CHAPTER 9

Social behaviour

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➲ Overview

Social structure and social behaviour are influenced by environmental factors. Hence, human-induced environmental changes are likely to have a variety of impacts on sociality and, because sociality often has demographic consequences, on population biology. We can learn a lot by capitalizing on intraspecific and interspecific variation in sociality to identify key environmental drivers of demography. In this chapter, I discuss some of the many ways that social behaviour and social structure are dependent upon the distribution and abundance of resources and other environmental factors. Armed with such knowledge, we can begin to develop individual-based models that will allow us to evaluate the relative importance of these anthropogenically-influenced environmental drivers and, ultimately, better predict the consequences of anthropogenic change on a variety of animals.

9.1 Introduction

Many anthropogenic activities ultimately influence the environment. These environmental changes affect the distribution and abundance of resources that animals use as well as the predators, parasites, and pathogens that they interact with. At the individual level, changes in resources influence the frequency and type of social interactions. Social structure, that includes the number and type of individuals in a group, and the duration and nature of their interactions, emerges through interactions between individuals (Hinde 1976; Whitehead 2008). We often assume that these social interactions are influenced by their benefits and costs, which may vary both temporally and spatially (Krause and Ruxton 2002) and will be influenced by the distribution and abundance of resources and predators, parasites, and pathogens. We should care about identifying the links between resources and other key factors influencing sociality because social structure has a variety of fitness and, hence, demographic consequences (Blumstein 2010; Blumstein and Fernández-Juricic 2010).

How can we learn about these links? In many cases the emergent social systems that describe patterns of space use and grouping, as well as breeding systems, vary both intra- and interspecifically (Lott 1991). It is the intraspecific variation in social systems that can help us understand the link between anthropogenic activities, their demographic consequences, and ultimately will influence whether a population goes extinct or persists in response to anthropogenic activities (Fig. 9.1). Identifying how populations vary may allow us to predict how anthropogenic stressors may cause systematic changes in key demographic parameters like survival and reproduction, and hence a population's persistence.

In this prospective review, I will describe some potential links between the environment and sociality that should influence demography. I will mostly focus on the individual, but clearly the links between anthropogenic activities and population persistence or extinction span multiple ecological levels (Fig. 9.1). Space prevents a comprehensive review of all possible relationships between sociality and envi-

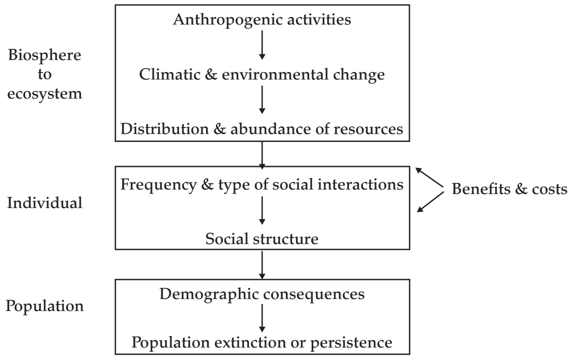

Figure 9.1 The relationship between anthropogentic activities and population extinction or persistence works through individuals interacting with important resources in their environment. The benefits and costs of interacting with others are influenced by the distribution and abundance of resources, and the benefits and costs of these interactions influence the resulting social structure.

ronmental and anthropogenic change. Suffice it to say that most aspects of sociality may be either directly, or indirectly, influenced by the environment. Rather, I selectively discuss some potentially important links between sociality and the environment focusing mostly on birds and mammals, but the ideas apply more generally to other taxa as well. I adopt a pluralistic approach when thinking about animal social groups and will discuss those that are simply ephemeral aggregations not characterized by strong social bonds, and those in which individuals may have more formal relationships, roles (e.g. breeder/non-breeder, territorial member/non-territorial floater), and bonds. Ultimately, any density-dependent activities may have fitness consequences and hence be important for understanding population biology (e.g. Courchamp et al. 2008). I will emphasize the importance of developing a mechanistic understanding of this social variation and will suggest that, once developed, we can use it to construct individual-based models that will allow us to predict the demographic consequences of anthropogenic factors, such as climate change and habitat alteration.

9.2 What environmental factors might influence sociality and how do humans impact them?

Whether directly through habitat destruction or modification, or indirectly through climate change, humans have a profound impact on the distribution and abundance of food and other essential resources that animals may require. Many factors influence where individuals are found and how they may interact in areas where they are found: food and predators are two important ones. For instance, consider two areas, one with predators and one without predators. All else being equal, more prey will be found in the area without predators than with predators. Humans may influence the distribution and abundance of predators both by killing predators and by introducing (or reintroducing them), or by modifying predators' food and creating mesopredator releases (Ritchie and Johnson 2009).

Animals often form groups when under predation threat because, simply by grouping, individuals may reduce their risk of predation. At least three models of predation hazard assessment (detection—Pulliam 1973; dilution—Pitcher and Parrish 1993; predator confusion—Landeau and Terborgh 1986; Krakauer 1995) predict that animals should forage more and allocate less time to antipredator vigilance as group size increases because predation risk declines with the addition of alternative prey. All three models assume a constant attack rate (i.e. that by grouping, individuals are not attracting more predators). This is likely not true in all cases (e.g. Cresswell 1994; Botham and Krause 2005), and if it is not, the form of density-dependence must be identified.

The distribution of predators may change naturally and independently from any changes in resources. For instance, if a predator's range is more closely tied with some environmental driver than its prey, under human induced environmental change, there could suddenly be more predators around, thus increasing predation risk, and the algebraic benefits of grouping shifts towards grouping. Yet the perception of risk may also drive intraspecific variation in grouping. Indeed animals may be more inclined to group in exposed areas to reduce their risk, as seen in coral trout *Plectropomus leopardus* (Goeden 1978), rainbow fish *Melanotaenia eachamensis* (Brown and Warburton 1997), and a variety of ungulates (Eisenberg 1981). Grouping in a specific habitat type influences resource depletion in those locations and may be a potent indirect effect of predation on the larger community (e.g. Laundré et al. 2010). And, if human activities force prey to group in a specific habitat type, there will be an enhanced effect of human activities on overall biodiversity.

Humans also move predators around (Bradshaw and Bekoff 2001). Consider the remarkable experiment that has been conducted in the Greater Yellowstone ecosystem since 1995 with the reintroduction of wolves *Canis lupus* (Smith et al. 2003). Wolves have directly and indirectly changed ungulate behaviour; ungulates flee them and avoid areas around willows *Salix* spp.—because these areas have limited visibility. The consequences of avoiding willows have led to an increased density of both willows and the birds that rely on them. Thus, the introduction of wolves led to an increase in breeding bird density. Grouping dynamics have also been changed by the reintroduction of wolves. Such changes in behaviour are not always expected. For instance, cape buffalo *Syncerus caffer* do not respond to spatial variation in lion *Panthera leo* predation risk, even though lions are a major source of predation (Prins and Iason 1989).

Similarly, humans may influence the distribution and abundance of pathogens and parasites. Parasites and pathogens are known to have a variety of direct and indirect effects by influencing, for example, mortality (e.g. Atkinson et al. 2009) or the behaviour of their hosts to facilitate disease transmission. In the case of the latter, we see direct links between the presence of a parasite or pathogen and host behaviour. Parasites and pathogens may also influence animals by affecting the abundance or distribution of their resources (e.g. changes in plant pathogens may influence the abundance of key plants). Human-mediated changes to the environment, such as climate change, are therefore expected to shift distributions of parasites and pathogens and create situations where animals may be suddenly exposed to novel parasites (Parmesan 2006).

We know from studies of birds (e.g. Brown and Brown 1986), mammals (e.g. Hoogland 1995), and lizards (Godfrey et al. 2009) that individuals in larger groups are more likely to have ecoparasites and other directly transmitted pathogens. Thus, changes in ecological factors that influence interaction rates can influence parasitemia. Such changes might be as simple as reducing available habitat, or as complex as changing the distribution of key resources to which individuals are attracted, or key players in the system, that is, individuals with a disproportionate effect on others (Borgatti 2006). In turn, parasetemia can directly influence mortality (Nunn and Altizer 2006), or indirectly influence mortality through making animals more susceptible to predation (Møller and Nielsen 2007). Parasites may change the adaptive value of sociality, and sociality may itself also select for antiparasite behaviour, such as allogrooming that mediates the effects of parasites (Bordes et al. 2007).

Human-mediated changes in the distribution of food and cover (e.g. through habitat fragmentation, habitat conversion and urbanization) can also be important in a social context. In particular, changes in resource distribution may influence the likelihood that individuals interact. Indeed, classic behavioural ecological models of sociality highlight the importance of resource distribution on group living (e.g. Johnson et al. 2002; but see Revilla 2003). If resources are clumped, individuals using those resources may aggregate to harvest them. This is seen in black-shouldered kites *Elanus caeruleus* (Mendelsohn 1988), golden jackals *Canis aureus* (MacDonald 1979), and spotted hyenas *Crocata crocata* (Kruuk 1972); three (of many) species for whom grouping varies intraspecifically and where more individuals are associated around locally dense food.

Clumping can occur along spatial and temporal domains and humans can create artificial clumps through agriculture, habitat fragmentation, or through our concentration of waste at dumps. Consider a fruiting tree that attracts frugivores. One benefit to group-living frugivorous primates (or bats) is that by living socially, individuals in a group are more likely to find these dispersed but important resources (Garber 1987). If resources have a more homogeneous distribution both in space and time, defence costs may exceed any benefits associated from defending them. A well-studied example of just how dynamic these decisions may be comes from a study of pied wagtails *Motacilla alba*. When food (aquatic insects that wash up on the shore) is scarce, individuals defend a territory on both sides of the bank. As food becomes more abundant, territory holders may share their territories with an associate without suffering any costs (Davies 1976). And, if food is superabundant, territoriality breaks down entirely. Humans, through our habitat modifications may thus affect territoriality.

Recent work (López-Sepulcre et al. 2010) illustrates that the relationship between resources, territoriality, and demography is not necessarily simple or straightforward. Seychelles magpie robins *Copsychus sechellarum* live on variable quality territories that are distributed in space. Individual robins compete more for access to the best territories. This territorial competition is 'bad' for the population as a whole because territorial replacements interfere with effective reproduction. Thus, dispersed resources—which are increasingly likely under human-induced environmental change—may be likely to enhance competition, and ultimately reduce population productivity.

Mating systems also illustrate the link between resources and distribution nicely. Here, female dispersion is often influenced by resource distribution. Males, in turn, track females. Thus, if resources are clumped, females may clump around those resources and males may compete for access to females. The underlying logic of this economic defensibility argument (Orians 1969; Bradbury and Vehrencamp 1977; Emlen and Oring 1977) is that we often assume that females, because they produce relatively fewer gametes than males, are a somewhat limiting resource. Importantly, female reproductive success can only increase by enhancing the survival of their young while males could conceivably mate with additional females. Thus, female fitness is strongly linked to resources whereas male fitness is linked to female distribution and abundance.

A nice example of this comes from a comparison of pinneped mating systems. On sea ice, females are widely distributed and males are unable to defend more than one or a few females. By contrast, on beaches, breeding colonies may have hundreds (or thousands) of females and dominant males can (and do) defend large harems (Le Boeuf 1978). Reproduction on these harems is highly skewed (Le Boeuf and Ritter 1988). As year-round sea ice melts out because of climate change (Markus et al. 2009), breeding females will be forced to have their pups on beaches and, if many of them aggregate on the same beaches, we may see greater reproductive skew.

Reproductive skew has genetic and hence potentially demographic consequences, particularly through its effects on a population's genetic heterozygosity (Anthony and Blumstein 2000). In a given year, with a fraction of males reproducing, the population will be more homozygous than in a mating system where all males have an equal probability of breeding. This reduced heterozygosity could enhance the likelihood of population extinction should a new parasite or pathogen infect the population. Indeed, if anything, we need more genetic heterozygosity to enable populations to respond to a variety of anthropogenic assaults, which will create variable environments, than is needed during periods of stasis.

Yet, the opportunity to have multiple mates need not be all bad. Because clumped females may attract more males, and because females may benefit from mating with more than a single male (Gowaty et al. 2010), it is conceivable that changes in resource distribution could influence the frequency of polygyny by females, and this could influence female fitness and hence population size. At this point, such effects are somewhat speculative and need to be studied in more systems.

9.3 Adaptive social behaviour has demographic consequences

I suggest that anything that influences demography—via its impacts on survival or reproduction—

is worthy of study if one wants to understand how to manage populations under human-induced environmental change (Anthony and Blumstein 2000; Blumstein and Fernández-Juricic 2010). Individuals may engage in social behaviour in an attempt to increase their fitness and it is largely through this enhanced survival and reproduction that social behaviour has its demographic consequences. Knowledge of social behaviour can be applied to wildlife management problems to either increase a threatened or endangered population, or to decrease a 'problem' population (Blumstein and Fernández-Juricic 2010).

However, social behaviour is complex and resources may drive aggregation but aggregation may not necessarily be beneficial to the population. Individuals react to other individuals in the environment and by doing so they also may affect the fitness of other individuals. It is important to realize that what is good for an individual may not be good for the population as a whole. Such 'Tragedy of the Commons' (Hardin 1968) may be common—particularly with respect to mating behaviour, where individual decisions may have negative population consequences (e.g. Blumstein 1998) and sexual conflict, where males may reduce female fitness (Rankin et al. 2011). However, as Rankin et al. (2007) point out, such conflicts are not restricted to reproductive behaviour. Indeed, any situation where individuals compete for depletable resources could lead to suboptimal outcomes for a population. For instance, the added value to a solitary animal joining a group might be positive, but beyond the optimal group size, individuals in the group may have their fitness reduced by the addition of extra individuals (Giraldeau 1988). And, when social cooperation has evolved, cheaters reduce the fitness of others (e.g. Rainey and Rainey 2003) and may drive a population extinct.

Animals living together often compete for depletable or patchy resources, and key resources such as nesting sites or burrows may be in short supply (Krause and Ruxton 2002). In many cases, individuals who have an option, opt out of social living. Such systems illustrate the often-facultative nature of sociality and group living. Indeed, observations like this suggest that sociality is sometimes environmentally forced because of resource limitations. This is most notable when we see subordinate animals failing to breed when living socially, but reproducing quite well when not, as seen in a variety of taxa (Brown 1987; Koenig et al. 1992; Brockmann 1997; Solomon and French 1997).

A defining characteristic of many species living in long-term social groups (*contra* those in social foraging aggregations) is the potential for reproductive suppression. Reproductive suppression is seen when potentially fertile females do not breed (Solomon and French 1997), although it also may occur in males, as seen in bluehead wrasse *Thalossoma bifasciatum* (Warner and Swearer 1991). It often emerges when key resources are limited and dominant (often older) individuals monopolize them (e.g. Komdeur 1992). Such resources may include burrow, nest, or shelter sites, or food. Importantly, reproductive suppression, which may reduce genetic variability, is another example of something that may be good for the dominant breeder, but may not be good for the population as a whole.

In an elegant and now classic experiment with Seychelles warblers *Acrocephalus sechellensis*, Komdeur (1992) demonstrated that habitat saturation explained variation in warbler nesting success. When individuals who were reproductively mature but failed to breed were translocated to an empty island, they bred. Until this habitat became saturated, breeding continued. This demonstrates a profound social cost to living in groups.

When anthropogenic disturbances influence the distribution or abundance of resources, the benefits or ability to aggregate will shift—as may the proportion of individuals that breed. Such effects may not be absolute, but socially induced suppression can also delay the onset of reproduction, as has been suggested in yellow-bellied marmots *Marmota flaviventris* (Armitage 2003). The age of first reproduction has profound impacts on individual fitness (Oli and Armitage 2003), and ultimately demography.

Kinship may also influence the adaptive value of sociality and the benefits of engaging in potentially cooperative behaviour that may enhance both individual fitness as well as group productivity. Human-induced habitat changes that affect where animals forage, or how animals group, may directly influence the likelihood that individuals interact with relatives. Consider a hypothetical species that lives in kin groups and defends a group territory. Imagine that suitable habitat that houses multiple groups is drastically reduced by habitat destruction (development, deforestation, desertification, etc.). As pressure to live in the remaining suitable habitat increases, social structure may break down and individuals are more likely to interact with non-kin. If cooperative behaviour is biased towards relatives, interacting with more non-relatives could reduce the benefits obtained by grouping, and thus reduce individual and perhaps group fitness.

9.4 Individual based models link environmental drivers with demographic outcomes

I suggest that the key to understanding how anthropogenic stressors may influence sociality and ultimately demography and population persistence is to build mechanistic models that link environmental drivers of sociality to individual social 'decisions' and then to demographic outcomes of these decisions. To do so, one must first identify the sorts of ecological drivers of sociality. Then, one could build individual based models and conduct sensitivity analyses to better understand the importance of climatic factors on emergent sociality.

Individual based models link behavioural decisions with demographic outcomes (Huston et al. 1988). To build an individual based model one must start with a clear question. These can be varied—but for now let's focus on models that have examined population persistence (e.g. Grimm et al. 2003; Rossmanith et al. 2006) and population regulation (e.g. Ridley et al. 2003).

Given a focused question, it's then important to identify key behavioural decisions that could influence this outcome as well as ecological drivers of these decisions. Such drivers could be specific sources of mortality (e.g. winter mortality, as shown in individual-based models in marmots), and the behavioural decisions could include dispersal (in marmots and Seychelles warblers), the frequency of polyandry (in woodpeckers), or the incidence of reproductive suppression (in Seychelles warblers).

With a set of decisions, it's important to then find a range of parameter values that will drive dynamics in a way that can be studied. Finding these may require a bit of computational work, but is an essential step. When possible, these parameters may be based on real parameter values from real systems (e.g. Grimm et al. 2003; Rossmanith et al. 2006).

Ultimately, the goal of building such a model is to look for emergent dynamics, but the relative importance of environmental drivers on demography can be identified using this approach. Let's review an example to better illustrate the method.

Lesser-spotted woodpeckers *Picoides minor* are typically monogamous, but sometimes mate polyandrously (Rossmanith et al. 2006). Such facultative polyandry is seen when a female has two separate nests, each with a male who helps care for chicks. However, the reproductive successes of the primary and secondary males are different; primary males have higher reproductive success. This polyandry is more likely in years when there are relatively more males in the population and is likely explained because secondary males are making the best of a bad job. At the population level, however, such polyandry is good in that it increases the population's growth rate. Thus, populations are expected to be more likely to persist with polyandry.

The individual-based model that Rossmanith et al. (2006) constructed to study behavioural flexibility of mating systems assumed that there were a series of annual time steps that followed each individual from birth to death. What happened in each time step was described by a series of rules. Such rules quantified the likelihood of a pair persisting, the probability of eggs not hatching, the probability of nest predation, the probability of an individual being killed, the probability of when an individual is killed its nestlings all die, and so on. Demographic noise was introduced by randomly distributed predation. The model was formally set up as a population viability analysis (Beissinger and McCullough 2002) in that the authors were interested in the estimated time to extinction. A sensitivity analysis was conducted where key parameters (such as juvenile survival rate and rate of polyandry) were individually varied and the resultant times to extinction estimated. The key result was that polyandry rate was negatively associated with time to extinction; polyandrous populations persisted longer.

To be particularly useful in predicting responses to anthropogenic change, models must parameterize and study the effects of environmental drivers on sociality. Such mechanistic, individual-based models may be best able to capture this variation and help us understand the links between the environment, sociality, and their consequences.

9.5 Possible consequences in the Anthropocene

Paul Crutzen, the Nobel Prize-winning atmospheric chemist who helped discover the effects of Freon on ozone, along with colleague Eugene F. Stoermer have described our current geological epoch as the Anthropocene because of humanity's profound impact on the environment (Crutzen and Stoermer 2000). Two of the drivers of this impact are anthropogenic climate change and anthropogenic habitat alteration.

Climate change will influence the distribution and abundance of plants and animals, and there will likely be 'winners' and 'losers' in both the shorter term and longer term. For instance, in the short term, we will have more (and more toxic) poison ivy *Toxicodendron radicans* (Mohan et al. 2006), and yellow-bellied marmots (in at least some locations) than before (Ozgul et al. 2010). Yet we also know that global warming is responsible for the local (and ultimately potentially global) extinction of many species and we currently see widespread evidence of changes in evolved phenologies (Parmesan 2006).

To better predict these winner and losers, we must understand the link between environmental variation and demographic success. In many cases the link goes through the social structure or breeding system. For these species, mechanistic models may be useful. Thus, when animals clump over a resource patch, they may be more likely to become diseased, but when living in groups with more males, females may have greater reproductive success through polyandrous matings. The devil of predicting a species' response is in the details of the complex algebra of the costs and benefits of sociality. However, behavioural ecologists are supremely well positioned to study these costs and benefits because of our well-developed toolkit studying the adaptive basis of behaviour.

With care, bioclimatic modelling may be a useful tool in helping to predict range changes for species with well-known thermal and moisture needs (Heikkinen et al. 2006; Jeschke and Strayer 2008). A bioclimatic model helps identify ecological drivers by mapping the current distribution and determining what potential ecological drivers best explain the current distribution. With some assumptions, it is possible to simulate into the future based on anticipated changes in environmental factors like projected rainfall and projected temperature. By creating bioclimatic models for both plants and animals we may find situations where one organism will face a thermal or moisture limit and thus its distribution will be limited, but the climate is nevertheless suitable for another organism. Species that are out of phase with their resources may be especially vulnerable (Parmesan 2006). However, the real utility may come from modelling the distribution of parasites and pathogens and projecting the vulnerability of populations to relatively unknown diseases. Such exposure may change the benefits of living socially, and in extreme cases potentially select for solitary living as an antiparasitic strategy.

The links between parasites and their social hosts is a fascinating one with some economic value. Studies of bovine tuberculosis *Mycobacterium bovis* in both territorial brush-tailed possums *Trichosurus vulpecula* and social (but not cooperative—Dugdale et al. 2010) European badgers *Meles meles* has shown that killing territorial residents in one location (whether they are infected or not) increases the movement of floaters and has the undesired consequence of increased movement of the disease (Smith 2001; Ramsey et al. 2002; Jenkins et al. 2007). Indeed, allowing infected residents to remain may be a superior strategy to widespread lethal control because of the tendency for non-territorial floaters to move into areas with other residents. In this case, it is the social behaviour (territorial defence) that reduces parasite transmission by reducing animal movement.

While there is some uncertainty over the rate of climate change, there is less uncertainty and more control over the rate of deforestation and other anthropogenic habitat modifications. With the possible exception of beavers, *Castor* spp., humans are the only animal that has had such a profound impact on the physical structure of the environment. This has led to homogenous stands of tarmac, trees, and vast monocrops of corn, soy, and potatoes. This extreme lack of habitat heterogeneity has either removed suitable habitat for many species, or created a place where pest species are favoured. Both of these influence the resultant social behaviour of species that relied on the original inhabitants.

9.6 Prospectus

Ecological models of sociality give us some predictive value assuming we know a sufficient amount about the resource needs of a given species. The challenge is to acquire this information. Additionally, while we can develop a laundry list of social factors that influence survival and reproductive success, we are far from developing the sort of broad conceptual understanding and detailed models that allow us to make more general predictions about how changes in the environment will influence a given species. Nor, I suspect, will we ever have many broad insights.

Much of conservation behaviour requires, by necessity, a single-species approach (Blumstein and Fernández-Juricic 2010). This should not be viewed negatively. Rather, by having a detailed and mechanistic understanding of the adaptive basis and value of sociality, we can predict how species will respond to anthropogenic assaults. I suggest that by adopting an individual-based modelling approach, we should be able to study one species at a time and better understand the links between the environment and demography.

Over time, we may be able to use empirical findings to make more general conclusions about the relationship between sociality and vulnerability. Nonetheless, our need for such approaches has never been greater. Behavioural ecologists will have an important role in these developing predictive models, and indeed in helping prevent extinctions (Schroeder et al. 2011).

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