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Animal Behavior as a Tool in Conservation Biology

J. Michael Reed

The behavior of animals is important to conservation biology because behavior affects species persistence through a wide variety of mechanisms. These mechanisms can include social disruption of breeding, dispersal and settlement decisions, learned and socially facilitated foraging, translocation success, and canalized behavior that is maladaptive (Reed 1999). In addition, understanding behavior can be critical to solving problems such as reserve design. As an example, one of the current controversies in conservation biology is how to create proper corridors to facilitate dispersal among protected areas (Beier and Noss 1998). Haddad (1999) showed how corridor use might be predicted from animal behavior at habitat boundaries. If we understood endangered species' behaviors as well as we do those of some domestic species, e.g., domestic sheep do not like walking into their own shadows (Kilgour and Dalton 1984), we could solve one aspect of corridor design. Behavior also can be critical to determining species' management goals. For example, a recent study of pilot whales (Globicephala melas) showed that its unusual group structure and mating system requires management for many pods rather than management for large numbers of individuals within a single pod (Amos et al. 1993). Even beyond setting management goals, behavior sometimes can be manipulated to achieve a particular goal. In nature we observe predators taking advantage of their prey's behavior (Jabłoński 1999), and there is no reason we cannot take advantage of species' behaviors to achieve conservation goals.

Despite the importance of behavior to species conservation, animal behaviorists only recently have entered the field of conservation biology (Clemmons and Buchholz 1997; Caro 1998; Gosling and Sutherland 2000), and have yet to do so en force. Sutherland (1998) demonstrated clearly the lack of overlap between the fields of animal behavior and conservation biology. He reviewed the subject matter of papers published in 1996

the census method to mercuse encetiveness			
Species (or taxon)	Census Method	Behavior(s)	Citation
		Exploited	
Black bear (<i>Ursus</i>	Counting opened cans of	Olfactory prey	Powell et al.
americanus)	sardines that were nailed to trees	detection	(1996)
Red-cockaded woodpeckers (<i>Picoides borealis</i>)	Counting "active" cavity trees	Excavating resign wells and scraping bark from nest	Reed et al. (1988)
,		and roost trees	
Most frogs	Counting calling males	Attracting mates by calling	Zimmerman (1994)

Table 12.1. Examples of how various species are censused and the behaviors exploited by the census method to increase effectiveness

in *Animal Behaviour* and in *Conservation Biology*; none of the 229 papers in the former journal dealt with conservation, and only 9 of 97 in the latter focused on animal behavior. It is possible that the lack of overlap so far in these fields is due to not understanding the myriad ways in which animal behavior can influence species' conservation. Of all areas of conservation biology, censusing and monitoring are the only ones where the methods center on species' behaviors. All animal censusing, monitoring, and inventory methods take some advantage of behavior (Table 12.1). When census methods are refined for particular target species, refinements often take advantage of specific behaviors, and the effectiveness of inventory and monitoring depend on the effectiveness of these methods (Bibby et al. 1992; Reed 1996).

In this chapter I present examples of the ways in which behavior can be used specifically as a tool to achieve conservation goals. Although most examples come primarily from birds and terrestrial mammals, behavior can be a tool in conservation of other taxa. Because of recent symposia (Clemmons and Buchholz 1997; Caro 1998; Gosling and Sutherland 2000), I do not review all the ways behavior can relate to species conservation. Rather, I address several important issues in conservation biology: finding behavioral indicators of ecosystem health, increasing reproductive success and survival, facilitating movement, improving population viability analysis, facilitating species translocation or reintroduction, and reducing loss of genetic variability. For each, I provide examples of how behavior might be manipulated to achieve specific goals. It is my intent to stimulate interest in considering and applying behavior to solve specific conservation problems.

12.1 Behaviors as Indicators of Ecosystem Health

Indicators are relatively simple measures intended to reflect complex phenomena (Bibby 1999). Popular biological indicators of ecosystem health or integrity include the presence or abundance of particular pollutants in wildlife, specific habitat

structures, and the presence or abundance of particular species (e.g., Furness and Greenwood 1993; Karr 1994). The disadvantages of many indicators include high economic cost of measurement, destruction of the individual being tested, necessity of long-term data, and a long time lag between the introduction of a problem and response of the indicator. Although not often used, particular behaviors or disruption of typical behaviors also can be indicators of ecosystem health, and they sometimes avoid the above problems associated with other bioindicators (Warner et al. 1966). Here I briefly review the use of behaviors to indicate the presence of pollutants, and their potential to act as indicators of other types of environmental impacts. The principles I present also can be applied to the presence of diseases, which can alter behavior or produce specific atypical behaviors.

Although most research on ecotoxicity focuses on determining lethal doses of toxicants, sublethal effects can result in population decline by disrupting normal behaviors (Cohn and MacPhail 1996) (Table 12.2). A wide variety of effects of pollutants on normal behaviors have been reported, including tremors in limbs, altered time/energy budgets, disrupted motor and sensory functions, and decreased performance in learned tasks (Peakall 1985; Døving 1991; Kulig et al.1996). For example, Galindo et al. (1985) found northern bobwhites (Colinus virginianus) exposed to methyl parathion were more susceptible to predation, and Nocera and Taylor (1998) found that very young common loons (Gavia immer) exposed to mercury spent less time brooding, resulting in decreased fledging rates. Despite the lethal impact of toxicants, however, not all studies find behavioral responses to sublethal doses (e.g. Fox and Donald 1980). Consequently, if one wants to determine specific responses or lack of response to particular chemicals, experimental work is needed. However, if one is interested in determining only if a toxicant in general is a problem in an ecosystem, rather than initially determining the specific toxicant, observing a suite of behaviors to determine if they deviate from typical behaviors can be sensitive indicators. Determining what constitutes atypical behavior requires fairly extensive data on the behaviors of healthy individuals for use in comparison (Døving 1991; Cohn and MacPhail 1996; Kulig et al. 1996). Given the rapidly expanding number of chemicals released into the environment with often-unknown effects (Colborn et al. 1998), this type of research should receive a high priority.

Although they have not been addressed formally, behaviors could be used as indicators of other types of ecosystem health. For example, it is reasonable to

Table 12.2. Population decline can result from a variety of sublethal impacts on behaviors

Type of Behavior	Impact to Population via:	
Parental Care	Fewer offspring produced	
Mating and Reproduction	Fewer matings, fewer offspring	
Predator Avoidance and Alarm Response	Increased mortality	
Behavior During Development	Increased mortality	
Predatory	Increased starvation	
Migration or Dispersal	Increased mortality, decreased colonization	

Source: Adapted from Døving (1991) and Cohn and MacPhail (1996).

assume that population density and habitat quality would be related for a given species. However, more-detailed studies have demonstrated this to be incorrect in many circumstances. For example, high population density might be associated with non-territorial (not breeding) animals, rather than with territorial (breeding) individuals (Van Horne 1983). Higher densities also could be associated with social disruption, and ultimately reduced reproductive success (Purcell and Verner 1998). In many species reproduction can be difficult to assess, and behavioral indicators of reproductive status might be used (e.g. Vickery et al. 1992). Changes in time budgets, such as time spent foraging, also can reflect changes in environmental condition, such as sea bird foraging time reflecting fish prey stocks (Montevecchi 1993).

Potential downsides to using behaviors as indicators include the necessity of deciding on discrete, quantifiable behaviors to measure, and the difficulty of determining specific cause and effect, particularly for identifying particular toxicants (Kulig et al. 1996; Peakall 1996). However, if one has as a goal to determine if there is a problem, rather than what the specific problem is, these concerns are less important. Developing behavioral indicators of ecosystem health will involve an interesting blending of experimental psychology, ethology, and field studies (Cohn and MacPhail 1996).

12.2 Increasing Reproductive Success

When the intrinsic rate of increase (r) of a closed population (one with no emigration or immigration) is less than zero, its numbers decline over time. Intrinsic rate of increase is a composite variable that combines death rate and birth rate. The birth rate in some species is dependent on behaviors that lend themselves to manipulation.

Many of the mechanisms by which behavior can affect reproductive success can be grouped under the rubric of social facilitation. Of conservation interest is the breakdown of these social factors at small population sizes, which can result in a sudden reduction in reproductive success or survival (Fowler and Baker 1991). Another behavioral problem related to small population size is increased frequency of hybridization, which results from inadequate behavioral barriers to mating (Rhymer and Simberloff 1996). The obvious solution to problems of inadequate population size is to increase its size. This option is not always available, such as with rare species or with some captive populations. Researchers working on captive populations of flamingos (Phoeniconais spp.) found a unique solution to the problem, however. Flamingos are social breeders and small groups of birds do not breed (Stevens 1991). Pickering and Duverge (1992) were able to stimulate pre-reproductive displays in a captive flock by putting up mirrors. This suggests the possibility of other methods for social stimulation, particularly in captive populations, such as showing still or videotaped pictures of conspecifics. Some species of birds and lizards are known to respond to projected images (e.g., Clark et al. 1997), though to my knowledge this method has not been used to facilitate breeding.

12.3 Increasing Survival

Survival rate is the other component of the intrinsic rate of increase in a closed population. Behavior contributes to individual survival in terrestrial vertebrates primarily through learned behaviors or responses. Here I show examples of two behaviors that affect survival rate, i.e., predator avoidance and learned foraging skills, and briefly discuss how they might be manipulated to increase survival rate.

Predator avoidance is key to survival for most species. For some vertebrates, effective predator avoidance is related to local habitat familiarity (Isbell et al. 1990; Clarke et al. 1993). For some other species, predator defense can be a social behavior that depends on a minimum group size. For example, when groups of pronghorn (*Antilocapra americana*) drop below 12-15 individuals, their typical defensive behavior breaks down, making them more susceptible to predation (Leopold 1933). These behaviors are important to decisions about how to release individuals when reintroducing them to a new site, but are not readily manipulated in wild populations. In contrast, for some species, recognizing predators and developing escape reactions are cultural skills that must be learned when the animals are young. This can be a problem when translocating animals or when introducing naïve (captively bred) animals to the wild because these skills might be lacking. Recently, researchers have used models of predators to condition wild and captive-reared animals to predators (e.g., McLean et al. 1995; Bunin and Jamieson 1996). Any increase in predator recognition escape proficiency could increase survival rate.

In many species, foraging efficiency increases with practice and learning (Kamil and Yoerg 1981) and social learning plays an important role in diet learning by juveniles (Provenza and Balph 1987). Work on domestic species (ruminants, goats, sheep) in particular has shown the importance of social learning of food selection. For example, experience early in life affects food selection by adults (Distel and Provenza 1991), food preference by mothers affects that of offspring (Mirza and Provenza 1990), and aversions or preferences to novel foods can be transmitted culturally to offspring (Thorhallsdottir et al. 1990). An extreme example of social learning affecting diet selection of young comes from research on domestic cats. Wyriwicka (1981) electrically stimulated pleasure areas in cats' brains while feeding them unusual foods (e.g., bananas). This resulted in a food preference for the cats, and this preference was learned by their offspring.

Social facilitation also affects proximate foraging behaviors. For example, group size can affect prey selection in species that sometimes cooperatively forage (Major 1978). In some species there is conspecific attraction to other foraging animals (Pöysä 1991b; Beauchamp et al. 1997), and decreased predation risk associated with large foraging groups can increase the amount of time spent foraging (Pöysä 1991a). Foraging behaviors in many species have already been manipulated to increase survival probabilities, particularly in the use of feeding stations (Helender 1978). For example, although diurnal cycles and weather affect white-tailed deer (*Odocoileus virginanus*) foraging patterns, Henke (1997) showed that deer enclosed in natural areas could be conditioned to feed at any time of day at feeding stations. Feeding stations can be used for more than just increasing food avail-

ability, however. They also could be used to train individuals on a new food type, to train aversion to a food type that is associated with increased mortality (such as crops, or a food type that has become poisonous through pollution), or to train animals to avoid high-risk areas. For species that feed in groups, decoys can be used to attract species to new feeding areas (Kear 1990).

Castro et al. (1994) used supplemental feeding to enhance habitat quality for endangered Hihi (Notiomystis cincta, a honeyeater) that had been translocated to an island for protection. They found that in the new habitat type, with the altered distribution of food (feeding stations) the birds adopted polygamous mating patterns not normally exhibited in this monogamous species. These accidental alterations of behavior could have negative effects on species and should be guarded against. For example, polygamous mating results in a lower effective population size than monogamous mating of the same number of males and females, thus increasing the rate of loss of genetic variability (see below) (Falconer 1989).

12.4 Facilitating Movement

The primary cause of species extinction worldwide is habitat loss and fragmentation. These mechanisms put species at risk by reducing population size and through edge effects, which are biotic and abiotic intrusion into interior habitat from an ecotone (Harris 1984). The isolation associated with habitat fragmentation has two components, physical isolation and psychological isolation. Physical isolation is a function of distance (MacArthur and Wilson 1967). Psychological isolation is based on behavior and has received less attention. Despite the capacity to disperse a given distance, many species will not cross a habitat gap or an ecotone (Desrochers and Hannon 1997; St. Clair et al. 1998). Not knowing the behavioral response of individuals can lead to incorrect predictions of the impacts of habitat isolation. For example, bighorn sheep (Ovis canadensis) tend to avoid entering timber when moving among feeding sites (Geist 1971). A resource manager unaware of this behavioral tendency would make incorrect predictions of species responses to some reserve designs and habitat management plans. Here I discuss three types of conservation problem associated with individuals moving among sites (dispersal, colonization, and corridor use), and methods that have been or might be used to manipulate behavior to help solve the problem.

12.4.1 Dispersal and Colonization

When a population becomes diminished and isolated, its chances of persistence are diminished because smaller populations are subject to stochastic factors affecting genetic variability, demography, chance environmental events (Shaffer 1981), and reduced opportunities for population rescue through immigration (Brown and Kodric-Brown 1977). Here I am concerned with the problems of reduced dispersal among populations because it is the driving force in metapopulation dynamics (Wu et al. 1993). Dispersal among populations typically is treated in population biology as a mechanical or diffusional process, where an

animal leaves its natal or breeding territory, travels in a random direction, and settles in the first appropriate site it finds (e.g., Johnson and Gaines 1990). However, dispersal in many species, particularly vertebrates, involves behavioral decisions regarding if or when to disperse, what path to travel, and where to settle (Stamps 1991; Reed et al. 2000).

In addition, the nature of the landscape that defines population distributions can affect the behavioral decisions involved in dispersal (Lima and Zollner 1996). For example, behavior can affect emigration decisions, either by increasing dispersal in response to local interactions or by inhibiting emigration. Inhibition can be due a reluctance to cross an ecotone (Stamps et al. 1987; Hansen and di Cristi 1992) or a gap in habitat (Desrochers and Hannon 1997; St. Clair et al. 1998), or avoidance of a particular habitat type (Geist 1971). An example of a behavioral inhibition to emigration comes from hyraxes (Heterohyrax brucei and Procavia johnstoni) living in the Serengeti (Hoeck 1989). These species live on isolated rock outcrops, and individuals tend to not disperse to other outcrops if they do no see or hear conspecifics at that outcrop (other examples given by Reed 1999). Similar behavioral mechanisms can inhibit immigration once an individual has dispersed, such as failure (or inhibition) to settle in suitable habitat because of the absence of some cue correlated with habitat quality (e.g., Stamps 1991; Weddell 1991). The most commonly studied behavioral mechanism affecting immigration is the effect of conspecific attraction on settlement decisions (e.g., Stamps 1987, 1991; Danchin et al. 1991). This can affect growth rates and persistence (Reed and Dobson 1993).

Behavior of emigration, immigration, and colonization (which I distinguish as a special case of immigration to empty habitats) can be exploited in conservation settings. Colonization of new or unused areas could be encouraged if the cues used by a particular species to assess habitat suitability were known and could be altered. Hunters have used cues to manipulate behavior for centuries, e.g., in attracting waterfowl by means of calls and decoys (e.g., Kear 1990). Along the same lines, nest boxes have been employed to attract cavity-nesting ducks to areas from which they had been absent (Kadlec and Smith 1992). Decoys and playback also have been used to induce colonially nesting birds to establish new colonies (e.g., Kress 1983), and dispersing Griffon Vultures (*Gyps fulvus*) were attracted to former breeding sites by spreading white paint to simulate droppings (Sarrazin et al. 1996).

Immigration rate or success could be enhanced for some species by creating breeding sites (e.g., Blanco et al. 1997), but this represents a change in habitat suitability rather than being a behavioral manipulation. The best examples of manipulating behavior to encourage natural colonization of suitable sites come from colonially nesting birds. This work was pioneered by Kress (1983), who presented painted decoys and played sound recordings of least terns (Sterna antillarum) to attract potential breeders to sites where he wanted colonies to be formed. These methods have been used successfully with at least seven other species of colonial seabird (Kress 1997; Veen 1997), and have potential for species with other breeding systems (e.g., Rodgers 1992). The goal of this work is to provide a conspecific cue of habitat suitability. This takes advantage of

prospecting behavior, which is exhibited by species across the animal kingdom, whereby animals gather information about potential breeding sites and make decisions based on expected reproductive success (Reed et al. 2000). Cues might include as widely differing actions as playing conspecific song (Verner 1992) and spreading white paint to simulate droppings (Sarrazin et al. 1996). Results from colonial waterbirds have been dramatic, and the approach used has potential for success for any territorial species.

Considering movement behavior and how it might be manipulated to solve conservation problems for the most part is poorly developed, but has many possibilities. For example, threats to amphibian persistence include roads bisecting breeding and adult habitats, and breeding pond loss. Efforts to provide tunnels under roads have shown that species can be very particular in their requirements for use (Langton 1989). Behavioral tendencies and restrictions should be considered in reserve designs (Schultz 1998) and in socalled sustainable development to ensure target species can take advantage of the landscape design.

12.4.2 Corridor Use

Another way to facilitate dispersal among patches of habitat is through corridors. Reserve designs and sustainable development plans often depend on corridors because of their theoretical importance to sustaining otherwise isolated populations (Saunders and Hobbs 1991). The efficacy of corridors in different situations, particularly what constitutes a corridor for different species, is controversial, but a recent review concluded that corridors can be effective (Beier and Noss 1998). Corridors can be as short as a highway underpass (Reed et al. 1975) or tens of kilometers long, such as buffer zones along railroads or highways (Walters et al. 1988). What constitutes a suitable corridor depends in a large part on behavioral decisions, which means corridor construction needs to take target species' behaviors into account.

Understanding how an animal uses its environment can help predict what will constitute a corridor. For example, some species use roads for foraging or dispersal (Munguira and Thomas 1992; Seabrook and Dettmann 1996), so roads might make useful corridors for some species of bat. In other taxa, roads can be barriers to dispersal (Richardson et al. 1997). Studies of movement behaviors and their consequences are critical to understanding corridor use. Rosenberg et al. (1998) found that Ensatina eschscholtzii, a plethodontid salamander, move across bare soil as well as across ground covered by vegetation, but the movements across the former habitat were much quicker. It is unknown, however, which cover type is better for the salamander. What actually constitutes a corridor for different species remains controversial (Beier and Noss 1998). The best approach for determining this is to develop replicated studies with different treatments for each species in question. However, time and money constraints often preclude this. Recently, Haddad (1999) provided a method that could shorten this process by showing that corridor use might be predicted from behaviors at ecotones. In looking at the behaviors of three species of butterfly, Haddad (1999) found that habitat specialists responded to ecotones by changing course and that they used corridors

to move among patches, while habitat generalists moved regardless of ecotones. Using simulation modeling of movement behavior, he showed that some increases in corridor width increased movement among patches, but that after some width the added benefit was minimal. Using his methods, combining behavior observations with simulation models, one might predict the efficacy of corridors for habitat specialists.

Behavior might even be influenced to encourage corridor use. White-tailed deer become more nocturnal and avoid roads and certain habitat types during the hunting season (Kilgo et al. 1998). For this species, placing corridors away from roads could result in increased use during the hunting season. The same type of detailed knowledge of behavior for species targeted for conservation might provide similar management tools.

12.5 Improving Population Viability Analysis

One basic problem in conservation biology is predicting population persistence, which can be done for some species through population viability analysis (PVA). PVA is a modeling tool that uses demographic data (survival and reproductive rates) and its relationships with environmental factors to project population sizes over time (Boyce 1992; Beissinger and Westphal 1998). Incorporating behavior in these models can increase prediction accuracy for some species. Because Reed (1999) recently discussed incorporating behavior into PVA models, I will only highlight some salient points.

Effects of behavior on survival and reproduction can be incorporated directly as a model parameter or indirectly by modifying the probability density function of a parameter. For example, density-dependent effects on survival or reproduction due to behavioral processes such as finding a mate, predator defense, or mating disruption (e.g., Hagan et al. 1996), can be incorporated as a parameter that modifies reproduction or survival. PVA models also can be modified to incorporate the results of altered mating preferences, or in metapopulation models, the results of altered dispersal patterns (e.g., Boulinier and Danchin 1997). Spatially explicit population viability models can be developed for single populations and for metapopulations (Dunning et al. 1995), and if the model is individually based, it has great potential for incorporating behavior. For example, one could incorporate decision-making during dispersal, mating preference, mate encounter rates, effects of habitat shape on encounter rate and selection, etc.

Incorporating behavioral data into PVA, however, is only simple in theory. Incorporating behavior into demographic models requires translating behaviors into demographic or spatial consequences (Beissinger 1997), which can be difficult because the data required for this incorporation normally will not exist and would be difficult to gather. As a consequence, one often must rely on best guesses of the effects of different behaviors on model parameters, and PVA predictions can be very sensitive to small changes in some parameter values (e.g., Stacey and Taper 1992). In addition, even if there is a demonstrated impact of behavior on any demographic parameter, it is not always necessary to incorporate it into a

PVA. Hanski (1994) developed a metapopulation model that can incorporate behavior in multiple ways, but the model predictions appear to be insensitive to its incorporation. Sensitivity analysis, or more specifically elasticity analysis (de Kroon et al. 1986), can be used to anticipate the potential importance of incorporating behavioral effects in modeling population persistence. If predicted persistence is insensitive to the degree of change in demographic parameters anticipated from incorporating behavior, it should not be incorporated into the PVA.

12.6 Successful Translocation and Reintroduction

Translocation and reintroduction are used commonly for species conservation (e.g., Griffith et al. 1989). They are used to create or augment populations and increase genetic variability. They can be done artificially, by moving adults, juveniles, or eggs (including by implanting ova), or more naturally by manipulating behaviors. The importance of behaviors in these processes varies by species and sometimes by individual, and could manifest at many stages. For example, behavioral adaptations of translocated individuals might not be suitable for local conditions (Warren et al. 1996), introduced animals might not be incorporated into local populations (Clarke and Schedvin 1997), or hybridization with related species could occur (Parkin 1996). How animals are reared in captivity also can have important impacts on the success of released animals. Rearing Nene (Branta sandvicensis) in captivity with adults increases survival of released birds over that experienced by young reared in the absence of adults (Marshall and Black 1992). Black-footed ferrets (Mustela nigripes) reared in seminatural pens have higher post-release survival than do those reared in cages without pen experience (Biggins et al. 1998). This pattern has been observed in other species as well, and can be a particular problem for species with complex social interactions (Watts and Meder 1996).

12.7 Decreasing Loss of Genetic Variability

Loss of genetic variability threatens species persistence by increasing the frequency of homozygosity of deleterious alleles and by decreasing the variability available for selection (Frankel and Soulé 1981). The rate of loss of genetic variability from a population is predicted by its effective size (N_e), which is determine by population size, sex ratio, skew in reproductive success, mating system, and similar traits (Parker and Waite 1997). Of most immediate concern to conservation biologists are problems associated with increased homozygosity within a population, which can result in inbreeding depression, which increases extinction risks (Allendorf and Leary 1986). One way to slow the rate of loss of genetic variability from a population is through immigration. The methods described above to increase dispersal or colonization would increase genetic variability. It is important to be aware of the potential problems created by these actions, such

as outbreeding depression or disruption of local adaptation (e.g., Frankel and Soulé 1981). Consequently, benefits of these actions need to be weighed against potential detriments.

Another method of decreasing the rate of loss of genetic variability is through selective breeding. By allowing more animals to mate and by reducing variance in reproductive success among individuals, a greater amount of variability is passed to the next generation (Ballou and Foose 1996). This possibility seems relatively simple for captive populations, but unlikely for wild populations. However, observations of mating preferences based on characteristics that can be manipulated suggest avenues for altering mate selection in wild populations of some species. Research on zebra finches (Poephila guttata) showed that colored leg bands could affect mate selection and reproduction (Burley 1986a). Reproductive success was twice as high for "attractive" birds (i.e., those banded with "attractive" colors) (Burley 1986b) and the sex ratio of offspring favored the "attractive" mate (Burley 1981, 1986a, c). In addition, mortality rates were higher for "unattractive" birds (60% vs. 13% for "attractive" birds during the time of the experiment; Burley 1985). Patterns of mating preference or reproductive success associated with artificial marking have been observed in some other species (Hagan and Reed 1988), but not in all (Weatherhead et al. 1991; Cristol et al. 1992). Whether band color affects reproduction and survival more generally is controversial, as are the proposed mechanisms driving these patterns (Ratcliffe and Boag 1987; Burley 1986a). However, recent manipulative experiments where unique adornments were provided to breeders reinforce some of Burley's ideas. For example, Witte and Curio (1999) provided novel traits (a colored feather to the head, altered bill color, and stripes under the tail) to Javanese mannikins (Lonchura leucogastroides) and found they affected mate choice and that males and females responded differently to the traits.

From a conservation perspective, if individual "attractiveness" could be manipulated in wild populations of a target species, it is theoretically possible to increase effective population size with a minimum of intrusion. This would allow slowing the rate of loss of genetic variability through two mechanisms, altering the breeding sex ratio and decreasing variance in reproductive success among individuals, which would reduce inbreeding depression. Blumstein (1998) modeled simple scenarios of the impacts of female mate selection preferences on effective population size. He focused strictly on the impact of mate selection on breeding sex ration, and some of his results can be shown simply using the following expression for calculating effective population size (N_e):

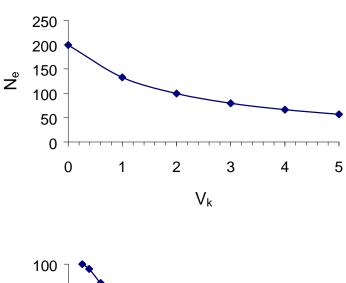
$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

where N_m and N_f are the effective number of males and females in a population; i.e., approximately the number of males and females breeding (Falconer 1989). For a fixed number of breeders, as the sex ratio becomes more skewed the effective size decreases (Figure 1). Altering mating preference also would affect variance among individuals in reproductive success. This relationship can be shown simply as

$$N_e = \frac{4N - 2}{V_k + 2}$$

where N is the number of breeders and V_k = variance in gamete production, or variance in family size (Falconer 1989). If all individuals have the same reproductive success (V_k = 0), N_e is maximized at 2N-1, and N_e declines with increased variance in among individuals (Figure 12.1).

Based on the above models, manipulating mate preference and relative reproductive success among individuals can increase effective population size. In fact,



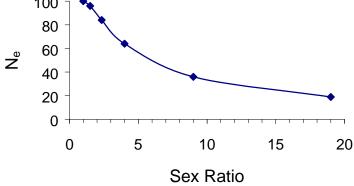


Figure 12.1. Effective population size (N_e) estimates for populations under different mating and reproductive scenarios. N_e is a measure of the rate of loss of genetic variability; the smaller N_e is the faster genetic variability is lost. Upper: N_e for a population with 100 breeders with different sex ratios of breeders (M/F). Lower: N_e for 100 breeders with different variances among individuals in reproductive success. In both graphs it is assumed that populations are ideal except for the variable being altered on the X-axis and that generations do not overlap; see text for equations.

even habitat manipulation can affect mating patterns in some species (Apollonio et al. 1998). Based on experimental manipulations of mate choice, these methods have the potential for working in both sexually dimorphic and monomorphic species. However, each species should be tested for an effect, and it should be determined whether the effect, if found, is enough to merit manipulation.

12.8 Conclusions

In this chapter I have shown that there are important problems in conservation biology that can be solved or ameliorated for some species by manipulating behaviors. Some of the solutions discussed here are being used for active conservation, while others are at the planning stage. My goal was to show the myriad and often quite creative uses to which behavior might be incorporated or manipulated to achieve specific conservation goals. More attention needs to be paid to the behaviors of wild animals, with particular reference to altering the environment to enhance reproductive performance, survival, and dispersal. I also encourage researchers to review methods used in domestic animal care and captive-breeding programs to look for other ways in which behavior might be manipulated. Researchers in these areas have long recognized the importance of animal behavior in their work, and have tools or approaches that could be adopted for in situ and ex situ animal conservation (e.g., Kilgour and Dalton 1984). Interesting introductions to behavior relevant to conservation, particularly for captive breeding of wild animals, exist for invertebrates (Demarest and Bradley 1995), fishes (Francis-Floyd and Williams 1995), reptiles and amphibians (Burghardt and Milostan 1995), birds (Hutchins et al. 1995), and mammals (terrestrial: Gittlemen and McMillan 1995; marine: Ellis 1995; non-human primates: Kholkute and Dukelow 1995). Greater interaction among conservation biologists, animal behaviorists, captive breeders, and domestic breeders would advance the field quickly. Not coincidentally, it is this type of disciplinary crossover that is necessary to develop the field of conservation medicine. Veterinarians, physicians, and biologists have been working in related and often overlapping fields of research. Conservation medicine will draw on all the sub-disciplines in these fields to develop the tools required to maintain ecosystem health.

References

- Allendorf, F. W., and R, F, Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in Conservation Biology: The Science of Scarcity and Diversity (M. Soulé, ed.). Sinauer Assoc., Sunderland, Mass.
- Amos, B., C. Schlötterer, and D. Tautz. 1993. Social structure of pilot whales revealed by analytical DNA profiling. Scince 260: 670-672.
- Apollonio, M., M. Festa-Bianchet, F. Mari, E. Bruno, and M. Locati. 1998. Habitat manipulation modifies lek use in fallow deer. Ethology 104:603-612.

- Ballou, J.D., and T.J. Foose. 1996. Demographic and genetic management of captive populations. Pages 263-283 in Wild Mammals in Captivity: Principles and Techniques (D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin, eds.) Univ. of Chicago Press, Illinois.
- Beauchamp, G., M. Bélisle, and L.-A. Giraldeau. 1997. Influence of conspecific attraction on the spatial distribution of learning foragesr in a patchy habitat. Journal of Animal Ecology 66:671-682.
- Bednarz, J. C. 1988. Cooperative hunting in Harris' hawks (Parabuteo unicinctus). Science 239:1525-1527.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12:1241-1252.
- Beissinger, S. R. 1997. Integrating behavior into conservation biology: potentials and limitations. Pages 3-22 in J. R. Clemmons and R. Buchholz, editors. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability analysis in endangered speceis management. Journal of Wildlife Management 62:821-841.
- Bibby, C. J. 1999. Making the most of birds as environmental indicators. Ostrich 70:81-88.
- Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird Census Techniques. Academic Press, London.
- Biggins, D. E., J. L. Godbey, L. R. Hanebury, B. Luce, P. E. Marinari, M. R. Matchett, and A. Vargas. 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. Journal of Wildlife Management 62:643-653.
- Blanco, G., J. A. Fargallo, J. L. Tella, and J. A. Cuevas. 1997. Role of buildings as nest-sites in the range expansion and conservation of choughs Pyrrhocorax pyrrhocorax in Spain. Biological Conservation 79:117-122.
- Blumstein, D. T. 1998. Female preferences and effective population size. Animal Conservation 1:173-177.
- Boulinier, T., and Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. Evolutionary Ecology 11:505-517.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigraiton on extinction. Ecology 58:445-449.
- Bunin, J. S., and I. G. Jamieson. 1996. Responses to a model predator of New Zealand's endangered Takahe and its closest relative, the Pukeko. Conservation Biology 10:1463-1466.
- Burghardt, G. M., and M. A. Milostan. 1995. Ethological studies on reptiles and amphibians: lessons for species survival plans. Pages 187-203 in Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Burley, N. 1985. Leg-band color and mortality patterns in captive breeding populations of zebra finches. Auk 102:647-651.
- Burley, N. 1986a. Comparison of the band color preferences of two species of estrilid finches. Animal Behaviour 34:1732-1741.
- Burley, N. 1986b. Sexual selection for aesthetic traits in species with biparental care. American naturalist 127:415-445.
- Burley, N. 1986c. Sex-ratio manipulation in color banded populations of zebra finches. Ecolution 40:1191-1206.
- Candland, D. K., and S. L. Bush. 1995. Primates and behavior. Pages 521-551 in Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Caro, T. M. 1998. Behavioral Ecology and Conservation Biology. Oxford University Press, New York.
- Castro, I., E. O. Minot, and J. C. Alley. 1994. Translocation of hihi or stitchbirds Notiomystis cincta to

- Kapiti Island, New Zealand: transfer techniques and comparison of release strategies. Pages 113-120 *in* Reintroduction Biology of Australian and New Zealand Fauna (M. Serena, ed.). Surrey Beatty & Sons, Chipping Norton, Australia.
- Clark, D. L., J. M. Macedonia, and Gh. G. Rosenthal. 1997. Testing video playback to lizards in the field. Copeia 1997:421-423.
- Clarke, M. F., K. B. da Silva, H. Lair, R. Pocklington, D. L. Kramer, and R. L. McLaughlin. 1993. Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. Oikos 66:533-537.
- Clarke, M. F., and N. Schedvin. 1997. An experimental study of the translocation of noisy miners *Manorian melanocephala* and difficulties associated with dispersal. Biological Conservation 80:161-167.
- Clemmons, J. R., and R. Buchholz. 1997. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom.
- Cohn, J. and R. C. MacPhail. 1996. Ethological and experimental approaches to behavior analysis: implications for ecotoxicology. Environmental Health Perspectives 104 (Suppl. 2): 299-305.
- Colborn, T., M. J. Smolen, and R. Rolland. 1998. Environmental neurotoxic effects: the search for new protocols in functional teratology. Toxicology and Industrial health 14:9-23.
- Cristol, D. A., C. S. Chiu, S. M. Peckham, and J. F. Stoll. 1992. Color bands to not affect dominance status in captive flocks of wintering dark-eyed juncos. Condor 94:537-539.
- Danchin, E., B. Cadiou, J.-Y. Monnat, and R. Rodriguez Estrella. 1991. Recruitment in long-lived birds: conceptual framework and behavioural mechanisms, Proceedings of the International Ornithological Congress 20:1641-1656.
- de Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.
- Demarest, J., and M. Bradley. 1995. Behavioral research with endangered invertebrate species. Pages 37-50 *in* Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204-1210.
- Distal, R. A., and F. D. Provenza. 1991. Experience early in life affects voluntary intake of blackbrush by goats. Journal of Chemical Ecology 17:431-450.
- Døving, K. B. 1991. Assessment of animal behaviour as a method to indicate environmental toxicity. Comparative Biochemistry and Physiology 100C: 247-252.
- Dunning, J.B., D.J. Stewart, B.J. Danielson, B.R. Noon, T.L. Root, R.H. Lamberson, and E.E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5:3-12.
- Ellis, S. Marine mammal behavior: conservation through research. Pages 441-463 *in* Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Falconer, D. S. 1989. Introduction to Quantitative Genetics, 3rd ed. Longman Scientific & Technical, New York.
- Fowler, C. W., and J. D. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. Report of the International Whaling Committee 41:545-554.
- Fox, G. A. 1978. Behavioral abnormalities of nestling Lake Ontario Herring Gulls. Journal of Wildlife Management 42: 477-483.
- Francis-Floyd, R., and J. D. Williams. 1995. Behavioral research on captive endangered fishes of North America. Pages 105-123 *in* Conservation of Endangered Species in Captivity: An Interdisciplinary approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.

- Frankel, O. H., and M. E. Soulé. 1981. Conservation and Evolution. Cambridge Univ. Press, U.K.
- Furness, R. W., and J. J. D. Greenwood. 1993. Birds as Monitors of Environmental Change. Chapman & Hall, London.
- Galindo, J., R. J. Kendall, C. J. Driver, and T. Lacher, Jr. 1985. The effect of methyl parathion on the susceptibility of bobwhite quail (*Colinus virginianus*) to domestic cat predation. Behavior and Neural Biology 43:21-36.
- Geist, V. 1971. Mountain Sheep: A Study in Behavior and Evolution. Univ. of Chicago Press, Illinois.
- Gittleman, J. L., and G. C. McMillan. 1995. Mammalian behavior: lessons from captive studies. Pages 355-376 *in* Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Gosling, L. M., and W. J. Sutherland. 2000. Behaviour and conservation. Cambridge Univ. Press.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477-480.
- Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. American Naturalist 153:215-227.
- Hagan, J. M., and J. M. Reed. 1988. Red color bands reduce fledging success in red-cockaded woodpeckers. Auk 105:498-503.
- Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151-162.
- Hansen, A. J., and F. de Castri. 1992. Landscape boundaries: consequence for biotic diversity and ecological flows. Springer-Verlag, New York.
- Harris, L. D. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. Univ. of Chicago Press, Illinois.
- Helender, B. 1978. Feeding white-tailed sea eagles in Sweden. Pages 149-159 *in* Endangered Birds: Management Techniques for Preserving Threatened Species (S. A. Temple, ed.). Croom Helm, Wisconsin.
- Henke, S. E. 1997. Do white-tailed deer react to the dinner bell? An experiment n classical conditioning. Wildlife Society Bulletin 25:291-295.
- Hoeck, H. N. 1989. Demography and competition in hyrax: a 17 years study. Oecologia 79:353-360.
- Hutchins, M., C. Sheppard, A. M. Lyles, and G. Casadei. 1995. Behavioral considerations in the captive management, propagation, and reintroduction of endangered birds. Pages 263-289 *in* Conservation of Endangered Species in Captivity: An Interdisciplinary Approach. (Gibbons, E. F., Jr., B. S. Durrant, and J. Demarest, eds.) State Univ. of New York Press, Albany.
- Isbell, L. A., D. L. Cheney, and R. M. Seyfarth. 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli national Park, Kenya. Behavioral Ecology and Sociobiology 27:351-358.
- Jabłoński, P. G. 1999. A rare predator exploits prey escape behavior: the role of tail-fanning and plumage contrast in foraging of the painted redstart (*Myioborus pictus*). Behavioral Ecology 10:7-14.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21:449-480.
- Kadlec, J. A., and L. M. Smith. 1992. Habitat management for breeding areas, in Ecology and

- Management of Breeding Waterfowl (Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A., and Krapu, G. L., eds.), University of Minnesota Press, Minneapolis, pp. 590-610.
- Kamil, A. C., and S. I. Yoerg. 1981. Learning and foraging behavior. Pages 325-364 *in* Perspecitives in Ethology (P. P. Bateson and P. H. Klopfer, ed.). Plenum, New York.
- Karr, J. R., 1994. Using biological criteria to protect ecological health. In: Rapport, D. J., Gaudet, C., Calow, P. (eds), Evaluating and monitoring the health of large scale ecosystems. Springer-Verlag, New York.
- Kear, J., 1990, Man and Wildfowl. T. & A. D. Poyser, London.
- Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida Panther. Conservation Biology 12:1359-1364.
- Kilgour, R., and C. Dalton. 1984. Livestock Behaviour: A Practical Guide. Methuen, New Zealand.
- Kress, S. W. 1983. The use of decoys, sound recordings, and gull control for re-establishing a tern colony in Maine. Colonial Waterbirds 6:185-196.
- Kress, S. W. 1997. Using animal behavior for conservation: case studies in seabird restoration from the Maine coast, USA. Journal of the Yamashina Institute of Ornithology 29:1-26.
- Kulig, B., E. Alleva, G. Bignami, J. Cohn, D. Cory-Slechta, V. Landa, J. O'Donaghue, and D. Peakall. 1996. Animal behavioral methods in neurotoxicity assessment. Environmental Health Perspectives 104 (Suppl. 2): 193-204.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution 11:131-135.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York.
- Marshall, A. P., and J. M. Black. 1992. The effect of rearing experience on subsequent behavioural traits in Hawaiian Geese *Branta sandvicensis*: implications for the recovery programme. Bird Conservation International 2:131-147.
- MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton Univ. Press, New Jersey.
- McLean, K. G., G. Lundie-Jenings, and P. J. Jarman. 1995. Teaching an endangered mammal to recognise predators. Biological Conservation 75:51-62.
- Mirza, S. N., and F. D. Provenza. 1990. Preference of the mother affects selection and avoidance of foods by lambs differeing in age. Applied Animal Behaviour Science 28:255-263.
- Montevecchi, W. A. 1993. Birds as indicators of change in marine prey stocks. Pages 217-266 in Furness, R. W., and J. J. D. Greenwood (eds.) Birds as Monitors of Environmental Change. Chapman & Hall, London.
- Munguira, M.L., and J.A. Thomas. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. Journal of Applied Ecology 29:316-329.
- Nocera, J.J. and P.D. Taylor. 1998. In situ behavioral response of Common Loons associated with elevated mercury exposure. Conservation Ecology [online] 2(2): article 10, 13 pages, (Available from the web at www.consecol.org
- Parker, P. G., and T. A. Waite. 1997. Mating systems, effective population size, and conservation of natural populations. Pages 243-261 *in* J. R. Clemmons and R. Buchholz, editors. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom.
- Parkin, D. 1996. Colonisation and hybridisation in birds. Pages 25-35 *in* The Introduction and Naturalisation of Birds (J. S. Holmes and J. R. Simons, ed.) The Stationary Office, London.
- Peakall, D. B. 1985. Ebhavioral responses of birds to pesticides and other contaminants. Residue Reviews 96:45-77.

- Peakall, D. B. 1996. Disrupted patterns of behavior in natural populations as an index of ecotoxicity. Environmental Health Perspectives 104 (Suppl. 2): 331-335.
- Pickering, S. P. C., and L. Duverge. 1992. The influence of visual stimuli provided by mirrors on the marching displays of Lesser Flamingos, Phoeniconais minor. Animal Behaviour 43:1048-1050.
- Powell, R. A., J. W. Zimmerman, D. E. Seaman, and J. F. Gilliam. 1996. Demographic analyses of a hunted black bear population with a refuge. Conservation Biology 10:1-11.
- Pöysä, H. 1991a. Effects of predation risk and patch quality on the formation and attractiveness of foraging groups of teal, Anas crecca. Animal Behaviour 41:285-294.
- Pöysä, H. 1991b. Does the attractiveness of teal foraging groups depend on the posture of group members? Ornis Scandinavica 22:167-169.
- Provenza, F. D., and D. F. Balph. 1987. Diet learning by domestic ruminants: theory, evidence and practical implications. Applied Animal Behaviour Science 18:211-232.
- Purcell, K. L., and J. Verner. 1998. Density and reproductive success of California Towhees. Conservation Biology 12:442-450.
- Ratcliffe, L. M., and P. T. Boag. 1987. Effects of colour bands on male competition and sexual attractiveness in zebra finches. Canadian Journal of Zoology 65:333-338.
- Reed, D. F., T. N. Woodard, and T. M. Pojar. 1975. Behavioral response to mule deer to a highway underpass. Journal of Wildlife Management 39:361-367.
- Reed, J. M. 1996. Using statistical probability to increase confidence of inferring species extinction. Conservation Biology 10:1283-1285.
- Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology 13:232-241.
- Reed, J. M., T. Boulinier, E. Danchin, and L. W. Oring. 2000. Informed dispersal: prospecting by birds for breeding sites. Current Ornithology 15: 189-259.
- Reed, J. M., J. H. Carter, III, J. R. Walters, and P. D. Doerr. 1988. An evaluation of indices of Redcockaded Woodpecker populations. Wildlife Society Bulletin 16:406-410.
- Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends in Ecology and Evolution 8:253-256.
- Richardson, J.H., R.F. Shore, and J.R. Treweek. 1997. Are major roads a barrier to small mammals? Journal of Zoology, London 243:840-846.
- Rodgers, R. D. 1992. A technique for establishing sharp-tailed grouse in unoccupied range. Wildlife Society Bulletin 20:101-106.
- Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83-109.
- Rosenberg, D. K., B. R. Noon, J. W. Megahan, and E. C. Meslow. 1998. Compensatory behavior of Ensatina eschscholtzii in biological corridors: a field experiment. Canadian Journal of Zoology 76:117-133.
- Sarrazin, F., C. Bagnolini, J.-L. Pinna, and E. Danchin. 1996. Breeding biology during establishment of a reintroduced Griffon Vulture Gyps fulvus population. Ibis 138:315-325.
- Seabrook, W.A., and E.B. Dettmann. 1996. Roads as activity corridors for cane toads in Australia. Journal of Wildlife Management 60:363-368.
- Sunders, D. A., and R. J. Hobbs. 1991. Natur Conservation 2: The Role of Corridors. Surrey Beatty & Sons, Sydney.
- Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conservation Biology 12:284-292.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.
- Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations.

- Ecological Applications 2:18-29.
- Stamps, J. A. 1987. Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. American Naturalist 129:629-642.
- Stamps, J. A. 1991. The effect of conspecifics on habitat selection in territorial species. Behavioral Ecology and Sociobiology 28:29-36.
- Stamps, J. A. 1994 Territorial behavior: testing the assumptions. Advances in the Study of Behavior 23:173-232.
- Stamps, J. A., Buechner, M., and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. American Naturalist 129:533-552.
- St. Clair, C. C., M. Belisle, A. Desrochers, and S. Hnnon. 1998. Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology [online] 2:13.
- Stevens, E. F. 1991. Flamingo breeding: the role of group displays. Zoo Biology 10:53-64.
- Sutherland, W. J. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56:801-809.
- Thorhallsdottir, A. G., F. D. Provenza, and D. F. Balph. 1990. Ability of lambs to learn about novel foods while observing or participating with social models. Applied Animal Behaviour Science 25:25-33.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.
- Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna sandvicensis* lath). Behaviour Suppl. 20:1-193
- Verner, J. 1992. Data needs for avian conservation biology: have we avoided critical research? Condor 94:301-303.
- Vickery, P. D., M. L. Hunter, and J. V. Wells. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. Auk 109:697-705.
- Walters, J. R., S. K. Hansen, J. H. Carter, J. H., P. D. Manor, and R. J. Blue. 1988. Long-distance dispersal of an adult Red-cockaded Woodpecker. Wilson Bulletin 100:494-496.
- Warner, R. E., K. K. Peterson, and L. Borgman. 1966. Behavioural pathology in fish: a quantitative study of sublethal pesticide tixication. Journal of Applied Ecology 3 (Suppl.):223-247.
- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zagers. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. Conservation Biology 10:547-553.
- Watts, E., and A. Meder. 1996. Introduction and socialization techniques for primates. Pages 67-77 in Wild Mammals in Captivity: Principles and Techniques (D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin, eds.) Univ. of Chicago Press, Illinois.
- Weatherhead, P. J., D. J. Hoysak, K. J. Metz, and C. G. Eckert. 1991. A retrospecitive analysis of red-band effects on red-winged blackbirds. Condor 93:1013-1016.
- Weddell, B. J. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? Journal of Biogeography 18:385-394.
- Witte, K., and E. Curio. 1999. Sexes of a monomorphic species differ in preference for mates with a novel trait. Behavioral Ecology 10:15-21.
- Wu, J., J. L. Vankat, and Y. Barlas. 1993. Effects of patch connectivity and arrangement on animal metapopulation dynamics: a simulation study. Ecological Modelling 65:221-254.
- Wyrwicka, W. 1981. The Development of Dood Preferences. Charles C. Thomas, Springfield, Illinois.
- Zimmerman, B. L. 1994. Audio strip transects. Pages 92-97 in Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians (W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L-A. C. Hayek, and M. S. Foster, eds.). Smithsonian Inst. Press, D.C.