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Behavioral Ecology and Conservation Policy:On Balancing Science, Applications, and Advocacy

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A Dilemma

Planet Earth is at risk. Rapid population growth, degradation of landscapes, extinction of species, and the pollution of air and water is creating a crisis for the biosphere whose unprecedented proportions are only just being defined, let alone understood. With respect to biodiversity alone, our efforts at eliminating species far outstrip our abilities for estimating the magnitude of the carnage we are inflicting. If ecology is the science concerned with the relationship of organisms to each other and their environment and conservation biology is the study of how to conserve and manage biological diversity, then behavioral ecologists have much to offer. Because behavioral ecology is about how ecology shapes behavior, it can help define conservation problems more precisely and show how understanding the function, or survival value, of behavior can help eliminate some of these environmental problems.

Accomplishing these two tasks, however, is not straightforward. Because two of the aims of conservation biology are the protection and sustainable use of Earth's biological diversity, human interventions—along with their conflicting interests and values—are inevitable. Consequently, conservation biology has a divided "personality," being composed of both basic and applied elements. While it is important to gain a detailed understanding of how species and their ecosystems function, it is essential that this knowledge be used to manage species and manipulate their ecosystems for desired ends. Thus behavioral ecologists addressing conservation issues must in part be research scientists learning about basic behavioral, life history, and ecological attributes of individuals so that they can monitor, or at times even predict, changes that will occur when environments are altered. But behavioral ecologists must also be environmental physicians, diagnosing the health of species and their ecosystems and offering treatments that can cure problems. Thus environmentally concerned behavioral ecologists are conservation biologists because they are in the knowledge business, unraveling the workings of the living world while using their skills and insights to conserve biodiversity and ensure the proper workings of pristine and perturbed ecosystems. As scientists they use experimental manipulations, systematic observations, and theoretical modeling with appropriate controls to guard against possible latent biases as they generate and apply new knowledge.

Behavioral ecologists and conservation biologists alike, however, face a special problem: they are also people. And as people, strongly held values color perspective and help shape personal goals and actions. Many behavioral ecologists are imbued with strong ideals that guide them to live in harmony with nature and encourage them to participate actively in the political arena. As such they are biological conservationists who are activists that use insights from ecology to guide their activism whose agenda is in part being shaped by beliefs, values, and intuition.

Consequently, behavioral ecologists feel a tension that clearly exists between the need to ensure, on the one hand, the objectivity that underscores the impartiality of research science, or the practice of clinical medicine with its deductive diagnoses and humane treatments, and on the other hand, the need to act, impelled by values based on environmental concern. Unfortunately, intellectually based activism can become confused with popular environmentalism and its zealous faith in absolute truths. Blurring the distinction between ecologists as research scientists and environmental physicians might not be all bad because it could both focus "pure" research that could too easily become esoteric and limit the implementation of mitigation strategies that are often superficial, if not simplistic. But if science is to influence the shaping of effective policy, then maintaining the distinction between the science of scientists and their political actions is critical.

It is the aim of this chapter to chart a course that can guide behavioral ecologists through the Scylla of rational but time-consuming research programs that provide basic insights that can shape effective management plans, and the Charybdis of forceful environmental action that sometimes compromises the biological foundations of accurate ecology. Being able to play these different roles without losing scientific credibility and without sacrificing the ability to shape conservation policy requires that behavioral ecologists know the players, scripts, and structural constraints associated with each of the theaters. By examining a series of case studies, we will see how the tenets of behavioral ecology and the results of long-term studies have already provided basic scientific insights that have helped formulate realistic management strategies. At the same time we will explore how such studies can be made more useful and help shape effective public policy and management practices, hence fostering the cause of environmentalism without sacrificing scientific credibility.

The Importance of Behavioral Ecology

Concepts from population and community ecology have had a dramatic impact on conserving species. Keystone predation (Paine, 1966), island biogeography (MacArthur and Wilson, 1967), harvesting theory (Beddington and May, 1980) and demography (Caughley, 1977) have all been used to shape strategies for increasing biodiversity, siting and sizing nature reserves, assessing maximal sustainable yields for fisheries and whaling industries, and determining minimum viable population sizes. Vigorous debate concerning the utility of using such theories for designing particular management plans has ensued (Mills et al., 1993), but without doubt such principles have provided valuable starting points for organizing thinking about how to solve real-world problems.

Can the first principles of behavioral ecology similarly serve to crystalize thinking about conservation strategies? The answer should be an unequivocal "yes." Although concepts from traditional population and community ecology have had tremendous impact, their utility is often limited because they essentially treat all individuals in populations as equals. Behavioral ecology, however, is about diversity and understanding why individuals respond differently to similar environmental circumstances. Ultimately such an understanding derives from the notion that differences among individuals are real, having been shaped by natural selection. Typically, selection maintains behavioral polymorphisms and favors individuals that facultatively respond to their environment, one which is often dominated by the actions of others. Thus, if conservation models, be they qualitative or quantitative, are to be used in predicting the dynamics of animal populations and the consequences of various conservation strategies, they must be made realistic. And this can best be accomplished by incorporating a detailed understanding of not only the behavior of the species but also the environmental selective forces responsible for shaping the behavior of the individuals that compose them.

Incorporating a focus on individuals and their variation into realistic models should not be difficult for two reasons. First, behavioral ecology is rich in "first principles." Optimal foraging and life-history theory, decision-making rules in competitive and predator–prey situations, as well as models of social, mating, and breeding strategy illuminate how individuals move, aggregate, acquire resources, and reproduce. In turn, these actions by individuals affect how their populations migrate, impact their landscape or habitats, and grow. Because these outcomes influence the genetic structure, demography, and dynamics of populations, concepts from behavioral ecology should be able to provide powerful insights into the functioning of populations. Moreover, behavioral ecology specializes in long-term field studies, so details on variation in birth and death rates as well as on lifetime reproductive success that are necessary to calibrate, or even generate, realistic models are often available. Thus incorporating a behavioral ecological approach into the study of conservation should not only help uncover subtle but important aspects of a species' or population's biology but also help in diagnosing and healing ailing populations or the ecosystems they inhabit.

Behavioral Ecology and the Science of Conservation Biology

Much basic behavioral ecological research has been focused on understanding the patterns and processes of individual species and the communities they inhabit. The empirical results and theoretical insights derived from these studies shed light on how systems work and often provide the framework upon which management and conservation decisions derive. Underwood (1995) describes this as "available and directed research"; level 1 (table 19-1). Observations on the ranging patterns of species to establish the boundaries of national parks is perhaps the most basic form in which this type of research is employed. Only after the seasonal migratory patterns of wildebeest were known were the boundaries of the Serengeti National Park and the Ngorongoro Conservation Area established (Grzimek and Grzimek, 1959). In this way a sustainable park was created and conflicts with humans were mitigated at the outset.

Although use of "off-the-shelf" knowledge has value, it often leaves the researcher in a defensive position; decision makers are asking the questions and hence setting the agenda. Because the data are often based on descriptions from different systems that are at best not too dissimilar from those needing assistance, it also puts researchers in the position of making difficult predictions about processes. When ordinary scientific uncertainty is added to the mix, ecologists often find themselves in untenable situations. Prescribed actions are

Table 19-1 Hierarchy of research types.

Level	Type	Purpose	Examples
1	Available and directed	Assess impacts of current action based on present observations. Use basic models tuned to existing patterns.	Viability analyses and impact statements
2	Applied and environmental	Assess impact of managerial decisions. Treat management actions as experiments in progress and test their predictions.	Reintroduction operations, environmental remediation schemes and alternative harvesting strategies
3	Basic and strategic	Design new experiments and develop new models based upon limitations or failures of implementing previous ones. Shift focus from understanding patterns to processes and mechanisms.	Consequences of individual decision-making; in particular dynamics of sex ratio adjustments, sex differences in behavior, Allee affects
4	Managerial and policy making	Understand how policy makers and managers make decisions and choose courses of action. Apply sociobiological reasoning to understanding the behavior of institutions as societies and actions of their members and other stakeholders.	Analyses of organizational structures, legal frameworks, legislative procedures, economic systems, and human motivations

rarely effective, and the effectiveness of science is doubted. As a result, Underwood (1995) argues that ecologists should become more proactive and expand their research to include three additional domains (table 19-1). First, even when providing existing "off-the-shelf" (level 1) research to managers, scientists should inform users about the generality and applicability of applying the findings to a particular problem because they were most likely obtained for a different population, in a different system, and at a different scale. Second, ecologists should begin researching the consequences of management and conservation decisions ("applied and environmental research"; level 2). In effect, decisions about whether to intervene, and in what ways, represent large-scale experiments. Because they are derived from hypotheses that make strong predictions, their outcomes can be measured, and the fit to the predictions can and should be evaluated.

Third, new research programs should be established when previous attempts at conservation or management have failed ("basic and strategic research"; level 3). Interventions are likely to fail for many reasons. To know whether they did so because the off-the-shelf research was applied at the wrong scale or to a system with novel processes, or to species or populations with different behavioral repertoires, it is necessay to perform postmortems if future attempts at solving real-world problems are to succeed. Generating fundamentally new understandings of ecological problems is perhaps the best way to ensure that basic research ultimately has ecological applications.

Last, ecological research must examine the dynamics of management ("managerial and policy making research"; level 4). Understanding why scientific knowledge is misapplied or often ignored when decisions are made will require an understanding of what motivations and rewards shape the behavior of managers. Underwood (1995) argues that leaving such inquiry to the domain of social scientists and humanists leaves scientists as servants of managers. If scientific thought is truly to inform policy, these roles must become more balanced. As many of the case studies described below will show, had behavioral research been performed at a level higher in the hierarchy, applications of the findings would have been more useful in shaping policy.

Certain tenets of behavioral ecology are shaping conservation strategy by offering insights into how to prevent the demise of species. Although most species will be lost due to habitat degradation, fragmentation, or loss, some have already succumbed to excess harvesting by humans. To stop these trends it is important to understand how animals behave and how their strategic responses have evolved so that their behavior can be exploited to develop strategies that enhance survival. Only in this way will it be possible to move beyond the most basic off-the-shelf research to the higher levels proposed by Underwood, where both effectiveness and the chances of adoption will be enhanced. Here I explore a number of case studies that show how the demise of species can be prevented by improving our understanding of how the tenets of behavioral ecology shape viable population sizes, strategies of sustainable resource use, and patterns of biodiversity by drawing upon theories of optimal foraging, life-history evolution, mating systems, and the dynamic relationships that exist between predators and prey.

Optimal Foraging and Applications of Bet Hedging

Because natural selection favors behavior that maximizes an individual's fitness, it often pays individuals living in temporally changing environments to hedge their bets. To do this they often diversify their behavior and reduce variance in offspring number, a major component of lifetime reproductive success (Seger and Brockmann, 1987). Sometimes such behavior coincides with maximizing a population's growth rate, but this need not be the case (Eadie et al., chapter 12, this volume). In fact, natural selection of the group selectionist kind is necessary if maximizing a population's success is to be favored directly. Much theory has been developed to explore the role of diversifying behavior with respect to life-history evolution (Schaffer and Gadgil, 1975; Stearns, 1976; Gillespie, 1977; Real, 1980; Rubenstein, 1982; Bulmer, 1984), but perhaps the best empirical examples showing that animals behave in accordance with predictions of the models emerges from studies of optimal foraging. Caraco and co-workers (1980), for example, showed that foraging birds did best if they were sensitive to the variability of food rewards in addition to the mean rate of return. When energy requirements were less than the expected reward of either foraging option, individuals avoided taking risks and chose the less variable one. Only when energetic needs exceeded either option's expected rate of return was the more variable option chosen.

Human exploitation of marine fisheries has often resulted in overfishing and in bringing fisheries to the brink of extinction. Reliance on standard principles of maximal sustainable yield (MSY) or even optimal sustainable use (OSU) has not worked. Most recently the highly productive cod fishery off the Canadian Atlantic coast has collapsed and has highlighted the problem of managing fisheries. An indefinite moratorium is in place for the Great Banks, and temporary moratoriums have been imposed on neighboring fishing groups with the hope that populations will grow and the fishery will recover.

Fishery biologists are well aware of the role that environmental fluctuations play in introducing uncertainty into estimating levels of sustainable catches. Typically managers use conservative catch criteria that attempt to maintain catch levels below MSY values or try to maintain stocks above the MSY level. Lauck et al (in press) argue that these recommendations are seriously flawed because they assume that current stocks are accurately known, which is never the case. Estimation errors of 50% are not atypical, but reliance on this method of determining a sustainable catch implicitly assumes that with better methods stock assessment can be improved.

The alternative view is that many aspects of the natural world are never knowable with sufficient certainty, and this leads Lauck and co-workers (in press) to favor a completely different management strategy. Rather than base quotas on a best guess that ignores uncertainty, they suggest that managers take a page from the behavioral ecological literature: use bet hedging to diversify their own behavior by managing fisheries to reduce variation in catch. An effective way of doing this would require exploiting only part of the resource while protecting the rest in Marine Protected Areas, or "no-take" zones (Shackell and Willison, 1995). Obviously, for any given level of harvesting, the average catch for the combined areas would be lower than if the entire area were open to fishing at this same level, and this would necessarily afford the fishery some protection.

But viewing the problem as only affecting the mean misses the point. If the entire stock were open to fishing, then any inadvertent overfishing generated by unpredictable appearances of extremely harsh environmental conditions would drive the entire population dangerously close to zero. Even though there will be intervening good years, damage associated with severe declines could make it difficult for populations to recover. With the entire fishery open to harvesting, variation in yield will be high. By setting aside a portion of the habitat to protect a fraction of the fishery, the likelihood of excessive depletions is reduced, which in turn reduces the variance of the harvest. As Lauck and his co-workers show, the larger the reserve, the better the policing, or the more fecund the species, the better such reserves will be at hedging against environmental uncertainty. Because yield increases with harvesting intensity but with diminishing returns, the percent decreases in the long-term yield for the population is likely be smaller than the percentage of the range that is set aside as the refuge. As a result, for whatever the size of the protected area, it is likely that the exploitable area can be harvested more intensively than would otherwise be the case.

Whether these ideas are adopted by managers and find their way into policy depends upon a number of factors. As Ludwig et al. (1993) argue, fishery management has been a spectacular failure despite much scientific analysis. Disagreements among scientists are common, and the prospects of resolving these disagreements are virtually nil because controlled experiments, even on a small scale, would involve short-term losses for the industry. As a result, Ludwig and co-workers suggest that effective management can only result when human motivations, usually greed, are incorporated into the system and when science is limited to identifying rather than remedying the problem. But a tenet of behavioral ecology as well as economics, bet hedging, may go a long way to mitigating the problem of over fishing precisely because it confronts the issue of uncertainty head-on (i.e., level 3 research) and provides a conservative means of managing when information about the state of the world is poorly known and when human greed and human error are likely to prevail.

Life-History Theory and Demography

Natural selection favors individuals who transmit the most genes to future generations. How this is best accomplished varies depending on environmental circumstances. In some situations, individuals that produce many small young early in life are favored, whereas under other circumstances individuals delaying maturity and investing lavishly in only a few young have the advantage (Horn and Rubenstein, 1984; Lessells, 1991). The allocation of limited resources to balance the conflicting demands of survival and reproduction defines a life history. From a conservation perspective, understanding why certain evolutionary patterns evolve and knowing when they are malleable is essential if intervention and management are to be successful. Knowing why a particular type of life history is adaptive under one set of environmental conditions and not another, or why some life histories are plastic while others are not, will make some interventions more effective than others in particular circumstances. Being armed with this understanding before a management problem is implemented or even designed is the best antidote to costly and possibly harmful practices.

Atlantic Salmon

One of the most important life-history stages is age of first reproduction because it tends to be correlated with many other features (e.g., longevity, fecundity) of a life history (Rubenstein, 1993). The benefits of breeding early in life are many. At least in expanding populations (hopefully the case for endangered, but now protected, or recovering species), maturing early tends to accelerate the spread of genes into future generations because offspring have their offspring quickly and they disproportionately contribute to the growth of the population. Also, breeding early reduces the period of juvenile vulnerability, which can be high and is typically greater than that of an adult. Nevertheless, there are costs associated with breeding early. Perhaps the two most important are small size and inexperience, both factors that could limit subsequent longevity or fecundity. For example, smaller size often means smaller ovaries and fewer eggs for females of many taxa, especially among invertebrates, whereas for males it typically means limited intrasexual competitiveness and hence lowered access to mates.

That human behavior can have an impact on changing this important transition is nowhere more apparent than in Atlantic salmon (*Salmo salar*) populations. In Atlantic salmon, increased fishing has changed not only the age of first reproduction but also the entire pattern of sexual development (Montgomery, 1983). Typically salmon develop in freshwater streams for 1 or 2 years and then smolt by migrating to the sea. There they forage on zooplankton and continue to grow. Once they attain a certain size, they become sexually mature and return to rivers, traveling upstream until they reach spawning grounds. Some parr, however, never reach critical smolting size. They remain in the stream and become sexually mature at small sizes and at early ages. Under pristine conditions, the fraction of the male population adopting this alternative route to maturity is small. With intensive fishing reducing the number of adults maturing at sea and thus reducing the number able to return to the rivers, the direct maturing parr that spend their entire lives in the streams are now no longer at such a competitive disadvantage. Their survival prospects are high and the number of large, superior competitors they are likely to encounter is reduced. Consequently, their life-history strategy is selectively advantageous and is increasing in frequency. The consequences on the fishery are likely to be profound. Fewer and fewer fish will migrate to the sea, and even with increased harvesting effort, catches will continue to decline. Fortunately, the species will survive but with morphologies and behavior quite different from what we are accustomed to seeing. By providing an explanation for why such profound populationwide changes are occurring, life-history theory can reveal where intervention is likely to be most effective (i.e., level 1 research).

As awareness of the likelihood of global change grows, ecologists have begun studying the responses of organisms to climate change (Peters and Lovejoy, 1992), especially with respect to life-history events (Rubenstein, 1992). Here too, anthropogenic actions are likely to impact salmon life-histories and the viability of the fishery. Because the salmon fishery is highly profitable and is dependent on species that spend part of their lives in fresh water and part out to sea, understanding how climate change will affect the growth of stocks, which in turn will determine optimal catch size necessary for sustainable harvesting. Mangel (1994a) modeled growth, development, and behavior of salmon in both streams and oceanic environments and found that, once at sea, increased water temperatures would lower growth and adult survivorship and induce earlier maturity. The combined consequence of these changes is an early return to natal streams in all but the fastest growing individuals. These fast growers actually delay maturing for an additional year. Such populationwide changes would be the indirect effect of temperature-induced increased winds that would disrupt zooplankton patchiness and lower feeding rates. For parr developing in streams, Mangel's models suggest that increases in water temperature will enhance growth and survival and induce smolting after 1, rather than 2, years. Changing the parr–smolt transformation point as well as the age at sexual maturity should have major implications for the fishery. As females accelerate development, they will mature earlier and at smaller sizes, thus lowering their fecundity. In addition, their survival will be reduced. Such changes do not augur well for the fishery and dictate that harvesting levels must be significantly reduced.

The implications of these hypothetical predictions are profound. Because many of the models' formulations are based on best-guess assumptions, their predictions should only be viewed as possibilities. Nonetheless, the models identify not only areas where further behavioral and developmental research is needed, but they also underscore the importance of "knowing your organism," something behavioral ecologists routinely do. Without understanding the intricate details about what behaviors salmon exhibit, it would be difficult to meld the physical dynamics of oceans with those driven by behavior and physiology. By appreciating that natural selection shapes life histories, more realistic understandings of how environmental changes will affect the survivorship and fecundity schedules that are so crucial for a species' survival (level 3 research) are possible.

Asiatic Wild Ass

Reintroduction of the Asiatic wild ass (onager) *Equus hemionus* into areas of Israel and Palestine, where it flourished until the turn of the century, provides another example of where attention to details of the dynamics of life-history evolution mean success or failure. One of the goals of the Israeli government is to reintroduce biblical animals to Judea and Samaria. In 1982 the first onagers were moved from a breeding reserve, Hai-Bar Yotvata, to Makhtesh Ramon, a large erosional crater in the center of the Negev Desert. The first release contained only males, and they quickly dispersed and many were shot when they moved near the Israeli-Jordanian border. A second attempt involving two males and six females took place in 1983 and was followed with additional releases in 1984 (two males and five females) and 1987 (five males and three females). All but two individuals were between 2 and 5 years of age, and the two older ones (aged 6 and 17) died shortly after release.

The population has been continually monitored since 1983, and it became apparent that the population was growing very slowly (Saltz and Rubenstein, 1995). By 1993 the population only contained 16 breeding females, up from the original 14. But recruitment has suddenly improved since there now are three 2-year old females, four female yearlings and nine female foals. With the ranks of reproductive females swelling, the population is growing. But why did this demographic transition take so long? And why is the population growing quickly now? These were questions that the government asked us to answer.

Much attention has been paid to the logistical features of reintroductions that are crucial for assuring success. That only males were initially introduced underscores the need to pay attention to detail. In accordance with International Union for the Conservation of Nature guidelines, a feasibility study was completed before the project began. Release sites were prepared so that the transplanted individuals could habituate to the habitat, and postrelease monitoring was performed. Nevertheless, the population size remained almost constant for nearly a decade. The problem underlying this stasis was that basic facts about the behavioral and evolutionary ecology of the species were not known. In particular, it was not appreciated that wild asses could facultatively adjust sex ratio nor that captivity could dramatically limit fertility.

Trivers and Willard (1973) were the first to suggest that differences in the ability of individual females to invest in the rearing of their young should lead to individual differences in primary sex ratios. They argued that mothers with sufficient resources should invest in the sex with the higher variance in reproductive success as long as this investment could increase the chances that such offspring would be those producing the most offspring. In polygynous species of ungulates, males exhibit higher variances than females, and in many species (Clutton-Brock et al., 1984) levels of parental investment affect the subsequent reproductive success of offspring. For species in which competition for critical resources is of the "contest" variety in which winners exclude losers from acquiring critical resources, females of high rank are often in above-average bodily condition and they produce more sons than daughters. When competition is of the "scramble" type in which success is shaped by utilization efficiency, dominance has little influence on who acquires the most resources. Instead, age seems to be the determinant of sex ratio bias; at least for Asiatic wild asses, middle-aged females give birth to sons, whereas both young and old females give birth to daughters (Saltz and Rubenstein, 1995) (fig. 19-1). Because all the females released into the crater were between ages 2 and 5—the male-producing years—very few females were recruited into the population, and the population did not grow. Over time, however, we predicted that the age structure of the population would change, and as more females begin to enter the female-producing years, the population should begin to grow. In fact this appears to be happening. Since 1993, 9 of the 13 foals born were female.

The population also initially failed to grow because the fecundity of females transferred to the crater was extremely low. Fewer than 30% of all reintroduced females had given birth within 2 years of the translocation, and for females aged 5 or less, fewer than 50% bore young (Saltz and Rubenstein, 1995). For females born in the crater, however, between 80% and 100% of females ≤5 years of age have given birth (fig. 19-2). Many hypotheses have been proposed to explain this abrupt change. Perhaps mating opportunities were reduced because of excessively small population size (an Allee effect; Allee, 1931). Although it is true that the population contained only one reproductively active male, he regularly pa-

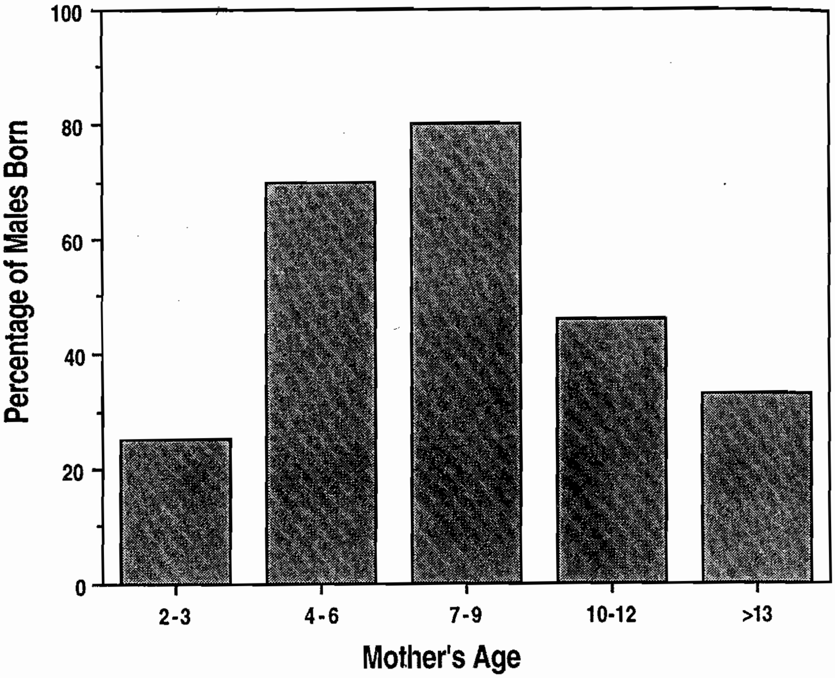

Figure 19-1 . Percentage of females in the Ramon onager herd giving birth to sons as a function of mother's age in years.

trolled the entire crater and made contact with females regularly. Thus sperm limitation is unlikely. Alternatively, it is possible that excessive vigilance or inefficient foraging by females, both consequences of small group sizes, might have lowered bodily condition enough to limit conception success. Given that female fat levels as judged by rump scores have always been high and have not changed over time, this additional Allee effect seems unlikely. Perhaps inbreeding depression could have been responsible for diminished reproductive success, although this also seems unlikely because per capita breeding success has improved over time. Similarly, youthful inexperience is unlikely to be the primary causative agent because young wild-reared females breed prolifically. Rather, it seems most likely that either stress associated with handling or some other residual, long-lasting effect of prolonged captivity prior to release is responsible for lowering the fecundity of the reintroduced females; evidence of handling reducing the reproductive capacity of wild dogs *Lycaon pictus* has just emerged (Creel, 1996).

Thus, had the Nature Reserves Authority been apprised of some basic tenets of behavioral ecology, the reintroductions might have succeeded more quickly and might have been more economic. By reintroducing older females, who were most likely to have given birth to a daughter, who in turn would most likely have given birth to a daughter, rather than middle-aged females, the population would have grown more quickly. But with the results of new studies to be built upon these initial insights, even this strategy could be improved upon. If we knew for sure that the lowered fecundity does not result from transport or the

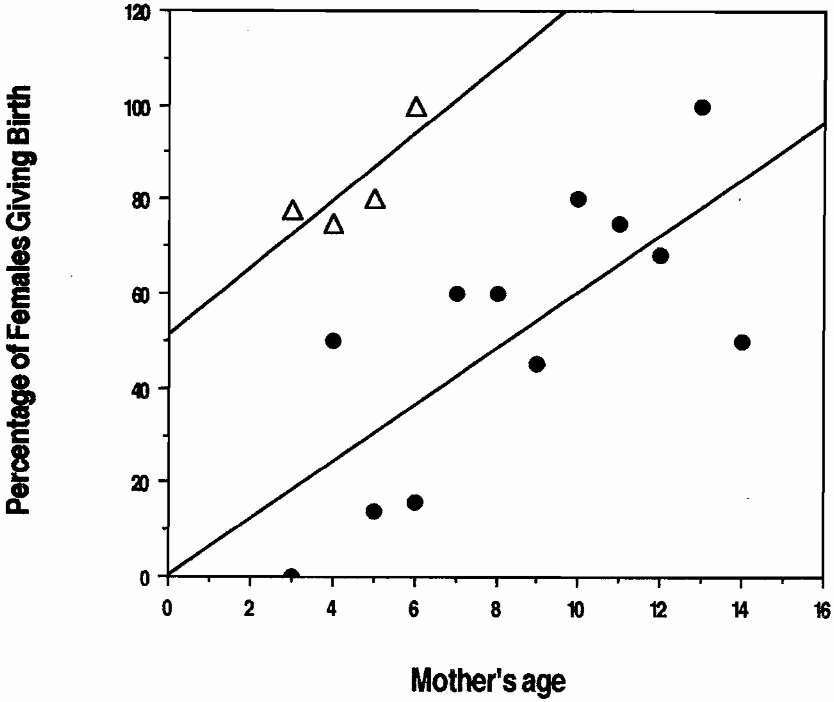

Figure 19-2 Percentage of adult female onagers giving birth at known ages. Filled circles denote translocated females ($y = 0.4 + 6.0x$; $F_{1,10} = 11.89, p = .006; R^2 = .54$). Open triangles indicate females born in the wild ($y = 51.3 + 7.1x$; $F_{1,2} = 3.74, p < .2; R^2 = .65$).

residual affects of captivity and if we assume that fecundity is enhanced after females acquire familiarity with the habitat and the all-important distribution of critical resources during the relatively peaceful prepubescent period, then introducing older females with their yearling daughters might be an even better strategy. Such a double addition of females producing mostly daughters would accelerate the recruitment process even more.

Clearly, the need to understand how environments shape behavior—the essential ingredient of behavioral ecology—would have been, and can still be, instrumental in devising effective and economical conservation strategy. Because the Nature Reserves Authority asked us to determine the problem and because they are planning to use our findings when designing further reintroductions, it is possible for scientific first-principles to make their way into effective management policy. That the Nature Reserves Authority has placed a behavioral ecologist as head of the reintroduction program shows that conservation planning is moving up the hierarchy to Underwood's (1995) basic and strategic research.

Mating Systems, Recruitment, and Population Viability

Perhaps the most powerful determinant of a population's ability to sustain itself is its ability to recruit new individuals. This can be accomplished either by increasing the survival prospects of females or by increasing their fecundity, and effective management should attempt to enhance both. By knowing something about mating systems and the processes of sexual selection that shape them, managers will gain insights into how to augment survival and fecundity by adjusting natural processes in meaningful ways. Unavoidable evolutionary trade-offs might limit any plan's effectiveness, but at least some undesirable and unintended consequences might be avoided.

Sexual selection often results in sexual dimorphism in morphology and behavior. In many polygyous species, only males exhibit weapons used in combat, and females invest more time and energy in rearing and protecting young. Appreciating that such differences are common can make a difference in ensuring that endangered species can increase their reproductive potential. This is likely to be especially true for those charismatic megafauna, where their extreme body size ordinarily limits their recruitment potential. Certainly, increasing either adult or juvenile survival is essential, and actions increasing both adult and juvenile mortality should be avoided. But doing so may not always be straightforward. Appreciating how prevalent and important sex differences are could complicate management by necessitating different action plans for males and females.

Black Rhinoceros

One species for which ignorance is particularly problematic is the black rhinoceros *Diceros bicornis*. Populations of black rhinos have been reduced by 97%, from 65,000 to less than 2500, in the last 25 years. Successful poaching for horns has led some nations to implement policies of dehorning in an attempt to reduce the slaughter by making rhinos less desirable to poachers (Berger, 1994). If effective, such a strategy would allow rhinos to continue roaming freely in their natural habitat. An alternative policy is to translocate rhinos to fenced areas where they can be monitored closely. Both strategies can foster ecotourism, but the former, by limiting the ability to monitor individual animals, still leaves rhinos at risk if dehorning fails.

Berger and co-worker's study (1994) of the behavior of horned and dehorned rhinos suggests that the dehorning strategy is likely to fail because horns regrow quickly and poachers appear to kill rhinos irrespective of horn size. Given that horns regrow at a rapid rate (anterior horns, 5.3 cm/year; posterior horns, 2.3 cm/year), rhinos regain value in just a few years if not dehorned again. But even if these assessments are overly pessimistic (Loutit and Montgomery, 1994), it is essential to know if dehorning disrupts normal behavior and puts individual rhinos at risk. According to Berger (1994) and Cunningham (Berger and Cunningham, 1995), the answer is unequivocally yes. Although dehorned mothers were no more likely to flee from predators than their intact counterparts, the disappearance of offspring being reared by dehorned mothers in areas of abundant spotted hyenas *Crocuta crocuta* and lions *Panthera leo,* but not those reared by normal horned females, suggests that horns play an important role in defense. Thus the population's ability to recruit is likely to be limited severely by dehorning; offspring appear to suffer immediate risks, and although dehorning might enhance a female's chances of survival in the short run, her medium- to long-term reproductive prospects are limited.

Despite morphological similarities among male and female rhinos, there are profound sexual differences in parental behavior. In response to predators, be they hyenas, lions, or humans, female rhinos with young are both more vigilant and more likely to respond actively than nonparous females or especially males (Berger, 1994). When offspring are older, mothers are likely to charge predators, but when offspring are young they tend to flee. Because repeated flight is likely to force all females to move long distances, chronic human disturbance is likely to put males at greater risk with respect to poaching because they stay put. In turn, as males become relatively rare, especially in small populations, sperm limitation of the kind generated by an Allee effect as described above and further elaborated by Dobson and Lyles (1989) and by Dobson and Poole (Chapter 8, this volume) could further limit the population's ability to grow.

Dunnocks

Knowledge of how changes in mating systems alter the per capita reproductive success of individual males and females should caution managers intent on altering a population's resource base or sex ratio. Davies's (1989) study on dunnocks *Prunella modularis* showed that changes in the ease at which females could acquire food dictated the size of their feeding territory. When food was made easy to acquire, territories were reduced in area. As a result, male territories became larger than those of individual females, and the mating system shifted from monogamy to polygyny. Conversely, when females defended large territories, especially if they were vegetatively and structurally complex, polyandry developed. Davies measured the reproductive success of individual males and females under these different mating regimes, so he was able to show convincingly that changes occurred and that their magnitudes could affect a population's recruitment. As fig. 19-3 shows, polygynous males have the highest reproductive success, but they contribute little apart from genes (unless an Allee affect limits sperm availability overall) to the growth of the population. And because females mated polygynously do much worse than if they were polyandrous or even monogamous, managers should do everything possible to avoid altering the landscape, or resource base, in ways that would encourage polygyny if it were important to promote population sizes of dunnocks or other species.

Sperm Whales

Direct application of these rules governing mating system and social evolution to conservation policy is rare. Ignorance of the dynamics of mating behavior has also led to a false sense of security when designing or implementing conservation plans for other large mammal populations. Models by Dobson and Poole (1997, Chapter 8, this volume) suggest that poaching the largest must males will prevent a large number of female elephants *Loxondata*

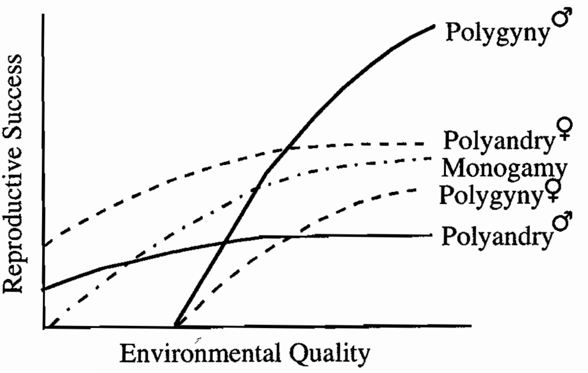

Figure 19-3 Environmentally induced sex differences in reproductive success (RS) for male and female dunnocks. Solid lines denote male RS, dashed lines denote female RS for polygamous mating systems. The dotted-dashed line depicts the RS for monogamous mates (adapted from Davies and Houston, 1984).

africana from mating. As a result, animals that exhibit low recruitment, in part because of large size and elephantlike "roving male" mating systems with strong male differentiation, will have a difficult time reversing long-term population declines once they begin.

In a similar way, ignorance about the mating system of sperm whales *Physeter macrocephalus,* the aquatic equivalent of elephants, has led to the implementation of inappropriate harvesting patterns that have almost resulted in their extinction. Because of their large size and extreme K-selected life-history characteristics, sperm whales were thought for years to exhibit harem-defense polygynous breeding systems. The reason for this mistaken classification was the result of using data from harvests in which the number of breeding females vastly exceeded the number of breeding males. Inferring that such ratios were the result of closed membership social groupings was uncalled for. Yet based on this assessment, it was assumed that most males would be superfluous. This inference encouraged the International Whaling Commission to allow the disproportionate hunting of males because most would be reproductively unnecessary and would be unable to fertilize females. Unfortunately for the sperm whale, the similarities with elephant societies are all too real (Weilgart et al., 1995). In both species, females are the core of the society and form permanent groups. In sperm whales these groups periodically merge when diving deep for squid. The young, which cannot follow their mothers for the entire dive, associate with adult female kin remaining on the surface. Males, however, leave their natal groups upon attaining sexual maturity, but they are excluded from associating with estrous females by older and more senior males. Consequently, the younger males remain at the higher latitudes in the cooler more productive waters when older males migrate with breeding females to the tropical breeding grounds. Once on the breeding grounds, mature males roam between female groups seeking reproductively active females.

Thus the mistaken notions that males are haremic and that subordinate males on the breeding grounds are superfluous has resulted in a severe reduction in the population of breeding males. And with the younger males thousands of kilometers away, it is not surprising that pregnancy rates among females have declined. Models developed by the scientific committee of the Whaling Commission predict that even a complete ban on sperm whaling will not result in an increase in the population for nearly 20 years. Such a complete ban would enable enough young males time to mature. Only then would all females be mated every year. Clearly, knowledge about the mating system of sperm whales could have prevented the overharvesting of mature males. Unraveling the mating system showed that all males found associating with females near the tropics were reproductively active and important for maximizing population recruitment. Their demise ensured the demise of the entire sperm whale population.

Understanding the dynamics of mating systems, especially the way in which environmental forces shape male–female relationships, can even have genetic implications for conservation. Although a severely reduced population must have its ecological population size boosted before its genetic effective population size increases, changes in mating system will influence both. Any move from polygyny to monogamy will increase the number of different males siring offspring. Because effective population size is essentially the harmonic mean of the reciprocals of the number of breeding males and females, any increase in the egalitarian nature of breeding will increase effective population size. So attention to mating system will influence both important demographic and genetic characteristics of a population (see Creel, Chapter 10, this volume). Unless behavioral ecologists work closely with managers and policy makers, this knowledge will be ignored because it cannot be gathered during simple surveys or short-term studies. Mating systems tend to be species specific with subtle details revealing if and how they can change facultatively as environmental circumstances change. It is only by arming managers with this detailed knowledge that a management plan will be effective. But before employing the power of these evolutionary rules becomes a regular part of any plan, managers must learn to appreciate their importance.

Predators, Prey, Arms Races, and Ecotourism

Predators and their prey are locked in struggles in which each is selected to counter the actions of the other. As predators move through a sequence of stages from detecting to approaching, to capturing and then consuming, prey attempt to disrupt this progression by either increasing vigilance, hiding, fleeing, or aggregating. Because the effectiveness of any particular tactic exhibited by the predator or the type of disruption selected by the prey depends on the costs and benefits of each and when in the sequence it operates (Endler, 1991), no one action will be best in every circumstance. Because the approach of even the most benign human, the ecotourist, is not unlike the approach of a predator, conservation biologists should be able to learn much about how to structure wildlife viewing so as not to disturb activities as important as foraging and mating.

It is true that wild animals often habituate more easily to tourists than to natural predators, but tourists often force wildlife to override this adaptive response by "pushing their luck" to get closer and closer to their subject. Any visitor to an African game park has seen a tourist van go off road to get close enough for that full-frame photo of an otherwise resting cheetah *Acinonyx jubatus*. Repeated disturbances of this kind can have profound consequences on altering the activity budgets of these creatures who are supposedly being protected in the reserve. It seems somewhat ironic that the increasing pressures by society and governments for wildlife protection to pay for itself, often via ecotourism, might end up hurting precisely those species that need the most help. Because the alternative of eliminating ecotourism is unacceptable, understanding how to control it requires research on how different species respond to different types and levels of human interference. Because behavioral ecologists are adept at identifying how environmental forces shape antipredator, foraging, and reproductive behavior, they are in a unique position to assess when and how different types of interference will have the greatest impact.

The finding that rhino females, but not males, run long distances from approaching humans highlights this problem and suggests that unless females can be habituated, their reproductive success could be hindered by frequent tourist visits. Although males will stay put, presumably because they are defending resources females desire, they may only do so as long as females regularly frequent their ranges. If the disturbance is too great, then it is possible that even males will leave the area, and the economic gains associated with tourism could be eliminated by the unintended consequences of its own popularity.

Such a dramatic effect in such an exotic site underscores the problem, but the consequences of visitations to nature reserves near urban centers in developed nations could be even more pronounced. Fortunately, studies on the impact of human visitation are emerging, but some of the results will challenge the ability of managers to balance the needs of wildlife with those of tourists. Klein and co-workers (1995) studied the impact of visitation on the activities of 49 species of waterbirds in a Florida wildlife refuge. Their results were striking. First, bird watchers, whether traveling on foot or in vehicles, not only displaced most species from preferred feeding sites, but they did so in ways that created nonlinear, or threshold, effects; only a few disturbances were enough to cause massive departures. Displaced birds took refuge with birds already foraging farther away, intensifying competition and reducing foraging success for all. Second, vehicular disturbance had more of an impact than did visitors traveling along footpaths. In part this resulted from the fact that there were more vehicles on the roadways than there were walkers on the paths. But in addition, 96% of the vehicles stopped and disgorged their passengers at least once, thus intensifying this type of disturbance. Different species were affected differently: some such as egrets *Egretta thula,* willets *Catotrophorus semipalmatus,* and sanderlings *Calidris alba* were more sensitive, but in general, migrants were more disturbed than were residents.

In one sense, the management implications of the study are obvious: human movements must be limited. But how should this be accomplished? Should quotas be imposed, or should more sophisticated rationing be instituted by restricting viewing times or access to routes? Deciding among alternatives will require better scientific data and will necessitate that refuge managers work with behavioral ecologists to decide what the next questions should be and what sorts of data should be collected. For example, determining which species need the most protection is essential and will only be possible from further studies on how diminished short-term foraging success influences longer-term reproductive success. Where species go when disturbed and whether the impact of disturbance is the same at different points in the tidal cycle or at different times of the year also must be ascertained. Answering these questions, however, will require more detailed studies on individually recognizable birds, a trademark of virtually all behavioral ecological studies (McGregor and Peake, Chapter 2, this volume). In addition, the detailed study of the behavior of individuals must be begun on the birdwatchers themselves. Any attempt at changing the behavior of birdwatchers will require an assessment of what they do in the reserve as well as knowledge about what they are least likely to give up when pursuing an activity they truly enjoy. Because their use of the reserve helps ensure that local, regional, and national governments continue to establish and maintain them, controlling human behavior will require delicate balancing of competing needs.

Understanding what shapes the behavior of prey in response to predators is only half the problem. Understanding what makes predators effective and how their actions change as environments change could provide insights into how better to control human predation, especially in relation to fisheries. Mangel (1994b) has developed spatially explicit models that predict the search patterns and movements of predators based on two factors: 1) the likelihood of additional prey being in the immediate vicinity if prey are already present; and 2) the likelihood that prey, once disturbed by the predator's presence, will reaggregate at given distances from the predator. The product of these two factors gives the probability that there will be undisturbed prey at various distances from the predator, so a clever predator should go where this probability is highest. From this simple formulation it is easy to see that predator search will be less area restricted when the initial distribution is more even or when the likelihood of predators dispersing prey is large. Thus, as fish shoals get smaller and more widely dispersed, it is clear why operators of fishing vessels have a tendency to concentrate their efforts into smaller and smaller areas. By increasing the pressure on the fishery in this way, the fishery is potentially further destabilized. In essence, the interaction of these two factors provides a mechanism to account for the searching movements of predators that goes beyond the mere descriptive patterns that emerge from recording the locations of sitings or attacks. By developing such models, behavioral ecologists can better understand the rules underlying searching patterns and thus forecast likely areas where impacts will be high. In turn, this should help in developing effective harvesting limits, deploying enforcement effort, and determining the appropriate size of protected areas, if such a strategy is adopted.

Keystones, Behavior, and Biodiversity

Not all species in ecological communities have the same impact in determining their structure. All play roles in recycling nutrients and in directing the flows of energy. But some organize and shape their communities out of proportion to their abundance (Paine, 1966). Such species are viewed as "keystones," and many conservation biologists appreciate that identifying the existence of a keystone species in a community will make preserving the functioning of the entire ecosystem that much easier. Moreover, the process of identifying the role every species plays in contributing to the fundamental organization of the assemblage has the added benefit of identifying the degree to which guild members are ecological, or functional, equivalents (Paine, 1995). This usually requires an understanding of the details of a species' foraging behavior, and this is where behavioral ecologists, armed with the tenets of foraging theory and the ability to follow the fates of individuals, become invaluable.

At the turn of the century, fur trappers had virtually exterminated the sea otter *Enhydra lutris* over most of its range. As conservation efforts led to the protection of sea otters, the species has begun recovering, and it is not uncommon to see areas along the Pacific coast where they are abundant. Sea otters are a keystone species (Estes and Palmisano, 1974), and where they are abundant the communities they inhabit are very different from those where they are absent. Because sea otters prefer to feed on sea urchins which consume aquatic vegetation, the removal of sea urchins has a dramatic affect on increasing the abundance and diversity of aquatic vegetation. In the presence of sea otters, kelp forests flourish, and their fronds provide refuges for juvenile and adult fish.

Although the effects of keystone species are typically felt across trophic levels, they can manifest themselves within tropic levels as well. The community of mammals grazing on North America's short-grass prairie represents a dramatic example. Prairie dogs (*Cynomys* spp.) live in reproductive groups called coteries, but these coteries aggregate into colonies that can cover hundreds of hectares. At the turn of the century these colonies occupied between 40 and 100 million ha of mixed short-grass prairie (Miller et al., 1994). Today their range has been limited to around 600,000 ha, largely as a result of government-sponsored control programs designed to help the livestock industry. Original estimates of prairie dogs reducing livestock range productivity by 50–75% (Merriam, 1902) appear to be exaggerated given that the level of competition between prairie dogs and livestock is only about 4–7% (Miller et al., 1994). In fact, detailed studies of prairie dogs' foraging and social behavior show that prairie dogs tend to facilitate the grazing of bison *Bison bison* and pronghorn antelope *Antilocapra americana,* two supposed competitors (Kreuger, 1986). Experiments with exclosures, coupled with detailed observations of bite and step rates along with nearest neighbor distances, showed that bison and prairie dogs feed better in the presence of each other on the edge of extant colonies and that the nitrogen content of the shoots growing there was also elevated when compared to controls. Pronghorn antelope also generally feed more efficiently at the center of prairie dog colonies, although there was no difference between existing and poisoned colonies. Apparently the behavior of prairie dogs, by altering the soil and increasing the abundance of dicots, have long-term effects on the structure of the community of grazing mammals.

Clearly, prairie dogs increase the diversity of the vegetation that ensures the existence of an abundant population of grazers. But their impact is felt even more widely; the poisoning of prairie dogs has been cited as a cause in the decline of the specialized predators such as the black-footed ferret *Mustela nigripes,* the swift fox *Vulpes velox,* and ferruginous hawk *Buteo regalis,* as well as the mountain plover *Charadrius montanus,* which needs open, short-grass habitats for nesting (Miller et al., 1994). It may prove that monies spent on prairie dog eradication will necessitate spending additional monies to protect a host of endangered species that would otherwise be thriving.

In communities of both prairie dogs and sea otters, attention to the behavior of certain species has illuminated the critical role that each plays in organizing the species assemblage in which it lives. Despite the clarity of the implications of these studies, segments of human society that want to exploit some of the other species intertwined in the community discount, ignore, or even attempt to discredit these scientific findings. Despite the economic boon that the charismatic sea otter provides to the Californian economy and the benefit it provides by creating a nursery and refuge for fish, local fisherman blame the sea otter for the demise of the local fishery and want otter populations reduced. Similarly, special interests that thrive on livestock grazing want prairie dog eradication programs to continue despite the fact that livestock could probably benefit from prairie dogs much as bison do. Moreover, it would appear to be more cost effective to protect prairie dogs rather than to protect the many individual species whose fates are tied to that of this keystone species. This antiscience sentiment frustrates conservationist biologists and will be difficult to overcome because it rises from deeply held attitudes and values that derive from myths, history, and greed. But is activism, often with its roots in environmentalist movements, an effective way of injecting science into the process of creating and then implementing effective policy? Much depends on the tactics that activist behavioral ecologists are likely to adopt.

Conservation Biology and Activist Behavioral Ecologists

Many behavioral ecologists want to apply their science to the conservation of biodiversity. As the previous examples have shown, understanding how the tenets of behavioral ecology and the methodology of following the actions and fates of individuals can make a difference in designing effective management programs and policies. Not wanting to sit passively and wait for their insights to be discovered and then applied, behavioral ecologists want to design relevant studies from the outset in order to accelerate the process. Such activism would move behavioral ecological research up Underwood's hierarchy to "applied and environmental research," and it would bring behavioral ecologists directly into the policy arena.

Problems and Pitfalls

Although behavioral ecologists conduct comparative or experimental studies in unbiased ways, the questions asked are often shaped by personal concerns, philosophies, and values. This injection of subjectivity into the selection of a research program should not matter as long as researchers ensure that conclusions and inferences are value-free. But activist scientists have to remain on their guard and be aware of what potential biases they can bring to their work. Because environmentalists typically pursue protectionist strategies based on a system of values, not on inferences derived from scientific study, tension can be created if activist behavioral ecologists align themselves with environmentalists. If behavioral ecologists are not careful and act upon their values instead of upon scientific knowledge, they can change from being "conservation biologists" into "biological conservationists," and as environmentalists, potentially jeopardize their scientific credibility. The dilemma is then how to balance actively influencing policy while remaining a respected and credible scientist.

The problem, and its ultimate solution, stems from the nature of how science is done and what it can tell the public, managers, policy makers, and leaders about how the natural world works. Good science rests upon assumptions that can be easily evaluated. If some are wrong, or cannot be substantiated, possibly because they rest upon hidden beliefs, then the conclusions, predictions, and applications of an empirical study or a theoretical model can be discounted or even rejected. If assumptions are sound and the study is well conceived and carried out expertly, then its results are typically accepted as valid. Unfortunately, neither the results nor the process of science is easily understood or readily accepted outside the scientific community. Not even environmentalists, let alone their adversaries, automatically accept the results of good scientific research; unless conclusions support preconceived notions, they are often discredited or ignored. What then is an activist conservation biologist to do?

Because conservation biologists are at times viewed as diagnosticians and healers, improving the health of species and habitats, examining the often-cited example of physicians and their proactive attack on the tobacco industry might provide some clues. It is often argued that medical researchers and clinical physicians rightly advocate banning cigarettes on behalf of their patients' health. The facts are abundantly clear that smoking kills, now that the haze of obfuscatory "science" generated by the tobacco companies has finally been blown away. Consequently, doctors would be remiss if they did not advocate a ban on the production and sale of cigarettes. Because no uncertainty remains about cause and effect, such activism is justified and called for. But whether such bans will become policy will depend as much on the desires of a supermajority of the populace as on their acceptance of the scientific evidence. Vested economic interests and the cry that millions of jobs will be lost are powerful forces for maintaining the status quo. Even economic arguments that medical costs will rise as a result of smoke-induced illness are weakened when viewed from the alternative perspective that more people living longer lives will in the long-run generate even higher medical costs. Despite all forms of advocacy, to ensure that the results of effective science can be applied to saving lives, individual physicians will continue to have to persuade individual patients to either stop smoking or never to start. If this analogy holds and offers any insights, then activist behavioral ecologists should be free to advocate on behalf of endangered species and habitats either from the bottom-up at the local level, or from the top-down in the larger policy arena.

Strategies: Purists and Pragmatists

Although activists come in many guises, they usually divide into two camps: "front-line purists" and "behind-the-lines pragmatists." Front-line purists do what it takes to protect an endangered species or a threatened habitat and its imperilled biodiversity. Typically they believe that only fundamental change in the way the system operates will lead to effective conservation. Behind-the-line pragmatists are more likely to accommodate existing structures and support actions that are more politically and economically palatable. They accept the notion that scientists are one of many stakeholders, each with a claim to "knowing what is right." Consequently, these pragmatists believe that science is only part of the solution, that scientists do not have all the answers. Science produces knowledge about how the natural world works and proposes ways to gain new knowledge when gaps in knowledge are identified. It can predict likely outcomes of various decisions, and it can identify acceptable boundaries within which human activity will not permanently harm the survival of species or the functioning of ecosystems. But science cannot specify where on this landscape of possibilities a local community, nation, or even an international community should be. Behind-the-line pragmatists realize that other stakeholders bring to the debate different perspectives, often with an antiscience bias, whereas front-line purists have a hard time accepting the distinction between the need to do good and the notion that what might be right may involve more than scientific fact.

Behind-the-line pragmatists will join with others to solve a problem mutually. But they assume that what other stakeholders expect of them—open mindedness—must also be accorded to them, and as a result, they believe that other stakeholders will allow science to play a critical role in shaping the solution. If this does not happen and front-line purists believe that it cannot, then collaborative and cooperative activities of stakeholders will disintegrate into arguments about beliefs, with those of the most powerful triumphing. Thus it is no wonder that pessimistic behavioral ecologists believing that science will always be superseded by powerful and entrenched political and economic pressures join the ranks of front-line purists. When they do so they will be free to advocate for one course of action or another. But to retain their credibility, they must clearly identify the facts and the existing limits to knowledge. Only by doing so can they highlight the origin of the uncertainties that lead to their best guesses about what is most likely to happen and what plan of action they champion pursuing. If the distinction is not made, then best guesses might be construed to be little more than value judgments, and both the public and policy makers could become confused and lose faith in the ability of science to suggest alternative courses of action and assess their biological and economic consequences.

For behind-the-line pragmatists, belief in the efficacy of discussion and negotiation is predicated on at least a partial leveling of the playing field by gaining acceptance of the value of science. But for behind-the-line pragmatic behavioral ecologists to succeed in shaping policy, their activism must take a variety of forms and operate on many fronts. Some of these efforts will produce results that percolate up from the bottom, whereas others will flow from the top.

Tactics: Activist Ways and Means

One way activist behavioral ecologists can make a difference is to use specific knowledge about particular endangered species or the degraded environments they inhabit for their protection and that of the additional biodiversity they harbor. Typically, behavioral ecologists study species in natural areas, such as reserves, parks, or ranches where access by the local populace is limited. Because these species and their lands represent resources with economic value denied to nearby residents, it is essential that local communities be made aware of what has been learned about the behavior of the animals and the ecology of their environments. In this way they may be able to derive some economic gain by acting in nonharmful ways. If this knowledge can be used to foster low-impact ecotourism or even to design resource harvesting schemes in accordance with Clark's proviso (1976) that harvesting be limited to species whose increase in value when alive is greater than the value of money, then by sharing the profits of these enterprises, local and hence broad based bottom-up support for conservation can be created.

Pragmatic behavioral ecologists must also be advocates for the utility of science and demonstrate the important role that science can play in informing conservationist policies. Educating other stakeholders about how science operates and what it can and cannot say about how species and their ecosystems work is an essential bottom-up strategy. To do this, science must be forced out of the ivory tower and scientific journals. Popular accounts of interesting studies, whitepapers and their shortened executive summaries, and editorials are all effective. Above all, these accessible publications should not shy away from stressing the fact that scientists are skeptics and that they make assumptions that often do not agree with those of others (but are usually transparent and open for debate) and that is why scientific disagreements about predictions are common. They should also underscore the notion that uncertainty is a pervasive part of the natural world and that not coming to grips with it has led to misguided and dangerous management strategies or no management at all (Ludwig et al., 1993).

Despite the ubiquity of uncertainty, there is no need to let the call for yet another study co-opt scientists and prevent them from drawing conclusions on the basis of data in hand. In fact, the widespread appreciation of uncertainty should serve as a clarion for more research into understanding complexity per se and how to manage in the face of it (level 3, basic and strategic research). The American public already cries out for just such research when it comes to understanding the weather, perhaps the most uncertain and complex process that individuals experience. Vast sums of money are spent on satellite data gathering and computer modeling so that individuals can organize their lives despite the inaccuracy of many of the model's predictions. Rather than ignoring spectacular failures, new research projects requiring ever more sophisticated and expensive science and technology are called for. It should be every behind-the-line pragmatist's hope that the need to understand how complexity and environmental uncertainty has put so many species in peril becomes part of every human's everyday consciousness.

But education should also be directed at the powerful interests residing at the top of the decision-making pyramid. Leaders in government and industry must be made aware that investing in science and then ignoring its findings is expensive and wasteful. The utility of behavioral ecology in identifying and then rectifying environmental problems must be highlighted, and examples of failed policy must be identified. Moreover, they must be shown, as do many of the case studies described above, how better science in the form of behavioral ecology could have done a better job if only its basic tenets had been included in the research program and decision-making process from the beginning. It must be the goal of all behind-the-line pragmatists to convince policy makers that science must be used to define the scope and nature of the problem. Activist scientists must help set the research agenda, not the managers, because the types of questions they can ask are limited by predetermined goals and the severe structural constraints under which they operate. It is also essential that science be used to monitor the effectiveness, as well as the unintended consequences, of whatever policy is implemented. The success of the Montreal Protocols in accelerating the reduction of Chlorofluorocarbon emissions should serve as a model and underscores the need to include science throughout the decision-making loop.

Stakeholders, Partnerships, and Valuing Science

To effect such a seismic shift will require a major change in the value that high-level managers and decision makers accord science. Only behind-the-lines pragmatists have a chance of effecting such a shift; continuing to shout all-or-nothing polemics simply polarizes the debate and hardens already entrenched positions. Using subtle powers of persuasion and keeping the faith that change is on the way is not enough, however. Activist behavioral ecologists must continue to use their novel approach to fight shoddy science that often ignores both the assumptions that underlie their studies of the environmental forces that shape behavior as well as the insights that are derived from detailed long-term studies on individuals. In this way the effectiveness and utility of good science is put continually on display. Then the challenge becomes making other stakeholders appreciate the value of good science. Otherwise there is no point in gaining important new knowledge if it is ultimately ignored. While lip service is often paid by some stakeholders to how useful science has been in cleaning up polluted air and water, they often claim either that the task is complete and that science has served its purpose or that the cost of regulation is too high. Changing the values that control the behavior of these powerful stakeholders will not be easy and will require that behavioral ecologists learn how managerial and policy decisions are made. In this way even if the topography of the so-called playing field is not leveled, at least the location of the hills and valleys will be understood.

Entering the fray at this level is the ultimate top-down gambit. Behavioral ecologists must learn how the legislative process operates, how judicial judgments are arrived at, where both political and economic power really resides, and how values and beliefs shape the perspectives of different stakeholders and motivate their actions (level 4 research). At the moment, however, there is no recipe for success that behavioral ecologists can use, but a perfect case—the controversy of managing livestock grazing on the grasslands of western Northern America—highlights what elements must be considered when joining with other stakeholders to solve collectively thorny real-world problems.

Grasslands and Grazers: Activist Science Pursuing Effective Policy

As discussed above, prairie dogs play a major role in structuring the community of grazers as well as many other species that benefit from their activities. Detailed community and behavioral ecological studies have revealed some surprising and unanticipated findings, in particular that some presumed competitive relationships are actually mutualistic. Other studies attempting to evaluate the extent to which native bison and cattle are competitors shows that the interactions are subtle. Bison show preferences for grasses and cattle show a limited tendency to specialize on forbs, but much depends on the patchiness of the landscape, whether the grazers are completely free-roaming or confined to fenced pastures, and at what time of year the measurements are taken (Plumb and Dodd, 1993). In fact, foraging theory is proving helpful in assessing the degree to which the decision rules employed by each species make them analogous herbivores. Still other studies (Dyer et al., 1993; McNaughton, 1993; Painter and Belsky, 1993) examine the extent to which grazing at different intensities changes the quality, abundance, and species composition of grasses on grasslands.

Clearly there is much scientific data emerging on the impact that different grazers have on each other and on the plants they eat. But as behind-the-line pragmatists realize, scientists are only one of many stakeholders involved in this controversy. Native Americans and early settlers have historical roots to the land and have harvested wildlife or raised livestock for generations. Residents of small rural communities and larger urban centers earn livelihoods from supplying livestock herders. Government employees facilitate (rangeland researchers) and regulate (local managers and more distant bureaucrats) these activities, groups with special interests profit from livestock grazing, lawmakers and judges make or interpret the rules governing the management of grasslands, and environmentalists and activist scientists care about the wild living resources that have to cope with the livestock. All have strong opinions because each is concerned about how changing the status quo in terms of altering what species are allowed to graze where and how extensively will impact either their pocketbook or the native species that inhabit the landscape.

There can be no doubt that grazing can and does have dramatic consequences for the structure and functioning of native grasslands. Not all studies purporting to document the harmful effects of livestock grazing are of high quality or apply across the landscape (Brown and McDonald, 1995), but enough are to warrant the involvement of scientists. And as the above case studies demonstrate, behavioral ecologists have the tools to enrich the scientific quality of the debate. But what should activists do? The editor of *Conservation Biology,* Reed Noss (1994) asked whether conservation biologists should "link arms with activists in efforts to reform grazing practices." Although he did not answer his own question, the debate raged on in the pages of the journal for over a year (e.g., Brussard et al., 1994; Fleischner, 1994). As we have seen, scientists can become activists, but the tactics they adopt will depend on how much faith they have in the system's ability to use science in deciding on the best course of action.

Front-line purists will take to the streets as citizen scientists and write, lobby, speak out, and generally agitate, but they will have to ensure that they identify where factual knowledge ends and where value judgments begin when making their case if they are to remain honest scientists and maintain their credibility. If behind-the-lines pragmatists have done their job by ensuring that scientific evidence will be used in deciding among alternative plans of action, then pragmatists can illuminate the debate by showing how different ecological factors (drought, fire, soil and nutrient heterogeneity, and species-specific behavior of wildlife and livestock) affect grasslands and the species they support.

Doing this, however, places the activist behavioral ecologist on the horns of a scientific dilemma. In its present form, most off-the-shelf research (level 1) is at best of marginal use because it was produced to solve a particular problem that typically has only limited similarities to the issue at hand. Yet real-world problems as thorny as the issue of grazing and multiple land-use schemes have an urgency that precludes the luxury of tailoring research to assessing and then solving the particular problem (level 2 and 3 research). To resolve the dilemma, activist behavioral ecologists must begin creating better, more generic off-the-shelf research. One way of doing this is to modify any level 3 study and extend its usefulness by making the models or findings more general. One such example comes from a study originally designed to evaluate alternative tactics for regulating a feral horse population by assessing the consequences of each tactic on the long-term demographic and genetic structures of the population. With minimal effort it has been possible to recast the model by parameterizing both ecological and life-history features in terms of size-scaling rules so that the model can be applied to the management of virtually any population ranging from mice to elephants (Rubenstein and Dobson, in preparation).

But making it easy to employ scientific thinking and the "what-if" theorizing in stakeholder discussions is only part of the solution. Activist behavioral ecologists will also have to change the values of the other stakeholders by demonstrating that the merits of managing the grasslands to ensure their ecological integrity is at least as valuable as managing them to maximize their primary and secondary productivity. To succeed at causing such a major shift in perspective will require understanding what values motivate the different stakeholders. Perhaps the interaction of values, beliefs, and scientific knowledge will convince all stakeholders that it will be possible to alter stocking levels, adjust patterns of herd movement, and modify the use of fire and a reliance on supplemental water in ways that minimize grazing impact without causing economic hardship for those seeking to enhance economic profit. Much of the rangeland is already degraded, and economic benefits will accrue simply by reclaiming them. Clearly, money will be needed to subsidize these changes, and healthy debate about the value of using such subsidies for these purposes rather than for other worthy causes (environmental or not) will necessarily ensue. But trade-offs and compromises will only emerge if desires, beliefs, and good science are all out in the open. By understanding both the cultural perspectives of the various stakeholders and the structures and operations of various legal, legislative, and regulatory institutions, laws and policies can be amended. New agendas for research will be necessary to predict and then validate the behavioral responses that will result from managing interactions between ecological forces and processes in novel ways. Partnerships among stakeholders that respect science and the scientists that uncover useful and fundamental knowledge offer the only hope for successful collaborations that will bring about these changes. Behavioral ecologists are one group of scientists that when active will have much to say when crafting these new policies and management practices.

Summary

Behavioral ecology has much to offer in solving real-world environmental problems. First, behavioral ecology focuses on the individuals and incorporating an understanding of how the environment shapes their behavior will make models more realistic. Second, behavioral ecology is rich in "first principles" that can provide insights into how recruitment can be enhanced in endangered populations.

Applying tenets of behavioral ecology will be difficult. Not only does the science have a "split personality," being part basic and part applied, but scientists' values color their perception and action. Scientists can improve the effectiveness of their science by moving from using the off-the-shelf research for gaining insight into analogous problems to performing postmortems on management interventions as if they were experiments or even to working with managers to design new management plans as experiments. Explorations of case studies highlighting how such large-scale experiments can be analyzed in retrospect, or how they can be designed a priori to be made more effective, illustrate the importance of drawing upon principles of optimal foraging theory, life-history evolution, individual decision-making, and mating strategy.

Activist scientists have to choose a strategy. "Purists" do what it takes to have their values or scientific understanding put into practice, while "pragmatists" will work with other stakeholders to come to some mutual understanding as to what is the best outcome given a series of constraints. Both have to ensure scientific objectivity by stressing that personal values only enter the scientific process at the point where questions are posed. Pragmatists must also stress if open mindedness is expected of them, then others must be open to the dictates of scientific study.

Activist tactics are varied, but common to all are needs to educate stakeholders as to the importance and utility of science and persuasive presence of uncertainty. Educational initiatives from top-down must stress the role that science can play in defining problems and monitoring their solutions at regular intervals, while those from the bottom-up must ensure that local stakeholders benefit from the eventual action plan.

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