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Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e

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Abstract

There has been a recent interest in integrating an understanding of behaviour into conservation biology. Unfortunately, there has been no paradigm for such a process. Without a clear framework for integration, conservation biologists may have difficulties recognising how behavioural knowledge can help solve real-world conservation problems. Effective population size (N_e) is a key demographic parameter used to understand population viability. A variety of behaviours and behavioural traits impact N_e, yet their importance for conservation is under-appreciated. We suggest that identifying behavioural traits that affect N_e provides a paradigm for integrating behavioural biology into conservation biology. Behaviour can affect N_e through at least three different mechanisms: reducing N — the population size; reducing r — the population growth rate, and/or by increasing reproductive skew. We discuss how nine common behavioural traits can reduce N_e, and suggest how an understanding of these traits may inform management of both free-living and captive animals. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Conservation biology is a crisis discipline aimed at saving biodiversity (Soulé, 1986). A common and important approach to saving biodiversity has been to preserve patches of habitat in order to maintain ecosystem-level processes which, in turn, preserves populations of species (Franklin, 1993). With these broad objectives and methods, conservation biologists have paid relatively little attention to how an individual animal's behaviour can help save biodiversity. Recently, a number of behavioural biologists have written reviews and book chapters on the role of behaviour in conservation arguing that a fundamental understanding of behavioural processes can contribute to conservation biology (Caro and Durant, 1995; Curio, 1996; Höglund, 1996; Lima and Zollner, 1996; Ulfstrand, 1996; Clemmons and Buchholz, 1997; Strier, 1997; Caro, 1998a,b; Sutherland, 1998). Despite this recognition that it may be important to apply knowledge of animal behaviour to conservation problems, there is no clear framework to help conservation biologists identify the specific cases when they should be concerned about behaviour, nor which behaviours they should be concerned about.

The number of individuals in a population, N, is a first approximation of endangerment. However, other factors influence the likelihood of a population going extinct over time. For instance, variation in the number of breeding individuals, variation in breeding success, the ratio of breeding males to females, as well as other factors influence the maintenance of genetic variation in a population (Falconer, 1989). Genetic variation influences long term sustainability because genetic variation is required to combat any negative effects of inbreeding, and to allow evolutionary adaptation to an ever-changing environment. To compensate for the inadequacy of N alone in predicting the likelihood of a population persisting over time, population geneticist's have developed the concept of the effective population size, N_e which better reflects the likelihood of a population persisting over time (Gilpin and Soulé, 1986). N_e is an estimate of the theoretical number of breeding individuals assuming

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they behave in an ideal way. N_e models an ideal population with the following properties: the population is split into sub-populations where there is no migration between sub-populations, generations do not overlap, the number of breeding individuals is the same for all generations and sub-populations, mating is at random and includes a random amount of self-fertilisation, there is no selection, and mutation is assumed to be unimportant (Falconer, 1989). N_e affects population viability by increasing homozygosity and decreasing the number of non-selected alleles. The loss of variation is compounded by an increase in linkage disequilibrium — nonindependent assortment of alleles — which reduces the frequency of novel gene combinations. N_e is influenced by factors that halt the passing of gametes to the next generation. Falconer (1989) identified six factors which influence N_e: (i) exclusion of closely related matings, (ii) skewed sex ratios, (iii) unequal generation size, (iv) unequal family size, (v) inbreeding, and (vi) overlapping generations.

A number of behavioural traits either directly or indirectly influence N_e by changing demographic parameters that contribute to N_e. We define behaviour broadly and recognise a hierarchy that begins with the neurobiological, genetic, and physiological processes that underlie observed motor patterns, includes the functional integration of those motor patterns into behaviours, as well as the integration of behaviours into behavioural traits. For instance, infanticide — a complex behavioural trait where adults kill young of their own species — directly influences N_e by reducing the population size, while another behavioural trait, reproductive suppression of adults, reduces the number of breeding individuals and may decrease a population's rate of increase — r — therefore reducing N_e. To integrate behaviour into wildlife conservation, we must understand how behaviour skews the operational sex ratio-the ratio of breeding males to females. Behavioural traits can influence the operational sex ratio in a number of ways. For instance, mature animals may be prevented from mating by dominant conspecifics or there may be active mate choice mechanisms that prevent certain animals from reproducing. Behaviour contributes to predation risk and skewed operational sex ratios emerge via differential mortality and survival — a 'double whammy' for species already in danger of extinction. Wright (1938) illustrated how skewed sex ratios influence N_e. Specifically,

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

where N_f is the number of breeding females and N_m is the number of breeding males.

From this we clearly see that N_e decreases by either decreasing the number of breeding individuals or by skewing breeding sex ratios.

Population viability analysis (PVA) is an important tool for managers because it provides an estimate of the viability and sustainability of a population. PVAs model the effect of certain biotic (fecundity, age of senescence) and abiotic factors (habitat availability) on N_e. It is through the calculation of N_e that a PVA predicts population persistence. N_e is therefore a central parameter determining population viability in PVAs.

As we will discuss in a number of following examples, individual behavioural strategies influence how individuals respond to habitat modification, hunting, fragmentation, corridor construction, reduced resource quality, and resource fluctuation. Understanding factors that influence behaviour over short time scales provides vital information for those developing more accurate population models as well as for those charged with managing populations. It is therefore surprising that most PVA models ignore behavioural variation (Derrickson et al., 1998).

N_e·s central importance in PVA models suggests that the best strategy for integrating behaviour into conservation will involve identifying behaviours and behavioural traits that impact N_e. N_e has already been recognised as one of a series of ways in which behavioural ecology can contribute to conservation biology (Parker and Waite, 1997; Caro, 1998a). Our approach differs in that we view that identifying and modeling the ways in which behaviour influences N_e as the perhaps the single most important way in which knowledge of animal behaviour can contribute to wildlife conservation.

When dealing with threatened populations, N_e is commonly quite low. Using knowledge of animal behaviour to design management regimes may only marginally increase N_e, yet this may be all that is needed to ensure population viability.

Behaviour can affect N_e through its effects on N, r, and reproductive skew. N, r, and reproductive skew influence N_e in at least five ways by their solitary and combined effects (Fig. 1). In this paper we discuss nine common behavioural traits that either directly or indirectly affect N_e. We focus on reproductive suppression, sexually-selected infanticide, mechanisms of mate-choice, mating systems, social plasticity, dispersal, migration, conspecific attraction, and reproductive behaviours which require special resources. These behavioural traits are found in many taxa. By discussing these, we hope to illustrate how behaviour can help inform conservation biology and how a wildlife manager might go about determining whether knowledge of behaviour should be applied to a particular conservation question.

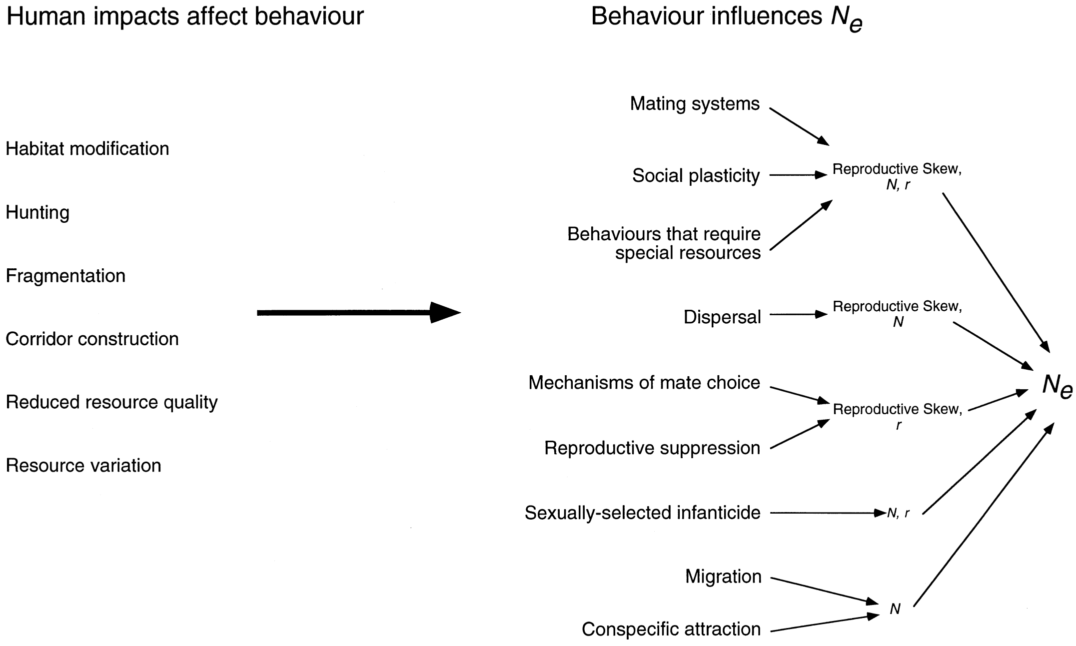

Fig. 1. Behavioural traits may decrease effective population size (N_e) in at least three ways: either directly by decreasing population size (N), or indirectly by increasing reproductive skew, or decreasing the population growth rate (r). A variety of human impacts affect these common traits.

2. Behavioural traits that influence N_e

Schematically we view N_e as being influenced by a variety of behavioural traits (Fig. 1). What follows is a discussion that illustrates how each influences N_e.

2.1. Reproductive suppression

When mature and potentially reproductive individuals in a social group do not breed, they are said to be reproductively suppressed (Wasser and Barash, 1983). Reproductive suppression is a key component of advanced sociality (Blumstein and Armitage, 1998, 1999), and is seen in many taxa (Wasser and Barash, 1983). Reproductive suppression influences N_e by reducing the proportion of individuals that breed and thereby decreasing r. If only one sex is reproductively suppressed, then suppression also increases reproductive skew. Reproductive suppression may be obligate or facultative (Creel and Macdonald, 1995) and can be viewed as the outcome of competition among potential breeders for the opportunity to breed when there are limiting resources. The effects of suppression leaves a population particularly vulnerable to hunting if the social group's suppressed individuals are unable to immediately breed when dominant individuals are killed (Greene et al., 1998).

Dominant breeders can suppress reproduction in subdominants via chemical or physical means (Wasser and Barash, 1983; Creel et al., 1992; Creel and Waser, 1997; French, 1997). Mechanisms may vary within a species as illustrated by dwarf mongooses, *Helogale parvula* (Creel et al., 1992). Mongoose females are suppressed by a series of rank-dependant dominance effects on ovarian function as well as behavioural mechanisms. Males are suppressed solely by direct intervention by dominant males which prevent them from mating with reproductive females.

The Seychelles warbler, *Acrocephalus sechellensis*, illustrates how a population may be constrained by reproductive suppression. Warbler population size was limited by the availability of nesting resources on the one island they inhabited (Cousin Island). Early attempts to save the species focused on creating more suitable habitat; once created the population size increased. However not all potential breeders reproduced — Seychelles warblers are facultatively cooperative breeders (Komdeur, 1992). Managers then decided to establish populations on other islands to reduce the risk of extinction. Between 1988 and 1990, 58 individual reproductively suppressed adult warblers (31 males and 27 females) were translocated to two nearby islands (Aride and Cousine Islands; Komdeur, 1994). Once translocated, both populations showed an explosive increase in population size. There was no reproductive suppression and individuals bred at younger ages than originally seen on Cousin. As the population increased, the highest quality habitat was fully occupied. At that point observers noted the onset of cooperative breeding and reproductive suppression.

The Seychelles warbler illustrates how knowledge of both resource and social constraints influences population size. Managers can use this knowledge to their advantage by creating habitat or potentially removing social constraints by translocating reproductively suppressed individuals. Such manipulations would not work for all species, so some knowledge of behaviour is required before planning intervention. For instance, species which have a naturally low *r* may not increase their reproductive output if more habitat is created. And, as we discuss below, some species require special places to breed. Creating new habitat for lekking species (species where males display on highly aggregated patches from which they obtain no resources other than mates — see section 2.9.2) may not help increase *r*.

Knowledge of the causes and mechanisms of reproductive suppression can allow managers to perform informed manipulations on populations. If suppression is due to resource limitation, providing more resources may increase *r*. However, in many species, dominant individuals suppress reproduction in subordinates and changes in social status clearly influence reproductive ability (Creel and Waser, 1997; Faulkes and Abbott, 1997; French, 1997). For these species, clustering resources to create several small groups, rather than one large group, may increase N_e because fewer individuals will be suppressed.

2.2. (Sexually selected) infanticide

In many species, when a new dominant male joins a social group or acquires a previous male's territory or status, the new male will kill offspring sired by the previous male, a phenomena known as sexually-selected infanticide (Hrdy, 1979). While initially thought aberrant and maladaptive, research in the past two decades has shown that for many species, sexually-selected infanticide is an adaptive reproductive strategy (Hausfater and Hrdy, 1984; Glass et al., 1985). Sexually-selected infanticide directly influences N_e by reducing juvenile survival and thus *N*, as well as indirectly by reducing recruitment and therefore population growth rate, *r*.

Infanticide occurs in a wide variety of taxa (Hausfater and Hrdy, 1984) and can cause as much juvenile mortality as predation. For instance, 50% of young golden marmots, *Marmota caudata aurea* — a large alpine ground-dwelling squirrel — that emerge above ground one year, survive to the next year (Blumstein, 1997). At least 22% of first-year mortality appears to be caused by infanticidal male marmots while predation is responsible for another 22% of mortality. New male immigrants apparently killed unrelated pups soon after they visited or joined a social group. This pattern is not restricted to marmots. While infanticide is best documented in rodents (Blumstein, 2000) and primates (van Schaik and Janson, 2000), it is seen in a variety of other taxa including canids, felids, birds and fish (Hausfater and Hrdy, 1984; Elgar and Crespi, 1992; van Schaik and Janson, 2000).

Infanticide has important implications for management. Typically, hunting males is not thought to decrease N_e because there are often unmated males that quickly replace missing males. However in this case of sexually-selected infanticide, hunting males significantly decreases effective population size because the unmated males kill their competitors progeny therefore reducing recruitment into the next generation (Caro, 1998c; Greene et al., 1998). In Sweden, where brown bears, *Ursus arctos*, are hunted, killing one adult male may lead to the deaths of non-hunted juveniles because other males may then kill the offspring sired by the previous male, with a resultant reduction in recruitment. Swenson et al. (1997) calculated that the demographic effect of killing a single adult male was equivalent to killing 0.5–1.0 adult female. Similarly the removal of a harem-holding male lion (*Panthera leo*) at low harem sizes allows un-related males to take over the harem and kill offspring (Greene et al., 1998). It is likely that sexually-selected infanticide may have similar effects on other species.

Management sometimes requires that individuals be moved. Movements, whether translocations or re-introductions, should be carefully evaluated with respect to whether or not a species is likely to exhibit sexually-selected infanticide. In some cases, moving females may be less risky than moving males who may, upon finding themselves in a novel social situation, kill unrelated young. Another situation where knowledge of infanticidal tendencies could be important is when habitat modifications change movement patterns. For instance designing a corridor might have unexpectedly large impacts on population growth rate if new males move through the corridor killing unrelated young that they encounter, or if increased movement allows greater contact between infanticidal males and family groups. Managers must consider whether or not a species of interest is infanticidal, especially when considering harvesting laws.

2.3. Mechanisms of mate choice

The way in which animals choose their mates directly influences N_e because some individuals are not chosen as mates, thereby reducing the operational sex ratio. Mate choice thus influences reproductive skew and potentially *r*. Active mate choice is found in many species (Bateson, 1983a) and may be accomplished by a variety of mechanisms (Andersson, 1994). While an understanding of mate choice mechanisms may be useful in captive breeding situations (e.g. Grahn et al., 1998), it is also important for managing wild populations.

2.3.1. Threshold assessment

Females rarely choose their mates randomly and often base their decisions about who to mate with after evaluating one or more male traits (e.g. Bateson, 1983a; Andersson, 1994). The assessment mechanisms or rules females use to assess male quality may directly influence N_e because only a subset of available males may be acceptable (Blumstein, 1998a). Females may use a 'fixed threshold' mechanism, meaning that they may choose not to mate at all in a given season rather than mate with a male with traits expressed below a certain threshold (Blumstein, 1998a). For instance, many females prefer males based on condition-dependent traits such as tail or antler length. The 'size' of condition-dependent traits depends on the male's ability to sequester resources from the environment (Andersson, 1994). In particularly bad years, such as during a drought or famine, or if human intervention influences the distribution of key resources required for trait expression, males may survive but not be able to grow long tails or large antlers. Additionally humans may preferentially harvest males with certain traits making it difficult for females to find acceptable mates. In these cases, and irrespective of mortality differences between the sexes, females using fixed threshold assessment mechanisms may chose not to mate, reducing r for a given season and therefore causing a decline in N_e (Blumstein, 1998a). Managers may increase the proportion of acceptable males by increasing resource quality, which in turn may enhance the expression of condition-dependent traits.

2.3.2. Non-independent mate choice

Females may not choose their mates independently of the behaviour of others, as assumed by many models of mate choice (Andersson, 1994). Non-independent mate choice is referred to as mate choice copying (e.g. Pruett-Jones, 1992; Dugatkin, 1998) and is documented in a number of promiscuous and lekking species (Höglund and Alatalo, 1995). Female copying occurs when females are more likely to mate with a male if they have witnessed him mating with another female. Female copying influences male mating success (Wade and Pruett-Jones, 1990) because some males mate most of the time while most males mate rarely. This leads to a skewed operational sex ratio, and thus influences N_e.

Mate choice copying may invalidate the random-mating assumptions of a non-behaviourally-informed PVA. Sage grouse, *Centrocercus urophasianus*, have several mechanisms for mate choice, one of which is mate choice copying (Gibson et al., 1991). Mate choice copying leads to highly skewed male mating success (Gibson et al., 1991). Whether or not females use copying as a mechanism of mate choice varies between years, and as yet is unpredictable (Gibson and Bradbury, 1987). Modelers and managers need to be aware of this behavioural plasticity when making assumptions about mating success parameters and management decisions.

At this point it appears that knowledge of mate choice copying would be best applied to captive management where more intimate intervention can take place. Regardless of whether or not we can manipulate copying, non-independent mate choice must be considered when constructing population viability models.

2.4. Mating systems

Mating systems affect N_e by determining which gametes are passed on to the next generation (Parker and Waite, 1997; Greene et al., 1998) by their effects on reproductive skew. Mating systems can therefore influence r, and whenever there is reproductive skew, animals may experience higher mortality associated with competing for limited breeding opportunities. Mating systems can also have a large effect on the way population size responds to natural and human-induced habitat changes, hunting, etc. (Komdeur and Dreerenberg, 1997; Parker and Waite, 1997; Caro, 1998c; Greene et al., 1998), as well as limiting the distribution of species (Höglund, 1996). Wildlife managers need to incorporate knowledge of mating systems into management plans (Greene et al., 1998).

Using a modification of Eq. (1), Parker and Waite (1997) illustrated how mating systems influence N_e. Assuming an N of 100, and a reproductive failure rate of 50%, a species displaying promiscuous mating (every male mates with every female) has an N_e of 67. Under the same conditions, a monogamous species (a single male mates with a single female) has an N_e of 50, an extremely polygynous species (males mate with multiple females, and not all males mate) has an N_e of only 19, while an extremely polyandrous species (females mate with multiple males, and not all females mate) has an N_e of only 9. Information about mating systems can be used by managers to understand the differential effects of habitat destruction or harvesting on N_e of different populations.

For example, Greene et al. (1998) modeled the effect of mating system and several other variables (harem size, infanticide, and reproductive suppression) on how a population would respond to three different types of hunting: trophy hunting of adult males only, hunting of all adults, and indiscriminate subsistence hunting. All forms of hunting are more detrimental to monogamous species than polygynous species: populations of monogamous species grew at slower rates when hunted. Hunting of only males had the greatest effect on infanticidal species as it increased the chance of sexually-selected infanticide and thus reduced population growth rate. Reproductively suppressed species were most impacted by hunting adults as female population size influenced population growth rate.

Mating systems may vary within and between species (Lott, 1991), making it difficult to always predict the relationship between N and N_e for a given species (see below). Thus, harvesting species with variable mating systems may require hunting laws to be tailored to each population, as well as to vary over time.

2.5. Social plasticity

Behavioural ecologists view species' social systems (which include both systems of space use and mating systems) as somewhat plastic traits that may change in response to environmental variation (Lott, 1991). As discussed above, the type of mating system a population employs effects N_e (Parker and Waite, 1997; Greene et al., 1998). Dunnocks, *Prunella modularis*, have one of the most variable mating systems known. One population may have individuals mating monogamously, polyandrously, polygynously, and polygynandrously (Davies, 1992), making it difficult to understand and to calculate male breeding success, and therefore N_e.

The decision about whether or not to associate with conspecifics may be influenced by external factors such as predation risk and resource distribution (Lott, 1991). For instance, fish may be more likely to school when they detect predators (Seghers, 1981). Group size varies as a function of the distribution and abundance of food in social carnivores (Gittleman, 1989). To guarantee access to needed resources, animals may defend territories or establish dominance hierarchies — behavioural traits which may expose individuals to greater mortality risk. Sunbirds, *Nectarinia reichenowi*, wagtails, *Motacilla alba*, and other territorial birds often shift between defending feeding territories and establishing dominance hierarchies as a function of food quality and quantity (Gill and Wolf, 1975; Davies and Houston, 1983). Resource variation may influence N_e both directly and indirectly. For instance, when mating systems vary as a function of resource distribution or abundance, different numbers of animals reproduce; a factor that directly modifies N_e. Resource variation may also indirectly influence N_e. For instance, engaging in aggressive behaviour may contribute to predation risk by increasing exposure to predators (Blumstein, 1998b). If rates of aggression are modified by whether a species is territorial or has a dominance hierarchy, switching between these social systems may modify predation rates for some classes of animal and this changes N_e.

Conservation biologists armed with a fundamental understanding of the mechanisms which cause shifts between breeding, social, or defense behaviour may have novel ways to manage populations. Understanding that social systems may vary in response to resource variation may allow managers to anticipate consequences of planned habitat manipulations, manage human hunting behaviour, and manipulate populations to facilitate viewing by ecotourists (Lott, 1991). Because the expression of many behaviours is flexible, proper management may require a detailed understanding of factors which trigger changes between one behaviour or social structure and another.

2.6. Dispersal

Dispersal is the one-way movement of animals from their natal territory or group to a place where they breed (Shields, 1987; Verhulst et al., 1997). Often one sex disperses and one sex remains philopatric (Greenwood, 1980; Nunes and Holekamp, 1996). Dispersal is a mechanism of gene flow (Shields, 1987; Brown and Brown, 1992): if a lack of suitable habitat prevents dispersal, then gene flow may be reduced (sensu Verhulst et al., 1997). Dispersal may be risky and is often a major source of mortality (van Vuren, 1998). If habitat fragmentation or loss forces animals to increase dispersal distance or spend more time in unsuitable habitat while dispersing, mortality rates may increase. Low dispersal rates may also increase extinction risk because individuals in highly localised populations cannot disperse away from disturbances. Thus, dispersal directly influences N_e by reducing population size and potentially by influencing the ability of a population to escape disturbance. Additionally, dispersal indirectly influences N_e through its influence on a population's genetic structure (Shields, 1987).

Habitat modifications may influence patterns of dispersal and may influence the distribution of parasites, predators or pathogens. For example roads built into the Luquillo forest reserve in Puerto Rico coincided with the invasion of this remnant habitat by pearly eyed thrashers, *Magarops fuscatus*, and their endemic botfly, *Philornis* sp. — a blood sucking-parasite (Snyder et al., 1987). Botflies subsequently infected the Puerto Rican parrot, *Amozona vittata*, and sharp-shinned hawks, *Accipiter striatus*. Both of these endangered species are less resistant to the parasite than its native host (Snyder and Taapken, 1978; Snyder et al., 1987; Delannoy and Cruz, 1991).

For some taxa that only mate within their social groups, dispersal is particularly important as it is a main mechanism of gene flow. If dispersal is reduced then gene flow may also be reduced.

Ecoclines as narrow as a road may deter some species from dispersing (Burnett, 1992). Lack of connectivity can also influence dispersal and therefore population persistence (Thomas et al., 1992). Long-term persistence of butterfly populations requires a network of suitable habitats sufficiently close to allow natural dispersal (Thomas et al., 1992). Lack of connectivity may be 'biological' as well as 'physical' and can result from introduced and feral species interfering with dispersal. In a study of frog metapopulation dynamics, local extinction was more prevalent after fish were introduced to dispersal corridors. Fish preyed upon tadpoles which isolated the remaining populations and halted successful dispersal (Bradford et al., 1993).

Dispersal may also be influenced by resource availability. The timing of Belding's ground squirrel, *Spermophilus* *beldingii,* dispersal is influenced by body mass which, in turn, is influenced by habitat quality. Squirrels on poor quality habitat delay dispersal and may not breed as soon as those on better-quality habitat (Nunes and Holekamp, 1996).

Dispersing individuals may have a higher rate of mortality than non-dispersers (Stenseth, 1984) for two main reasons. First, dispersers may have to move through novel environments. If they are unfamiliar with the terrain, it will be harder to find refuges from predators (Metzgar, 1967; Ambrose, 1972), shelter, and resources required for survival while dispersing. Second, dispersers may move through relatively narrow corridors (Machtans et al., 1996) making it easier for predators to find them.

Poor dispersal abilities may be a contributing factor for extinction. For instance, without intervention, Seychelles warblers could not have moved from Cousin Island to Cousine and Aride Islands; a distance of 1.6 and 9 km, respectively (Komdeur, 1994). A relatively small-scale natural disaster such as a cyclone or bush fire on Cousin, could have led to the extinction of the entire species. Additionally, the poor dispersal abilities of the pancake tortoise *Malacochersus tornieri* seems to hinder population recovery (Klemens and Moll, 1995). And, as mentioned before, human-induced habitat modifications may make dispersal more difficult for dispersers. Knowledge of dispersal behaviour is thus vital knowledge for designing functional reserve boundaries (Beissinger, 1997; van Vuren, 1998).

2.7. Migration

Migrating animals move across habitat types in search of favorable resources, and migratory species may be more vulnerable to extinction (Pimm et al., 1988). Migration is common and is found in many taxa (Dingle, 1996). All migratory species are vulnerable in at least three ways that may reduce N_e. First, they are vulnerable to factors that may change migratory patterns. Second, they are particularly vulnerable to habitat loss because they have wide-ranging habitat requirements. Third, while migrating, they may suffer increased mortality.

Migrating animals may rely upon chemical and visual cues to properly orient while migrating (e.g. salmon — Hasler et al., 1978). Such cues may be modified or destroyed by humans which may either change migratory patterns or completely block migration (sensu Hasler et al., 1978). Changed migratory routes increases the chance of populations encountering predators they have not had to deal with before, including humans, and for which they have not evolved defenses.

Migratory species are vulnerable to modification or destruction of their breeding grounds, the area they migrate though, and of their wintering area (Berthold and Terrill, 1991). Because migratory behaviour may be highly heritable (Berthold and Querner, 1981), migratory species may not have the ability to naturally modify their migratory patterns in the face of habitat destruction or loss (Dolman and Sutherland, 1994). However, human interventions with young birds have shown that it is possible, in some cases, to change migratory patterns (Temple, 1978). Regardless, without human interventions, migratory species may be more vulnerable to extinction because it is difficult to protect all of their required habitat (Powell and Bjork, 1995).

In some cases wintering grounds can be highly localised. For instance monarch butterflies, *Danaus plexippus*, winter in large aggregations in Mexico and California. These aggregations and the large scale movements are of aesthetic interest. The species is not hunted or otherwise endangered but habitat loss in its wintering grounds make migratory populations, and therefore the entire spectacle of migration, vulnerable (Brower and Malcolm, 1991; Malcolm, 1993).

Like dispersing animals, migrating animals move through unfamiliar terrain during which time they may be fatigued and physiologically stressed. Migration is risky and migrators may be more exposed to predation (Rubenstein, 1998; Caro, 1998b). Migrating animals may move in large groups and along narrow corridors, making them easy prey for human and non-human predators. For instance, migrating Atlantic salmon, *Salmo salar*, are more vulnerable to being caught by fishermen than individuals which remain at sea (Rubenstein, 1998), and most people are familiar with the spectacle of bears and eagles hunting migrating salmon in the streams of North America.

Migratory species may have evolved high fecundity to compensate for the high mortality associated with migration. If numbers fall below a certain level due to excess mortality, a species will no longer be able to sustain the high cost of migration (Dingle, 1996), and its population may decline or go extinct.

A fundamental understanding of migration is required for proper landscape management. For instance, the present boundaries of the Ngorongoro Conservation Area were formed to accommodate wildebeest migration (Caro and Durant, 1995), and managing the greater Yellowstone ecological region relies on an understanding of migratory patterns. To adequately protect a migratory species, reserves must be established in all used areas (Powell and Bjork, 1995).

2.8. Conspecific attraction

Animals may not independently decide where to settle or defend a territory; their behaviour may be influenced by the behaviour of other members of their own species. The importance of conspecific attraction on decision making has recently been pointed out by a number of workers (Stamps, 1988; Smith and Peacock, 1990; Reed and Dobson, 1993; Muller et al., 1997), but wildfowl hunters have recognised the usefulness of decoys for centuries. Conspecific attraction has a variety of indirect influences on N_e by its influence on the amount of available habitat (sensu Reed and Dobson, 1993), population density (Smith and Peacock, 1990), and dispersal (Reed and Dobson, 1993).

Conspecific attraction is found in both colonial and non-colonial species and in a variety of taxa. There have been several experimental studies documenting the importance of conspecifics on settlement decisions. For instance, juvenile *Anolis* lizards prefer to settle in habitat patches already occupied by other juvenile anoles (Stamps, 1988). Playbacks of conspecific vocalisations induce preferential settlement in several species (pied flycatchers, *Ficedula hypolecua* — Alatalo et al., 1982; Laysan albatrosses, *Diomeda immutabilis* — Podolsky, 1990; and a grasshopper, *Ligurotettix coquilletti* — Muller, 1998). These studies, and others, suggest that conspecifics may have an important impact on where animals settle. How specifically does conspecific attraction influence N_e?

Conspecific attraction can affect population dynamics and persistence, particularly in small or establishing populations (Reed and Dobson, 1993). When conspecifics influence settlement decisions, patches of suitable habitat are left vacant and there will be greater competition for occupied patches. Sometimes, stochastic factors influence which patches are occupied and which patches are left vacant. Thus, it is not always correct to assume that occupied patches are the highest quality (Reed and Dobson, 1993), and populations may have higher growth rates or carrying capacities on other patches. Conspecific attraction can also lead to an increase in population density without increasing population size (Reed and Dobson, 1993). Increasing density modifies population growth parameters in any density-dependent population (Reed and Dobson, 1993).

As previously discussed (Section 2.6), dispersing animals may be particularly exposed to predation and other sources of mortality while dispersing. Because animals may search for other conspecifics, species that use conspecifics as cues for habitat quality will have modified dispersal behaviour. For instance, the direction an individual disperses may be influenced by cues from conspecifics (Hoeck, 1982). Hoeck (1982) suggested that rock hyraxes, *Procavia johnstoni*, do not willingly disperse from their kopjes without cues from other Hyraxes at a potential destination. However, the exact nature of this influence will ultimately depend upon a given species' spatial distribution.

Some PVA models assume random dispersal (e.g. Lindenmayer and Possingham, 1996a). For a variety of reasons discussed, dispersal is far from random if conspecifics are used as cues for habitat settlement. Thus, knowledge of the degree to which conspecifics are important cues for habitat settlement decisions can make modeling exercises more realistic, and their predictions more accurate.

In addition to helping model N_e, knowledge that a species uses conspecifics as cues for settlement decisions can inform conservation programs. For instance, animals could be 'seeded' into suitable habitat to attract others. Or, artificial cues could be broadcast or placed in appropriate habitat as a way to attract others. Ultimately it may be possible to attract enough individuals to form a sustainable population (Reed and Dobson, 1993).

It may not always be necessary to collect original data to determine whether or not a species uses conspecifics as cues for habitat settlement decisions. Muller et al. (1997) used archival data on a wren, *Troglodytes aedon*, collected over 50 years ago for other purposes to demonstrate that a species' settlement decisions were influenced by the presence of conspecifics. The statistical method they developed could be used by others with either archival or contemporary data.

2.9. Reproductive behaviour that requires special resources particularly impacted by human development

Some species have reproductive behaviour that requires special resources. For instance, cavity-nesting animals require trees characteristically found in established forests which may be particularly impacted by human development. Leks are locations where males of a species gather to display for females who visit the site to mate (Höglund and Alatalo, 1995). Often leks are very traditional locations that have been used for many generations; once destroyed, animals may not find new mating grounds. Bowers are complex mating structures produced by an Australasian group of birds *Ptilinorhynchidae*. The bowers may capture people's attention who may then observe the birds or collect ornaments from the bower that are required for successful mate attraction. Either way, the natural breeding behaviour may be influenced by humans. Any species that requires special resources to reproduce may be especially vulnerable to human impacts leading to a decline in N and N_e.

2.9.1. Cavity-nesting

Many species (birds — Eadie et al., 1998; mammals — Lindenmayer and Possingham, 1996b) nest in tree cavities which may be a very limited resource. Logging old growth forests destroys natural tree cavities (e.g. Lindenmayer and Possingham, 1996a). A common remedial activity is to create artificial nest boxes as habitat for cavity nesters. However, nest boxes are not a panacea; when nest boxes are spatially clumped, conspecific brood parasitism may increase (Eadie et al., 1998), social patholgies may result (Semel et al., 1988), and disease transmission may increase. The frequency of extra-pair copulation, and thus gene flow, as well as sexually transmitted diseases (Hart, 1990; Thrall et al., 1998), may be influenced by the spatial distribution of nest boxes.

An example of the ingenious use of nest boxes was to alleviate nest predation by pearly-eyed thrashers on Puerto Rican parrot nests. This required a detailed understanding of pearly-eyed thrasher territorial behaviour. Pairs of nest boxes were established — one for the Puerto Rican parrot, and one for pearly-eyed thrasher. Resident thrashers are highly territorial and chased away all other conspecifics. In doing so thrashers themselves helped reduce the amount of predation on the parrot nests by non-nesting thrashers (Wiley, 1985). Nest boxes, however, should be used with caution (Semel et al., 1988; Eadie et al., 1998), and should not necessarily be considered equivalent to natural tree cavities.

2.9.2. Lekking

Lekking occurs in many taxa including arthropods, fish, amphibians, reptiles, birds, and mammals (Höglund and Alatalo, 1995). Lekking species have very specific habitat requirements during the breeding season; they not only need refuge, foraging and breeding areas, but also a place to lek. Destruction of leks may directly influence N_e in that a population will no longer have a breeding ground, and thus rate of breeding will halt or be reduced, and indirectly influence N_e by causing females to travel farther to find a suitable lek.

As previously discussed with respect to dispersal and migration, moving over unfamiliar terrain is risky. Females typically visit a lek fewer times than males (Höglund and Alatalo, 1995). Their reduced familiarity may increase their predation risk while approaching the lek or while on the lek. In contrast, males of some species may spend a considerable amount of time at a lek but also leave it regularly to forage. While on the lek they are preoccupied and may be at a greater predation risk, and repeated trips to and from a lek may also increase the chance of mortality if the approach is hazardous.

Changes to the lekking habitat may indirectly influence N_e by the differential mortality of males and females. Differential mortality creates skewed sex ratios within the population, which in turn leads to an even lower N_e (Creel, 1998).

While on a lek, the aggregation of potential prey may attract predators (Balmford and Turyaho, 1992). Because males spend more time on a lek and make more trips to a lek than females, they are particularly likely to be killed. Strong sexual selection on a lek (Gibson et al., 1991) may compound the effects of differential mortality, making lekking species likely to have much smaller N_e's than would be expected by simply counting individuals.

Leks may be at locations with quite specific environmental characteristics. For instance, the light environment may highlight an individual's ornamentation to its best advantage (Endler, 1992; Endler and Théry, 1996). Generally, though, we have little understanding about what specific factors are required for a suitable lek in most species. Thus, any habitat manipulations around leks, or that may affect lekking species, may have unpredictable and potentially irreversible consequences. Environmental changes can have enormous impacts on the population biology of lekking species. For instance, sage grouse apparently find their leks using unspecified landmarks on the ground because when there is substantial snow cover, birds do not aggregate on the lek for mating (Gibson and Bradbury, 1987). It is clear that more information is vital to a better understanding of how lekking affects a population's N_e.

2.9.3. Bowers — specialised mate attraction structures

Some species, such as bower birds, build structures which humans may destroy or damage. Because, males build bowers, male mating success is impaired. N_e is thus reduced because of a skewed operational sex ratio.

3. Discussion

We hope to have demonstrated a variety of ways that behavioural knowledge can inform conservation. Why then has behaviour been ignored by many conservation biologists? One reason may be related to the different levels of analysis used by most behavioural biologists and most conservation biologists (Höglund, 1996; Lima and Zollner, 1996; Clemmons and Buchholz, 1997; Strier, 1997). Behavioural studies focus on individuals, whereas conservation studies focus on populations and higher levels of ecological organisation.

Another reason behaviour is often overlooked by conservation biologists is that conservation biology is a crisis discipline. While knowledge of population biology and genetics have obvious implications for population persistence, behavioural impacts on population persistence are thought to be less direct. Perhaps this is because behaviour was considered to be species-specific and hence idiosyncratic. We hope to have offered a number of examples that illustrate how behavioural traits widely shared among species can directly and indirectly influence N_e, and therefore population persistence time. Understanding which, and how, behaviour influences N_e is a central organising principle for applying behavioural knowledge to conservation biology. It gives us a starting point to focus studies, as well as giving us a solid theoretical base from which to work.

This has been a brief overview of selected common behavioural traits that we believe may be of particular importance for determining N_e, and about which wildlife managers might be particularly concerned. Many other behavioural traits can influence N_e (Clemmons and Buchholz, 1997; Caro, 1998a,b) either directly or indirectly. Strategies, such as allogrooming (Hart, 1990), that control parasites and pathogens have obvious impacts on N_e. Many social behaviours are density dependent (Goss-Custard and Sutherland, 1997) and may not occur if population size dips below a threshold (Allee, 1931). We have not explored interactions between different behaviours that may have additional impacts on N_e (Kilgo et al., 1998).

As other behavioural biologists have pointed out (Caro and Durant, 1995; Lima and Zollner, 1996; Clemmons and Buchholz, 1997; Strier, 1997; Caro, 1998a,b), behavioural knowledge can be used by conservation biologists in other ways. For instance, because an animal's behaviour is affected by a wide range of factors which act on many levels of organisation (i.e. genetic, individual, population, and the environment in which a individual exists), behaviour can be used as an valuable indicator of population 'health'. The relationship between foraging effort and resource quality provides an obvious example of how behaviour can be used in this way. In a study of four species of seabirds, foraging behaviour was the best indicator of the size of off-shore fish stocks (Monaghan, 1996). The study was conducted before and after an oil spill that reduced fish stocks. Analysing dive depth and the length of foraging trips over different years provided an accurate picture of normal foraging, and of foraging in depleted stocks. Behavioural biologists are best equipped to study and interpret these sorts of changes (Curio, 1996; Clemmons and Buchholz, 1998).

Unrecognised natural behaviour can also create special problems when animals are captively bred. Sexual imprinting is a natural behaviour where mate choice preferences are influenced by early social interactions (Bateson, 1983b; McFarland, 1987). When an endangered species is hand-reared in captivity or cross-fostered with another less-endangered species, there is a risk of abnormal reproductive behaviour and mate choice (Primack, 1993). As we have already discussed, mate choice preferences directly impact N_e. Eliminating unwanted sexual imprinting may require animals to be hand-fed by puppets, rather than by keepers, as seen in the case of the California Condor, *Gymnogyps californianus* (Primack, 1993).

Skeptics may claim that behaviour provides us with little useful information for conservation, or that the cost of obtaining this information is too high, and indeed that it is not needed for effective conservation. However, without critically examining the relationship between a species behaviour and N_e we will not be able to estimate its impact. Certainly, we can envision situations where ignoring behaviour may result in a sub-optimal management decisions (e.g. moving infanticidal males around, or establishing nest boxes for cavity nesters). And, we can envision situations where applying behavioural knowledge to a conservation problem can reduce mortality rates enough to allow r to be greater than 1.0. If nothing else, understanding which behaviours may influence N_e will increase the diversity of a wildlife manager's tool kit. It is through the application of these tools that we will ultimately help conserve biodiversity. We look forward to the more comprehensive integration of behavioural biology and conservation biology.

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