VERTEBRATE MATING SYSTEMS, ALLEE EFFECTS AND CONSERVATION

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ABSTRACT

Recent interest has focused increasingly on the role of behavioural research in conservation. Within this field, the study of mating systems can make a highly important contribution. Mating systems both affect, and are affected by, interactions between conspecifics. Of particular importance are Allee effects, which arise as a result of the benefits of conspecific presence. Recognition of the consequences of Allee effects for mating systems, conservation, and behaviour, has also increased recently. The inter-relationship between these areas is highly complex, and both mating systems and Allee effects have consequences for each other, as well as for conservation. In this way, both have direct and indirect consequences for conservation. We discuss these in the light of current, and potential, contributions of the study of mating systems to conservation.

Introduction

In recent years, increasing emphasis has been placed on the potential contributions of behavioural science to conservation1-4. A key area is the study of mating systems. Different mating systems may explain differential susceptibilities of species to certain conservation risks, and a thorough understanding of mating systems is essential for many aspects of conservation intervention and management. Recently, attention has also focused on the role of Allee effects in both behaviour and conservation5-7. Allee effects, named after the pioneering work of W.C. Allee8-10, arise as a result of the benefits of conspecific presence, and manifest as reductions in individual fitness as populations become smaller and these benefits are lost11. The types of Allee effect to which a species is susceptible may both affect, and be affected by, the species' mating system. The inter-relationship between mating systems, Allee effects and conservation is illustrated in Figure 1.

In this chapter, we discuss the relationships between mating systems and Allee effects, and we explore the consequences of these relationships for conservation. We discuss each of the four links shown in Figure 1, although inevitably, there is some overlap between these. We begin with an assessment of how Allee effects can affect mating systems (and thus can have indirect consequences for conservation), and how mating systems may affect a species' vulnerability to Allee effects (also with indirect consequences for conservation). We go on to look at the more direct consequences of both Allee effects and mating systems for conservation.

Mating systems

Allee effects

Conservation

Fig. 1. The inter-relationship between mating systems, Allee effects and conservation. Both mating systems and Allee effects have a direct bearing on many conservation issues. However, Allee effects are important factors underlying the mating system of a species, whilst mating systems can also affect the types of Allee effects to which a species is vulnerable. In this way, both mating systems and Allee effects can also have indirect implications for conservation.

1. Allee effects and their consequences for mating systems

At their most basic, Allee effects arise because self-incompatible species require conspecifics with which to mate. As population densities or sizes decrease, availability of potential mates is reduced. This type of mate limitation is perhaps the most widely cited mechanism of the Allee effect but many others are also recognised. Examples of these have been divided into seven categories, presented in Table 1. For completeness, the table lists examples from a range of taxa, both plant and animal.

Recent evidence suggests that the factors underlying mating systems are considerably more complex than was thought previously\(^\text{12}\). We believe that Allee effects form an important factor in this complex relationship (Fig. 2). Allee effects are important determinants of the spatial distribution of a species (Fig. 3), and hence are significant factors underlying the type of mating system that a species adopts. For example, African wild dogs (\textit{Lycaon pictus}) are among the smallest members of the large carnivore guild of sub-Saharan Africa. The resultant susceptibility of this species to intraguild kleptoparasitism leads to an Allee effect at small group sizes which is an important determinant of group living in this species. This Allee effect can therefore be said to underlie the 'obligate communal breeding'\(^\text{13}\) seen in the African wild dog. Similar arguments can be made for many other species of obligate cooperators.

As a second example, the relatively low metabolic rate of large antelope might account for the lack of selectivity in their diet, which in turn allows them to survive on the open grasslands\(^\text{14}\). However, it is likely that within this extensive habitat, it is Allee effects, due to antipredatory behaviours, that promote herding behaviour among many of these species. Those same Allee effects may therefore be responsible for the ease with which single males can monopolise large groups of females, leading to the polygynous, harem systems, typical of such species.
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### 6. Demographic stochasticity

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### 7. Genetics

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Finally, in pukeko (*Porphyrio porphyrio*), territorial defence has been postulated as a major factor promoting polyandry\(^62\). Males that do not ally with extra male defenders risk losing their territory to those that do, and consequently risk losing the opportunity to breed. Thus Allee effects arising from inadequate territorial defence by individuals appear to promote polyandry in this species.

From the above examples, it is clear that Allee effects can have major implications for the type of mating system adopted by a species. Understanding the relationship between Allee effects and mating systems is therefore an important element in understanding both the social and breeding behaviour of the species. In particular, this is important for understanding how social dysfunction can result from rarity and impair a species' chances of recovery. It can also be relevant to successful captive breeding. In helping to shape the mating system of a species, Allee effects may also have indirect implications for conservation, as outlined in section 4.
Fig. 3. Several component Allee effects may act on a species simultaneously. The relationship between these and any negative density dependent factors will be important in determining the degree of aggregation and thus the spatial distribution. Component Allee effects 1 and 2 may represent, for example, ease of mate finding and benefits of "safety in numbers". These have the effect of increasing fitness from its basic level in the absence of conspecifics ($F_0$), up to some point where increased aggregation brings no further benefit through these mechanisms. Negative density dependence by contrast, may result from increased competition for food or mates, or increased depletion of resources. This will tend to decrease fitness from $F_0$ as degree of aggregation increases. The cumulative fitness represents the relationship between all the density dependent factors, and dictates an optimal degree of aggregation $A_0$.

2. **Mating systems and their consequences for Allee effects**

In section 1, we discussed how Allee effects can affect the spatial distribution and, hence, the mating system of a species. However, many other factors, including environment, mate choice and parental care systems also dictate the mating system of a species. These can, in turn, influence the nature of associations between individuals and groups, and can thus affect the type of Allee effects to which a species is susceptible. For example, more solitary, monogamous species might be more vulnerable to certain Allee effects than are aggregative or polygamous species. In particular, these might include mate finding Allee effects when at low densities\textsuperscript{63}, and problems due to skewed sex ratios when population sizes become small. Polygamous breeding systems might also be more susceptible to certain Allee effects. Most notably, these include some of the genetic problems associated with small population sizes.
As observed in section 1, mate limitation is an important mechanism of the Allee effect. In small populations, or populations at low density, this may arise simply as a result of infrequent encounters with potential mates, as has been demonstrated for some insect species (see Table 1, 5.1-5.3). Similarly, unequal sex ratios which arise stochastically in small populations, may also lead to mate limitation. As an example, chance differences in the numbers of males and females in a small population of reintroduced sea eagles (*Haliaeetus albicilla*), in Scotland, led to a significant number of individuals failing to form pairs. A further, less obvious form of mate limitation results in species in which sexual selection plays an important role in the mating system. Females have been shown to have higher reproductive success when breeding with males of perceived high quality, even where differential male quality is based entirely on nonfunctional ornaments. The differential-allocation hypothesis suggests that females may allocate more reproductive effort to offspring sired by higher quality mates. It follows from this, that if mate choice is restricted in small or low density populations, then low parental investment and low reproductive output may result. Such a phenomenon would certainly correlate with low reproductive rates and success in many species of zoo animals, where forced matings with apparently suitable mates are conducted without regard for mate choice. Leks provide a forum for mate choice in a variety of species. It would be interesting to know whether species which rely on such communal displays are particularly susceptible to small population extinctions. Finally, mate limitation may also arise where individuals are highly related, and animals avoid breeding in preference to breeding with a close relative. This has been shown for acorn woodpeckers (*Melanerpes formicivorus*) (see further below) and is also thought to be a feature of the meerkat (*Suricata suricatta*) mating system.

For polygamous species, genetic issues may be of particular concern. Genetic mechanisms are perhaps the most widely discussed mechanisms of the Allee effect (although rarely by that name), but their importance to declines in survival and fecundity is still widely debated. Three genetic mechanisms of the Allee effect are given in Table 1: inbreeding, genetic drift, and hybridization. Hybridization is discussed in greater detail in section 4; in the current section we will concentrate more fully on inbreeding and drift.

Both inbreeding and genetic drift lead to a reduction in heterozygosity and allelic diversity. Of considerable concern is inbreeding depression, the increased expression of deleterious, recessive alleles that can result from reduced heterozygosity. The negative effects of inbreeding depression have rarely been documented in natural populations of vertebrates, but potentially costly behavioural mechanisms aimed at avoiding inbreeding in natural populations, suggest that its consequences may be severe. Given that genetic mechanisms are dependent on effective population size, $N_e$, it may be expected that polygamous mating systems will increase rates of inbreeding and loss of genetic variation, and experimental data support this prediction. Frankham calculated that genetic management could potentially increase the ratio of $N_e/N$ almost 20-fold, and discussed several methods by which this could be achieved. These included: equalising family size; reducing reproductive skew by decreasing polygamous mating strategies; minimising population fluctuations; and minimising kinship between breeding individuals. All of these strategies are clearly far more easily implemented in captivity than in the wild, whilst such intensive manipulation of natural breeding strategies and, potentially, disproportionate selection for less fit phenotypes, remain contentious. In particular, as discussed above,
interfering with free mate choice might well be detrimental to the health of captive populations. Different species react in different ways to inbreeding. It has been observed that many species have relatively high inbreeding coefficients, and yet remain unaffected. These differences may reflect differences in the natural abundance of the species, but will also be dependent on their mating systems. For many vertebrates, dispersal is an important behaviour relating to the mating system, and obviously functions to reduce inbreeding. However, in fragmented habitats, dispersal is frequently highly risky, or indeed, impossible. Understanding the natural behaviour of a given species may therefore have important consequences for issues such as reserve design, corridor use, or translocation.

There is some support for the idea that repeated inbreeding of healthy individuals can 'purge' a population of deleterious alleles and thus prevent inbreeding depression, although evidence for this process is limited and the method is not without considerable risks. Knowledge of the species' natural mating system may be important in determining the merits of this process. More commonly, efforts are directed towards maximising heterozygosity within populations of rare species. Encouraging gene flow between subpopulations, or introducing individuals from elsewhere can improve reproductive fitness; however, risks associated with disease transmission, dilution of locally co-adapted genes and other costs of translocation, mean that this must be judged on a case by case basis, and only with a sound knowledge of the mating system of the species involved.

To summarise, mating systems can impact on the type of Allee effects to which a species is susceptible. As a result of this, mating systems and other associated behaviours can also affect the vulnerability of a given species to certain types of conservation risk. An understanding of mating systems is thus an important component in assessing and treating the causes of population declines.

3. **Allee effects and their direct consequences for conservation**

The major consequences of Allee effects for conservation have been reviewed recently. Allee effects often result in aggregative behaviour or group living, which can render species more susceptible to certain types of conservation threat. Examples include disease outbreaks, which models indicate can more readily establish in aggregated host populations, and harvesting, which may be more efficient and damaging, when the target species is highly aggregated. Beyond these specific examples however, the principal implications of any type of Allee effect can be inferred from incorporating Allee effects into simple models of population dynamics (Box 1 and Fig. 4). The most important conclusion of this simple modelling approach is that at reduced numbers or densities, Allee effects reduce the viability of groups, populations, or species. Furthermore, where Allee effects are strong, lower threshold group or population sizes result, below which growth is negative, and extinction is highly likely.
Box 1. Allee effects and models of population dynamics

Allee effects can be described, for example, by either a negative exponential or a rectangular hyperbola function. Due to its mathematical tractability, the rectangular hyperbola function is most easily incorporated into models. This function takes the form:

\[ p = \frac{n}{(\theta + n)} \]  

(1)

where \( p \) is the fitness due to the component Allee effect, \( n \) is the population size and \( \theta \) is the population size at which \( p = 0.5 \). The value of \( \theta \) allows the strength of the Allee effect to be scaled (Fig. 4a).

The specific growth rate of populations limited by the “carrying capacity” of their habitat is often given by the logistic equation:

\[ \frac{dn}{dt} = r - \frac{rn}{k} \]  

(2)

where \( t \) is time, \( r \) is the intrinsic growth rate of the species, and \( k \) is the carrying capacity. When \( n < k \), the specific growth rate is positive and \( n \) increases. When \( n > k \), growth is negative and \( n \) decreases. Thus the population always tends towards \( k \) (Fig. 4b).

Given that equation (1) gives relative fitness under an Allee effect, the reduction below optimal fitness which results from that effect can be derived as:

\[ 1 - p = \frac{\theta}{(\theta + n)} \]  

(3)

An Allee effect can thus be incorporated into the logistic equation by subtracting a term proportional to equation (3) from equation (2). Whilst \( \theta \) will scale the Allee effect, a term of proportionality, \( \alpha \), will allow the severity of the Allee effect to be modelled. Logistic growth subject to an Allee effect will thus be given by:

\[ \frac{dn}{dt} = r - \frac{rn}{k} - \frac{\alpha \theta}{(\theta + n)} \]  

(4)

The result of this additional term is that the specific growth rate is depressed at any given population size, and that this reduction is most marked at low values of \( n \) (Fig. 4c). The population will have two equilibria - a lower, unstable equilibrium and an upper, stable equilibrium. The lower equilibrium is critical; below this, growth is negative and the extinction of the group or population becomes highly likely.
Fig. 4. Allee effects and simple population dynamics. a) A function such as the rectangular hyperbola can be used to describe Allee effects. Allee effects increase in severity from left to right, with values of θ of 2, 10, and 20. b) The standard logistic model of population growth accounts for negative density dependence only. Below the carrying capacity (k), growth is positive, and the population increases towards k. Above k, growth...
is negative. Thus $k$ is a point of stable equilibrium. c) When an Allee effect from (a) is incorporated into the logistic equation, the dynamics are radically altered. The population now has two equilibria, $C$ and $U$. The upper equilibrium, $U$, is stable, at a point somewhat below $k$ from the logistic equation. The lower equilibrium, $C$, is unstable and critical. Below this, the population is highly likely to tend towards extinction. Population growth is positive, only in the interval between $C$ and $U$. The distance between these equilibria depends on the severity of the Allee effect.

Depending on the mechanisms involved, the implications of these simple models may apply at either group, aggregation, or population level, whilst a similar mathematical approach can also be applied to the persistence of metapopulations\textsuperscript{78}. Where the model is considered at a group level, there is a lower, unstable equilibrium, analogous to some minimum group size, below which, mortality is likely to exceed natality. Such thresholds are typical of obligate cooperators\textsuperscript{6}. These are species in which helpers are required for survival or reproduction, for example, for antipredatory measures; defending territories, nests or dens; transporting young; or provisioning young, gestating or incubating females. Examples of these include saddle-back tamarins ($Saguinus fuscicollis$), that rarely or never attempt breeding as lone pairs, probably as a result of energetic restrictions on females, for whom foraging, lactation and transport of infants would be too costly without additional helpers to share infant carrying\textsuperscript{79}. Similarly, reproductive success for pairs of dwarf mongooses ($Helogale parvula$) without helpers is negligible\textsuperscript{13}. A more extreme example has recently been demonstrated for meerkats. In an area of high predation, juvenile mortality in this species is inversely related to group size, and is extremely high for groups of less than four individuals. Small groups of meerkats thus have extremely limited reproductive success, particularly in harsh environmental conditions\textsuperscript{70}.

Many group-living species show dominance hierarchies and some form of reproductive suppression, such that only one pair in any group will breed. In such cases, differences between actual population size, $N$, and effective population size, $N_e$, can be striking. Examples include the gray wolf ($Canis lupus$), where the number of breeding groups, rather than the number of individuals, controls increases in population persistence\textsuperscript{80}. Such dynamics have been suggested to account for the slow recovery of the Ethiopian wolf ($Canis simensis$), following disease epidemics a decade ago\textsuperscript{7}.

At the level of the aggregation, Allee effects can also impair reproduction when individuals are present in low numbers, leading to unstable equilibria at minimum flock or colony sizes. The example of reduced reproductive success in small colonies of guillemots ($Uria aalge$), due to less effective predator swamping, is given in Table 1. The inability of small flocks of some species of flamingo ($Pheniconaias spp.$) to reproduce due to a lack of social stimulation is indicated by studies of captive populations\textsuperscript{81}, and provides another example of an Allee effect at this level.

Of considerable concern to conservation biologists, is the interval between the upper, stable, and the lower, unstable, equilibria. Populations fluctuate as a result of a range of factors, including weather, disease, food supply, predation, or even overcompensating density dependence\textsuperscript{82}. If the amplitude of population fluctuation is of a similar order of magnitude to the interval between the population's equilibrium sizes, then this leads to the possibility of extinction. This has been suggested as an additional factor leading to the dramatic extinction of the North American passenger pigeon ($Ectopistes migratorius$)\textsuperscript{83}. 

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Finally, Allee effects may also have potential as a conservation tool. Conspecific presence can be an important factor influencing patch choice, especially for younger individuals\textsuperscript{84}, and thus decoys or call playback can be employed to encourage preferential colonization in protected areas, or recolonization of deserted or recently restored patches of habitat\textsuperscript{85,76}.

To summarise, the major direct consequences of Allee effects for conservation arise from the change in population dynamics, particularly at low population sizes or densities. Conservation is usually required because habitat loss or fragmentation, exploitation, or the impacts of introduced predators, competitors or disease, have led to increased mortality in a species or population. Species which are subject to strong Allee effects are likely to be far less able to withstand these additional sources of mortality, far less likely to recover, even after the source of mortality is checked, and far more likely to decline to extinction, than are other species.

4. Mating systems and their direct consequences for conservation

The study of mating systems is crucial to many areas of conservation, not only those concerned with assessing, understanding and treating risks due to Allee effects. Two of the most important causes of anthropogenic extinctions, are over-exploitation and the impact of introduced species.

Overexploitation accounts for almost one quarter of all extinctions of species since 1600, for which the cause can be identified\textsuperscript{86}. In general, exploitation will cause increases in mortality which, for species subject to Allee effects, may have unforeseen consequences (see section 3). However, exploitation may have other consequences also, on which the study of mating systems may have a more direct bearing.

Differential mortalities due to harvesting can affect mating systems and reproductive parameters. Sport hunting is usually biased towards larger animals, and frequently towards males. Selective removal of adult male ungulates by tourist hunters is believed to reduce female fecundity, and modelling indicates that it could lead to population collapses\textsuperscript{87}. A classic example of a species subject to differential harvesting pressure between sexes, is that of the African elephant (\textit{Loxodonta africana}). Traditionally, this species has been harvested for ivory. Tusk size varies between sexes and also with age, so that ivory based exploitation very rapidly leads to populations with distorted sex ratios and age structures\textsuperscript{76}. These authors concluded that selective removal of males can lead to sperm limitation, whilst selective removal of females would reduce the size of female herds, decreasing the incidence of males finding female herds and, consequently, also lowering per-capita fecundity.

In fisheries, sexual dimorphism can also lead to differential exploitation. Young gag groupers (\textit{Mycteroperca microlepis}) are predominantly female, transforming into males as they grow larger, a trait known as protogyny. Differential mortality of the larger males has been shown to lead to highly skewed sex-ratios, potentially leading to sperm limitation (Koenig \textit{et al.} 1996, cited in\textsuperscript{88}). Other species of fish provide a range of examples of the complex effects of exploitation on reproductive strategies\textsuperscript{88}. Fish species which mature late are also more susceptible to overexploitation\textsuperscript{89}.
Study of mating systems of exploited species may suggest a range of different approaches to methods of exploitation. First, contrary to traditional approaches, where larger adults are removed throughout the population, removal of whole groups might be preferable to removal of small numbers of individuals from many different groups. Depending on the mating system of the exploited species, this could prevent the reproductive output of remaining groups from being compromised, permitting them to increase and fractionate, and allowing vacant habitat to be recolonised. Second, selective removal of males can have a particularly serious effect on monogamous species by reducing local male densities and creating a mate finding Allee effect. For these species, removal of pairs, rather than individuals at random, might also be preferable. Third, where habitat is exploited, either for agriculture or, for example, timber production, knowledge of the biology of resident species will be important in determining whether utilisation should be intensive or extensive. Where a species is sensitive to habitat degradation, intensive utilisation might be favoured; whilst this will reduce the quantity of available habitat, remaining habitat will permit species to remain at natural local densities. If, by contrast, animals are more tolerant towards habitat degradation, extensive utilisation will be favoured, as this will maximise available habitat, and thus will be more likely to support populations above critical threshold sizes.

The study of mating systems can also have an important bearing on the problem of hybridization. Almost 40% of all extinctions of species since 1600 for which the cause can be identified, can be attributed to introduced non-native species. Introduced species can impact on populations of native species in a wide variety of ways, including by direct predation, by competition, by spreading diseases to which native species are naïve, or, if closely related to a native species, by hybridization. The effects of predation, competition or disease were alluded to in section 3, above, and derive mainly from the increased mortalities which these cause. In this section, we will focus on the problem of hybridization.

Hybridization and genetic introgression have been reported in all five classes of vertebrates. These processes underlie concerns for the future of the rare white-headed duck (Oxyura leucocephala) that can hybridise with ruddy duck (O. jamaicensis) introduced to Europe from North America. Similarly, the Ethiopian wolf is threatened by genetic introgression by feral domestic dogs (Canis familiaris), and concern exists over the extensive hybridisation between native red deer (Cervus elaphus) and sika deer (Cervus nippon) introduced to Scotland from Japan. Susceptibility to genetic introgression will depend on many aspects of mating systems, including modes of fertilisation, degree of promiscuity, and nature of courtship behaviours. However, examples exist for almost all conceivable breeding systems, across a range of taxa with many elaborate forms of courtship behaviour. Viability of hybrid offspring can also be crucial in determining the extent of the problem, although even where introgression is prevented by inviable hybrids, loss of breeding potential can threaten the parental populations, as in European mink (Mustela lutreola), whose females generally abort after mating with introduced male American mink (M. vison).

A detailed knowledge of the mating systems and breeding biology of species which can hybridize might render policies for prevention more effective. Understanding patterns of mating and cues for mate attraction can help to identify the potential for hybridization. Slight differences in timing of breeding between the two species might be exploited to
cause disruption at the time favoured by the non-native species. Alternatively, hybridization might be unidirectional. For example, studies of the Ethiopian wolf mating system indicate that male dogs can mate with female Ethiopian wolves, but hybridization is unlikely between female dogs and male Ethiopian wolves. Selective control of free-ranging males may thus be sufficient to prevent hybridization.

In general, the best way to avoid hybridization, or other risks of introduced species, is to prevent the introductions from occurring. It is likely that many countries could adopt much more stringent measures for preventing accidental spread of exotic species and diseases, both by adopting stricter hygiene rules at docks and airports and by preventing introduced species from becoming established. The potential impacts of roads, railways and canals should also be considered in the light of their potential as corridors for the movement of alien species. Even the use of deliberate habitat corridors has been criticised on the basis that connectivity can accelerate the spread of introduced species. Most introduced species will be most easily eradicated whilst few individuals remain, and Allee effects may make this even easier. However, Allee effects will also tend to depress population increases whilst an alien species is present in low numbers, potentially promoting complacency at the time when the species is most vulnerable to eradication.

The study of mating systems can also make a major contribution to conservation through captive breeding and reintroductions. For many species, available habitat has been so reduced, or remains threatened to such an extent, that the persistence of those species in situ cannot be assured. Habitat destruction is widely believed to be the predominant cause of extinction and accounts for over a third of all recent extinctions for which the cause can be identified. For species threatened by habitat destruction, it might often be necessary to take representative individuals into captivity, maintaining a reservoir population until habitat can be restored, and other forms of threat neutralised. Despite continued debate regarding the economic prudence of this approach, this rationale has led to a widespread commitment of zoos to captive breeding, and to the formation of a Conservation Breeding Specialist Group (CBSG) within the World Conservation Union (IUCN). Genetic considerations for captive breeding and release were discussed by Frankham but it has been observed that for captive breeding at least, some of the commonest difficulties are behavioural. It is worth commenting on the contribution that research into social and breeding systems can make to several aspects of these processes.

Social conditions may play an important role in encouraging captive animals of many species to breed. Classically, most species kept for breeding are housed in male-female pairs. However, these arrangements might not always reflect the natural social conditions of the species concerned. Some temporal variation in social organisation is also common for many wild vertebrates. Allowing free mate choice may be an important aspect of enhancing reproductive success in captivity, even though this may conflict with genetic considerations (see also Section 2). Detailed knowledge of mating and post-natal behaviours may also reduce breeding failures, abandonment or death of young. Wielebnowski cited the example of the cheetah (Acinonyx jubatus). As with several other carnivore species, cheetah move their young when disturbed. Disturbance in captivity may provoke this behaviour, and it is therefore important that more than one den site is both available and provisioned.

Social facilitation of reproduction has been shown to be important in captive bred lemurs. A study of the worldwide pattern of captive reproduction in Eulemur species over
the past 20 years showed that female black and mongoose lemurs (E. macaco and E. mongoz, respectively) housed with additional conspecifics, have higher reproductive rates than those maintained as part of an isolated pair. As discussed in section 3, social enhancement of group displays has also been indicated as an important element increasing breeding success in several species of captive flamingos (Phenicconais spp.)101,81. It has been shown that the incidence of breeding displays in smaller flocks can be increased by the use of mirrors in indoor enclosures102. Mirrors provide the appearance of more birds taking part in marching displays, which has a synergistic effect in encouraging other birds to join the display.

Maintenance of natural social organisations may be especially important for species intended for reintroduction. Previously, callitrichid primates were believed to breed in isolated pairs. This is likely to be an artefact of captivity however, where energetic constraints to breeding are far less significant than in the wild, and where the type of cooperative polyandry seen in many wild callitrichids is thus not necessary103. Evidence from studies of captive callitrichids suggests that experience of alloparenting and family life are important determinants of future reproductive ability104. Callitrichids bred for release in the wild should thus be housed in social conditions which more closely mirror those experienced in natural habitat.

Studies of social behaviour and breeding strategies can also be of benefit to introductions and re-establishment, particularly in making informed decisions regarding founder population sizes, release sites and release procedure. Perhaps unsurprisingly, number released has been shown to be positively related to likelihood of establishment for both insects105 and birds106. Release procedure can be tailored to prevent Allee effects which might result from aspects of the breeding behaviour. A tendency for long-range, post-release dispersal may favour soft-release protocols involving temporary penning at the release site. For example, simultaneous releases of male and female brush-tailed phascogales (Phascogale tapoatafa), an arboreal Australian marsupial, resulted in dispersing males failing to find the few females released. Staggered releases allowed females to establish territories prior to the release of males, increasing the success of this programme107.

To summarise, the study of mating systems can play an important role in many areas of conservation, including management of exploited species; identification of the risks, and subsequent control, of hybridization; and in captive breeding and reintroductions. However, the capacity of the study of mating systems to contribute to conservation, has yet to be fulfilled, and the links between these fields continue to offer enormous potential for research.
References