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Social behaviour in conservation

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Overview

This chapter develops links between social behaviour and demography, and illustrates how knowledge of social behaviour may be used to manage populations for conservation. The chapter is necessarily speculative, both because the 'formal' field of conservation behaviour is still only a decade old, and because explicit applications of social management are still relatively uncommon. I summarise case studies where social behaviour has been manipulated to manage populations, and suggest possible ways that behaviour could be used to manage populations. After defining effective population size, I list a number of ways that social behaviour may influence it, via genetic variation, survival and reproductive success. Reproductive skew emerges from unequal reproduction, which may be caused by (among other things) social stress, reproductive suppression and infanticide. Social aggregation may reduce natural mortality, and the observations that animals seek conspecifics may be used as a management tool to attract individuals to protected locations. But conspecific attraction and social aggregation may also predispose a population to be vulnerable to human exploitation. Social factors (including reproductive opportunities) may drive dispersal and movements between groups. Humans can influence the structure of social relationships in animals, and these manipulations may influence group stability. Knowledge of these and other mechanisms arms managers with tools to manipulate the habitat or relationships to favourably influence social behaviour and structure, and thereby better manage a population.

20.1 Introduction

Conservation behaviour applies behavioural principles to help conserve (or manage) animal populations (Blumstein & Fernández-Juricic 2004). The link between social behaviour

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and conservation works through demography. Many wildlife conservation problems are demographic, where a major objective is to increase (or maintain) a population's growth rate, or to increase its likelihood of persisting over time. Demography thus provides a unifying principle that links behaviour and conservation (Anthony & Blumstein 2000). The social structure, social interactions or social behaviour of a population or species may affect persistence via its effects on reproduction or survival. For instance, mating systems influence a population's genetic structure, and therefore population viability. Reproductive competition, a defining feature of highly social species, influences demography via reproductive suppression and infanticide, and these behaviours may influence sustainable harvesting levels in European brown bears *Ursus arctos*, African lions *Panthera leo*, and capybara *Hydrochoerus hydrochaeris*. A feature such as conspecific attraction may generate insights to attract animals to particular locations, but it may also make a species more vulnerable to exploitation. Grouping may reduce predation risk. Finally, because social structure and social behaviour are often adaptive responses to environmental variation, anthropogenic changes may have a profound influence on social behaviour, and consequently on demography and population viability. In this chapter I will describe these and other potential links between social behaviour and wildlife conservation, and provide examples to illustrate them.

What is best for individuals is not necessarily best for the population. This tension is no better illustrated than when we wish to understand how (and why) social behaviour influences demography, and thus population biology. Conservation biologists are obsessed with the number of individuals because they focus on population persistence. An important sub-discipline of conservation biology develops *population viability analyses* (PVA), where the goal is to estimate the likelihood of a population persisting over a given time (Soulé 1987, Beissinger 2002). The process requires decision makers to compile or estimate demographic parameters and to have a clear underlying demographic model (Beissinger & McCullough 2002). All else being equal, a large population is more likely to persist over a given amount of time than a small one.

Remarkably, many PVA models do not include relevant behavioural parameters (Derrickson *et al.* 1998). Whether and how behaviour may affect population persistence is an empirical question, but factors such as Allee effects (negative density dependence: Courchamp *et al.* 1999), conspecific attraction (Stamps 1988), reproductive suppression (Wasser & Barash 1983) and sexually selected infanticide (Ebensperger 1998) all are likely mechanisms through which behaviour influences population persistence. It is by developing explicit models of how these behaviours may influence demography that we will gain fundamental insights into the relationship between social behaviour and population persistence.

The relationship between behaviour and conservation should be explicitly experimental (Blumstein 2007). Wildlife managers are often reluctant to consider that behaviour may influence demography, or to consider potential behavioural interventions. This may be because they have not been formally trained in behaviour (for instance, to be a 'Wildlifer' certified by the US Wildlife Society, a course in behaviour is one of only many electives: www.wildlife.org/certification). Alternatively, it may be because they may believe that behaviour has a relatively small effect on population persistence. Thus, behavioural ecologists who wish to fundamentally influence wildlife conservation should be trained in adaptive management (Walters & Holling 1990, Johnson 1999), and should design their studies to measure the effect size of behaviour on population persistence (admittedly, this may require long-term studies and controlling for a variety of extrinsic and intrinsic factors that influence population persistence). If behaviour has a strong and compelling link to demographic processes, wildlife managers must seriously consider it – much as they already consider the relationship between genetic diversity and extinction risk (Frankham *et al*. 2002). (Remarkably, many decisions in conservation management are not based on adaptive management (Pullin *et al*. 2004, Sutherland *et al*. 2004, Blumstein 2007, Seddon *et al*. 2007). Thus, intrepid behavioural biologists who seek to integrate behaviour into conservation biology may face two sources of opposition: that against behaviour, and that against active adaptive management.)

The field of conservation behaviour is young (Buchholz 2007), and we are still at the stage of creating the toolkit for wildlife managers to deploy when they face a particular problem. The topics in this chapter should be viewed as ripe for exploration. Thus, this chapter is more a prospective review than a definitive summary. Students should realise that there is a lot to work on, and that they can make significant advances by integrating theoretical behavioural ecology with wildlife conservation biology.

20.2 The effect of social behaviour on effective population size (N_e), and its importance to conservation behaviour

20.2.1 Defining N_e

While the number of animals (N) in a population is a first approximation of endangerment, other factors may influence the likelihood of a population going extinct over time. One of these is the population's genetic variation. The effective population size (N_e) of a population better reflects the likelihood of extinction due to genetic homozygosity (Gilpin & Soulé 1986).

N_e is an estimate of the theoretical number of breeding individuals, assuming they behave in an ideal way. An ideal population has the following attributes: the population is split into subpopulations without migration between them, there are no overlapping generations, the number of breeding individuals is the same for all generations and subpopulations, individuals mate randomly, there is a random amount of self-fertilisation, there is no selection, and mutation is assumed to be unimportant (Falconer 1989). Clearly, these assumptions are not likely to be met in most populations of interest to conservation behaviourists. Regardless, low N_e may affect population viability by increasing homozygosity and decreasing the number of non-selected alleles. This loss of genetic variation may be compounded by an increase in linkage disequilibrium, which itself reduces the number of novel gene combinations.

N_e is influenced by factors that impinge on the ability of gametes to be passed to the next generation. Such factors include: exclusion of closely related mating, biased sex ratios, unequal generation sizes, unequal family sizes, inbreeding and overlapping generations (Falconer 1989).

We can see how behaviour may influence N_e by examining an equation to calculate N_e assuming no overlapping generations:

$$N_e = \frac{1}{\frac{1}{4N_m} + \frac{1}{4N_f}} \tag{20.1}$$

where N_e = the effective population size, N_m = the number of breeding males in the population, N_f = the number of breeding females in the population. Calculations of N_e explicitly acknowledge that not all individuals breed (e.g. Nunney 1993, Parker & Waite 1997).

Anthony and Blumstein (2000) suggested that behaviour influences N_e by influencing reproductive skew, the number of breeding individuals and the reproductive rate (Fig. 20.1). They suggested that by focusing on these pathways we could better integrate behaviour into PVA models. I will reiterate some of these suggestions as well as expand our previous discussion to include other social behaviours.

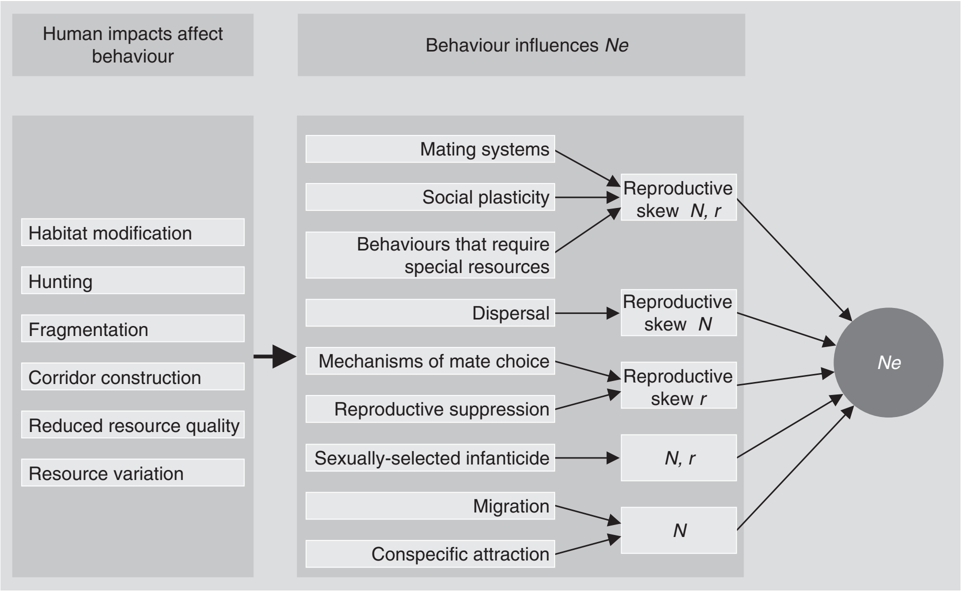

Figure 20.1. Conceptual links between behaviour and demography, and between anthropogenic impacts and behaviour. From Anthony & Blumstein (2000); used with permission.

20.2.2 How mating systems may affect N_e

Mating systems influence N_e by determining which gametes will be passed on to the next generation (Anthony & Blumstein 2000). Contrast a genetically promiscuous duck, a harem-polygynous elephant seal *Mirounga* sp., and a genetically monogamous goose with biparental care. Parker and Waite (1997) illustrated (using a modification of the above equation) how mating system influences N_e. They assumed that the population size was 100 and there was a 50% failure rate. The promiscuous species (characterised by each male mating with each female) had an N_e of 67. The monogamous species (where each female mated only with a single male) had an N_e of 50. And the highly polygynous species (where males mated with multiple females but some males did not mate) had an N_e of 19. Interestingly, a highly polyandrous species (where males mated with multiple females but not all females mated) had an N_e of only 9.

Greene *et al*. (1998) explored the effects of mating system on the consequences of hunting. They incorporated breeding systems into demographic life-table analyses and subjected their populations to different types of hunting. The effect was profound: populations of monogamous breeders always grew at a slower rate than those of more polygynous breeders. This is because in monogamous systems both males and females are limited in their ability to obtain fertilisations. Hunting strategy (trophy or subsistence) interacted with mating system, but highly polygynous species were less susceptible to hunting-related mortality.

20.2.3 Managing N_e *for conservation*

A discussion of mate choice, while it may have an effect on N_e (Blumstein 1998), is beyond the scope of this review (see Chapter 10; Swaisgood & Schulte in press). However, mate choice can be manipulated experimentally, as the large literature on sexual selection demonstrates (Andersson 1994), and manipulating mate choice has been used to address conservation problems (e.g. Fisher *et al*. 2003). For instance, male pygmy lorises *Nycticebus pygmaeus*, an endangered nocturnal primate that relies heavily on olfactory communication, could be made more attractive to females when females had olfactory experience with the males, and when the males' scent over-marked the scents of other males. Manipulating attractiveness is a conservation behaviour tool that can be used in other captive breeding situations.

Because the population sex ratio will influence N_e, and the adult sex ratios of endangered birds are often male-biased (Donald 2007), sex ratios may also need to be adjusted to manage N_e. In an elegant study of the endangered kakapo *Strigops habroptilus*, Robertson *et al*. (2006) capitalised on the evolutionary theory of sex allocation (Trivers & Willard 1973), which suggests that the offspring sex should be a function of maternal body condition. Kakapo managers wanted to ensure all females were in good condition, so they initially provided them ad lib food. This created an unexpected problem: clutches from these extremely well-fed females were highly male-biased!

Robertson *et al*. (2006) then successfully shifted the offspring sex ratio by strategically manipulating breeding females' body condition. This technique could be employed in other captive breeding programmes where sex ratios became unnaturally biased towards one sex.

20.3 Other effects of mating systems on population structure and genetic variability

Patterns of reproduction in a group will influence the genetic properties of the subpopulation and population. Traditionally, population geneticists focused on three types of heterozygosity: variation within individuals, variation among individuals in the same subpopulation, and total population variation (Sugg *et al*. 1996). Sewall Wright (1969, 1978) developed fixation indices (F_{IS} – within subpopulations, F_{ST} – among subpopulations, and F_{IT} – within the entire population) that calculate an observed value of genetic variation compared to what would be expected in an ideal population (e.g. with random mating and no mutation or selection). These fixation indices can be used to estimate the degree of inbreeding and therefore the rate at which genetic variation is lost.

Species with social structure, however, violate a fundamental assumption of such models, namely that animals mate randomly within a subpopulation (Sugg *et al*. 1996, Dobson 1998). Does this make a difference in predicting the rate at which genetic variation is lost? Sugg *et al*. (1996), Dobson and Zinner (2003) and Dobson (2007) reviewed a series of studies that concluded it does. The key is that kinship relationships (coancestry), which develop from mating tactics and sex-specific dispersal strategies, develop more quickly than inbreeding in social groups. Historically, kinship and inbreeding were the only mechanisms proposed to account for genetic similarity. Yet the formal models developed to study gene dynamics describe how genetic variation changes as a function of social structure. And it is this genetic structure that it is essential to quantify if one is to properly calculate effective population sizes.

The argument is based on a formal model called the *breeding group model* (Chesser 1991a, 1991b, Chesser *et al*. 1993, Sugg & Chesser 1994). Sugg *et al*. (1996) evaluated the breeding group model by applying it to black-tailed prairie dogs *Cynomys ludovicianus*. These social rodents meet a key assumption of the model: populations are subdivided into groups comprised of kin. Several studies reported that the rate of female dispersal would influence the rate at which genetic variation was lost (Dobson *et al*. 1997, 1998, 2004). As female dispersal rates increased, heterozygosity was lost faster. This finding has a somewhat counterintuitive implication for a commonly used population recovery technique, translocation, which involves moving animals from one location to another to recover a locally extinct population (Kleiman 1989). By moving females from their original colonies to found new colonies, genetic variation was more quickly lost. The results from Dobson and colleagues suggest that it is essential to understand the effect of sociality on gene dynamics when designing management strategies to preserve genetic diversity (see also Chesser *et al*. 1996).

20.4 How relatedness among group members and reproductive skew influence reproduction and population size

Relatedness among group members is likely to influence cooperative and competitive social behaviour, and these are likely, in turn, to influence reproduction and population size. As one example, consider reproductive skew. Unequal sharing of reproduction (i.e. skew) within cooperative groups is a pervasive phenomenon. Vehrencamp (1983) was the first to explicitly propose that the ability to behaviourally create reproductive skew may play an important role in stabilising group cooperation. Her initial models of reproductive skew have been greatly elaborated to focus on the relative control of reproduction within groups by dominants and subordinates (e.g. Emlen 1982, Reeve & Ratnieks 1993, Reeve *et al.* 1998). Such 'transactional' skew models may explain shared reproduction because both dominants and subordinates can increase fitness by living in the groups relative to living alone (Nonacs 2001). Interestingly, transactional models predict that genetic relatedness can strongly influence skew, but this effect also depends on the environmental constraints on group and solitary living (Johnstone 2000, Nonacs 2001).

Because skew influences who breeds, anything that influences skew can affect gene dynamics, and therefore will effect N_e. Ecological constraints have long been known to be important factors explaining social-system variation (Crook 1970, Wilson 1975, Lott 1991) that may affect both social and non-social species. For instance, cooperatively breeding and reproductively suppressed Seychelles warblers *Acrocephalus sechellensis* that were translocated to an isolated island without resident warblers suddenly reproduced. As the small island began to saturate with breeding territories, newly born residents became reproductively suppressed (Komdeur 1992). Similarly, the removal of resident breeding male superb fairy-wrens *Malurus cyaneus* led to the immigration of males that were previously helping their parents raise young (Pruett-Jones & Lewis 1990). In both cases, the lack of available breeding vacancies was identified as an ecological constraint on breeding which consequently generated reproductive skew.

Patchy environments limit dispersal ability and form another possible constraint implicated in the origin of reproductive skew. For instance, in the family of rodents that includes the eusocial naked mole-rat *Heterocephalus glaber*, widely scattered food, arid habitats and hard soils are hypothesised to select for group living (Lacey & Sherman 1997, Lacey 2000). Interspecific variation in mole-rat group size is associated with food density and rainfall (Faulkes *et al.* 1997). However, such constraints are likely to be relatively rare compared to more dynamic variation in ecological factors, such as climate, that affect growing season.

Thus we should generally expect animals to engage in dynamic skew games that may have consequences for population persistence. Identifying the causes and consequences of skew within a species may provide strategies by which managers may increase the likelihood of a population persisting over time. In particular, reducing ecological constraints, and thereby reducing reproductive skew, should increase N_e.

20.5 How reproductive conflict may affect demography

Clearly, reproductive skew has demographic consequences. Skew results from competition among potential breeders, and we generally expect animals to compete for breeding opportunities. Here I discuss two mechanisms of reproductive conflict that may create reproductive skew and have profound effects on demography and population persistence: reproductive suppression and sexually selected infanticide.

20.5.1 Reproductive suppression

Complex sociality is characterised by a reduced probability that all individuals reproduce (Blumstein & Armitage 1998, Cahan *et al.* 2002). Often this is accomplished through reproductive suppression, whereby potentially fertile females do not breed (Solomon & French 1997), and such suppression is often a mechanism that leads to reproductive skew (see Chapter 14). If females living closely with others compete reproductively, then not all females breed or litter sizes are reduced. Reproductive suppression therefore reduces the population size and the effective population size by reducing the number of potentially reproductive females who are able to breed (Anthony & Blumstein 2000).

Habitat saturation may be a direct cause of reproductive suppression and alloparental helping (see Chapter 12). Some species, when faced with no chance to breed independently, engage in alloparental care, and therefore may obtain indirect fitness benefits. Such helping behaviour has been demonstrated to be a strategy whereby individuals make the 'best of a bad job' because, as discussed above, when individuals are translocated to a location with potentially available territories, they immediately begin breeding independently (e.g. Komdeur 1992). Thus, identifying species where habitat saturation suppresses independent reproduction gives us a tool to use should managers need to increase the number of breeders.

Alberts *et al.* (2002) experimentally removed dominant male Cuban iguanas *Cyclura nubila* from a population where they prevented subordinates from breeding. This removal led to formerly subordinate males taking over vacated territories and winning more fights. While the authors were unable to directly study the effect on reproductive success, such interventions might help increase the number of breeding individuals and thus, they argued, prevent the loss of genetic variation.

Mechanisms of suppression can be sophisticated, and they may also affect captive animals that, in theory, have sufficient resources to breed independently. One mechanism of suppression is via social stress (Wingfield & Sapolsky 2003). Such stress-induced sterility works through both the hypothalamic–pituitary–adrenal (HPA) and the hypothalamic–pituitary–gonadal (HPG) axes. Life-history theory leads us to expect that reproduction is traded off against growth and maintenance. Thus, when animals are particularly stressed, they should allocate energy away from reproduction and growth, and mobilise energy to facilitate escape. It is this reallocation of energy that leads to stress-induced sterility. If social animals, in which reproductive suppression is known or suspected to occur in the wild, fail to breed in captivity, then a strategy to increase reproduction might be to reduce the opportunity for social stress by moving animals apart. In some species social facilitation is required for breeding (Hearne *et al.* 1996, Swaisgood *et al.* 2006). It is therefore essential to conduct formal experiments to see whether stress-induced reproductive suppression is reduced by moving potential breeders apart, or whether grouping facilitates reproduction.

20.5.2 Sexually selected infanticide

In harem-polygynous species, sexually selected infanticide is seen when males kill the unrelated offspring of a female to whom they have just acquired access. Access may result from the previous male dying (either naturally or via hunting), or it may be the outcome of a territorial take-over. Regardless, by killing unrelated young, the new male need not allocate time or energy to care for someone else's offspring and, by eliminating maternal care, he either reduces the time until the female can breed again or increases the likelihood of her breeding with him the next season. Infanticide mainly affects the population size by decreasing the survival rate of infants and reducing juvenile recruitment (Anthony & Blumstein 2000).

Such sexually selected infanticide has been reported in a variety of carnivores, including European brown bears, African lions, non-human primates and many rodents (see Sarah Hrdy's profile; Packer & Pusey 1984, Blumstein 2000, van Schaik & Janson 2000, Swenson 2003, Ebensperger & Blumstein 2007). It has a profound effect on demography because typically males are ignored when modelling population persistence. In populations or species that engage in sexually selected infanticide males (specifically fathers) suddenly become important for persistence, because their presence prevents other males from coming in and killing young.

Sustainable hunting models, in particular, can become more realistic when sexually selected infanticide is considered. For instance, brown bears in Scandinavia engage in sexually selected infanticide (strangely, North American brown bears, i.e. grizzlies, do not). Swenson *et al.* (1997) found that killing a single adult male would decrease the population growth rate by 3.4% and disrupt male social organisation for 1.5 years. However, models that explicitly examined the effects of killing male lions (another species that exhibits sexually selected infanticide) found that current hunting levels should not drive the population to extinction (Greene *et al.* 1998). A capybara harvest model that explicitly compared the effects of sexually selected infanticide by males and reproductive suppression on population size found that the effect size of infanticide was small compared to that of reproductive suppression (Maldonado-Chaparro & Blumstein 2008). Such behaviourally informed models are important tools for the managers of species that exhibit sexually selected infanticide, many of which exhibit declining populations.

20.6 Social aggregation reduces mortality

In some cases it is safer to be in a crowd than alone, and there are many ways that individuals may aggregate (see Chapter 9). For instance, animals may live in temporary or more stable social groupings, or they may breed in a colony site with many other conspecifics. Several models of predation hazard assessment note that per-capita risk declines as group size increases (Krause & Ruxton 2002). This may result from the confusion that multiple prey create when moving around, or it may result from the collective vigilance that emerges when animals are in groups. Regardless of the precise mechanism, for species that benefit from aggregation, predation rates may be density-dependent, and at lower densities there may be a greater risk of predation (e.g. Sandin & Pacala 2005).

The relationships between time allocation and group size are referred to as *group-size effects* (Bednekoff & Lima 1998). Importantly, group-size effects are not restricted to highly social species. Many species form transient foraging aggregations despite no long-lasting social bonds. Group-size effects are typically studied by looking at the relationship between group size and time allocation to foraging and anti-predator vigilance. The general assumption is that if group size provides safety, then we should expect to see that as group size increases, individuals allocate more time to foraging and less time to anti-predator vigilance. In most species, we assume that foraging and vigilance are mutually incompatible: thus time allocated to vigilance cannot be allocated to other beneficial activities, such as foraging.

There are a few difficulties with quantifying group-size effects. The first is that determining whether vigilance behaviour is directed to predators or conspecifics is difficult and not always possible. There have been some attempts in primates by looking at gaze direction (Treves 2000), but most studies are unable to precisely identify the target of vigilance. The second is that there are other reasons why animals might forage more in larger groups. For instance, if feeding competition increases, then animals will forage more because of increased competition, rather than decreased risk. This is particularly a concern for species that engage in scramble competition on exploitable patches of food (Beauchamp 1998). However, if food is more or less abundant and not particularly patchy, then we should be able to infer that individuals benefit from aggregation if the time allocated to foraging increases as group size increases.

For such species, translocations or reintroductions may need to be carried out with complete social groups. Many translocations and reintroductions for conservation fail because recently introduced individuals end up being killed by predators (Beck *et al.* 1991, Short *et al.* 1992, Miller *et al.* 1994). This creates an ethical issue – animals die because of our actions (Bekoff 2002) – and a practical issue – the recovery may not work (Kleiman 1989). Doing anything to increase the survival of these animals is an important goal of much reintroduction and translocation research (Kleiman 1989, Seddon *et al.* 2007). Thus, by moving animals in social groups, predation rates may decline, and individuals may survive longer. The best evidence that social translocations may improve reintroduction success comes from a study of black-tailed prairie dogs (Shier 2005, Shier & Owings 2007a, 2007b). By moving intact social groups, individuals survived longer because the likelihood of predation was reduced.

20.7 Potential effects of conspecific attraction on survival and management

The presence of other conspecifics may provide compelling evidence that a particular location is suitable. There is a growing body of evidence that animals use conspecifics as cues when assessing habitat suitability and making habitat settlement decisions (Stamps 1988). This phenomenon has been used by conservation biologists to help attract individuals to a particular location (Schlossberg & Ward 2004).

For instance, on the Fort Hood military base in Texas, conservation biologists were trying to recover the endangered black-capped vireo *Vireo atricapilla*, a species that was negatively impacted by brown-headed cowbirds *Molothrus ater* (Ward & Schlossberg 2004). Cowbirds are brood parasites and lay their eggs in other species' nests. Cowbird nest parasitism is responsible for the decline of a number of species, including the black-capped vireo. On the base, cowbirds were eliminated and wildlife managers wanted to attract black-capped vireos to nest in areas where cowbirds were controlled. To do so, they played black-capped vireo song from 04:00 to 10:30 h during the nesting period. They found that in locations where song was played more vireos nested, and these nests were successful. Thus, by capitalising on conspecific attraction, conservation biologists were able to locally recover a population.

Social grouping (and conspecific attraction) may make a species more vulnerable to exploitation. Consider the large colonies of nesting seabirds and marine mammals that made them ripe for exploitation by sailors upon discovering the islands. And consider herding ungulates, such as the plains buffalo *Bison bison*, a species for which Richard Irving Dodge noted that in 1871, while riding through a 25-mile-long herd, 'the whole country seemed to be one mass of buffalo moving slowly northward' (Dodge 1877, p.120). This species was hunted almost to extinction. Or consider the extinct passenger pigeon *Ectopistes migratorius*, a species that lived in such large populations that 'flocks in the migratory period partially obscured the sun from view' (Anonymous 1910).

From the perspective of a hunter, hunting success may be higher on grouped than on solitary individuals. This is because in some situations there is a positive density-dependent relationship between population size and predatory success (Sih 1984). Such a relationship may arise from individuals forming search images, whereby hunting success increases with experience (which is correlated with population size), or because once a patch is located hunting success may increase. For any given predator–prey system, it is an empirical question whether there is positive or negative density dependence, and the specific nature of this relationship may inform conservation.

20.8 How social factors may influence dispersal and movement between groups

In many species, dispersal is influenced by social structure or group size. Residents may disperse if there are no breeding opportunities but remain if there are opportunities within the group. Such facultative dispersal increases the variation in the nature and types of interactions found.

In some cases, wildlife managers wish to eliminate individuals that may have a transmissible disease. However, the outcome of such culling may be an influx of immigrants, and these immigrants may have to form social relationships anew. Such a strategy of killing residents has proved counterproductive in at least two instances where residents were killed to reduce the spread of a disease.

Localised killing of resident European badgers *Meles meles* to eliminate outbreaks of bovine tuberculosis (TB) was found to be counterproductive because this led to the influx of immigrants (Woodroffe *et al*. 2006, Jenkins *et al*. 2007). Badgers can be carriers of TB, and for many years they were locally killed when infections were discovered. However, badger immigrants ranged widely and visited more settes (and communal latrines) than residents. This increased movement was counterproductive because it could increase the rate of transmission of TB between badgers, and potentially from badgers to livestock.

Such a result is generally expected (Smith 2001), and similar findings emerged from a study of brushtail possums *Trichosurus vulpecula* in New Zealand. Killing residents led to increased movement of males in controlled areas, which potentially exposed more possums (and livestock) to TB (Ramsey *et al*. 2002).

20.9 How phenotypic plasticity in social structure may predispose species to respond to anthropogenic activities

The social structure of many species is phenotypically plastic. Such intraspecific variation in social systems is thought to be adaptive (Lott 1991), but it raises the possibility that anthropogenic change can modify social structure. It could do so through at least two mechanisms: modifying the habitat, or modifying the nature of the social relationships.

20.9.1 Modifying the habitat may modify social structure

Modifying the habitat is easier to envision, because many models of social evolution are based on the link between the distribution and abundance of resources and social system. For instance, the classic Emlen and Oring (1977) model of mating systems is based on the distribution of females being determined by the distribution of food, and the distribution of males being determined by the distribution of females. If females are clumped, and therefore defensible, polygyny may result. Thus, by modifying the distribution of critical resources, either intentionally (as part of a management intervention) or unintentionally (via anthropogenic changes), the mating system may vary. The genetic consequences of a variable mating system were discussed above, as were the consequences of variable group sizes. Thus, habitat modifications may influence survival and reproduction via its effects on mating systems.

20.9.2 Humans may change the nature of social relationships

To understand how human activity may affect the structure of groups, a very brief introduction to social network analysis is required. Social network analysis is a tool that can be used to study the structure of groups (Chapter 9; Croft *et al*. 2008). Social groups (and structure) emerge from interactions among individuals. In a network, individuals are nodes, and interactions between them form the links. By developing an association matrix of social interactions, it is possible to plot the social network, and to calculate a number of network statistics, both for individuals and for the overall group. These social network statistics formally describe attributes of sociality and, as such, provide a more comprehensive understanding of structure than simple measures like group size (Wey *et al*. 2008).

One insight from social network analysis is that all individuals in a group may not be equivalent. A network approach to studying sociality suggests that certain individuals may be ‘key players’ (Borgatti 2003). The removal of key players might have a disproportionate influence on social stability. For instance, in pig-tailed macaques *Macaca nemestrina*, adult males engage in third-party policing whereby they break up fights among females. By doing so, they have a stabilising influence on the rate of agonistic interactions among a group’s females. Interestingly, their importance is even greater than would be predicted by a network analysis. Flack *et al*. (2006) created experimental groups, observed social interactions, and then graphed the resulting network. They then removed certain males from the simulated network, and recalculated network structure (this served as a control). Compared to this control, the network changed even more when males were experimentally removed from the social group.

In African elephants *Loxodonta africana*, female matriarchs possess knowledge that helps increase a group’s per capita reproductive success (McComb *et al*. 2001). These large individuals are often targeted by hunters, and their removal may have disproportionate effects on group productivity. Importantly, their removal has long-term deleterious consequences for young males, who grow up without proper adult control/supervision and become a real problem when they become adolescents (Bradshaw *et al*. 2005).

Network analyses, and analyses of the pattern of social interactions, can be used to study the consequences of anthropogenic disturbance. For instance, social relationships can be influenced by tourism, as has been found in bottlenose dolphins *Tursiops* spp. (Lusseau 2003a). Specifically, Lusseau used Markov-chain analyses to quantify how behavioural patterns of dolphins were modified by ecotourists. He found that the presence of boats truncated dolphin social interactions. Such interactions are essential for structuring the social group of this fission–fusion species (Lusseau *et al*. 2005). Lusseau (2003b) also used insights about the scale-free nature of the structure of dolphin social networks to predict that the loss of individuals would not fragment the cohesiveness of a group.

20.10 Conclusions and future directions

This chapter has highlighted selected links between sociality and wildlife conservation. Because wildlife conservation biologists are often faced with relatively small populations, it is essential to understand behaviours that influence demography. I have illustrated how a variety of social behaviours may affect reproduction and mortality. I have also discussed how behaviour may influence gene dynamics, which itself may influence population persistence.

A criticism of conservation behaviour is that there are a lot of implications, but few applications in the form of practical examples of behavioural knowledge helping recovery (e.g. Caro 2007). While not entirely true, this is a valid concern, and conservation behaviourists should work to apply their knowledge to species recovery (Buchholz 2007, Swaisgood 2007). One impediment to application is that wildlife managers are often not trained in animal behaviour. It is by working closely with behavioural ecologists that they will learn how behavioural ecology may be helpful to them. Through such collaborations, they will see if this knowledge can help develop better population viability models, increase the likelihood that animals breed in captivity, and increase the success of population recovery tools such as translocation and reintroduction. Such studies should be designed in the context of adaptive management, whereby experiments are designed to see if a changed model, or a changed management option, has a significant and substantial outcome. If not, the extra costs associated with behaviourally based management may not be that useful. If so, then behavioural ecologists will have made a fundamentally important contribution to wildlife conservation.

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