Whereas the study of animal behavior is mainly concerned with the causes, development, and adaptive significance of variation in behavior of individuals, conservation biology is concerned with the behavior of populations, especially their response to disturbance caused by humans, and in preventing their extinction. Nonetheless, an increasing number of people studying animal behavior have become concerned about species’ extinctions and habitat loss, sometimes for professional reasons because their study populations are under threat, or for personal reasons (Rubenstein 1998). Consequently, since 1995, there have been several attempts to point out the relevance of animal behavior to the field of conservation biology. The purpose of this chapter is to:

1. outline briefly the history of these attempts;
2. describe the major areas of animal behavior that have the potential to address conservation problems; and
3. discuss why connections between these disciplines have failed to solidify as quickly as expected.

At the end of the chapter, we suggest ways in which those embarking on new studies in animal behavior can tailor their research to solving urgent conservation problems.

Attempts to Link Animal Behavior to Conservation Biology

Although interest in conservation increased steadily from 1950 onwards (see articles in the journals Oryx, Journal of Wildlife Management, Environmental Conservation, and Biological Conservation), one can argue that the discipline of
Conservation biology was born officially in 1987 when the first issue of an influential journal of that name appeared. Conservation biology is a multidisciplinary science that documents the extent and distribution of biodiversity; examines the nature, causes and consequences of loss of genes, populations, species, and habitats; and attempts to develop practical methods for stemming species’ extinctions and allow for continuation of functioning ecosystems (Wilson 1992; Meffe & Carroll 1997). Initially, it used principles from ecology, population genetics, and systematics to describe biological diversity and seek ways to conserve it (Simberloff 1988) but as the discipline grew it embraced economic, sociological, anthropological, and philosophical constructs to understand and change the impacts of human activity on species and habitats. Animal behavior was deemed to have little relevance to the study of changes in population size and composition since the behavior of a population necessarily encompassed the sum of the behavior of individuals within that population. Two exceptions were zoo managers, who recognized that individual behavioral idiosyncrasies could influence breeding success in very small captive populations, and those in charge of reintroduction programs, who saw behavior following release as a key element of success (Kleiman 1989).

Recognition that advances in animal behavior might be pertinent to conservation issues came with the realization that a species’ biology could predispose it to changes in habitat, to predation or competition from introduced animals, or to hunting (Caughley & Gunn 1996); that knowledge about mating systems (see Chapters 11 & 12) and social organization (see Chapter 14) could influence effective population size and population growth (Caro & Durant 1995); and that knowledge of learning mechanisms (see Chapters 7 & 8) could revise predictions about breeding success in captivity (Curio 1996) and prey species reintroductions (McLean et al. 1994). These and other ideas were brought together in a special edition of the journal *Oikos* (volume 77) and in three wide-ranging edited volumes by Clemmons and Buchholz (1997), Caro (1998a) and Gosling and Sutherland (2000), in short syntheses that championed the importance of behavior for conservation (Martin 1998; Sutherland 1998; Caro 1999), and in taxonomically restricted review articles (Strier 1997; Reed 1999; Shumway 1999; Colishaw & Dunbar 2000). This sudden burst of interest signifies a new awareness of the way in which principles of animal behavior can be used to redirect conservation programs (Caro 1998b).

**Conceptual Links Between Animal Behavior and Conservation Biology**

**Behavioral methodology**

In order to monitor populations so that conservation action can be implemented well in advance of crises, it is necessary to estimate population size and growth rate regularly. Although ecologists have developed many indirect methods of doing this (e.g., catch per unit effort, transects, acoustic surveys, point counts, and live trapping), fieldworkers studying behavior have needed to develop specific techniques to identify individuals
since behavioral biologists are interested in causes and consequences of individual variation. Their techniques fall into two categories (McGregor & Peake 1998).

1 Artificial markers, such as leg bands placed on birds, numbered collars on mammals, radio and satellite transmitters, and modifying the appearance of individuals using fur dyes and bleaches, freeze branding, ear notching, and toe clipping.

2 Using natural markings for field identification, such as coat markings in cheetahs (*Acinonyx jubatus*), facial characteristics in Bewick’s swans (*Cygnus columbianus*), scars in dolphins (*Tursiops truncates*), footprints in cougars (*Puma concolor*), acoustic signals in blue monkeys (*Cercopithecus mitis*), and genetic markers in marine turtles. Natural markings are superior to artificial techniques in that they avoid risks inherent in capturing and marking animals (Cuthill 1991; McGregor & Peake 1998).

Individual identification has several advantages. First, the researcher sometimes knows all the individuals in the population instead of a sample, and can thereby assess the resolution of more conventional and widely used ecological census techniques. For example, Gros et al. (1996) were able to gauge the accuracy of interviewing people about cheetah numbers against known population sizes of cheetahs gleaned from long-running behavioral studies. Second, if individuals’ reproductive careers and survival are followed over time, the causes of changes in population size can be discerned. Third, if properties of calls can be individually recognized, researchers can estimate the population size of secretive species such as corncrakes (*Crex crex*) or bitterns (*Botaurus stellaris*) (McGregor et al. 2000).

Other methods, such as playing back the recorded songs of birds, can also be employed to calculate population size (Baptista & Gaunt 1997). Although ornithologists have long used birds’ vocalizations to elicit answering calls and count individuals in thick vegetation, mammalogists now use similar techniques, for example playing whooping calls to call in spotted hyenas (*Crocuta crocuta*) from a known radius (Mills et al. 2001). This method is well suited to censusing rare species at low densities, the very populations of concern to conservation biologists.

**Ontogeny**

Two elements of behavioral development (see Chapter 6) have a direct bearing on restoration projects in conservation biology: acquiring antipredator behavior and imprinting. Ability to recognize predators is influenced by genetic processes (Hobson et al. 1988) and learning processes (Curio et al. 1987). For example, New Zealand robins (*Petroica australis*) from mainland New Zealand that have been exposed to (introduced) small carnivores for over 100 years respond immediately to stoats (*Mustela erminea*) whereas those from an outlying island with no such experience do not. Yet after only one exposure to a stoat, the naive robins show full response intensity (Maloney & McLean 1995).
Practical methods have been used to train naive birds and mammals prior to reintroduction, particularly in Australia where remnant native fauna has been subject to intense predation from introduced placental carnivores (Short et al. 2002). Mammalian examples include rufous bettongs (*Aepyprymnus rufescens*) and quokkas (*Setonix brachyurus*) being conditioned to respond fearfully to a fox (*Vulpes vulpes*) by pairing a stuffed fox with a live domestic dog (*Canis familiaris*) that harassed them (McLean et al. 2000), and rufous hare-wallabies (*Lagorchestes hirsutus*) being trained to avoid a model fox or cat (*Felis catus*) by pairing the predator’s appearance with a conspecific alarm call or loud noise or, alternatively, with a moving predator puppet and squirt of water (McLean et al. 1995). These and other studies (Griffin et al. 2000) raise a host of applied developmental questions, including how frequent and for how long should training last, how natural should it be, will it transfer to future generations, and whether responses are specific to different predators (McLean et al. 1994; Griffin et al. 2001).

Currently, the beneficial consequences of predator avoidance training on survival following reintroduction are equivocal; for example, rufous hare-wallabies (*Lagorchestes hirsutus*) failed to respond to the predators 8 months later, and the very small number of studies that have monitored long-term survival have yet to reach any consensus (McLean et al. 1994).

More generally, animals reared in isolation or in peer groups without parents face problems if they are reintroduced into the wild, including loss of dominance (Marshall & Black 1992) and lack of knowledge about poisonous foods (Beck et al. 1994) and migratory routes (Baskin 1993). Furthermore, captive-reared individuals can imprint (see Chapter 6) on their human caretakers, heterospecific foster parents, or even on their captive surroundings, resulting in inappropriate breeding behavior. Captive-rearing institutions have known about these problems for years and have developed elaborate programs to deal with them (McLean 1997; Curio 1998). There are many examples. California condor (*Gymnogyps californianus*) chicks are fed in the nest using hand-held puppets of a parent’s bill and head to avoid chicks making attachments to humans (Toone & Wallace 1994). Endangered whooping cranes (*Grus americana*) cross-fostered to sandhill cranes (*Grus canadensis*), so as to induce the whooping crane parents to produce a second clutch, have difficulty in forming pair bonds (Kepler 1977) and therefore workers disguised as whooping cranes (dressed in sheets with a puppet head on one hand) feed the chicks in the field. To prevent released California condors from roosting on power lines, chicks are fledged in large flight pens with tree branches and are conditioned to avoid a model power pole that gives moderate electric shocks (Wallace 2000).

Unfortunately, most of the progress in the area of reintroductions has been on a case-by-case basis, dealing with developmental problems as they arise. Progress in understanding behavioral development, on the other hand, has been based on studies of relatively few model species. Consequently, there are few guidelines to inform us about relatively unknown endangered species other than obvious concerns about predators needing to acquire hunting skills and migratory species requiring knowledge of migratory routes. At present, application of knowledge of behavioral ontogeny to conservation is largely by trial and error.
Mechanisms

Hormones

Environmental stressors can trigger a cascade of hormone secretions (Wingfield et al. 1997). For example, glucocorticosteroids play a central role in physiological and behavioral responses to stress and field assays of these hormones have been used to evaluate levels of stress in wild populations. In the Western fence lizard (*Sceloporus occidentalis*), adrenal responsiveness was higher in individuals from populations on the periphery of the species’ range (Dunlap & Wingfield 1995); habitat fragmentation may cause similar effects (Wingfield et al. 1997). Following an oil spill near a colony of Magellanic penguins (*Spheniscus magellanicus*) in Argentina, birds with light oil contamination (<5% of body surface) returned to the colony but did not breed (Fowler et al. 1995). Field assays revealed a reduction in sex steroids and an increase in stress hormones. Heavily oiled birds that were rescued and washed not only exhibited higher levels of corticosterone than nonoiled birds but also significantly higher levels than oiled birds that were not washed, indicating that considerable stress is involved in restraining and cleaning oiled birds (Fowler et al. 1995).

Hormonal therapy can be used to enhance breeding in captive animals or in populations that exhibit low reproductive rates in the wild (Wingfield et al. 1997). Conversely, hormone therapy could be used to suppress reproduction in overcrowded populations or in predators or parasites of species in peril (Seal 1991). Finally, some pollutants may mimic natural hormones and have unanticipated impacts on wild populations. Several components of petroleum-related products have estrogenic properties and have potent effects on reproductive behavior and development (Hose & Guillette 1995).

Behavioral toxicology

Direct assays of behavior have been used to measure stress. Behavioral assessments are rapid and sensitive, and are likely to detect sublethal effects of an environmental perturbation before impacts at the population level are manifest (Smith & Logan 1997). Most applications of behavioral toxicology involve controlled laboratory studies of chemical contaminants and focus on behaviors such as orientation, locomotion, or preference/avoidance (reviews in Little et al. 1993; Smith & Logan 1997), although the methodology can be readily applied in the field. For example, Krebs and Burns (1977) documented the long-term effects of an oil spill on the population dynamics and behavior of a saltmarsh crab (*Uca pugnax*). Many crabs died or left the area; those that remained displayed aberrant locomotor and burrowing responses, slow or impaired escape behavior, and molted and developed mating colors at the wrong time of the year. These changes impaired successful reproduction and increased exposure to predators. Consequently, densities were reduced for at least 7 years after the spill. Understanding behavioral abnormalities induced by oil provides insights as to why this population failed to recover.
Information on the behavioral flexibility of a species may be useful in predicting the degree to which a population would be placed at risk by environmental change, since specialists may be more vulnerable to disturbance than generalists (Arcese et al. 1997). Nonetheless, species with highly specialized behaviors may be able to expand their repertoire when opportunity or necessity dictate. For example, the Mauritius kestrel (*Falco punctatus*) is an obligate cavity-nesting bird requiring large tree holes in which to nest. Loss of nest sites and increased nest predation by introduced macaques (*Macaca fascicularis*) resulted in the population being reduced to only two pairs in the wild. In 1974, however, one pair nested on a cliff and was successful. Offspring from this pair also nested on cliffs and recruits to the population have come predominantly from cliff-nesting birds (Temple 1986). This example illustrates that shifts in behavioral preferences may be transferred between generations, highlighting the importance of learning and imprinting. Understanding whether a species is capable of such behavioral flexibility and determining how such shifts occur and are maintained may be critical for conservation efforts, especially for species where it is impossible to restore specialized resources upon which they depend.

Behavioral flexibility may also predict whether a species is likely to invade novel environments and thus become a conservation concern for other species. Sol et al. (2002) found that bird species with relatively large brains and which exhibited foraging innovations were more likely to become established when they were released into a new region.

**Interference with sensory modalities**

Introduction of detrimental light into the environment (photopollution) can disrupt behaviors such as orientation, timing of periodic behavior, and visual communication. Eggs of endangered sea turtles hatch at night and young turtles move immediately to sea using a complex phototaxis toward the brightest horizon (the open ocean on unlit beaches; Witherington 1997). Artificial lighting from roads or houses along the beach disrupts this orientation mechanism; in Florida alone, approximately 1 million hatchling sea turtles are misdirected by lighting each year, resulting in hundreds of thousands of hatching deaths. Changing the spectra of artificial lights could reduce misorientation deaths of hatchlings (Witherington 1997).

Orientation behaviors of large numbers of nocturnally migrating birds are also affected by artificial light sources such as lighthouses, aircraft beacons, and office towers (Reed et al. 1985). Interference with visual systems impacts many other behaviors, particularly those that rely on color for signaling or display, such as birds lekking in fragmented forests (Endler 1997). Altered light has also interfered with the mating displays of cichlid fishes in the African Great Lakes. Members of this speciose group are sexually isolated by mate choice, determined on the basis of body coloration. Increased turbidity of the water, brought about by increases in lake productivity, deforestation, and agriculture, constrains color vision such that the mating displays maintaining reproductive isolation are no longer functional. Accordingly, there has been a drastic loss of
species in areas of the lakes with high turbidity due to the breakdown of reproductive barriers (Seehausen et al. 1997).

Interference with animal auditory systems can have similar effects (McGregor et al. 2000). Density of breeding birds was reduced by 20–95% in areas adjacent to busy roads and highways in the Netherlands (Reijnen et al. 1995) and there was a negative correlation between noise level and bird density (Reijnen et al. 1997). Male willow warblers (*Phylloscopus trochilus*) experienced difficulties attracting or keeping females near roads, possibly due to distortion of male song (Reijnen & Foppen 1994). Underwater noise may affect marine mammals in a comparable manner. Some whales communicate vast distances underwater using vocalizations, but the present level of anthropogenic oceanic noise now precludes such communication (McGregor et al. 2000). The effects of this interference on the population and social structure of marine mammals are unknown.

Habitat selection

Understanding the habitat needs for a species is a basic requirement of any conservation program. However, the study of habitat selection has been fraught with difficulties, including debate over operational definitions of habitat use, preference, selection, availability or suitability (Hall et al. 1997), concerns over methodology used to measure habitat selection (Garshelis 2000), and uncertainty about the appropriate scale at which to do so (Arthur et al. 1996). Most empirical studies of habitat selection involve a comparison of the habitat types used to those available (Garshelis 2000). Assessments of “availability” assume that researchers can measure habitat in the same way as that perceived by the study animal. This is problematic because different estimates of availability can lead to very different (even opposite) indices of habitat selection for the same species (Arthur et al. 1996; McClean et al. 1998; Mysterud & Ims 1998). Uncertainty over the scale at which to measure habitat use and availability has further resulted in debate over habitat needs for threatened species, such as the northern spotted owl (*Strix occidentalis*) (Buchanan et al. 1995; Meyer et al. 1998; Folliard et al. 2000).

Efforts to link habitat selection to fitness consequences have centered on the concept of habitat sources and sinks (Pulliam & Danielson 1991; Pulliam 1996). Animals experience different local birth and death rates in different areas and reproductive surpluses from productive habitats (sources) could maintain populations in unproductive habitats (sinks). A critical question for conservation biologists is whether animals are able to discriminate between the two types of habitats.

Delibes et al. (2001) examined the effects of habitat selection on the degree to which increasing amounts of sink habitat would impact population growth rates. When animals use source and sink habitats at random (no habitat preference), population growth rate declines once a critical amount of sink habitat is exceeded. However, when animals can identify and avoid sink habitats, population growth rates remain high until most of the habitat is converted to sinks. There is a third, more worrisome possibility: animals can be attracted to sink habitats. In this case, there may be dramatic impacts on population growth rates, causing rapid reductions once a critical level of sink habitat is reached. Such attractive sinks, or ecological traps (Donovan & Thompson 2001;
Woodward et al. 2001), exist because the cues that animals use to select habitat are indirect; animals cannot predict breeding success directly and must use other cues to assess habitat quality (Kokko & Sutherland 2001). When those cues become uncoupled from the underlying fitness value of a habitat (by changes in the quality of a site but not its appearance), attractive sinks can develop. Understanding the cues animals use to assess habitat quality, and the degree to which such preferences can be altered, may be critical in evaluating the consequences of anthropogenic habitat change.

Foraging and patch choice

The conceptual framework for the study of foraging behavior has a long theoretical history and strong links with behavioral ecology (Stephens & Krebs 1986; Giraldeau & Caraco 2000). The most effective use of foraging theory in a conservation context has come from efforts to link foraging behavior and density-dependent habitat selection using the ideal free distribution and ideal despotic distribution (Sutherland 1996). For example, Goss-Custard et al. (1995a,b) developed individual-based models for the oystercatcher (Haematopus ostralegus) in which the location, behavior, and body condition of each individual was tracked. A game-theory approach was then used to determine where each individual feeds, its body reserves, and the survival consequences for the individual and all others in the population (Stillman et al. 2000). Using this model, the effect of habitat loss to oystercatchers can be calculated and the most vital habitats determined. Stillman et al. (2001) extended this approach to examine the impact of shellfish harvest and found that although current levels of harvest were sustainable, increased fishing effort would greatly affect oystercatcher mortality and population size. Parallel studies have examined loss of winter habitat, breeding habitat, and migratory strategies on bird populations (Dolman & Sutherland 1995; Sutherland 1996) and have used foraging models to develop baseline expectations of habitat use against which effects of disturbance can be evaluated (Gill & Sutherland 2000).

Foraging behavior has also been used in other conservation contexts, such as examining the influence of human hunters on animal populations, including indigenous peoples (Winterhalder & Lu 1997), fishermen (Abrahams & Healey 1990), and whalers (Whitehead & Hope 1991). Studies of the foraging success of seabirds provide reliable indices of the abundance and distribution of commercially important fish species and do so less expensively than conventional fisheries surveys (Monaghan 1996).

Allee effect and conspecific attraction

When populations decline to exceptionally low densities or groups dwindle to very small numbers of individuals, per-capita rates of increase can decline to zero or become negative (Fig. 16.1). This is called the Allee effect and it arises for a number of reasons: (i) genetic inbreeding and loss of heterozygosity leading to reduced fitness; (ii) random demographic stochastic effects that include highly skewed sex ratios, resulting in a paucity of mates; or (iii) a loss or reduction in opportunities for cooperative interactions.
between individuals, for example the inability to find receptive mates (e.g., African elephants, *Loxodonta africana*, Dobson & Poole 1998; Glanville fritillary butterfly, *Melitaea cinxia*, Kuussaari et al. 1998) or lack of group defense (Courchamp et al. 1999; Stephens & Sutherland 1999).

Once regarded as idiosyncratic and of limited relevance to natural populations, the Allee effect is now seen as potentially significant when populations dwindle to very low densities, when populations are heavily harvested, when reductions in group sizes of susceptible hosts prevent disease from spreading (Dobson & Poole 1998), when small numbers of individuals are reintroduced in the course of a restoration project, and when individuals are encouraged to congregate and breed in safe habitats (Jeffries & Brunton 2001).

One of the ways in which an Allee effect might be mitigated is through conspecific attraction. Here, animals use the presence of conspecifics to select a habitat in which to live or breed. For example, pelagic marine invertebrates use chemicals released by conspecifics to settle close to established conspecifics (Meadows & Campbell 1972), and juvenile lizards (*Anolis aeneus*) settle next to areas where they have seen conspecifics in experiments that control for habitat quality (Stamps 1988). Conspecific attraction is thought to be particularly important in colonial seabirds choosing where to nest (Danchin & Wagner 1997). Using presence of conspecifics as a proxy for suitable habitat may
also serve to reduce settlement costs if it is difficult or time-consuming to assess components of habitat quality, or, at a coarser level, conspecifics may simply be used to locate suitable habitat (e.g., listening for and moving toward frogs chorusing at an ephemeral pond; Greene & Stamps 2001).

Conspecific attraction is an important tool in reintroduction programs because it can be employed to draw released individuals into a safe target area; thus the use of decoys, artificial droppings, and tape lures are common in bird reintroduction attempts (Jeffries & Brunton 2001). It is also important in reserves designed to protect metapopulations (spatially discrete subpopulations connected by occasional dispersal). Without knowledge about conspecific attraction, suitable habitats may appear to be unsuitable simply due to an absence of conspecifics and unwittingly be omitted from inclusion in a reserve (Smith & Peacock 1990).

**Movement, ranging, and dispersal**

If habitats differ in risk, for example if one lies inside a reserve but the other does not, movement of individuals between habitat patches will dictate patterns of mortality and reproduction inside and outside the protected area. Unfortunately, we know surprisingly little about the permeability of habitat edges, let alone about individual movements in their vicinity. Edges are detrimental to many forest-loving species because forest edges receive more sunlight, are less humid, and suffer greater wind shear than forest interiors. Edges are also detrimental to some specialists that cannot compete with generalist and commensal species that make forays in from the surrounding area. From this follow two predictions: certain species should avoid edges, and species that range widely will be more likely to encounter and cross boundaries and suffer problems there. Regarding the second point, Woodroffe and Ginsberg (2000) documented very high levels of human-induced mortality among large carnivores living in protected areas and reasoned that species with large home ranges would be more likely to encounter human activities because they were more likely to leave reserves than those species with smaller ranges. Woodroffe and Ginsberg then derived a measure of critical reserve size necessary to maintain each carnivore species. Critical reserve size correlated positively with female home range size after controlling for phylogeny (see Chapter 13) and population size. Moreover, female home range size was larger in species listed as threatened by the International Union of Nature and Natural Resources (IUCN) and was correlated with proneness to extinction (Woodroffe 2001). Thus, patterns of ranging are an important predictor of effective reserve size and extinction risk (see also Harcourt 1998 for a parallel finding in primates).

Reserve design has been a central focus in conservation biology for 25 years, with early debates focusing on the appropriate size and number of reserves and current interest on the importance of connecting reserves. Since large reserves are preferable to smaller reserves, an important conceptual question is whether to sacrifice reserve size for a corridor (narrow strips of land that differ from the habitat on either side and are attached to somewhat similar patches of vegetation; Fig. 16.2). Benefits of corridors include exchange of individuals among previously connected populations, which could lower regional
extinctions, reduce inbreeding depression, and increase recolonization in unoccupied patches. Corridors may also act as suitable habitats in their own right. Disadvantages include facilitating spread of disease or fire between patches, and attracting edge-loving and introduced species (Hobbs 1992; Rosenberg et al. 1997).

A key issue in this debate is whether corridors facilitate movement between patches and, as a consequence, increase population viability within those patches (Beier & Noss 1998). The problem has been addressed either demographically, by comparing patch occupancy and abundance in patches that are or are not connected (but usually failing to observe whether animals move down corridors), or behaviorally, by observing whether animals are found in, or better still, move along corridors (but often failing to document whether movements occur across the surrounding habitat as well). Studies that have observed animal movements in corridors are beginning to paint a complicated picture that includes closely related species using corridors but not others (e.g., butterflies, Sutcliffe & Thomas 1996; vole species, Mech & Hallett 2001), some species refusing to cross even small gaps (e.g., dormice, Muscardinus avellanarius, Bright 1998) but others doing so easily (e.g., tigers Panthera tigris, Johnsingh et al. 1990), and juveniles using corridors for dispersal but adults of the same species settling there (e.g., songbirds, Machtans et al. 1996). Only a few generalizations can be made at this stage: animals are more likely to select pathways that include components of their habitat, to move more rapidly through low- than high-quality habitat, and to avoid using the
surrounding area the more it contrasts with their own patch (Rosenberg et al. 1997). We foresee a rapid growth in studies observing movements of animals in corridors in the next few years.

Movement and dispersal are also important for discrete populations connected by migration (a so-called metapopulation). The probability of extinction of a metapopulation can be highly influenced by factors such as habitat loss and emigration rates between patches. In turn, emigration is influenced by the size of the subpopulation, the suitability of each habitat patch, and distance between patches. Understanding behavioral patterns of movement between subpopulations is critical for maintaining the metapopulation (Hanski 1998).

Mating and social systems

Studies of mating systems and social systems (see Chapters 11, 12 & 14) have contributed to two areas in conservation biology: determining effective population size, and evaluating effects of exploitation on harvested species.

Effective population size

The effective population size \( N_e \) is a measure of the ability of a population to maintain genetic diversity (defined as the size of an ideal population that would lose genetic variation via genetic drift at the same rate) and has been a central component of conservation planning for small populations (using population viability analysis). \( N_e \) can be substantially lower than the actual population size due to variance in sex ratio, variance in reproductive success among individuals, or changes in population size over time which can be influenced by the mating system.

Parker and Waite (1997) examined the effect of mating system and reproductive failure on \( N_e \). With increasing levels of failure (as might occur in a declining population), \( N_e \) declines (Fig. 16.3a). However, \( N_e \) is also strongly affected by the mating system. As the mating system deviates from monogamy to increasing extremes of polygyny or polyandry, \( N_e \) is reduced substantially because fewer males (polygyny) or females (polyandry) contribute genetically to the next generation. Conversely, increased promiscuity leads to larger \( N_e \) than would be expected under monogamy because members of the more abundant sex have greater opportunities to breed. The influence of mating system applies across most ranges of failure, although the rate at which \( N_e \) is impacted differs with mating system.

Application of molecular genetic techniques to studies of mating systems has revealed the presence of extrapair young in many vertebrates. A consequence of increased extrapair young is increased reproductive skew (see Chapter 14) because fewer males dominate more of the breeding opportunities. Increased reproductive skew, in turn, leads to a reduction in \( N_e \) (Fig. 16.3b). Patterns of mate choice can further impact \( N_e \) (Blumstein 1998). Females rarely chose mates randomly; typically, females select males on the basis of one or more traits and they may do so using a relative or an absolute assessment rule. Females using absolute threshold assessment rules select mates which exceed some threshold, and reject males falling below. Blumstein (1998) examined
situations where the distribution of male trait values was reduced, as might occur following disease or environmental hardship that reduced animals’ body condition. This, in turn, resulted in a smaller proportion of males being “acceptable” to females and a consequent reduction in $N_e$.

Despite the growing number of models examining the effects of mating and social systems on $N_e$, empirical data are scarce. However, Creel (1998) collected data from species of African carnivores in order to examine the relative influence on $N_e$ of variance in population size, sex ratio, and reproductive success, as well as social and behavioral
factors such as dominance, reproductive suppression, reproductive skew, and dispersal behavior. Social and behavioral features had the greatest impact on \( N_e \). Variance in population size or sex ratio resulted in \( N_e \) being reduced to 75–95% that of the actual population size (\( N \)), whereas incorporation of behavioral factors reduced \( N_e \) to 15% of \( N \) for some species.

**Effects of exploitation**

The study of social systems provides insight into the effects of harvest and over-exploitation on populations in the wild. For example, Greene et al. (1998) considered the interaction of breeding systems with hunting intensity and harvest strategies for several African ungulates and carnivores. In their baseline population (assumed to be polygynous), the population growth rate was related to harem size. Population growth rates were lower for small harems because of low male survivorship and an insufficient number of males to fertilize all females (Allee effect). Fecundity also decreased in very large harems because of competition among females. The authors examined the effects of three different hunting regimes (on adult males, all adults, or adults and juveniles) and found similar effects on population growth. Under baseline conditions, the model population could sustain hunting intensities of 30–40% and was resilient to the hunting of males when harem size was large (Fig. 16.4a). When infanticide by males was included in the model, the population could no longer sustain the same levels of hunting and now the removal of males resulted in reductions in population growth because replacement males killed offspring (Fig. 16.4b). If the effects of reproductive suppression were included (i.e., dominant individuals prevent reproduction by subordinates), the population could sustain only very low levels of hunting for the adult and adult-and-juvenile harvest regimes. Conversely, if the harvest was restricted to only males, much higher intensities could be tolerated (Fig. 16.4c). Greene et al.’s study illustrates how breeding system attributes can significantly influence the magnitude of a population response to hunting pressure.

Other studies have examined the relationship between the degree of plumage dimorphism and introduction success on islands. McLain et al. (1995, 1999) found that introduction success rate was lower for species of birds with sexually dichromatic plumage than for species with monochromatic plumage. They argued that species subjected to intense sexual selection (i.e., those with dichromatic plumage) may have a reduced evolutionary potential to respond to natural selection pressures and so may be at greater risk of extinction when populations are small.

**Demography and life histories**

Overexploitation can also impact life histories, as illustrated by coho salmon (\textit{Oncorhynchus kisutch}). Male salmon have two life-history tactics: jacks mature precociously (6 months in the ocean) at small size, whereas hooknose males delay maturity until they reach a larger size (18 months in the ocean). These alternative life histories correlate with different behavioral tactics to obtain mates: large hooknose males fight
for access to females whereas small jacks attempt to sneak matings (Gross 1991). Each tactic does better when rare and the relative value of the two life histories is negatively frequency-dependent (Fig. 16.5). In undisturbed conditions, an equilibrium balance of jacks and hooknoses could be maintained at the frequency $p_1^*$ where the fitness of the two tactics is equal. Humans, however, have altered this relationship through harvest. Fishing removes the largest individuals, typically the hooknose males. Accordingly, the survivorship of hooknose males is reduced, lowering the fitness surface for that life-history tactic (Fig. 16.5). This results in a shift in the equilibrium frequency of jacks in the population (from $p_1^*$ to $p_2^*$ or $p_3^*$, depending on fishing pressure). Hence,
Size-selective fishing leads not only to changes in the demographic dynamic (reduced population size, especially of large males) but possibly the evolutionary dynamic as well. Overexploitation of the large males could result in an evolutionary shift favoring the jack life history and in doing so would reduce the proportion of large economically desirable males. This situation is further complicated by the observation that being a jack or hooknose may be conditional, with faster-growing fish turning into jacks and slow growers into hooknoses. Artificial selection in fish hatcheries for fast growth may actually increase numbers of small animals because managers were unknowingly selecting for jacks.

Consideration of alternative reproductive behaviors may have important consequences for population dynamics as well. For example, conspecific brood parasitism in birds can lead to population fluctuations, cycles, or even local extinction (Eadie & Fryxell 1992; Nee & May 1993). Provision of high densities of artificial nest sites, a common restoration practice, may exacerbate this problem (Semel & Sherman 1995; Eadie et al. 1998).

The study of life histories has also been used in conservation biology to identify species that may be vulnerable to perturbation. Detailed demographic data are frequently unavailable for many species, yet conservation managers require some method to evaluate species at risk. One possibility is to employ ecological characteristics that correlate with some measure of vulnerability. For example, Harcourt (1998) examined the response to logging of a number of primate species and evaluated the utility of ecological traits in predicting whether a species was impacted (as measured by an index of density before and
after logging). Of the variables examined, only home range size was a strong predictor; species with large home ranges were vulnerable to the effects of logging (Harcourt 1998).

**Relaxed selection**

Recolonization is a fundamental goal of conservation biology and endangered carnivores are being reintroduced regularly around the world (Gittleman & Gompper 2001) despite a persistent worry that prey populations may suffer reductions or extinctions without knowledge of contemporary predators. In the absence of predation, selection for predator evasion strategies may become diminished or relaxed.

For example, populations of California ground squirrels (*Spermophilus beecheyi*) are more resistant to northern Pacific rattlesnake (*Crotalus viridis*) venom where snakes are abundant than where they are absent (Poran et al. 1987) even though all California populations are able to recognize snakes (Coss 1999). Estimated maximum time since release from snake predation ranges from 70,000 to 300,000 years. In contrast, Arctic ground squirrels (*Spermophilus parryii*), whose ancestors have experienced relaxed selection for 3–5 million years, show an inability to recognize snakes and exhibit inappropriate antipredator behavior (Goldthwaite et al. 1990). Similarly, Byers (1997) noted that specific forms of antipredator behavior of pronghorn (*Antilocapra americana*) have persisted despite the extinction of predators such as North American cheetahs (*Miracinonyx* sp.) in the last ice age (10,000 years ago). Furthermore, in laboratory experiments, tammar wallabies (*Macropus eugenii*) that had been isolated from mammalian predators since the last ice age responded to visual presentations of evolutionarily and ontogenetically novel predators (fox and cat) by reducing their foraging and increasing their vigilance in comparison with controls. However, they did not respond to acoustic signals, such as howls of dingoes (*Canis lupus*) (Blumstein et al. 2000).

In contrast to these studies, Berger (1998; Berger et al. 2001) found a rapid decrease in predator recognition abilities of North American ungulates isolated from large predators for only 40–75 years (10 generations). Specifically, moose (*Alces alces*) living in areas where predators have been recently extirpated reduced their feeding rate in response to wolf urine, wolf howls, and raven (*Corvus corax*) calls (ravens are associated with carcasses) compared with moose in predator-rich habitats, although all populations reduced their feeding rate in response to grizzly bear (*Ursus arctos*) feces. Thus we currently face a complicated picture where responses to novel predators vary across species, across populations of the same species, differ according to the behavior under consideration (Table 16.1), differ between predators, and even between different cues provided by the same predator.

From a conservation perspective, however, it is clear that individuals can learn about predators rapidly. Predator-naive moose mothers whose calves were killed by wolves during the recent wolf recolonization in Wyoming elevated their vigilance in response to playbacks of wolf howls by 500% in years after the predation event and were four times as likely to abandon their feeding sites following playbacks (Berger et al. 2001). In some species, at least, offspring loss causes hypersensitive maternal behavior that must ameliorate actions of novel predators.
Relaxed selection is also seen as a separate problem confronting breeding institutions (Wallace 2000). Here there is concern that species bred for generations in zoos may lose their ability to cope with environmental stresses, including food shortages, competition over resources, challenges from conspecifics, as well as appropriate antipredator behavior outlined above. At present, there has been no systematic study of this topic.

Table 16.1 Summary of the behavioral consequences of relaxation of predation in North American ungulates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Extinct predators</th>
<th>Effects*</th>
<th>Repeated at other sites</th>
<th>Time frame (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group size Pronghorn</td>
<td>National Bison Range, Montana</td>
<td>Cheetah, short-faced bear, lion†</td>
<td>No change</td>
<td>No</td>
<td>10,000+</td>
</tr>
<tr>
<td>Pronghorn</td>
<td>Great Basin Desert, Nevada (paired sites)</td>
<td>Human‡ vs. none</td>
<td>Smaller</td>
<td>No</td>
<td>25</td>
</tr>
<tr>
<td>Musk ox</td>
<td>Alaska, Canada and Greenland (19 sites)</td>
<td>Wolf</td>
<td>Smaller</td>
<td>Yes</td>
<td>25–50</td>
</tr>
<tr>
<td>Vigilance Caribou</td>
<td>Peninsular, Alaska and Kangerlussuaq, Greenland</td>
<td>Wolf</td>
<td>Reduced</td>
<td>No</td>
<td>4000+</td>
</tr>
<tr>
<td>Bison</td>
<td>Badlands, South Dakota and Wood Buffalo, Canada</td>
<td>Wolf</td>
<td>No change</td>
<td>No</td>
<td>75</td>
</tr>
<tr>
<td>Location in group Pronghorn</td>
<td>Badlands, South Dakota</td>
<td>Wolf, grizzly bear</td>
<td>Vigilance differs</td>
<td>No</td>
<td>75</td>
</tr>
<tr>
<td>Bison</td>
<td>Badlands, South Dakota and Wood Buffalo, Canada</td>
<td>Wolf, grizzly bear</td>
<td>No change</td>
<td>No</td>
<td>75</td>
</tr>
<tr>
<td>Raven response Moose</td>
<td>Alaska and Wyoming</td>
<td>Wolf, grizzly bear</td>
<td>Decreased</td>
<td>Yes</td>
<td>40–75</td>
</tr>
</tbody>
</table>

* Changes at sites lacking in predation.
† Pleistocene extinctions.
‡ Modern humans.
Human behavioral ecology

Until recently, indigenous people hunting wild vertebrates or harvesting wild plants were seen as good conservationists (and termed “ecologically noble savages”), but this view has come under sharp scrutiny from anthropologists using sophisticated behavioral, ecological, and economic theory. One problem is that claims of resource conservation were often made on the basis of reports, about food taboos for instance, rather than from empirical data. Another problem is that it cannot be concluded that native groups are conservationists because they are not overexploiting their resources; they may simply live at a low density that is not yet resource limited (Alvard 1998a; FitzGibbon 1998). Clearly, conservation needs to be defined carefully and must incorporate two criteria. It must prevent or mitigate resource depletion, species extirpation, or habitat degradation, and it must be designed to do so in order to separate it from epiphenomenal conservation such as exploiting males from a polygynous species simply because males are easier to catch (Alvard 1998a). Conservation, thus defined, often involves a short-term loss in order to reap a long-term gain (Smith & Wishnie 2000).

Accordingly, human behavioral ecologists have generated predictions that contrast true conservation with behavior designed to maximize food intake based on optimal foraging theory (Alvard 1998b). To illustrate, a conservation hypothesis predicts that hunters will choose species that are less vulnerable to local extinction, and will choose young and old age classes that have lower reproductive value than prime-aged individuals. In contrast, an optimal foraging model (the prey model discussed in Chapter 9) predicts that choice will be based on prey types that maximize return rates and that hunters will select any age class that they encounter but ignore immatures if they fall below the range in body size as predicted by the diet breadth model. In the first instance, prey species can now be ranked according to (i) their maximum intrinsic rate of increase ($r_{\text{max}}$) (Robinson & Redford 1991) or (ii) according to their profitability based on handling (pursuing, killing, and processing) prey or on mean return rates from continued search for higher ranked prey (i.e., return in calories for higher ranked prey divided by both handling and search time). All these variables can be estimated or measured empirically.

Among the Piro of south-eastern Peru who use shotguns, prey items closely matched those predicted by optimal foraging theory. Thus, large species such as spider monkeys (Ateles paniscus), howler monkeys (Alouatta seniculus), capybara (Hydrochaeris hydrochaeris), deer (Mazama americana), and tapir (Tapirus terrestris) were pursued at nearly every encounter despite monkeys and tapir having a low $r_{\text{max}}$. Similarly, the ratio of immatures to adults killed was indistinguishable from that in the census population for peccaries, deer, and capybara, whereas primate prey were significantly biased toward adults; old prey made up a small proportion of kills (Alvard 1995). Thus predictions of optimal foraging were better supported than those of conservation. More generally, field studies from many different parts of the world show that humans follow the predictions of optimal foraging theory rather than conservation (Table 16.2).

Another branch of human behavioral ecology is examining apparently altruistic conservation acts among people in production systems where they have control over resources.
Pastoralists, who graze cattle, have long been credited with protecting grasslands from overuse by means of grazing regimes, stocking regulations, and institutional land-use practices. Borgerhoff Mulder and Ruttan (2000) used game theory to model the payoffs of rich and poor herders grazing their cattle between wet and sensitive dry season pastures. Payoffs are asymmetrical because their value depends on the number of cattle owned by the herder. Borgerhoff Mulder and Ruttan found situations in which poor and rich herders should cooperate in reducing grazing in dry-season areas, in which neither poor nor rich should cooperate, and a large number of situations in which the rich should cooperate but poor should defect. In this modeling space, rich herders could obtain even higher payoffs if they coerced poor herders to leave the dry-season reserve

Table 16.2 Field studies using optimal foraging theory (OFT) with results that bear on the issue of conservation.

<table>
<thead>
<tr>
<th>People</th>
<th>Primary hunting technology</th>
<th>Prey</th>
<th>Location</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ache</td>
<td>Shotgun and bow</td>
<td>Large/medium-sized ungulates, rodents, primates</td>
<td>Paraguay; rainforest</td>
<td>OFT predictions upheld</td>
</tr>
<tr>
<td>Cree</td>
<td>Rifle and trap</td>
<td>Large ungulates, small mammals, birds, fish</td>
<td>N. Ontario; boreal forest</td>
<td>OFT predictions upheld</td>
</tr>
<tr>
<td>Wana</td>
<td>Trap, spear, blowgun, and dog</td>
<td>Large ungulates, primates, rodents, birds, bats, fish</td>
<td>Sulawesi, Indonesia; rainforest</td>
<td>No obvious conservation</td>
</tr>
<tr>
<td>Piro</td>
<td>Shotgun and bow</td>
<td>Large/medium-sized ungulates, rodents, primates, birds</td>
<td>Amazonian Peru; rainforest</td>
<td>OFT predictions upheld</td>
</tr>
<tr>
<td>Inujjuamiut</td>
<td>Rifle and trap</td>
<td>Large marine and terrestrial mammals, birds, fish</td>
<td>Canadian arctic; tundra</td>
<td>OFT predictions upheld</td>
</tr>
<tr>
<td>Yanamomo, Ye'kwana</td>
<td>Shotgun and bow</td>
<td>Large/medium-sized ungulates, rodents, primates, birds, fish</td>
<td>Venezuela; rainforest</td>
<td>“Hunters and fishers that have depleted resources hunt and fish more intensively”</td>
</tr>
<tr>
<td></td>
<td>Bow</td>
<td>Large terrestrial mammals</td>
<td>Tanzania; savannah woodland</td>
<td>“A hunter maximizes average rate of meat acquisition by ignoring small prey”</td>
</tr>
</tbody>
</table>

Source: Adapted from Alvard (1998b).
when the wet season begins. The importance of this work is that, in contrast to the hunter-gatherer studies, it shows that some people (here the rich) can be good conservationists while pursuing selfish goals.

In both the foraging and pastoralist context, a dispassionate understanding of the conditions under which people switch to and away from conservation strategies is central to programs designed to develop sustainable patterns of resource use, conservation of biodiversity, and protection of human rights (Robinson & Bennett 2000).

### Impediments to Applying Animal Behavior to Conservation Biology

Although the number of connections between animal behavior and conservation biology is impressive, many of the links take the form of “how knowledge of animal behavior might influence conservation.” There are remarkably few examples that meet three criteria: (i) how behavior varies in response to social or environmental factors, (ii) how this variation changes the way a population responds to exploitation or to a restoration project, and (iii) how management takes note and alters its conservation program as a consequence. We regard this three-stage process as the yardstick of success in linking these disciplines. There are three classes of problems that impede rapid integration of these two fields.

#### Conceptual problems

Many studies of animal behavior are interested in how natural selection shapes the behavior of individuals and how this affects reproductive success and survival. Conservation biologists and managers, on the other hand, focus on population size and structure and are interested in individual fitness only if it directly influences the response of populations to anthropogenic disturbance (Fig. 16.6). Differential emphases on individuals and populations remain a key impediment to linking these fields (Beissinger 1997).

![Fig. 16.6](image_url)

**Fig. 16.6** Principal foci of attention (ovals) of studies of animal behavior and conservation biology. Connections between foci are also shown.
In addition, many aspects of animal behavior do not have direct consequences for populations. For example, grooming, song learning, and play are almost irrelevant to decision-makers trying to save a dwindling population. Moreover, many issues in conservation biology are simply unlikely to benefit from knowledge of animal behavior (Table 16.3).

### Social problems

Many population biologists view behavior studies as difficult to conduct or as too time-consuming when conservation decisions need to be made rapidly. Interest in relating animal behavior to conservation biology has come principally from undergraduates and graduates, who do not yet have the training to develop sophisticated or rigorous analyses. University faculty and managers who guide these students have training in more traditional disciplines and often lack the ability or willingness to make bridges between fields. Finally, the short time span over which tentative links have been made has been insufficient for many intellectually rich areas to have surfaced, let alone to have been debated or tested; consequently there are remarkably few well-worked examples demonstrating how knowledge of behavior is important for conservation management.

<table>
<thead>
<tr>
<th>Area</th>
<th>Likely to benefit</th>
<th>Unlikely to benefit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extent of biodiversity</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Loss of biodiversity</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Genetic stochasticity and (N_e)</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Demographic stochasticity and PVA</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Environmental stochasticity</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Habitat fragmentation and metapopulations</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Prioritizing management plans</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Reserve connectivity</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Extractive reserves</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Managing reserves</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Trade in wildlife</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Captive breeding</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Species reintroductions</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Philosophical issues</td>
<td>✓</td>
<td></td>
</tr>
</tbody>
</table>

*Source:* Adapted from Caro (1998a).
Institutional problems

Last, animal behaviorists come from a different “culture” than managers and, to a lesser extent, conservation biologists. Managers view behavioral research as too esoteric whereas animal behaviorists view conservation as being too applied. They do not go to each other’s meetings, nor do they read each other’s journals (Sutherland 1998). Most damaging, there are very few sources of funding available to provide graduate training to link the two fields. Indeed, in the USA the National Science Foundation does not even have a panel that specifically considers or funds conservation research.

How to Move Forward

For a study of animal behavior to be taken seriously by conservation biologists, it must help solve a conservation problem. The onus is on animal behaviorists to be aware of, and take an active interest in, conservation issues so that they can grasp research and management opportunities as they arise. Aside from being conservation “savvy,” we suggest future animal behavior studies stay mindful of five issues.

Focus on a species or system of conservation concern

Choose a study animal of conservation concern

Studies of animal behavior conducted on endangered or rare species have a better chance of being relevant to conservation than studies on common species, all else being equal (Caro 1998c). What are the advantages and disadvantages of this research gambit? First, with endangered species there may be questions relating to population size or restoration to which managers need answers. Thus, from the onset, the behaviorist will be working in collaboration with, and under the auspices of, a conservation team: hence behavioral findings will have a greater chance of being acted upon. Second, any findings about behavior that affect juvenile survival and reproductive rates and hence population size and structure (Fig. 16.6) are likely to be important in helping bolster populations that are, by definition, at risk. Against these benefits, there will be difficulties in obtaining large samples (although any results are likely to be interesting; Bunin & Jamieson 1996), animals may be difficult to observe if they are sensitive to disturbance or have been hunted, and permits may be difficult to obtain.

Work on several species simultaneously

Although it is unusual for an observational behavioral study to focus on more than one species, conservation biologists often do so in order to make better management decisions. Working on several species allows researchers to maximize behavioral data collected during a period of fieldwork. If responses to, say, an environmental perturbation are
common to several species, it highlights the importance and robustness of the results; if they are different, it alerts researchers and managers to additional causal factors affecting behavior, or the need to consider differences in species’ behavioral ecology.

Choose a study area of conservation relevance

Given that habitat fragmentation, pollution, direct exploitation, and the introduction of exotic species are the four most devastating forces affecting habitats and species, we advocate research that compares behavior of animals in such areas to control areas. For example, one might compare behavior before and after a perturbation such as habitat fragmentation or impending translocation. Or one might contrast behavior in areas impacted by oil slicks or in populations suffering from disease or overharvesting with control sites. At a broader scale, we would welcome more research in the tropics since this is where most of the world’s biodiversity is found, where habitats are disappearing most rapidly, and where fewest researchers work.

Avoid surrogate species

Several colleagues have advocated the use of surrogate species to explore processes by which animal behavior affects conservation but we are leery of transferring results between even closely related species. For example, our own work shows that ungulate species with slightly different breeding systems respond quite differently to hunting pressure (Greene et al. 1998). Similarly, conspecific brood parasitism occurs frequently in wood ducks (Aix sponsa), which compromises the efficacy of using nest boxes to bolster populations, but occurs to a lesser extent in Barrow’s goldeneye (Bucephala islandica) because of territoriality, enabling nest boxes to be used (Eadie et al. 1998). A further limitation of studying substitute species is that some managers are not comfortable or willing to draw comparisons between systems and will only utilize behavioral data if they come from the species at risk. Finally, and more worrying, we perceive a growing trend in which researchers attempt to relate a behavioral project on a common species to conservation in an offhand and indirect fashion on grounds that any findings about, say, dispersal, mating systems, or antipredator behavior are relevant to population persistence; such an approach avoids responsibility for making firm and useful connections to a specific conservation problem.

Focus on behavioral factors that influence population dynamics

Any attempt to integrate animal behavior with conservation biology must link behavior with fundamental demographic processes (birth, death, immigration, emigration; see Fig. 16.6). It is not sufficient to suggest that a given behavior “might” impact population growth rates; rather, one must demonstrate that it does, and specifically how. Behaviors that affect age at first reproduction (e.g., dominance), clutch size (e.g., life-history tradeoffs), offspring sex ratio (e.g., age or dominance), or survival (e.g., mating or resource competition) and which are conditional on environmental or social
circumstances will modify population growth rates and can be incorporated into a population viability analysis. Similarly, behavioral factors that alter breeding sex ratios, mating system, or variance in family size will influence $N_e$. Conditions under which infanticide, siblicide, and intrasexual competition over mating opportunities are expressed each bear on this important parameter in conservation biology.

**Identify the specific behaviors involved and determine the effect size**

Even when it can be demonstrated that behavior has an influence on the demography of a population of conservation concern, it is not always clear what specific component of the behavior system has been affected. For example, debate on the effect of dehorning black rhinos (*Diceros bicornis*) as a conservation measure was swayed only when Berger and Cunningham (1994) were able to highlight specifically how dehorning reduced a female’s ability to defend her young against predators. To be most useful to conservation efforts, animal behaviorists need also to determine the effect size of a given behavioral perturbation to help prioritize conservation efforts. Simulation models provide one method (e.g., Greene et al. 1998); an alternative approach is to compare populations in areas where they have been impacted to those where they have not (Berger & Cunningham 1994).

**Identify possible solutions**

If there is a case that behavior influences a conservation problem, then animal behaviorists are likely to be in a good position to propose or develop possible solutions. The same training that allows an animal behaviorist to identify a behavioral problem can equally be applied to finding practical ways to alleviate that behavioral perturbation. Moreover, the personal experience than an animal behaviorist may have through several years of field study may prove invaluable to a conservation planning team (Arcese et al. 1997).

**Get the data into the hands of those who need it and will use it**

Academic researchers are trained that the culmination of a research project is publication in a peer-reviewed journal, with the assumption that those who need the information can find it easily there. Unfortunately, conservation managers rarely read journals such as *Animal Behaviour* and, even if they do, the time delay between the behavioral study and applying its findings to a field situation may be too great. It often takes more than a year between submission and publication. Populations can become extinct in less time. If animal behaviorists are serious about playing an active participatory role in conservation biology, they must become engaged in the process at the outset.
SUMMARY AND CONCLUSIONS

Animal behavior is concerned with variation in the behavior of individuals, whereas conservation biology is concerned with the response of populations to environmental factors, often anthropogenic disturbance. Nonetheless, knowledge of how animal behavior varies in response to environmental or social factors, and how such variation changes the way a population responds to exploitation or a restoration project, can alter management decisions about a conservation program. In this chapter, we explore how the study of animal behavior can play an important role in conservation biology. For example, we consider how knowledge of behavioral methods and behavioral ontogeny can provide practical tools to aid monitoring programs and to develop successful captive-rearing and release efforts. We also consider how a greater understanding of the proximate mechanisms underlying behavior may help develop useful assays for populations under stress and enable us to predict which species may be most vulnerable to the effects of anthropogenic change. We then examine how habitat selection, foraging and patch choice, the Allee effect and conspecific attraction, movement, ranging and dispersal behavior may be critical elements in determining why some populations decline and what must be done to remedy the situation. Similarly, we consider how analysis of mating and social systems, demography and life histories, and relaxed selection bear on contemporary conservation issues. Finally, we examine how human behavior relates to conservation. It is clear from even a cursory review that the study of animal behavior has much to offer conservation biology; indeed, we believe that many conservation plans may be at best incomplete and at worst misleading without a more careful consideration of how individual behavior influences population dynamics in species of concern. Nevertheless, there are still conceptual difficulties in applying animal behavior to conservation biology, as well as social and institutional problems. The way forward may be to focus behavioral research more closely on conservation problems, especially those that relate to important demographic parameters. Animal behaviorists need to form a new dialogue with conservation managers.

FURTHER READING

For those who have interest in the topic of conservation and behavior we recommend the following three books: Behavioral Ecology and Conservation Biology (Caro 1998a), Behaviour and Conservation (Gosling & Sutherland 2000), and Animal Behavior and Wildlife Conservation (Festa-Bianchet & Apollonio 2003). These three books together present a series of subject areas where scientists have tried to relate animal behavior to conservation biology. We recommend readers think carefully as to whether the chapter authors have actually demonstrated that knowledge of a behavioral system changes the way that conservationists think about a problem and that, as a consequence, alters management strategy, or whether the authors simply indicate that behavior might be relevant to conservation.

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