Int. Zoo Yb. (2011) **45:** 203–212
DOI:10.1111/j.1748-1090.2010.00123.x

Can conservation-breeding programmes be improved by incorporating mate choice?

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Captive populations are managed to promote demographic growth or stability and preserve genetic variation. Current protocols use survival rates to estimate the number of offspring needed to achieve target population size, while pedigree analysis is used to select breeding pairs to retain genetic diversity and minimize inbreeding. Despite these efforts, many captive populations fall short of programme goals. Reproductive failure of breeding pairs is a contributing factor, often as a result of pair incompatibility. Because choice is a component of most mating systems, providing a choice of mates could improve the sustainability of captive populations through increased fecundity and offspring survival while enhancing animal well-being. However, allowing mate choice might undermine genetic goals if those choices are inconsistent with genetic management objectives. Strategies for incorporating mate choice into management include: (1) using mate choice to increase reproduction of genetically valuable animals; (2) providing multiple genetically acceptable mates; (3) assessing mate preferences via odour or other cues before animal transfer; (4) using alternate breeding strategies, such as specialized breeding centres. Research is needed to determine whether incorporation of mate choice in breeding programmes can increase reproductive success without compromising genetic health and the potential to contribute to the conservation of wild populations.

Key-words: captive breeding; genetic management; mate choice; population management; reproductive success.

BREEDING STRATEGIES FOR GENETIC MANAGEMENT

Captive-animal populations are carefully managed to promote their demographic growth or stability and preserve genetic variation, which increases their long-term viability as educational zoo exhibits, source populations for research, and their potential to serve as a demographic and genetic resource to supplement wild populations when needed (Lacy, 1994). To serve these functions, captive populations need to maintain a healthy age and sex structure, maintain genetic diversity, avoid inbreeding effects and minimize adaptation to captivity (Ballou & Foose, 1996). Because exhibit space and other resources are limited, zoos can only maintain relatively small populations of each species, amplifying the risks of stochastic (chance) processes, such as fluctuating birth and death rates, and loss of genetic diversity through genetic drift. This means that captive populations are managed tightly to maintain a specific target size and to maximize the retention of genetic diversity (Earnhardt *et al.*, 2001). The selection of breeders, their mates and their reproductive success can have profound impacts on the viability of these populations in captivity and their usefulness to reintroduction efforts.

Current population-management strategies rely on accurate demographic and pedigree information maintained in studbook databases. Age- and sex-specific survival and fecundity rates allow managers to estimate the number of offspring needed to achieve a certain population growth rate and target population size. By anticipating deaths over the subsequent year, given the age and sex structure of the current population, and calculating average litter/clutch size and juvenile survival, managers are able to estimate the number of offspring (litters/clutches) needed to increase, decrease or maintain the population to meet desired goals.

The appropriate number of breeding recommendations is made to meet these reproductive needs, with the selection of breeders based upon genetic considerations to the extent possible. Pedigree analysis enables managers to determine the relative genetic value of each individual in the population as a potential breeder. A mean kinship (MK) value is calculated for each animal, which represents its average relatedness to the population. Animals that represent common genetic lines and have many relatives in the population have a high MK value and are not as desirable as future breeders. Conversely, animals that carry rare, under-represented genetic lines and have few or no relatives in the population have a low MK value and are priority candidates for breeding. Breeding individuals with low MK values serves to equalize the representation of the distinct (founder) genetic lines and the retention of genetic diversity; breeding common gene lines hastens the loss of genetic diversity through genetic drift. This strategy of genetically managing captive-animal populations through minimizing mean kinship has been shown through modelling to be an effective strategy for retaining genetic diversity, and is the recognized strategy used by regional zoo associations worldwide today (Ballou & Lacy, 1995). The ultimate focus of such a strategy is to preserve the population as closely as possible to the genetic composition of the wild source population (Lacy, 2009) and to retain evolutionary potential. Although these goals are not focused on maximizing individual reproductive success, without reliable breeding none of the population goals can be attained.

Selection of breeding partners is also important to avoid the potential harmful effects of inbreeding, that is, the mating of related individuals, impacting both individual fitness and population health (Lacy, 1997). Once managers have determined the desired number of breeding pairs and the priority animals for breeding, they are able to recommend pairs based on many factors, such as location, age and reproductive history, while avoiding pairing closely related animals as much as possible. In this way, managers determine not only who has the opportunity to breed but also breeding partners – be it for a monogamous pair with long-term pair bonds or for a group- or herd-living species with a polygynous mating system. For example, one criterion for assigning priority animals to breeding pairs is to avoid pairing genetically valuable animals to non-valuable ones. In this way we can avoid combining rare and common genes within the same offspring, which could prevent us from optimally managing the genetic lineages in future generations.

IMPORTANCE OF REPRODUCTIVE SUCCESS

Although captive-animal programmes are designed to be sustainable, this has not been achieved for many species (Lees & Wilcken, 2009). Possible causes for the unsustainability of these populations are being analysed and further analyses would be highly desirable. One factor that has already been identified is the failure of many assigned pairs to reproduce, often as a result of pair incompatibility. The standard strategy for pairs that do not reproduce is to assign another breeding partner and transfer one or both animals to another location. Such sequential pairings may, by chance, result in a more successful match, but meanwhile valuable time and reproductive opportunities are lost.

The reproductive success of breeding pairs has significant consequences for both the demographic and genetic status of the population. Poor reproductive success may reduce population growth or even lead to population decline and may reduce genetic diversity if animals of high genetic value to the population reproduce poorly. In fact, some individuals are genetically valuable precisely because their reproductive success has been low (prolific individuals with many offspring are more likely to be well represented in the population). Uncertainty in predicting and controlling reproductive success is problematic, handicapping managers in their ability to manage tightly population size and growth, leading them to make some recommendations for already proven breeders that are less likely to be genetically rare and valuable to the population.

POTENTIAL IMPACT OF MATE CHOICE

For at least some species, mate choice may well influence acceptance and, therefore, reproductive success and, ultimately, programme effectiveness. It is entirely possible that continued 'forced' pairings and the lack of opportunity for natural mate-choice mechanisms to operate in zoo breeding programmes may alter this natural mating process and lead to adaptation to the captive conditions of human-controlled matings. However, it is also possible that allowing for mate choice under novel conditions could accelerate adaptation to captivity if traits used in mate choice are altered under captive conditions. Mate choice may also provide a natural mechanism for maintaining genetic diversity in zoo populations, as has long been known to occur in experimental laboratory populations (e.g. Ehrman & Probber, 1978; Spiess & Ehrman, 1978; Lacy, 1979). Allowing mate choice could be particularly valuable to zoos when the relationships of individuals are uncertain or unknown, such that we cannot identify the genetically optimal pairings from pedigree analysis. A better understanding of mate choice will aid population managers in achieving their goals for a viable, genetically healthy population, help to minimize selective changes to captivity and, potentially, may provide insight into developing a more effective breeding management strategy for captive-animal populations.

In the natural environment, animals often have the opportunity to choose their own mates, depending upon the social and breeding system of the species. The importance of female choice in mating systems and strategies (Bateson, 1983) has been documented in numerous taxa, including many mammalian species (e.g. Krackow & Matuschak, 1991; Stumpf & Boesch, 2006; Hoffman *et al.*, 2007), birds (e.g. Bateson, 1982; Buchholz, 1995; Bennett *et al.*, 1996; Bluhm & Gowaty, 2004), amphibians (Chandler & Zamudio, 2008) and invertebrates (e.g. Eberhard, 1996). Indeed, Darwin (1871) proposed that mate choice was a major selective force in evolution. The paradigm of competing males and choosy females (see Kokko *et al.*, 2003) has been used widely to explain the specialization of the sexes and characterizes the polygynous mating systems of the majority of species studied.

The role of mate choice in mating strategies and reproductive success in a variety of species ranging from fish to amphibians, birds and mammals, including humans, is an area of active research. Some studies focus on the mechanisms used in making choices, particularly olfactory communication (e.g. Johnston, 2003; Novotny *et al.*, 2007; Charpentier *et al.*, 2008), some on the genetics of choice (e.g. Penn, 2002; Charpentier *et al.*, 2008), particularly the influence of the major histocompatibility complex (MHC) (e.g. Penn & Potts, 1999), and others on male versus female mating strategies (e.g. Tregenza & Wedell, 2000; Moore, 2001). Although the phenotypes and underlying genetic bases of partner preferences are often not known, mate choice has been found to reflect finely tuned assessments of genetic commonness in the population or similarity between potential mates (e.g. Ryan & Lacy, 2003). In addition, choice can be employed not only during courtship but also post-copulation via cryptic female choice (Eberhard, 1996), a term that has been used to describe sperm competition as well as female ejection of sperm and control over litter or clutch size (e.g. Birkhead & Moller, 1993; Birkhead *et al.*, 1993; Pizzari & Birkhead, 2002). Although virtually all mate choice research has focused on female choice, an argument can be made that males may also be selective (Dewsbury, 1982; Ryan & Altmann, 2001; Clutton-Brock, 2007). In particular, males of monogamous and, especially, polyandrous species should also be choosy, because they forgo reproducing with other females and invest considerable effort in the offspring of their mate. In fact, even in polygynous House mice *Mus musculus*, mutual choice improves reproductive output (Drickamer *et al*., 2003).

The mechanisms and factors affecting mate choice are not yet well understood but allowing animals to choose partners has been shown to increase pregnancy rates, litter sizes and offspring survival (e.g. Keane, 1990; McClain, 1998; Drickamer *et al*., 2000; Ryan & Altmann, 2001; Anderson *et al*., 2007). There are multiple points in the reproductive process where choice can influence overall reproductive success. At the simplest level, compatible pairs are more likely to copulate. A female that rejects mating attempts from a particular male will not conceive unless forced. Even then, post-copulatory cryptic female choice can impede or prevent fertilization. Best described for birds, females may be able to eject or even influence the ability of sperm to fertilize following forced copulation or mating with a non-preferred male. If fertilization does occur, in some species embryo survival and litter size may be lower, probably through restricted allocation of nutrients. The survival of offspring born as a result of a non-preferred mating may be compromised by inadequate parental care. However, in some cases female preferences may be obscured by the effects of male competition or by male attempts to constrain female choice (see Clutton-Brock & McAuliffe, 2009).

Also in keeping with the goals of modern zoos is enhancing animal well-being. Compatible pairs that result from allowing animals to select preferred partners could clearly contribute to the well-being of those individuals. It could be argued that such pairs would be more likely to exhibit good parental care, also improving offspring well-being and survival. For monogamous species in which males share parental duties, pair compatibility could be particularly critical not only to successful courtship and mating but also to the care provided to offspring.

Mate choice may not be important in all species and in fact some studies have failed to find an effect (e.g. Paterson & Pemberton, 1997; Huchard *et al*., 2010). However, studies differ in focus and methodology, which can affect outcome, and choice can act at many levels, some much less apparent than others (e.g. cryptic female choice and extra-pair copulations). For example, as pointed out by Huchard *et al*. (2010) investigations into the involvement of the MHC analyse limited segments, so the results may not be generalizable to the whole MHC region and absence of effect may be owing to the selection of an inappropriate segment for analysis.

INCORPORATING MATE CHOICE INTO CAPTIVE MANAGEMENT

If choice is a natural component of most if not all mating systems and is indeed as important to reproductive success as research suggests, the implications of preventing choice in captive-breeding programmes are potentially counterproductive and detrimental to achieving programme objectives. The major benefits from allowing choice are increased reproductive success, that is, higher birth and hatching rates and higher offspring survival, plus enhanced animal well-being. Nevertheless, an important concern among zoo-based population managers is that allowing mate choice might undermine current genetic goals if animals make choices not consistent with breeding recommendations. Considerable literature indicates that females make good genetic choices in terms of individual fitness. The two genetic qualities so far identified include preferring males: (1) with 'good genes' (e.g. males that are healthy, strong and parasite resistant) or (2) that are of the optimal genetic distance (i.e. not too close in order to avoid inbreeding effects or too distant, which can compromise fertility) (see Roberts & Gosling, 2003; Mays & Hill, 2004; Neff & Pitcher, 2005).

Wedekind (2002) discussed the possible benefits of allowing free mate choice in captive-breeding programmes as a means to promote reproductive success and to improve the genetics of a population, but he also identified the risk that free mate choice might cause much greater variance in reproductive success, thereby decreasing effective population size. Thus, while the natural mate-choice criteria may result in increased fitness of the female and her offspring, such mate-choice strategies may not result in maximal retention of genetic diversity in the population, at least not with the same efficiency as might be achieved when breeding pairs are designated based on detailed pedigree analyses. Moreover, free choice of mates would not likely balance founder representation (done to maintain the genetic characteristics of the source founder population) or avoid loss of adaptations to wild environments, which together with maximal protection of genetic diversity are the primary goals of captive-breeding programmes (Lacy, 1994).

When females use the 'good genes' criterion, only a limited number of males exhibiting those preferred qualities are selected by all females. The result is that the remaining males are not represented in subsequent generations, although the offspring sired by the few preferred males may be healthier and have a higher survival rate under certain conditions. In other ways, however, natural mating systems might abet rather than compromise attaining the genetic goals of captive-population management. Another strategy that females use in selecting a mate reflects her own genotype and assumes that she will produce more and healthier offspring if the sire's genes differ enough to result in relatively heterozygous offspring. Such a strategy avoids inbreeding, with the potential for expression of deleterious alleles, but also avoids excessive outbreeding with a male so different from her genetically that fertility might be compromised. This propensity to select for optimally heterozygous mating could be more consistent with current captive-population management goals than selection for good genes. Moreover, because mating preferences evolved in natural environments, mate choice in the captive descendants may actually help to preserve the wild-adapted characteristics of the species. Mating preferences could partly counter the inadvertent selection for adaptation to captivity that is likely quite strong in our breeding programmes (Frankham *et al.*, 1986; Frankham & Loebel, 1992), despite of our attempts to slow it through pedigree management (Frankham *et al.*, 2000).

Given the potential for mate choice to change not only the genetic balance in these populations but also the logistics of establishing pairs, it is critical that all the possible detrimental effects be carefully considered along with the potential advantages. The discriminatory selection of mates can reduce gene diversity, perhaps rapidly if only a subset of potential mates is preferred (Wedekind, 2002). The traits used in mate choice can be under strong selection, with such sexual selection not always favouring traits that otherwise are advantageous, as in 'run-away' sexual selection (Fisher, 1930). If the captive environment obscures or alters the cues used, mate choice in captive-breeding programmes might not operate effectively or might lead to selection for traits that are maladaptive or that have no genetic basis. Even if animals make optimal mate choices to maximize genetic quality and diversity in their own offspring, population-level diversity may not be maintained as well as when strict pedigree analysis is used to select an optimal set of breeders. In addition, a reduced number of successful breeders can cause rapid loss of genetic diversity at loci not involved in mate choice.

The value and application of opportunities for mate choice in breeding programmes also needs to consider the considerable differences in husbandry practices among species, which vary with taxonomy and also social and mating systems. Group-living species vary in the composition of the primary breeding unit in the wild and include those that would comprise only females with their young, those with a single male and multiple females along with young, and those with multiple males as well as females and young. More solitary species as well as monogamous ones are typically maintained either alone or in pairs. Each of these would require a different strategy to allow individuals to choose a preferred mate.

UNDERSTANDING MATE CHOICE

In order to allow animals to play an active role in selecting mates, an understanding of the signals or mechanisms used in mate assessment is necessary. For some species, the signal modality may already be known or a literature review may uncover the appropriate information, but for others some preliminary research may be needed. For example, in considering a study of mate choice in Cheetahs *Acinonyx jubatus*, some Cheetah managers warned that only males, not females, paid attention to male scent marks. However, the females not only pay attention to urine samples from males but also they distinguish between males according to genetic distance (Mossotti, 2009).

The method that many species appear to use in evaluating potential mates is olfaction. Chemical communication has been best studied in mammals (e.g. Johnston, 2003) but more recent work is demonstrating the importance of olfactory communication in birds as well (Soini *et al*., 2007; Balthazart & Taziaux, 2009; Whittaker *et al*., 2010). The use of olfactory signals may provide a more efficient approach to providing choice to a female or in evaluating her potential acceptance of a mate. That is, rather than transfer a potential mate to a new location, the male's urine or other scent sample, as appropriate for the species, could be sent instead for the female to assess. The rationale for this strategy is based on extensive data from rodents indicating that male urine or soiled bedding contains all the olfactory information a female needs to make such a choice, and that the choice matches the one she makes when presented with the males themselves. Furthermore, females may be able to assess mate quality (i.e. good genes) from male scent marks (Rich & Hurst, 1998).

However, olfaction is not the only sensory modality implicated in mate assessment. Visual signals are important for many species, especially birds. Although visual displays are often considered to be merely mechanisms that highlight colour patterns and ornaments, or convey the condition of feathers or fur, the motor performance involved in displays has been shown to be itself an indicator of male quality (reviewed in Byers *et al*., 2010). In other species, auditory communication is important to females in judging male quality; for example, bird song (Lampe & Saetre, 1995), frog calls (Gerhardt *et al*., 1996) or Red deer *Cervus elaphus* stag roars (Charlton *et al*., 2007). Thus, allowing males to engage fully in species-specific displays may be critical to insuring that females are presented with adequate information for making selections.

Females of some species are more likely to mate with males with which they are already familiar (Tang-Martinez *et al*., 1993), which affords an opportunity for managers to influence mate selection by presenting the scent of a partner that would fulfil programme goals before presenting the partner himself. In other species, increased rates of scent marking stimulate a female, presumably by representing male vigour and territory ownership (Roberts & Gosling, 2004), another scenario that could be manipulated to influence choice. Female hamsters (Cricetinae) prefer the last male to scent mark over another's mark, where overmarking is possibly indicative of male–male competition, with the winner being the last to overmark (Johnston, 2003). If this response applies to females of other species where males overmark, managers could use this strategy to create a 'winner' by adding scent samples sequentially so that the sample from the male best for achieving population goals is added last. Females may also be influenced by the behaviour of other females (Dugatkin, 1992), preferring males that other females have chosen, suggesting that social groupings appropriate for the species may facilitate mate acceptance, even for males that might not have been selected were the females housed alone. However, the selective pressure for some females to cluster as a predator-avoidance strategy may sometimes result in association with a particular male and be misinterpreted as copying mate choice (Clutton-Brock & McComb, 1993).

Although there are likely species differences, considerable data suggest that preferences for particular mates are not entirely genetically based, even at the level of the MHC. Experience or learning during development also can play a role, something demonstrated by cross-fostering experiments.

For example, female mice avoid mating with males that carry the MHC genes of the family in which they were reared rather than with males carrying their own MHC genes (Yamazaki *et al*., 1988; Penn & Potts, 1998). Cross-fostering is a useful management tool in some captive-breeding situations but the potential effects on the outcome of future breeding recommendations should be considered in weighing these benefits. It is also important to note that female preferences can change throughout the oestrous cycle and between oestrus and pregnancy, with preferences for genetically dissimilar males only clear during oestrus (Egid & Brown, 1989).

NEXT STEPS IN INCORPORATING MATE CHOICE

Given the clear importance of mate choice in so many species, we believe that the zoo community should carefully consider its implications for captive-breeding programmes. Mate-choice mechanisms are likely affecting current population management efforts and a greater understanding of these mechanisms would be beneficial. Not only is the phenomenon of mate choice very complex and multifaceted (Candolin, 2003) but also the potential incorporation of mate choice into breeding recommendations would be challenging, both in terms of logistics of offering choice in a zoo setting and in implementing choice in a way that augments rather than hinders our population management goals. In our discussions of mate choice with numerous colleagues in the zoo community, many admit that they would be interested in including mate choice but simply do not know how to go about it and/or are unsure of the implications for genetic management.

To explore these issues, a mate-choice symposium was held in March 2010 at the Saint Louis Zoo, MO, USA, that brought together 70 participants, including the top researchers in the field of mate choice as well as zoo population managers, including studbook keepers, species coordinators and population-management advisors. The first day consisted of a series of research presentations by the academic community outlining the mechanisms and consequences of mate choice across a variety of taxa, and the subsequent 2 days were spent in taxon-based working groups to discuss the implications of mate choice, opportunities for incorporating mate choice into captive management and identification of potential research projects to investigate these issues.

The meeting participants identified several potential strategies for incorporating mate choice into our current breeding management, including: (1) using our knowledge of mate choice to increase the reproductive success of genetically valuable animals, especially habitually poor breeders; (2) providing multiple genetically acceptable mates rather than a single mate; (3) conducting long-distance assessment of mate acceptability (via testing of odour or other cues) before actual animal transfer; (4) considering alternate breeding strategies, such as focusing on specialized breeding centres or using intra-institutional management that optimizes reproductive success combined with periodic exchange of individuals among institutions. While many of these strategies may have merit, there are many data gaps in our knowledge of mate choice, under both wild and captive conditions, that need to be addressed before the implementation of mate choice into effective population management can be considered. Also critical is an evaluation of those factors that lead to low reproductive success in some captive populations, and particularly the extent to which mate choice or the lack of choice is contributing to reproductive failures.

Potential research projects have been identified across a variety of taxa and mating systems to investigate these data gaps; these research ideas are being explored in terms of potential facilities, collaborators and funding for implementation. The result of such research efforts will provide guidance regarding how, and if, the incorporation of mate choice in breeding recommendations can increase reproductive success in captive, managed populations without compromising the genetic health of these populations and their potential to contribute to the conservation of wild populations.

ACKNOWLEDGEMENTS
The authors thank all the workshop and symposium participants, in particular Karen Bauman and Joanne Earnhardt, for critical input and discussion, and the Institute for Museum and Library Services and the Saint Louis Zoo for workshop and symposium support.

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Manuscript submitted 6 May 2010; revised 13 August 2010; accepted 7 October 2010

