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"IN MY OPINION . . ."

MANAGEMENT OF SMALL POPULATIONS: CONCEPTS AFFECTING THE RECOVERY OF ENDANGERED SPECIES

GARY E. BELOVSKY, *Conservation Biology Program, Department of Fisheries and Wildlife and Ecology Center, Utah State University, Logan, UT 84322-5210*

JOHN A. BISSONETTE, *National Biological Survey, Utah Cooperative Fish and Wildlife Research Unit and Conservation Biology Program, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

RAYMOND D. DUESER, *Conservation Biology Program, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

THOMAS C. EDWARDS, JR., *National Biological Survey, Utah Cooperative Fish and Wildlife Research Unit and Conservation Biology Program, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

CHRISTOPHER M. LUECKE, *Conservation Biology Program, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

MARK E. RITCHIE, *Conservation Biology Program, Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

JENNIFER B. SLADE, *Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210*

FREDERIC H. WAGNER, *Conservation Biology Program, Department of Fisheries and Wildlife and Ecology Center, Utah State University, Logan, UT 84322-5210*

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Based on survey responses from state agencies, Hayes (1991) examined which mammalian orders were most vulnerable to becoming endangered, threatened, or of special concern, and the perceived causes. Habitat destruction was listed most frequently as the cause of a species' vulnerability, whereas overexploitation was only considered important for some Carnivora and Artiodactyla. Reviews of extinctions through history have documented the overriding significance of habitat destruction (Hester 1967, Diamond 1984). Therefore, wildlife biologists and conservationists have long considered habitat destruction to be the critical initial threat to plant and animal populations (Terborgh and Winter 1980). However, we wish to caution that the elimination of the initial causes of endangerment, such as habitat destruction, may not remove the threat to populations and may not be the prime concern in developing recovery plans.

Wildlife biologists should work to preserve and restore habitat for plants and animals, assuming that many populations of plants and animals are threatened as a result of habitat loss and degradation. Unfortunately, although the preservation of suitable habitat is necessary, it may no longer be sufficient to ensure the recovery of small populations because the appropriation of habitat and "letting nature take its course" (i.e., management by "benign neglect") may no longer be sufficient; rather,

innovative and active management may be needed. Especially when considering habitat loss and degradation, we should include human-induced factors, such as climate change (e.g., global warming) and habitat fragmentation, as well as the elimination (e.g., gray wolf, *Canis lupus*, in the Greater Yellowstone Ecosystem) and introduction of species (e.g., rainbow trout, *Oncorhynchus mykiss*, into cutthroat trout, *O. clarki*, streams and lakes).

We and others (e.g., Ehrlich and Ehrlich 1981) fear that managers and agencies might become complacent, operating under the premise that the protection of a piece of habitat ensures population persistence. Hayes' (1991) survey supports our concern, because state agencies never attributed population declines to the special demography of small populations and only once attributed declines to the special population genetics of small populations.

Confusion between the initial causes of endangerment and concerns for the persistence or recovery of precarious populations was cautioned against by Ehrlich and Ehrlich (1981), because the causes for reduced populations may not be the same as the causes for further declines and possible extinction. Although recovery cannot proceed without curtailing habitat loss and degradation, once a population becomes small its existence is threatened even after the original causes of endangerment are controlled. The recovery or persistence of small populations cannot occur without considering the special demographic and genetic traits of small populations. These considerations are the essence of population viability analysis (Shaffer 1987), interagency cooperation in management (Salwasser et al. 1987), reserve design (Diamond 1986), and captive breeding programs (Thorne and Belitsky 1989).

HISTORICAL INSIGHTS

Hester (1967) reviewed the historical and scientific literature on mammalian and avian endangered species and their extinction or recovery in North America since European colonization in the sixteenth century. Hester's conclusions paralleled those of Hayes' (1991) survey of state agencies: habitat destruction has been the major cause of endangerment, and overharvesting has been a secondary cause. However, we examined the traits of endangered species (and several subspecies, e.g., heath hen [*Tympanuchus cupido*]) that have either survived ($n = 34$) to the present (still endangered or recovered) versus those that have gone extinct ($n = 34$), as reported by Hester (1967). These data are crude, but simple statistical tests based on binomial estimates of the 95% confidence intervals for percentages illustrate interesting contrasts between the 2 groups of species. Species names used as examples follow Hester's (1967) listing for easy comparison.

1. Endangered species that have survived are represented by a greater proportion of species with low reproductive rates (i.e., long generation time, or small clutch or litter size) than those that went extinct: 29% (15–49%) versus 3% (0–7%). For example, the Haitian hutia (*Plagiodontia hylaeum*) with its low reproductive rate survived, while other Caribbean island hutias with higher reproductive rates went extinct (*Geocapromys columbianus, G. ingrahami, Hexolobodon phenax, Isolobodon portoricensis*, and *I. levir*). Species with low reproductive rates often are assumed to be more vulnerable to extinction, but the data do not support this. The observed opposite pattern might be explained if high reproductive rates correlate with high mortality rates (low life expectancy), then small populations might be more precarious, even though high reproductive rates permit populations to recover quickly (Belovsky 1987, Pimm 1991). Furthermore, high reproductive rates may produce populations that fluctuate more over time and periodically approach very low numbers (Pimm 1991).

2. Endangered species that have survived and those that have gone extinct did not differ in subjective estimates of their population densities (number/area) at the time of European contact: 44% (26–63%) versus 41% (23–60%) had low densities. For example, the sea mink (*Mustela macrodon*) a species with a high density went extinct, whereas the marten (*Martes americana*) a species with a low density survived. Low population density often is assumed to make a species vulnerable to extinction due to Allee Effects (e.g., difficulties in finding mates), but no evidence for this emerged; however, this might not be expected for several reasons. First, population density may not be the critical means of assessing a small population because a population can be large even if it is at a low density when it inhabits a large area. Second, it is possible that a number of populations, even at low density, that are spread over a wide area can create a "rescue-effect" from extinction by migrants moving between the populations (see below).
3. Endangered species that went extinct differed from surviving species in having populations restricted to small areas: 74% (60–88%) versus 35% (20–56%). This is illustrated by the large number of island dwelling species that have gone extinct. The extent of a species' habitat may have been the principal determinant of its vulnerability to extinction, because even high population density may not be associated with large population size when the population is restricted to a small area, and small population size predisposes a population to extinction (see below).

The above contrasts are no doubt confounded by body size, trophic level, and life history attributes of the species (e.g., large animals and carnivores tend to have lower densities and will be affected by small area more than smaller animals or herbivores, see below). Nonetheless, the association between extinction and small area is very strong. Many of the extinct species (<30%) reported by Hester (1967) were naturally confined to small areas, especially islands, and consequently may have had small populations, but many became restricted to small areas that could only support small populations through habitat destruction by humans (e.g., the heath hen). Habitat destruction can occur by either a large loss of habitat area or by changing the spatial distribution of the habitat, i.e., fragmentation. In either case, small populations often are created.

The number of species becoming threatened or extinct has increased over time (Fig. 1). As in the past, the initial threats to biodiversity are largely caused by habitat destruction creating small populations, especially as species' original ranges become restricted to subregions (e.g., the grizzly bear, *Ursus arctos*, in the continental U.S.). However, Hester's (1967) historical review provides a glimmer of hope for this situation. Sixty-eight species of birds and mammals in North America have been threatened with extinction since the sixteenth century, and 50% of them have gone extinct. However, in the 14 cases where people have attempted to recover an endangered species, only 1 species (7%) has gone extinct, but most have not recovered to the point that they are not still considered threatened over their entire previous range. Therefore, wildlife and fisheries managers concerned with protecting threatened species should be hopeful, but success will depend on better understanding the special demographic and genetic traits of small populations.

A FUTURE WITH SMALL POPULATIONS

In the past, biologists or conservationists wishing to protect a species would argue for habitat protection assuming that success in this activity and protection of the species from further deleterious factors such as harvesting

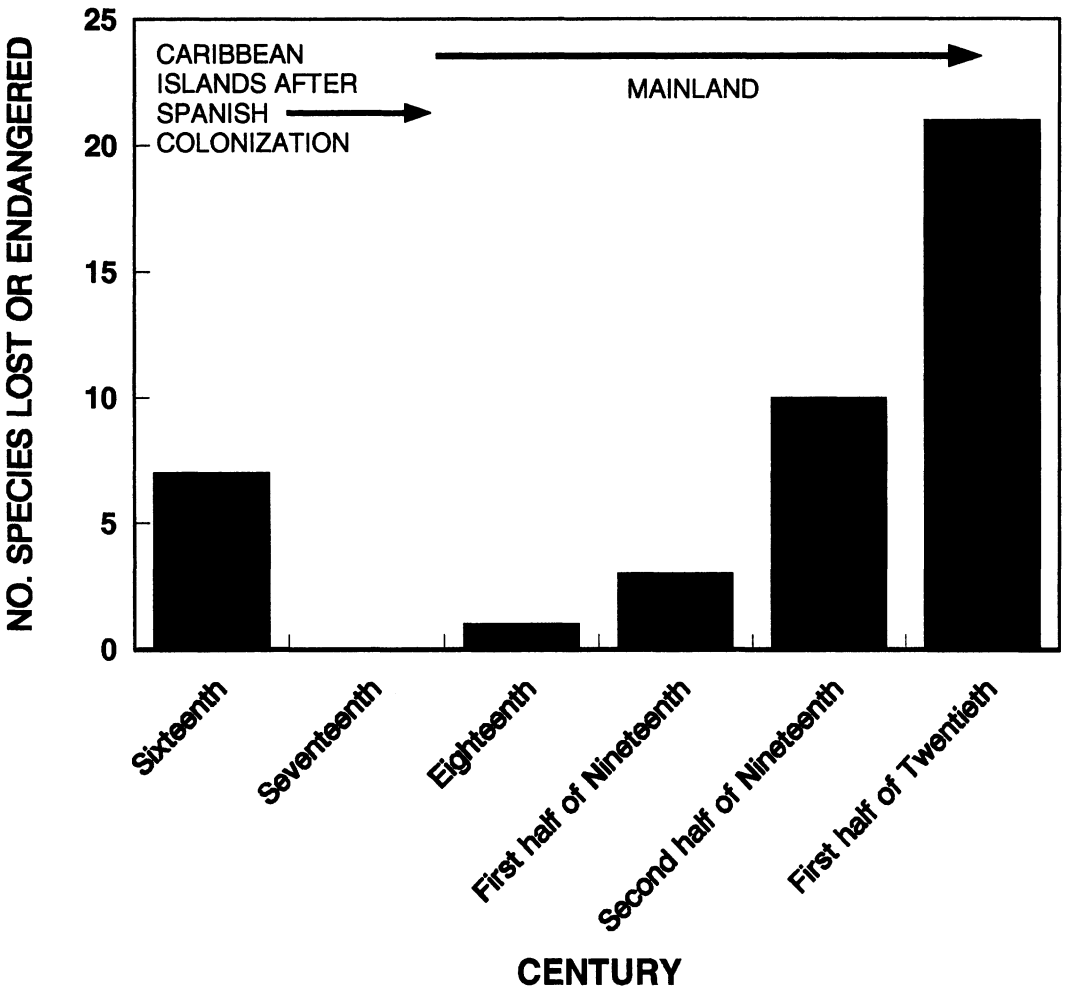

Fig. 1. The chronology of human-caused endangerment of bird and mammal species in North America since European colonization (from Hester 1967). After an initial pulse of extinctions on Caribbean islands after Spanish colonization, the number of endangered species has increased rapidly on the North American mainland.

would ensure persistence of the species. Although setting aside habitat is the only feasible option for protecting ecological communities and their biodiversity, this alone may no longer be sufficient to ensure the long-term persistence of the component species' populations.

Habitat protection as the sole action now may be insufficient because: (1) the amount and distribution of undisturbed habitat available for protection has been affected by human activities; (2) public funds for the purchase and protection of these lands is always limited and land prices have increased dramatically; (3) human demands on lands already protected have increased because of increasing human populations and their resource demands; (4) protected habitats may no longer be refuges as exotic species are introduced (e.g., the zebra mussel, *Dreissena polymorpha* [Roberts 1990]), species important to the functioning of ecological communities are eliminated (e.g., gray wolves in Yellowstone and their predation on

elk, *Cervus elaphus*), and global environmental changes modify preserved habitats (e.g., global warming); and (5) natural succession in ecological communities changes habitat suitability.

Simply identifying the patchwork of habitat fragments has become a major effort (e.g., Gap Analysis [Scott et al. 1993]), but this action cannot guarantee any level of habitat protection, nor can it guarantee protection of sufficiently large areas to ensure the persistence of populations. Therefore, without the unlikely event of setting aside larger tracts of habitat than we already have (see Mann and Plummer 1993), we may be faced with increasing numbers of small populations of many plant and animal species that are vulnerable to the demographic and genetic problems that reduce persistence.

CONCERN FOR SMALL POPULATIONS

Early wildlife managers and ecologists had concerns about "edge-effects" and "edge- and core-sensitive species" (Leopold 1933) that relate to problems created by habitat loss and fragmentation, as well as the large areas of habitat required by some species (Leopold 1949, Shelford 1963). But the increasing potential for the creation of small populations and how this reduces population persistence first was addressed formally in MacArthur and Wilson's (1967) pioneering work on island biogeography. They realized that habitat fragments were "islands" surrounded by an "ocean" of inhospitable habitat; as island size decreases, a population's size diminishes because habitat availability declines and the population's vulnerability to extinction increases. Furthermore, a population's vulnerability to extinction increases as the distance between islands increases because individuals from one population will be less likely to immigrate to a declining population and help rescue it from extinction (Brown and Kodric-Brown 1977). The ability of individuals to move between habitat islands often decreases as greater human disturbance either increases distances between habitat islands or makes the ocean separating the habitat islands less hospitable. These theoretical predictions of extinction vulnerability have been empirically supported (e.g., bird populations on islands [Diamond 1984, Pimm et al. 1988]; mammals on mountain tops [Brown 1971]; fish in lakes [Magnuson 1991]).

From a management perspective, the isolation of units of preserved habitat (fragmentation) has been demonstrated to cause local or regional extinction of populations (Harris 1984, Lovejoy et al. 1986). Newmark (1987) reported that western U.S. national parks may be too small to support some mammal populations after the populations were isolated and prevented from using previously suitable habitat surrounding the parks. The persistence of gray wolves at Isle Royale National Park, where a large island of pristine habitat was set aside, prey were sufficient, and wolves were at maximum density (no./area) just a decade ago, would not seem to be a concern, but wolf numbers in this small population have declined and they may become extinct (Rolf Peterson, Michigan Technological Univ., Houghton, Mich., pers. commun., 1993). Plants and animals in U.S. national parks have received more protection than most, but setting aside habitat may not be sufficient if the area needed for population persistence is not encompassed in the park and the continuing habitat loss and fragmentation surrounding the park are not considered (Newmark 1987).

THE SPECIAL BIOLOGY OF SMALL POPULATIONS

Conservation biologists provide 2 reasons for concern for small populations when designing management plans to foster their persistence and recovery (Gilpin and Soule 1986, Soule 1987).

1. Genetic considerations dealing with "founder effects", genetic drift, and in-

breeding depression can reduce genetic variability and increase the expression of deleterious traits. These factors reduce survival and reproduction as well as long-term evolutionary potential and adaptability to changing environmental conditions.

2. Demographic considerations emerge from random variations in birth and death rates. These rates are averages of probabilistic occurrences for the individuals composing the population even in a constant environment (e.g., probability that a female will give birth to 0, 1, 2 . . . offspring in a time period; probability of dying in a time period [Raup 1991]). Whereas these probabilities produce the expected birth and death rates given sufficient time or averaging over many individuals, the smaller a population at a point in time the greater the likelihood that it will exhibit birth and death rates very different from expected values (e.g., the probability of getting all heads in 2 coin tosses is 0.5^2, but the probability of getting all heads in 5 tosses is 0.5^5). Consequently, small populations are more vulnerable to extinction because they are more likely to experience a "run of bad luck" (a series of periods with low birth rates and high death rates). Furthermore, as the population becomes smaller, the likelihood of a run of bad luck increases; this has led Gilpin and Soule (1986) to refer to this process as a "vortex".

Given sufficient time the probability that a finite population will persist, not experience a run of bad luck that leads to extinction, is infinitely small; this is analogous to the eventual loss of a complete bankroll by a gambler ("gambler ruin" analogy *sensu* [Raup 1991]). For example, assuming a constant probability of persistence/time period (s), which ignores the decreasing probability as the population becomes smaller during a run of bad luck, the cumulative probability of persisting (p) rapidly approaches zero as the number of time periods (t) increases (e.g., $s = 0.99$ and $p = 0.99^t$: at $t = 1$, $p = 0.99$; at $t = 10$, $p = 0.90$; at $t = 100$, $p = 0.36$). The probabilistic nature of population persistence and the increasing probability of extinction as population size decreases are often confused; some examples of this difficulty are presented below.

The genetic and demographic effects are magnified by environmental stochasticity (e.g., annual variation in food, cover, etc.), catastrophic events (e.g., epidemics, floods, etc.), and interactions with other species (e.g., competitors, predators, diseases, etc.) (Soule 1987, Lande 1988). The more a population's carrying capacity and birth and death rates vary with environmental fluctuations over time (Roughgarden 1979, Goodman 1987), the more frequent and severe the occurrence of catastrophes (Ewens et al. 1987); the more severe the interactions with other species (MacArthur 1972), the more vulnerable is the small population.

The above factors are not the initial cause for a population's small size, but they make it vulnerable to extinction because population declines easily can continue after the original cause for small population size is eliminated (i.e., the extinction vortex discussed by Gilpin and Soule [1986]). Scientists need to study the dynamics of small populations and provide this information to managers who can improve their strategic and tactical planning for species protection.

MANAGING SMALL POPULATIONS

A better understanding of the theoretical concepts for small populations will enable managers to develop better plans for species recovery and persistence. These concepts provide critical insights into management questions, such as: (1) how much total habitat must be provided? (2) how should the mosaic of habitat units be arranged? and (3) will habitat protection be sufficient and, if not, what other actions are necessary? Failure to consider these

factors will doom many preservation plans to failure.

Ideally, the proper management of small populations requires biologists to have knowledge of a population's carrying capacity, birth and death rates, and other parameters such as: (1) variability of birth and death rates caused by stochastic differences between individuals; (2) temporal variability in carrying capacity and birth and death rates caused by environmental fluctuations (e.g., annual changes); (3) frequency and severity of catastrophes; and (4) intensity of interactions with other species that affect birth and death rates (e.g., competitor-induced declines in birth rates and survival). By considering these factors (this does not necessarily mean absolute measurement) managers can begin to ask whether enough and the correct mix of habitats have been provided. If insufficient habitat has been provided and more is unavailable, managers must enhance the chances for a species' persistence in the available habitat (e.g., increasing carrying capacity, predator control, supplementing populations, etc.).

Rudimentary guidelines are available for assessing whether sufficient habitat area has been provided or is even available (Belovsky 1987). Furthermore, these guidelines for managers have been validated using data for the extinctions of mammals on Great Basin mountaintops since the end of the Pleistocene (Belovsky 1987). These guidelines include: (1) larger areas are required to support larger species; (2) carnivores need larger areas than herbivores; (3) larger areas are required in tropical than temperate regions; (4) larger areas are required in forests than grasslands; and (5) larger areas are required in more variable environments than less variable environments. While estimates of required habitat area and population size needed by a species of a given body size in each of the above categories to persist for a given time (e.g., 100 years) with a given probability (e.g., 95%) can be computed, a specific species' habitat area and population size can differ from these estimates based on its unique traits.

If the above habitat guidelines cannot be satisfied, the population cannot be benignly neglected. Rather, active management must be performed to make the available habitat capable of supporting a sufficiently large population or to assist small population persistence. An example is provided by the recent demise of the remaining wild black-footed ferret (*Mustela nigripes*) population caused by canine distemper (Thorne and Belitsky 1989). The disease is not density-dependent, but a catastrophe that would have little impact on a larger population where some individuals may be immune, develop immunity, or not be exposed (Dobson and May 1986). The study of small populations tells us to expect this type of vulnerability and to consider these situations in our planning.

Some wildlife biologists already are empirically considering the minimum population size needed for persistence; while this is encouraging, there also is misunderstanding. For example, Berger (1990) found that desert bighorn sheep (*Ovis canadensis*) populations of 50 or less went extinct, while those of 100 or more persisted for 70 years. These results were questioned by Krausman et al. (1993), because they know of populations of 50 or less in Arizona that have persisted. Berger (1993) responded by asking whether these data were statistically valid. Neither statistics nor Berger's (1990) inability to include Arizona population data may be the issue, rather the debate may be moot because the dynamics of small populations inform us that there is never a guarantee of persistence. Some populations less than 50 will persist and others that are greater than 100 will disappear. The management issue is how the probability of persistence changes with population size and what probability of persistence is acceptable to society. Therefore, managers will have to deal with uncertainty, even when sound strategies are adopted.

How to employ the dynamics of small pop-

ulations in management becomes even less clear when existing theoretical models are used. These models are simplistic and have not been validated (Boyce 1992, Stacey and Taper 1992). This was a critical debate in developing the recovery plan for the Northern spotted owl (*Strix occidentalis*, Murphy and Noon 1992). Nonetheless, the theoretical models often provide results consistent with observations (Belovsky 1987, Thomas 1990) or with population sizes that have evoked concerns over persistence from managers (Wilcove et al. 1993).

Theoretical models, even though they are simplistic and have not been validated, do provide certain robust rules for the management of small populations. If a more complex model or management plan violates one of these rules, the complex model's predictions or the management plan must be reevaluated. For example, an innovative management proposal to balance economic development and persistence of a mountain lion (*Felis concolor*) population in a region of California was based on population persistence times (Beier 1993). Persistence times were computed using a complex simulation model because existing theoretical models were thought to be too simplistic, especially given their density-independent construction, and to provide persistence times that were too pessimistic (short). However, two of the simulation model's predictions violated the rules established by theoretical models:

1. The theoretical models are called density-independent, because population growth abruptly stops when carrying capacity is attained, rather than birth and death rates changing gradually as density increases (Boyce 1992, Stacey and Taper 1992). Therefore, Beier's (1993) claim that these models frequently produce populations larger than carrying capacity is not possible.
2. Theoretical models employ two forms of variation in birth and death rates: random variation in births and deaths between individuals (i.e., demographic variability); and variation in birth and death rates over time (i.e., environmental variability). Environmental variability enhances demographic variability and is more important, reducing persistence times by an order of magnitude or more than when demographic variability only is considered (Boyce 1992, Stacey and Taper 1992). Beier (1993) does not include the environmental variability referred to in theoretical models; therefore, we would expect his persistence times to be much longer than those from the theoretical models. Furthermore, regardless of the rescue effects of migrants, the 15–20 adult mountain lions predicted to guarantee persistence also is expected, because this is the value predicted by theoretical models when environmental variability is not incorporated. Perhaps a complex model was unnecessary and the management conclusions are too optimistic.

The theoretical models also indicate the types of data that will be needed to compute persistence times so that sound management strategies can be developed. For example, to estimate demographic variability in the mountain lion case, observations of a sufficient number of individuals in a given year are needed to estimate the probability of survival and probabilities of different levels of female reproductive output. To estimate environmental variability, observations of a sufficient number of individuals over a sufficient number of years are needed to estimate the variation in birth and death rates between years.

Small populations are an important subject for today's wildlife and fisheries managers. This is still a new area of study; it will strain the adequacy of our knowledge of each species, modify how we study populations, and force biologists to expand their perspectives on management. Considering these problems when developing management plans may not require costly monitoring programs by state agencies. Rather, existing information on small populations can be incorporated into recovery

plans, and continued research advances can be used to update plans. This will require better communication between biologists working on small populations and those developing and implementing recovery plans.

IMPLICATIONS

Wildlife and fisheries managers no doubt will devote more of their time to dealing with small populations and the recovery plans for threatened species because the threat to species throughout the world is increasing (Wilson 1989). A hands-off preservationist approach to the maintenance of biological diversity may no longer be realistic, rather the maintenance of precarious species' populations may require new and more intensive management activities. Understanding the demography and population genetics of small populations as studied by conservation biologists will provide some insights for this management. However, communications have been strained between more traditional wildlife and fisheries biologists and conservation biologists, and cooperation has been jeopardized by the creation of professional dichotomies based upon different philosophies (consumptive versus nonconsumptive) and levels of investigation (population versus community versus ecosystem ecology) (Temple et al. 1988, Anonymous 1989, Bolen 1989, Edwards 1989, Gavin 1989, Hunter 1989, Teer 1989, Wagner 1989). Nonetheless, it is logical that these two groups should join forces to solve this pressing set of problems.

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