The Importance of Behavioral Ecology for Conservation Biology: Examples from Serengeti Carnivores

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Biologists working in East Africa and elsewhere are usually assigned to one of two camps: those who conduct "research" and those who practice "conservation." Though camp members may view each other amicably, often as not researchers see conservation as uninteresting or as a second-rate discipline, while conservationists regard research as irrelevant or esoteric. Conservationists often ask research biologists, and those studying animal behavior in particular, the galling question of whether their years in the field amount to anything.

In the past, the answer to this question often amounted to "no," but it is increasingly clear that biological research has an important role to play in conservation. Growing concern about rates of species extinction and habitat loss has led to the formation of a new applied discipline called conservation biology (Ehrlich and Ehrlich 1981). Conservation biology addresses processes by which populations go extinct (research-oriented questions) and strategies for preventing extinctions (conservation-oriented questions), and thus provides many important bridges between entrenched camps. The discipline draws upon population biology, biogeography, community ecology, and genetics to meet its objectives (Simberloff 1988). For most biologists, then, the links between their work and conservation are now much more obvious than in the past. For behavioral ecologists, however, who formed the majority of research personnel in the Serengeti during the 1980s, difficulties remain in justifying their work on conservation grounds because their field has been largely ignored by conservation biology (but see Soulé 1983; Simberloff 1986).

In this chapter we demonstrate the crucial role played by behavioral research in conservation biology by exploring the links between behavioral ecological research conducted on Serengeti carnivores over the last 15 years and conservation science. Large carnivores have a special sig-

nificance for conservation biology for four reasons. First, they live at lower densities than the species on which they feed and are hence more vulnerable to extinction. Second, because they are at the top of the trophic pyramid, their presence is dependent on many lower trophic levels remaining intact. Third, they may therefore be sensitive indicators of ecosystem perturbations, since changes in the reproduction and population size of a predator may be easier to monitor than those in prey or vegetation (Landres, Verner, and Thomas 1988). Fourth, large carnivores are "flagship species" (Western 1987) capable of attracting disproportionate attention and funding (e.g., Rabinowitz 1986). Though their import is acknowledged (Terborgh 1988), as yet little attempt has been made to translate knowledge of carnivore population dynamics into conservation theory or practice.

To date, research on Serengeti carnivores has lain squarely within the realm of behavioral ecology. The principal studies, on black-backed jackals, cheetahs, dwarf mongooses, lions, spotted hyenas, and wild dogs, have each monitored recognized individuals over long time periods and have been concerned primarily with understanding aspects of their diverse breeding systems. Based on papers in print and manuscripts made available to us at the time of writing, we have summarized the main achievements of Serengeti carnivore studies in table 21.1. It should be noted, however, that useful work has also been conducted on bat-eared foxes (Lamprecht 1979; Malcolm 1986), banded mongooses (Rood 1975; Waser et al., chap. 20), slender mongooses (Waser et al., chap. 20), white-tailed mongooses (Waser and Waser 1985), golden jackals (Moehlman 1983), aardwolves (Kruuk and Sands 1972), striped hyenas (Kruuk 1976), and leopards (Bertram 1982; Cavallo 1990).

In this chapter, we first outline the reasons that populations go extinct. Then, using examples from Serengeti carnivores, we show how knowledge of an animal's behavior can assist in all key facets of conservation biology, including management strategies. Finally, we briefly discuss how diverse conservation studies of endangered species outside Serengeti have profited from consideration of behavior, reinforcing the point that behavioral ecologists have an important role to play in a biological world rapidly becoming dominated by conservation issues.

CAUSE OF POPULATION EXTINCTIONS

Populations can go extinct as a result of deterministic processes such as sustained habitat destruction or overhunting. Populations may also succumb to chance or stochastic events of either a demographic or environmental nature. Demographic stochasticity, which results from individual variation in birth and death rates, occurs in all populations, but its effects

Table 21.1 Principal topics in studies of Serengeti carnivores.

Species	Topics	Selected references[a]
Black-backed jackal	Helpers at the den	Moehlman 1979
	MtDNA sequence divergence	Wayne et al. 1990
Cheetah	Reproductive strategy	Caro and Collins 1987; Caro, FitzGibbon, and Holt 1989
	Consequences of grouping	Caro 1994
	Interspecific predation	Laurenson 1994
	Parental care	Caro 1987; Laurenson, 1994
	Hunting behavior	FitzGibbon 1990
	Genetics and reproduction	O'Brien et al. 1987; Wildt, O'Brien, et al. 1987
Dwarf mongoose	Social organization	Rood 1978, 1980, 1990
	Kin selection	Creel and Waser, 1994
	Dispersal	Rood 1987
	Reproductive suppression	Creel et al. 1991, 1992
Lion	Reproductive strategies	Bygott, Bertram, and Hanby 1979; Packer and Pusey 1982; Packer, Gilbert, et al. 1991
	Infanticide	Bertram 1975; Packer and Pusey 1983
	Dispersal and philopatry	Hanby and Bygott 1987; Pusey and Packer 1987
	Consequences of grouping	Packer, Scheel, and Pusey 1990
	Hunting behavior	Schaller 1972; Scheel and Packer 1991; Scheel 1993
	Comparative genetics	Wildt, Bush, et al. 1987; Packer, Pusey, et al. 1991
Spotted hyena	Social organization	Frank 1986a, b; Hofer and East 1993a
	Siblicide	Frank, Glickman, and Light 1991
	Hunting behavior	Kruuk 1972
	Ranging behavior	Hofer, East, and Campbell 1993; Hofer and East, 1993b
	Vocalizations	East and Hofer 1991; Hofer and East, 1993c
	Parental care	
Wild dog	Social organization	Frame et al. 1979; Malcolm and Marten 1982
	Dispersal	Frame and Frame 1976
	Hunting behavior	Fanshawe and FitzGibbon 1993

[a]Based on published material and preprints sent to the authors, excluding chapters in this volume.

increase as population size declines (Goodman 1987; Durant and Harwood 1992). Similarly, environmental stochasticity, which results from external factors such as drought or disease, acts on all populations, but its effects remain substantial even in large populations. In general, populations outside protected areas are most likely to be subject to deterministic extinction processes, whereas those inside are expected to increase or remain stable but be more vulnerable to stochastic events.

If a population remains at low numbers for a sustained period, genetic problems may also arise. Small populations may be subject to inbreeding depression during initial years of population decline since there is an increased chance of deleterious recessives being expressed, which may be manifested in high infant mortality (Ralls, Brugger, and Ballou 1979; Templeton 1987). In addition, small populations may suffer a loss in genetic variance (Miller 1979; Gilpin and Soulé 1986). It has been hypothesized that a population with a low level of genetic diversity has less ability to respond to natural selection under changing environmental conditions and may thus be more susceptible to environmental stochasticity (Dobzhansky and Wallace 1953; Franklin 1980; Selander 1983).

Conservation biologists and geneticists relate the census population size to the number of individuals contributing genetic material to the next generation by using a theoretical quantity called the genetic effective population size. It employs the concept of the ideal population in which each individual has an equal chance of mating with every other individual (including itself). In reality, individual lifetime contributions to fitness in most populations are nonrandom because of phenotypic differences (Clutton-Brock 1988), and accurate estimates of the effective population size strongly depend upon detailed knowledge of individuals' contributions to the next generation (Crow and Kimura 1970).

THE INFLUENCE OF BREEDING SYSTEM ON EXTINCTION PROBABILITY

Grouping Patterns

The extent to which individuals are grouped together alters the way in which a population is subdivided. If populations are subject to strong independent environmental stochasticity, then population subdivision (i.e., its metapopulation structure) can promote chances of persistence through time because of the "spreading of risk" (den Boer 1968): for example, while a catastrophic event could wipe out one group, the odds are that others would survive. In addition, theory suggests that grouping may influence effective population size and genetic differentiation within populations, both of which affect the rate at which genetic diversity is lost from a population (Gilpin 1991); however, few empirical studies have tested these hypotheses.

Carnivore species show striking differences in group size and the extent to which they are social (table 21.2; see also Bertram 1979). For example, leopards of both sexes live alone as adults (Bertram 1982), whereas female cheetahs are solitary while males either live alone or in small groups of two or three individuals (Caro 1989). Lionesses live in groups ranging in size from two to eighteen females, and these groups are held by coalitions of between one and nine males (Packer et al. 1988;

Table 21.2 Behavioral ecology of some Serengeti carnivores.

	Cheetah	Dwarf mongoose	Lion	Spotted hyena	Black-backed jackal	Wild dog
Grouping						
	Primarily asocial	Large social groups	Large social groups	Large social groups	Small social groups	Large social groups
Mating system						
	Polygynous and polyandrous	Monogamous with reproductive suppression	Polygynous and polyandrous	Polygynous	Monogamous with reproductive suppression	Polyandrous with reproductive suppression
Dispersal						
	Male-biased with kin	Both sexes with kin	Male-biased with kin	Male-biased	Both sexes	Both sexes with kin[a]
Intraspecific interactions						
	Infrequent	Intense	Common	Intense	Intense	Intense
Interspecific interactions[b]						
	Rare	Rare	Rare	Common	Common	Common
Range size						
	Some very large	Small	Medium	Very large	Small	Very large

[a] Frame and Frame 1976; Fuller et al. 1992
[b] With other carnivores.

Packer, Gilbert, et al. 1991). Knowledge of social structure contributes to predictions about population persistence and highlights the problems in ascribing different species a single group size value. In addition, studies that collect demographic and genetic information, such as those on lions (Packer, Gilbert et al. 1991), are in a good position to relate grouping patterns to genetic differentiation.

Mating Systems

In species that breed polygynously, many males fail to reproduce; this reduces the effective population size below the actual population size. In species that are reproductively suppressed, in which typically only one male and one female breed per group, these effects may be even more striking: here the number of breeding individuals becomes equivalent to the number of groups. Furthermore, under panmictic breeding conditions the variance in birth rate is inversely related to population size. In reproductively suppressed populations the variance in birth rate is inversely related to the proportion of breeding individuals, and is thus higher than in monogamous populations.

Reproductive suppression is characteristic of several carnivores (Creel and Creel 1990; table 21.2). For example, in Serengeti, three species show some form of reproductive suppression or delayed breeding in which nonreproductives help in different ways. In wild dog packs usually only the alpha female and male breed; subordinate males normally stay on to help

their brother raise the litter, regurgitating food for the pups, while females disperse to form new packs (Frame et al. 1979; Fuller et al. 1992). Similarly, only the alpha pair of dwarf mongooses normally breeds, while subordinates guard, carry, and bring food to the alphas' offspring (Rood 1980); subordinate females can also provide milk for the alphas' young (Creel et al. 1991). Offspring of black-backed jackals from the previous year often remain on their natal territory, helping to rear their full siblings by bringing food back to them, and do not reproduce in their first year (Moehlman 1979). As a consequence, wild dog and dwarf mongoose populations are subject to higher levels of demographic stochasticity than, for example, those of leopards or banded mongooses. Reproductive suppression also reduces the number of individuals contributing to the gene pool, and therefore greatly increases the rate of loss of genetic diversity.

DNA fingerprinting techniques now used extensively in behavioral ecology can shed additional light on the number and identity of individuals contributing to the next generation. For example, Packer, Gilbert, et al. (1991) have shown that certain males in large coalitions of male lions do not father any offspring; this finding alters assessments of effective population size based on behavioral observations.

Dispersal

Effective population size is also influenced by the extent and costs of dispersal between groups (Lande and Barrowclough 1987; Rogers 1987). Dispersal is defined here as movement from group of origin to the first or subsequent breeding group (Chepko-Sade et al. 1987). Evidence from computer simulations shows that both dispersal and metapopulation structure affect population persistence, but the manner in which they do so depends on dispersal costs and the types of stochastic events involved (Durant 1991; Hansson 1991). If, for example, dispersal reduces survivorship substantially, perhaps as a result of predation, it will reduce population persistence in comparison to populations in which dispersal costs are low. In saturated habitats where territorial openings become available only as a result of death or ousting of residents, however, dispersal costs may have little influence on population persistence. Kin-structured migration, in which relatives disperse together, also influences effective population size, although its effects depend on interactions with group size and dispersal rates. In general, however, genetic differentiation between groups increases when kin migrate together.

Behavioral ecological studies sometimes obtain good data on these aspects of dispersal. For example, it is known that dwarf mongooses normally transfer between packs with overlapping home ranges, with median dispersal distances being 0.5 km for males and 1.0 km for fe-

males (Rood 1987). In regard to costs, dispersing lionesses breed at a later age in Serengeti than do nondispersers, whereas in Ngorongoro Crater they suffer greater mortality than do nondispersers (Pusey and Packer 1987). Finally, the proportion of dispersers that transfer alone or in groups and the degree of relatedness between dispersers may also be known. For instance, simultaneous primary transfer by littermates is commonplace in cheetahs, dwarf mongooses, lions, and wild dogs (table 21.2).

THE INFLUENCE OF INTRASPECIFIC BEHAVIOR ON POPULATION SIZE

Intraspecific behavior strongly influences the intrinsic rate of increase for populations. In spotted hyenas, offspring are born with fully erupted canines and incisors and attack their siblings at birth, often killing like-sexed littermates in the narrow burrow where the mother cannot intervene (Frank, Glickman, and Licht 1991). This results in a mortality rate of approximately 20% in the first few weeks of life. Among wild dogs, in those rare instances in which a subordinate female gives birth, the alpha female attempts to control access to the litter, which interferes with pup provisioning and results in litter loss (Frame et al. 1979).

On entering a pride for the first time, male lions often kill cubs sired by former male residents and this accounts for 27% of all cub mortality in the first year of life (Packer et al. 1988). Infanticide also occurs in leopards (Ilany 1990; Cavallo 1991). The conservation implications of this behavior are severe. If resident males are shot and new males replace them, small cubs will be killed and subadults evicted (Packer and Pusey 1983). Frequent replacements can actually halt recruitment altogether in both species. On the basis of this information derived from behavioral and ecological research, Packer (1990) recommended that lion and leopard hunting be stopped in the Loliondo and Ikorongo Game Controlled Areas. Behavioral data on habitat requirements and recruitment rates can therefore help to determine hunting quotas or the level of trade that can be sustained.

Social behavior can also have negative consequences for genetic diversity, the most obvious example being male-male competition over access to females. Indeed, in Ngorongoro Crater, large coalitions of male lions have prevented any immigration of males from outside since 1970. This, together with a population crash in the early 1960s (Fosbrooke 1963), has resulted in the current Crater population of 75–125 animals being descended from just 15 founders (Packer, Pusey et al. 1991). In effect, the population is genetically isolated for behavioral reasons. Simulations show that heterozygosity has been declining since the mid-1970s and that

female reproductive performance may have suffered as a result (Packer, Pusey et al. 1991).

Further research is required to determine the range of population sizes over which these intraspecific behaviors are manifested, but such behaviors can potentially reduce recruitment rates even at low population sizes.

THE INFLUENCE OF INTERSPECIFIC BEHAVIOR ON POPULATION SIZE

Predation and Competition

Predation and competition are important determinants of population size. Although these processes are usually studied by ecologists, they are now under increasing scrutiny from behavioral ecologists because direct observation of individual predators minimizes bias in diet estimation (Caro and FitzGibbon 1992). For example, by studying individually recognized female cheetahs intensively, Laurenson (1994) found that cheetah cub mortality was extremely high, with only 5% of cubs reaching independence. This mortality stemmed primarily from predation by lions, which kill cheetah cubs both in their lair and soon after emergence.

Laurenson (chap. 18) has argued that the principal factor limiting cheetah population size in Serengeti and probably in other protected areas is cub mortality due to sympatric predators. Predation is likely to be a far more important factor affecting this species than is its reduced genetic variability (Caro and Laurenson 1994). Litter loss may depend on the density of other predators and perhaps the availability of safe lair sites. Under current conditions cheetahs may fare best in game reserves or multiple-use areas where other predators are hunted or harassed, but where prey densities remain relatively high (Laurenson, Caro, and Borner 1992).

Disease

Disease epizootics may exert a particularly strong effect on the probability of population extinction (Scott 1988; Thorne and Williams 1988). Behavioral studies are crucial to understanding the epidemiology of disease and in designing disease management programs such as vaccination schemes. The incidence of epizootics depends upon the contact rate between and within subpopulations and the number of susceptible individuals (Anderson and May 1979). Disease will therefore affect social species with a high rate of contact between individuals most strongly (table 21.2). If disease is transmitted between groups or individuals intraspecifically, outbreaks are likely to be correlated in time between groups. However, in low-density species or where intraspecific interactions are infrequent,

interspecific transmission may assume greater importance (see also Dobson, chap. 23).

As a result of long-term monitoring, we know that disease has affected both the lion and wild dog populations in the Serengeti ecosystem. Lions in Ngorongoro Crater underwent a population crash in the early 1960s as a result of a plague of *Stomoxys* biting flies, which reduced the lion population from about 60–75 to 10–15 animals (Fosbrooke 1963; Packer, Pusey et al. 1991). Lions are also suffering a new outbreak of disease at the time of writing.

Wild dogs in Serengeti may also have declined as a result of disease. The population dropped from 110 adults in 1970 to 26 in 1977 as a result of high pup mortality (Malcolm 1979), and clinical signs of disease were observed on several occasions (Schaller 1972; Malcolm 1979). In 1990 rabies was confirmed as the cause of death of one dog, and clinical signs were seen in other pack members (Gascoyne et al. 1993). A study of seroprevalence to rabies antibody showed that over 40% of wild dogs sampled had been exposed to the virus (Gascoyne et al. 1993). Knowledge of behavioral interaction rates between different wild dog packs and between packs and domestic animals would shed light on the relative importance of intraspecific and interspecific disease transmission in this species.

SPECIES-SPECIFIC BEHAVIOR AND EXTINCTION PROBABILITY

The probability that a species will go extinct depends on numerous ecological, behavioral, and life history factors. For example, large species and those with large ranges occur at low population sizes and are more vulnerable to extinction (see Gilpin and Diamond 1980; Higgs and Usher 1980). In addition, some evidence suggests that risk-prone species have low rates of dispersal, slow rates of reproduction, or specialized diets (Terborgh 1974; Wilcox 1980; Fowler and MacMahon 1982). Other, poorly understood behavioral factors, such as willingness to cross open areas (Willis 1974) and susceptibility to nest predation (Sieving 1992) have also been implicated in local extinctions. The relative importance of behavioral factors in promoting extinction requires urgent investigation since these factors greatly affect a population's response to range fragmentation.

THE IMPORTANCE OF BEHAVIORAL STUDIES FOR MANAGEMENT OPTIONS

Ranging Behavior

Many protected areas in Africa have been delineated to take account of the movements of species they are trying to protect. For example, the

present boundaries of the Serengeti National Park and Ngorongoro Conservation Area were formed only after wildebeest ranging patterns were known (Grzimek and Grzimek 1959; Turner 1987). If intact ecosystems are to be conserved, it is essential that they account for the ranging behavior of large carnivores (table 21.2).

Serengeti cheetahs and wild dogs have enormous home ranges because they follow the movements of migratory prey (Durant et al. 1988) (an average of 833 km² and 777 km² for female and nonterritorial male cheetahs respectively: Caro 1994; 1,500–2,000 km² for wild dog packs: Frame et al. 1979). Both species range outside the park. Fortunately, buffer zones afford protection to both species, but their population sizes would almost certainly be reduced if agriculture directly abutted the park. Elsewhere in areas of high prey density, wild dog ranges are smaller, at about 600 km² (Reich 1981). Nonetheless, even in such favorable circumstances Frame and Fanshawe (1991) estimate that a reserve 2,300 km² in area could support only six packs or 30 adults maximum. Very few reserves in Africa are large enough to contain the 200–300 individuals thought to be a rough minimum figure for long-term population persistence, disregarding genetic deterioration (East 1981; Fanshawe, Frame, and Ginsberg 1991). In comparison to one large reserve, several small reserves with no gene flow between them would be completely inadequate for wild dog protection (Diamond 1976; Terborgh 1976; Newmark 1987).

While spotted hyenas occur at higher densities than wild dogs or cheetahs, they also range over huge areas. Hyenas commute from a core clan range to the wildebeest migration in order to hunt, with the result that a large proportion of the hyena population may converge on one small area (Hofer, East, and Campbell 1993). If this area is subject to snaring, as occurs in the west of the park and in the Grumeti and Ikorongo Game Controlled Areas, the whole population is at risk. Indeed, Hofer, East, and Campbell (1993) calculate that over 10% of adult spotted hyenas on the plains-woodland border are killed in snares each year.

Carnivores also cross large areas while dispersing. For example, male lions occasionally move from the central Serengeti plains to Ngorongoro Crater or into the Loliondo Game Controlled Area, where they have been shot (Packer 1990). Reserve designers must take the movements and dispersal patterns of wide-ranging species into account, but can possibly take advantage of long dispersal distances to construct corridors leading to other protected areas (Johnsingh, Narendra Prasad, and Goyal 1990; but see Hobbs 1992).

Calculating Minimum Viable Populations

One of the most important parameters for conservation is the size below which a population ceases to be viable over the long term. A minimum

viable population (MVP) can be defined in two ways. First, the demographic MVP is the population size able to persist with a particular probability over a specified number of years (Shaffer 1981). The genetic MVP, however, is the size of the population able to maintain a particular level of genetic diversity over a specified time period (Foose et al. 1986; Ralls and Ballou 1986; Soulé et al. 1986). In general, the genetic MVP is higher than the demographic MVP, depending on factors such as the species' behavior and the risks of extinction that management is willing to accept (Soulé et al. 1986). In Serengeti, only wild dogs and possibly cheetahs fall below generally accepted MVP levels (table 21.3).

The demographic MVP can be calculated only by estimating the probability distribution of the time to extinction. Some models rely on mean population growth rate and variance estimates but need a long-term demographic data set characteristic of behavioral ecological studies in order to be accurate (Durant 1991). The genetic MVP is generally calculated using detailed life history statistics. Demographic records therefore have an important role to play in calculating both sorts of MVP.

Monitoring Populations

Management requires regular monitoring of species in order to protect them effectively, and knowledge of behavior underlies many different population monitoring schemes. For example, ungulate censuses rely on knowing of the whereabouts of species at different times of year (Sinclair and Norton-Griffiths 1982). Similarly, in species that commute, population estimates will be greatly affected by when and where censuses are conducted (Hofer and East, chap. 16). Transects use assumptions about the distribution of group sizes and how different habitats are utilized, and will be affected if group sizes vary between habitats. Capture-mark-recapture techniques assume an equal chance of recapturing or resighting individuals, which in turn depends on their tameness following handling and their activity schedules. Conversely, behavioral observations are useful in assessing whether monitoring techniques, such as radio-collaring, have an effect on study animals (Laurenson and Caro 1994).

Interventions

In some circumstances interventions may be desirable when populations exhibit low densities and poor recruitment, or when sex ratios become skewed. For example, when rabies was implicated in the reduction of the Serengeti wild dog population to very low levels, two packs were vaccinated against rabies following a trial program with four wild dogs at the Frankfurt Zoo (Gascoyne et al. 1993).

Reintroductions, another form of intervention, can best be applied in two situations (Stanley Price 1989): first, when a localized extinction has occurred; second, to bolster an existing population that has declined to

Table 21.3 Approximate 1991 population sizes of some carnivores in the Tanzanian and Kenyan portions of Serengeti ecosystem combined.

Species	Estimated numbers of adults	Source
Cheetah	200–250	Authors' estimate
Leopard	800–1,000	Borner et al. 1987
Lion	2,800	Packer 1990
Banded mongoose	43,000	Waser et al., chap. 20
Dwarf mongoose	94,000	Waser et al., chap. 20
Slender mongoose	30,000	Waser et al., chap. 20
Black-backed jackal	6,300	Authors' estimate[a]
Spotted hyena	9,000	Hofer and East, chap. 16[b]
Wild dog	50	Burrows 1991

[a]Based on dividing 11,425 km² of woodlands with >5% canopy (Tanzania Wildlife Conservation Monitoring database) by average home range size (Fuller et al. 1989).
[b]An estimated 1,500 spotted hyenas living in the Masai Mara (Hilborn et al., chap. 29) were added onto the rounded 7,500 quoted for the Tanzania ecosystem (Hofer and East, chap. 16).

low levels; and third, to introduce new genetic material into an inbred population. Successful reintroductions critically depend upon accurate behavioral data, including knowledge of a species' activity cycle, diet, and social behavior. Stanley Price (1989) has outlined a number of behavioral factors that can facilitate reintroductions: being tolerant of a broad range of habitats and thus adaptable to new situations; having a wide range of foods available; being exploratory and hence able to move into new areas; and being amenable to behavioral manipulation.

Currently, reintroducing cheetahs into reserves in Russia and India is under discussion, since their numbers increase rapidly in the absence of lions and spotted hyenas (Anderson 1984). The cheetah has many of the traits highlighted by Stanley Price. For example, Adamson (1969) was able to release a captive cheetah successfully by gradually reducing the amount of food it received from her.

In summary, it is clear that behavioral ecology can contribute to many critical facets of conservation biology, such as predictions of population persistence, reserve design, and management. The most important facts it can contribute are size and number of social or geographic units, knowledge of the mating system and dispersal, interaction rates, ranging patterns, and species-specific behavior (table 21.4).

LINKS BETWEEN CONSERVATION AND BEHAVIOR OUTSIDE SERENGETI

In this chapter we have shown how knowledge of behavior and ecology enhances conservation using data from Serengeti carnivores. Since large carnivores hold such a prominent place in conservation biology, it could be argued that our examples are special cases. Yet an examination of

Table 21.4 Relationships between behavioral ecology and conservation biology.

Aspect of behavioral ecology	Relevant information	Principal conservation significance
Demographic records	Mean and variance in reproductive success	Calculating MVPs
Grouping patterns	Mean and range	Population persistence Genetic diversity Monitoring
Mating system	Polygyny/monogamy, reproductive suppression	Population persistence Genetic diversity
Dispersal	Rate, costs, and kin structure	Population persistence Genetic diversity Reserve size and corridors
Ranging patterns	Overlap and home range size	Reserve size Monitoring Interventions
Intraspecific interactions	Rate	Population persistence Disease transmission Interventions
Interspecific interactions	Rate	Population persistence Disease transmission
Species-specific behavior	Various	Population persistence Monitoring Interventions

other conservation studies and programs shows that behavioral ecology has important ramifications for a wide variety of conservation agendas.

First, dispersal behavior is increasingly being incorporated into extinction models to make them more precise (Chepko-Sade et al. 1987). Durant and Mace (1994) showed that monk seals became increasingly vulnerable to extinction as migration increased because they risked moving to uninhabited localities where breeding was impossible, but mountain gorillas became less vulnerable with increasing migration because females transferred to breeding groups. Indeed, dispersal and colonization of new areas may be enhanced by the presence of conspecifics, thereby altering metapopulation dynamics (Smith and Peacock 1990). Similarly, knowledge of dispersal distances helps to address the related issue of how habitat fragmentation affects population persistence, and is now being incorporated into plans for the recovery of the northern spotted owl (Murphy and Noon 1992).

Second, empirical conservation studies now attempt to collect data on life histories and the ecological and social factors affecting individuals.

As illustrations, Laurance (1991) found that rainforest mammals in northern Queensland, Australia, were more prone to extinction if they had low fecundity and high longevity, or if they had specialized diets; while Soulé et al. (1988) showed that the occurrence of chaparral-requiring birds was positively associated with the presence of coyotes, since the latter reduced the abundance of avian "mesopredators" such as gray foxes and domestic cats.

Third, conservation strategies are now beginning to account for behavior even in their initial stages. For example, female grouping patterns and mating preferences in African elephants are seen as critical in predicting the chances of subpopulation recovery following poaching (Dobson and Poole, in press).

Fourth, as with carnivores, ranging patterns of other species have helped to delineate the size and location of reserve boundaries. Based on measurements of the huge territories of rainforest raptors, Thiollay (1989) argued that the size of proposed national parks in French Guiana should be as large as 1–10 million hectares in order to encompass a sufficient number of breeding pairs.

Fifth, rehabilitation programs have relied extensively on behavioral insights to be successful. In attempting to increase the number of nest sites for the highly endangered Puerto Rican parrot, researchers found that the pearly-eyed thrasher was driving parrots away from nesting holes or breaking their eggs. By carefully determining the size and shape of artificial nest boxes preferred by each species and erecting both in close proximity, the researchers enabled each species to lay, since the aggressive thrashers drove intruding conspecifics away from the parrots' nests (Snyder and Taapken 1978). Similarly, the successful reintroduction of Arabian oryx into Oman rested heavily on advance knowledge of the ranging patterns, diet, grouping, and reproductive behavior of the species (Stanley Price 1989).

Finally, the effects of tourism can be determined in part from observing animals' responses to human disturbance. For instance, Burger and Gochfeld (1991) showed that distances at which birds were flushed by humans were shorter in residents that were regularly exposed to people than in migrants, indicating that habituation had occurred. More studies of this nature would be useful in East Africa, where national revenue depends so much on the presence and viability of mammal populations in the face of mass tourism (see Burney and Burney 1979).

Though space limits us to these few examples, it should be clear that the bridges between behavioral ecology and conservation biology are numerous, and are often pivotal to conservation programs. Indeed, the benefits of knowing species' habitat requirements for in situ conservation and their behavioral needs for ex situ conservation are self-evident. Currently,

however, links between the disciplines are constructed by conservation biologists seeking to make their models more realistic, or their management plans more successful. We additionally need behavioral ecologists to give more weight to conservation concerns in the course of their research and to present data in a form more suitable for the purposes of conservation biology, since their findings can greatly assist in predicting imminent population extinctions.

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TWENTY-TWO

Population Structure of Wildebeest: Implications for Conservation

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The Serengeti ecosystem is often defined as the area encompassed by the wildebeest migration (McNaughton and Campbell 1991), and this definition has provided a compelling justification for shaping and reshaping the boundaries of a vast protected area. If one goal of protected areas is to maintain genetically intact wildlife populations, however, it is still unclear whether this definition is ecologically appropriate for other species in the ecosystem, or even for wildebeest. For example, effective conservation plans rest on assumptions about the spatial limits of populations and their interactions with one another. The problems involved in making such assumptions are shared by all protected areas whose fate it is to become "islands in a sea of humanity" (Leader-Williams, Harrison, and Green 1990). Nevertheless, we are rarely certain of the extent to which protected areas are conserving "intact" populations and communities. Two possibilities arise: (1) protected areas may represent natural islands that were maintaining independently evolving lineages at their inception; or (2) they may contain populations now confined within unnaturally isolated parks that were once linked by dispersal and gene flow. I suggest that answers to such questions are essential for the long-term management of protected areas as functionally intact communities. Ecological processes that operate over large areas and long time spans may be drastically modified when habitat fragments are set aside for conservation and the intervening lands are developed (Pimm 1991; Saunders, Hobbs, and Margules 1991). In this chapter I explore the questions raised above for wildebeest within Serengeti and several other protected African savannas.

Studies of large herbivore populations have typically been confined to single species in one area over a few years. The monitoring of the size of the Serengeti wildebeest population over 30 years provides an exceptionally long and intensive example (McNaughton and Campbell 1991). On occasion, migrations have also been followed by radiotelemetry, and such techniques are useful for revealing present-day movement patterns.

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