viable, genetically healthy populations, while potentially helping minimise selective changes to captivity and providing insight into developing a more effective breeding management strategy for captive animal populations.

Acknowledgements

We thank Regina Mossotti for use of the cheetah images.

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