

Mate choice and its implications for conservation and management

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The potential contribution of behavioural principles to conservation is not widely appreciated despite a recent burst of interest in the interface between the two disciplines. Many aspects of behaviour, including social interactions, foraging, habitat selection, imprinting, and antipredator strategies, are relevant to the propagation and preservation of species. In this paper, I focus on what we know about how individuals choose mates, a subject in which tremendous advances have been made in the past two decades. I discuss how current understanding of patterns and causes of mate preferences can address conservation problems. By viewing the behaviour of individuals as being adapted to their circumstances, robust predictions can be made about the consequences of environmental change. For example, changes to natural habitats alter the mating decisions of individuals, and thus the genetics and demography of populations; this has clear conservation implications. Further, individuals are expected to make mate choice decisions that maximize their reproductive success, and this insight can be used while planning captive breeding strategies. In addition, knowledge of the development of mating preferences and of the mechanisms of mating decisions allows us to influence mating behaviour to meet conservation goals. Managers would benefit by considering the ways in which mate choice behaviour might help or hinder their conservation interventions.

Keywords: Conservation, management, mate choice.

How to conserve and manage biodiversity and ecological processes has typically been thought of as an ecological and economic question. Basic themes in conservation science include the resilience of natural systems to disturbance, the susceptibility of species to extinction, the causes and consequences of population change, and the problems of preserving small populations¹. Although the behaviour of individuals is relevant to several of these themes², behavioural biologists have played a smaller role than they should³ and behavioural articles in conservation journals are rare^{4,5}. This lack of involvement is beginning to change, with four edited volumes on the role of behaviour in conservation^{6–9} and many articles on this subject (e.g., refs 10–16). The general message that emerges from these discussions is that conservation can benefit from recent deve-

lopments in our understanding of animal behaviour, and that students of behaviour should develop research ideas relevant to conservation problems.

Contributions to conservation come from both evolutionary and mechanistic approaches to behaviour. Evolutionary questions are concerned with understanding behaviour in terms of its evolutionary history and function. Explanations of behaviour in this domain are called ‘ultimate’. Ultimate questions help us understand the adaptive value of behaviour (e.g., *how does alarm calling increase the probability of survival?*) and allow us to make predictions about change (e.g., *in what ways should animals alter their foraging behaviour when a predator is present?*). Ultimate causes are linked to evolutionary fitness, which in turn is closely related to individual reproductive output. Because population growth is a result of the cumulative reproduction of individuals, an understanding of ultimate causes may allow us to predict population-level consequences of specific changes in the environment^{16–18}.

Mechanistic questions about behaviour deal with the ontogeny and control of behavioural patterns. Questions such as *how does foraging behaviour develop in a young animal?* and *what is the neuronal control of cricket song?* belong to this approach. These are also called ‘proximate’ questions¹⁹. In the conservation context, a detailed understanding of proximate mechanisms allows us to influence the behaviour of individuals and anticipate problems when animals are placed in novel situations (such as in captivity).

Many aspects of behaviour are relevant to conservation, but perhaps none more so than reproductive behaviour, because this is directly related to population dynamics. In this paper, I focus on mate choice, an aspect of reproduction that has received much attention from evolutionary biologists, but has been largely neglected in more applied contexts. I examine how the ways in which individuals make choices about whom to mate with can inform conservation efforts. An understanding of the causes and consequences of these choices may help us anticipate and alleviate certain conservation problems.

I first provide a brief historical treatment of the field of sexual selection (of which the study of mate choice is a subset). I then discuss the reasons animals choose one mate over another and what kinds of partners are preferred. Given this background, I examine the application of our understanding of mate choice to issues in conservation and

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management. I end with some suggestions for how mate choice studies can better inform conservation issues, and how conservationists can benefit from a greater familiarity with mate choice research. Note that although this discussion is restricted to animals, similar ideas can and should be applied to issues of plant conservation.

Sexual selection and mate choice: what do we know?

In *The Descent of Man and Selection in Relation to Sex*, Darwin²⁰ identified an important evolutionary process with curious outcomes. Because individuals must survive and reproduce if their genes are to pass to the next generation, and because obtaining a mate is integral to reproduction in sexual organisms, any trait that enhances the ability of an individual to obtain access to mates and gametes of the opposite sex will be favoured. Darwin called the process by which such traits evolve Sexual Selection, and suggested that it explains the existence of bizarre and costly traits like elaborate weaponry and ornamentation. He proposed that males often compete for access to females, and that females are typically choosy about whom they mate with.

Why should there be such a difference between the sexes? Anisogamy (differences in gamete size) provides part of the answer. In most sexual organisms, some individuals (males) produce many small mobile gametes, and other individuals (females) produce fewer large, nutrient-rich gametes. This initial asymmetry, in combination with differential post-mating investment in offspring²¹ results in females tending to be choosy, and in males competing over females^{21–23}. In some species, however, this pattern is reversed, with males investing more in offspring, and consequently being the choosy sex (reviewed in refs 24 and 25). Mate choice, then, is not a strictly female phenomenon, although I will refer to it as female choice because this seems to be the most common pattern. Note also that although I focus on mate choice in this paper, competition over mates (most often male–male competition) is also an important part of the sexual selection evolutionary process^{20,26}.

What do females choose and why?

Why might female preferences for particular traits evolve? In addition to a null model proposed by Fisher²⁷ (called ‘runaway selection’), females preferences may arise as a by-product of selection in other contexts (the sensory bias hypothesis²⁸). But the main reason that females choose among males appears to be related to measurable benefits of such choice. There are two main categories of benefits: genetic and nongenetic (see ref. 26 for a review).

Good genes: If males differ in their genetic quality, it might pay females to choose those males with ‘good

genes’^{29,30}. An obvious example is female preference for mating with conspecifics over heterospecifics¹⁹. However, variation in genetic quality also occurs among conspecifics, and may be related to, for example, foraging skill, disease resistance, or general body condition^{26,31,32}. Genetic quality appears to often be displayed through the degree of exaggeration of secondary sexual traits^{26,31}. Across species, females mated to males with such exaggerated traits have offspring who survive better^{33,34}, but the precise fitness benefits females gain through good genes remain difficult to estimate³⁰.

Female preferences need not be unanimous; in some cases, females might be expected to differ in terms of which male is the most suitable. Here, the search is for males with compatible genes³⁵ rather than for those with the ‘best’ genes, because the genetic quality of a male may depend on which female is doing the choosing. A classic example is inbreeding avoidance. Inbreeding (breeding with relatives) leads to an increase in homozygosity, the expression of recessive alleles (many of which may be deleterious), and often a consequent reduction in offspring fitness (‘inbreeding depression’^{36,37}). Accordingly, females appear to pay attention to relatedness while choosing mates³⁸. Exceptions to this general pattern do exist, and females may show different tolerance to inbreeding depending on inbreeding load³⁹. For example, in the dwarf mongoose *Helogale parvula* there appears to be no inbreeding avoidance or depression⁴⁰, while song sparrows *Melospiza melodia* show no inbreeding avoidance despite strong inbreeding depression⁴¹.

Recently there has been much interest in mate choice in relation to genes in the major histocompatibility complex (MHC). Resistance to some diseases is enhanced in individuals with high heterozygosity at MHC loci⁴², and such individuals may be of high overall quality⁴³. In such a case, one would expect females to choose males genetically dissimilar to themselves at these loci, and there is increasing evidence that females use odour cues to do this^{42,44,45}.

Direct benefits: Nongenetic or ‘direct’ benefits to females from choosing mates are likely to be greater than genetic benefits, but empirical measures of the magnitude of direct benefits are quite variable⁴⁶. Direct benefits come in many forms⁴⁷. In some species, males feed females during courtship and pair formation, or transfer nutrients in several ways, including through semen and specialized male organs eaten by the female²⁶. Such courtship or nuptial feeding may help females in the nutritionally expensive task of producing offspring. Females who mate with good feeders produce larger and more eggs than those mated with poor feeders²⁶. Other benefits females may receive for themselves by choosing among potential mates include avoiding sexually transmitted diseases⁴⁸, escaping harassment by other (often younger) males⁴⁹, and possibly

lowering the risk of predation when associating with males at the centre of a territorial aggregation⁵⁰.

Apart from benefits to the females themselves, mate choice is often associated with benefits to their young. In those species in which males provide paternal care to the offspring, females evaluate aspects of males that correlate with such care^{51–53}. Paternal care may also be indirect, for example, through territory quality, and females may base their choice on territory attributes⁵⁴ or on male traits that are correlated with territory quality⁵⁵. It may sometimes pay a female to pair with the owner of a high quality territory even if he already has a mate. Thus, according to the polygyny threshold hypothesis⁵⁶, large variation in territory quality may lead to the appearance of a polygynous mating system in which some males acquire many mates. In contrast, when paternal care is vital for offspring survival, the costs of sharing a male are high, and monogamy is likely to be the prevalent mating system.

Implications for conservation

What lessons can conservationists learn from the wealth of theoretical and empirical work on mate choice? It turns out that patterns of mate choice can have implications for the genetics of populations⁵⁷ and their risk of extinction^{58,59}, and may allow us to predict some consequences of habitat alterations, population changes, and human disturbance (Figure 1). Captive breeding efforts may also benefit from mate choice theory. Many of these implications depend on precisely what females are choosing, and for what reason.

The genetics of populations

Ever since the discovery that inbreeding can lead to a reduction in the survival and fecundity of individuals, there has been concern about maintaining genetic diversity and heterozygosity in captive and wild populations. In captivity, this is done mainly by arranging matings to minimize inbreeding and to maximize the number of breeding individuals⁶⁰. In the wild, much effort has focused on understanding factors affecting genetic drift (and thus loss of alleles) in a population. The effective size of a population (N_e) is the number of breeding individuals that in an ideal population would undergo genetic drift at the same rate as the actual population⁶¹. Populations with small N_e lose genetic variation faster than those with large N_e , and their status is thus of greater concern.

Mate choice and mating system directly influence N_e by their effect on the breeding sex ratio and on the distribution of reproduction^{15,61,62}. The precise effect will depend on whether females preferences are uniform (as perhaps for healthy males) or variable (as in the avoidance of inbreeding⁶³). Uniform mate preferences cause a greater

skew in the breeding sex ratio and a larger inequality in the distribution of reproduction among males, leading to reduced N_e . Mate choice copying has a similar effect¹⁵. If, on the other hand, mate preferences are variable, there is a smaller reduction in N_e ⁶³. In general, variation in reproductive success can strongly influence N_e . For example, Creel⁶⁴ found that, in carnivores, unequal reproductive success was related to a greater reduction in N_e than was skewed sex ratio or variation in population size.

One problem in calculating N_e is that outward patterns of mating are often misleading in estimating the distribution of reproductive success. For example, extra-pair fertilizations (EPFs) are well-known in birds (including in outwardly monogamous species⁶⁵). Similarly, extra-pair and extra-group matings mean that apparent mating pattern is of limited utility in inferring genetic breeding system in primates, even in seemingly monogamous species like gibbons⁶⁶. While costs to females of mating with several partners may be substantial, there are likely to be many benefits (reviewed in ref. 67), including insurance against genetic incompatibility⁶⁸, and choice of males with the best sperm (cryptic female choice⁶⁹), or least-related sperm (e.g., in *Drosophila*⁷⁰). While calculating N_e , such multiple matings must be taken into account. In theory, they can either increase or decrease variance in reproductive success among males^{61,71}. However, in outwardly monogamous birds, EPFs are usually found to increase variance in male reproductive success (e.g., ref. 72), and thus decrease N_e .

Clearly, conservation biologists must consider the effects of mate choice patterns and the mating system of target

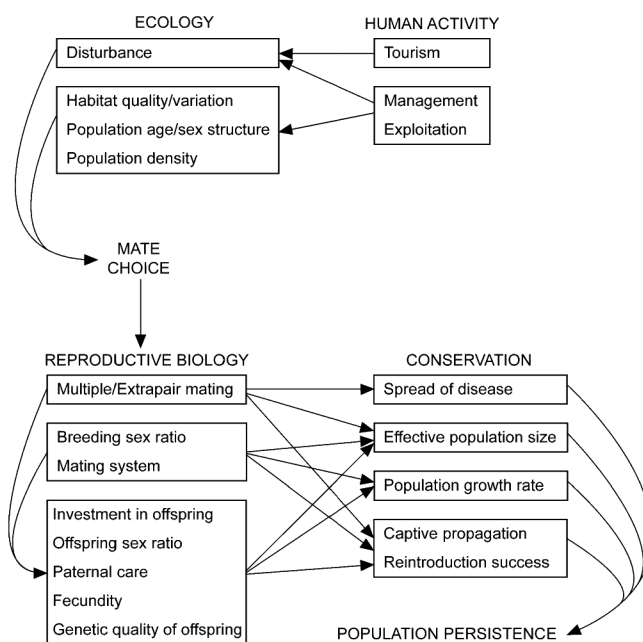


Figure 1. Schematic diagram of the relationship between mate choice and conservation issues. Human activities change ecological factors, which can influence mate choice and thus affect population patterns.

species on N_e while conducting population viability analyses or calculating minimum viable population sizes. It is also important to note that changes in habitat or population structure may alter female choice (see below), and thus the distribution of reproduction.

Small population problems

Small populations suffer from various problems, including increased genetic drift (random fluctuations in allele frequencies), and increased demographic stochasticity (random fluctuations in population growth rates). In addition, when populations reach low densities, not only is it difficult for females to find mates, but they may also be unable to sample a large enough number of potential mates before making mate choice decisions. At worst, this may deter females from breeding⁷³; or they may mate with low-quality males, and thus suffer reduced genetic and direct benefits. When their ability to choose is constrained, females may also reduce their fecundity and their investment in individual offspring. All these responses would exacerbate the Allee effect (low or negative population growth rate at low densities; see also ref. 74). However, female choice can sometimes ameliorate certain problems of small populations. For example, while inbreeding tends to increase at low population sizes, this may be countered by female choice for non-kin⁷⁵.

Predicting population or species extinction

Sexual selection and mating system may play a role in the extinction and persistence of populations. For example, the intensity of sexual selection (as measured by sexual dichromatism) predicts extinction risk. Dichromatic bird species were less likely to establish in Hawaiian islands⁷⁶ and in New Zealand⁷⁷, and had a 23% higher local extinction rate in North America⁷⁸ than monochromatic species. Causal links are not well known, but sexual selection may act by decreasing effective population size, by increasing demographic stochasticity, or by driving traits away from their natural selection optima, thus increasing their cost⁷⁹.

However, the pattern of increased vulnerability of sexually selected species is not universal and much remains unclear about the links between sexual selection and population persistence and extinction⁵⁸. For example, polygynous species are thought to typically show a large reproductive skew (and thus low N_e) and hence such species are expected to be more vulnerable to genetic stochasticity than monogamous species. However, the model of Legendre *et al.*⁸⁰ shows that in certain situations, monogamous species should be more, not less, susceptible to extinction than polygynous species because the death of a single individual may mean that its mate does not reproduce. Consistent with this, Brashares⁸¹ found that monogamous and

mildly polygynous West African mammals were more prone to extinction than highly polygynous species.

Clearly, the predictions depend on whether genetic or demographic stochasticity is the more important in population decline. If genetic effects are most important, highly skewed reproduction associated with strong sexual selection will make populations vulnerable. On the other hand, if demographic stochasticity predominates, monogamous species may be worst off⁸⁰. While it is clear that there is a link between mating behaviour and the vulnerability of populations to extinction, further work is needed to obtain reliable generalizations that can be used in drawing up priorities for conservation.

Effects of changes in population structure

Changes in the sex- and age-structure of a population can occur through various human activities, including hunting, culling, and translocation. Removal of individuals from populations due to these activities is usually highly non-random. Trophy hunting may focus on larger and older males, and poaching and culling, even when undirected, may remove mostly males in species in which males have larger home ranges, or mostly females in species in which females group together in herds. Similarly, translocation efforts may target specific sex and age classes.

Any change in population structure may have important effects on female choice and its consequences^{82,83} (but see ref. 84). Changes in the relative number of breeding males and females may lead to changes in mating system⁸² and hence the genetics and demography of the population (see above). There may also be consequences of changes in age structure. If high quality (often older) males are removed, female choice for genetic or direct benefits, or both, may be less effective⁸⁵. The precise effects will depend on the nature of the benefits that females receive. If territory quality (e.g., food and safety) is important, replacement males are likely to step in and effects on female reproduction may be small. On the other hand, if paternal care is important and high quality males are removed, this could seriously affect reproduction.

The proximate rules that females use are likely to influence the outcome of changes in population structure. Possible rules include 'best-of- n ', in which a female samples a certain number of males, and chooses the one with the 'best' attributes. Another might be a threshold rule, in which a female will mate with any male above a threshold, but not with any other (e.g., ref. 86). The rules that females follow may help in making predictions. For example, when female preferences are based on a threshold this will lead to low N_e if large males are killed¹⁵. In the Dungeness crab *Cancer magister*, size limits on catching mean that large adult males are removed from the population, and mature females have difficulty finding a sexual partner⁸⁷.

There may be other consequences as well. Harassment of females by males may increase if adult males are removed, and harassment in fish can reach levels at which females do not spawn⁸⁸. In such cases, removal of young males could increase female survival and reproductive success. Removal of males could be catastrophic in certain species. For example, a high turnover of pride male lions *Panthera leo* (perhaps due to shooting) may lead to increased infanticide by replacement males⁸⁹ and this can have drastic effects on population growth⁹⁰. One would expect a similar pattern in other species with infanticide by males (e.g., langurs⁹¹, fish⁸⁸) or by females (e.g., jacanas⁹²). In rigid monogamists (e.g., seahorses, cranes), removal of an individual means the effective removal of its partner. Facultative monogamist/polygamist species should be better able to tolerate the removal of breeding individuals⁸⁸. However, mate removal is likely to increase the vulnerability of the remaining individual to predation while seeking a replacement mate (e.g., seahorses⁸⁸).

Non-destructive harvesting can also have effects. In Portugal, male fiddler crabs *Uca tangeri* are caught, their larger claw is removed, and they are then released. The broken claw is eventually regenerated. Even though individuals are not removed from the population, there may be negative consequences at the population level in part because both females and intact males respond to clawless males as females⁹³, and thus these males may not be able to reproduce.

It appears then, that when evaluating the effect of hunting or large-scale translocation of animals, it is important to take mate choice and mating behaviour into account. For example, using a modelling approach, Greene *et al.*⁹⁴ found that monogamous and weakly polygynous species were more susceptible to hunting of males than were highly polygynous species, and infanticide reduced the resilience of a population to hunting. Hunting that targets adult males or adults of both sexes reduced population growth rate more than hunting of all age- and sex-classes⁹⁴.

Effects of habitat fragmentation and change

The causes of habitat fragmentation and change are usually outside the control of conservationists and managers. But this is not always so, and habitats may even be deliberately changed to meet conservation objectives. Restoration of degraded habitats is an example, as is habitat management in general. Natural changes in habitat (e.g., vegetational succession from grassland to scrub or forest) also occur, even when not deliberately induced. Could habitat change affect mate choice and its consequences?

One effect may be a change in mating system⁸². The polygyny threshold model⁵⁶ holds that the extent of variation in habitat quality affects mating system through its effects on female choice. If habitat quality varies widely, then females should prefer to settle in high quality habitats, even if this means sharing a territorial male with other

females. Such a pattern is seen in, for example, prairie dogs *Cynomys gunnisoni*⁹⁵ and red foxes *Vulpes vulpes*⁹⁶. Habitat fragmentation is an obvious example of increased variation in habitat quality, and by altering the distribution of resources, it may also change female distribution and hence mating system even when mate choice is unimportant⁹⁷. In addition, changes in overall abundance of food may promote one mating system over another and may alter patterns of communal breeding⁸². Variation and abundance of resources are often affected by management practices such as providing food or salt-licks in specific places, enriching natural food sources (e.g., planting grass plots), or encouraging regeneration. For example, planting trees in grassland areas is likely to change the mating system of blackbuck *Antelope cervicapra*, a species in which mating system varies with habitat openness⁹⁸.

Occasionally, habitat changes may lead to disastrous consequences through a complete breakdown of female choice mechanisms. For example, increased turbidity in the waters of Lake Victoria has led to increased hybridization (and thus loss of species diversity) because female haplochromine cichlids are no longer able to distinguish the colour of conspecifics from that of heterospecifics⁹⁹ (see also ref. 100 for the relationship between light quality and behaviour). Similarly, water pollution may hinder the ability of aquatic organisms to choose appropriate mates based on chemical cues.

Effects of disturbance

Human-caused disturbance in wildlife reserves includes poaching, resource extraction, monitoring activities, and tourism. To animals, disturbance (like predation risk) can be thought to be traded off against resource use¹⁰¹. The major effects of disturbance are often thought to be on foraging success, increased tendency of parents to desert young, increase in generalist predators (e.g., crows, rodents) associated with humans, or even a complete avoidance of the area. In addition, there may be subtler effects through female choice.

Because sampling males often takes time, and may increase travel time of females (and thus conspicuousness), one would expect females to be less choosy when predation risk is high than when predators are absent, and this is a common pattern (e.g., ref. 102). If human disturbance causes females to perceive a higher risk the consequences of disturbance may be important in species in which females must find and mate with an appropriate male within a short time window. For example, many antelope, including the blackbuck, have a period of oestrus that lasts only 24 h¹⁰³. If human disturbance prevents females from following their mate-sampling rules, they may not mate at all. Mating in the next cycle may be possible, but fawns are then likely to be born later in the year, possibly under suboptimal conditions. In addition, disturbance is likely

to increase mate-sampling costs to females, and it may increase mating by subordinate males who would otherwise be excluded by dominants⁸³. In some species of conservation concern, then, it may be important to minimize disturbance when females are sampling and mating with males. This is particularly critical in species that mate in large, spectacular aggregations (e.g., colonial waterbirds, lekking antelope, schooling fish).

Captive breeding issues

Although the role of captive breeding in conservation suffers from severe limitations¹⁰⁴, this approach will sometimes be needed for a small number of species. Basic behavioural knowledge, including that of mating system and mate choice, is essential for most captive breeding¹⁰⁵. Knowing how mate preferences develop is a good example. Females often prefer to associate and mate with males who look, smell, or sound like their fathers or other males in the vicinity while they were young. Such a learned preference is called imprinting, and is well-known in a variety of species (e.g., refs 106 and 107). Problems of sexual imprinting in captivity are widely recognized and are minimized by using puppets while hand-rearing¹⁰⁸. When endangered species are cross-fostered¹⁰⁹, inappropriate imprinting or the expression of inappropriate sexual preferences must be prevented by limiting access to the foster species as adults^{110,111}.

In captivity, one has the unusual ability to directly influence mating between individuals. Often, in species with small populations, the overriding goals are minimizing inbreeding by mating nonrelatives and maximizing N_e by minimizing variance in reproduction among individuals. Hence, females are usually given no choice of mate. As discussed earlier, this may lead to problems such as social incompatibility, genetic incompatibility, lowered offspring quality, and a reduction in female fecundity and investment in each offspring.

Because maximizing genetic diversity does not distinguish between beneficial and deleterious alleles, ensuring that all individuals breed may not be the best strategy if there is heritable viability⁶³. For example, in whitefish *Coregonus* sp., optimal mate choice would increase offspring survival during a bacterial epidemic by 12% as compared with random mating¹¹². Grahn *et al.*¹¹³ provide another example of the possible negative effects of removing mate choice. Captive bred Atlantic salmon *Salmo salar* are released on a large scale to supplement wild populations. This species is cultured by mixing eggs and sperm of wild-caught individuals in such a manner as to maintain the greatest genetic variability. When allowed to, however, females prefer more ornamented males (those with large adipose fins), which are of high quality. Grahn *et al.* argue that preventing female choice for high-quality males may be contributing to the high incidence of mortality related to a deficiency of thiamine. They suggest

that mate choice be given more room in conservation breeding programmes, especially where effective population sizes are adequate.

Other consequences of preventing mate choice in captivity include altering female investment in offspring (e.g., fecundity and egg or birth mass) and altering offspring sex ratio. Females in several species are known to change investment in offspring according to the attractiveness of their mate^{114,115}. Not only do females vary investment according to the status of their partners, they also may vary the sex of their offspring. For example, female zebra finches *Taenopygia guttata* prefer males with leg bands of certain colours, and avoid those with leg bands of other colours¹¹⁶. Females mated to preferred males invest more in their offspring and show a male bias in the sex ratio of their offspring, compared with females mated to nonpreferred males^{51,117}. In house mice *Mus musculus*, free mate choice has a dramatic effect on various measures of fitness. Using a behavioural assay to measure female preferences, Drickamer *et al.*¹¹⁸ found that females mated to preferred males had litter sizes 31% larger than those mated to nonpreferred males. Mutual mate preference trials showed that pairs who preferred each other had lower pre-weaning pup mortality (8.1%) than pairs who did not prefer each other (23.9%, ref. 119). Similarly, reproductive output was found to be higher in free-mated pairs than assigned pairs of domestic pigeons *Columba livia*¹²⁰ and Mauritius kestrels *Falco punctatus*¹²¹.

Despite the advantages of free mate choice, it may in some cases be unwise to allow mate choice to dictate captive breeding, and intervention may be needed to circumvent natural breeding systems and enforce mating to meet genetic or other goals^{63,122}. For example, female investment in young should be maximized when the goal is to produce many offspring of high quality. However, increased investment in current reproduction is likely to decrease female longevity and future reproduction, and hence in some cases one may want to maximize female survival by reducing investment in offspring. Regardless of the specific goal, knowledge of the proximate mechanisms that influence female decisions about mate choice, offspring number, offspring sex, and investment in young, will allow us to manipulate these decisions.

Various techniques to influence female preferences are known. For example, Fisher *et al.*¹²³ showed that a female pygmy loris *Nycticebus pygmaeus* can be induced to preferentially associate with a particular male by exposing her to his urine for several weeks. Similarly, Roberts and Gosling¹²⁴ were able to manipulate the preferences of female harvest mice *Micromys minutus* by increasing the familiarity of particular males to the target females, and also by inducing males to increase olfactory signalling. In some species females may reduce their investment in offspring when allowed to sample only a single male. Letting females sample (see, smell, or hear, if not actually mate with) other

males may counter this. If females use a relative evaluation rule, it may be possible to artificially raise the target male's attractiveness relative to others. In birds that use ultraviolet sexual signals, for example, this is easily done by placing other males behind a glass partition, thus blocking ultraviolet light and reducing the perceived quality of these males relative to that of the target male¹²⁵.

Choosing the best management option, then, requires some knowledge of what females choose for, what the benefits of choice are, and what investment decisions females make when mated to males of different kinds. This information must then be weighed against the genetic costs of allowing free mate choice. Benefits of allowing female choice, and costs of denying it may not all occur in all species, just as inbreeding depression may be critical for some, but not other, species. Studies are needed that evaluate the costs and benefits of breeding programmes based on population genetic considerations alone and those that allow room for female choice¹¹³.

Conclusions

Disciplines like behavioural ecology are based on firm underlying theory – that of evolution by natural and sexual selection¹⁹. Such disciplines aim to be strongly predictive, with the predictions coming from robust first principles. We expect organisms to have evolved rules that allow them to behave in a manner that maximizes their fitness, at least in environments similar to those in which they evolved. Changes in the environment should lead to predictable changes in behaviour and, through behaviour, reproductive success. This contrasts with most ecological models (e.g., of population change), which are primarily descriptive and statistical, and cannot be used to predict the consequences of novel changes¹⁶.

Much remains to be done by students of behaviour who want to contribute to conservation efforts. A key area of study is what changes in social behaviour (including mate choice, but also territoriality, grouping, dispersal, etc.) result from changes in the environment (habitat attributes as well as population size and structure). Is there variation among taxa in these changes? Similarly, a deeper understanding of the behavioural determinants of species endangerment and extinction will allow us to better construct priorities for conservation action⁷⁹. Strong generalizations are needed if behavioural concepts are to be of use to conservation.

For their part, conservationists should begin applying behavioural ideas in their work. Where behaviour-mediated outcomes (like mating system) are important, it may be necessary to implement measures to influence the behaviour of individuals in the target population. Even if influencing behaviour is not the goal, managers should not ignore behavioural consequences of their actions. Simple management actions like providing supplemental water or food may change habitat quality and thus mate choice and

mating patterns (and through this, population persistence; Figure 1). In the same way, habitat restoration (or any other change) may have foreseeable (and undesirable) consequences. Ideally, all management interventions would be viewed as formal field experiments and their consequences studied, so that progress could be made in identifying generalizations about the reactions of animals to habitat and population changes.

Similarly, some knowledge of behavioural and evolutionary principles would clearly be useful for those breeding animals in captivity, especially if the goal is to maintain healthy, disease-resistant individuals, perhaps for later release. Captive breeders require good advice on the relative costs and benefits of allowing free mate choice versus breeding to maximize genetic variation. Experimental studies are needed to address such issues, and to explore variation across taxa in the appropriate mixture of approaches. These studies are often best carried out on surrogates, common species that are closely related to endangered taxa (e.g., ref. 126). Students wishing to do behavioural ecological work with conservation implications would do well to focus on such surrogate species. Those managing breeding facilities should also be aware of the diversity of tools available to modify an animal's behaviour using established ethological principles, although much work still needs to be done on such proximate questions as mate-search rules and cues used in mate choice.

All possible tools must be brought to bear in the struggle to conserve biodiversity and natural resources. One suite of tools is provided by recent advances in our understanding of behaviour. Ultimate and proximate considerations of the causes and consequences of mate choice (and sexual selection in general) yield new predictions and new opportunities in our efforts to preserve species and the habitats they live in.

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