POPULATION VIABILITY ANALYSIS: ADAPTIVE MANAGEMENT FOR THREATENED AND ENDANGERED SPECIES

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Introduction

Population viability analysis (PVA) is the process of estimating the probability of persistence of a population for some arbitrary time into the future (Soulé 1987, Boyce 1992). PVA has its origins in the conservation biology movement; indeed, it is one of the keystone ideas of conservation biology (Wagner 1989). Performing a PVA entails compiling available biological data on a species and using these data as the basis for a simulation model for the population. The model then can be used to project future population trajectories from which one may estimate the probability that it will persist, for say 100 years, or other related estimates such as the probability of extinction or expected time extinction (Dennis et al. 1991).

The probability of extinction emerging from PVA would appear fundamental to establishing priorities for conservation based on guidelines that have been proposed for the categorization of species by International Union for Conservation of Nature and Natural Resources (IUCN) (Macė and Lande 1991). In other applications, attempts are made to determine the minimum viable population (MVP) necessary to meet conservation objectives. Unfortunately, such applications are premature because we cannot reliably estimate the extinction probability for any species (Lebreton and Clobert 1991, Boyce 1992).

Yet, I believe that PVA can be enormously valuable if viewed in the context of adaptive management. The process of pulling together all available data and building a simulation model constitutes a synthesis of our current understanding of the population. Simulation models can be used to generate hypotheses of how we expect the system to respond to perturbations or management manipulations (Boyce 1991b). If this is followed by monitoring the consequence of management actions, PVA clearly is within the framework of adaptive management (Walters 1986).

Limitations

We do not know how many individuals are necessary to prevent population extinction, and there is insufficient empirical and theoretical basis on which to make such extrapolations. Small populations may remain viable over quite long periods of time. For example, the Socorro Island red-tailed hawk (*Buteo jamaicensis socorroensis*) has persisted for well over 40 years with a population of only 20 ± 5 (Walter 1990). Although small populations gradually lose genetic variability due to drift, these populations may be important because geographic isolates often are genetically distinct (Lesica and Allendorf 1992). Small populations clearly are much more prone to extinction due to chance events, inbreeding depression, or an Allee effect (Soulé 1987, Dennis 1989). But we do not have sufficient knowledge of any of these processes to make defensible proclamations of a minimum viable population for any species.

Lack of Genetic Basis for Assigning MVP

It is common to place a target of an effective population size (N_e) of 50 for a short-term MVP, presumably based on the assumption that a 1 percent loss of heterozygosity is acceptable (Frankling 1980, Lacava and Hughes 1984). Then what often follows are calculations to estimate N_e based on data on sex ratio and mating system (Harris and Allendorf 1989).

Although N_e may give insight into the consequences of drift to loss of genetic diversity, there are numerous measures of effective population size depending upon the mechanisms affecting drift. Ewens (1990) reviews calculation of N_{ei} relative to inbreeding, N_{ev} for the variance in gene frequencies among subpopulations, N_{ee} targeting the rate of loss of genetic variation and N_{em} for mutation effective population size. Yet another measure, $N_e^{(meta)}$, defines the effective population size in a metapopulation experiencing repeated extinction-recolonization events (Gilpin and Hanski 1991). Each of these basic measures of N_e then is subject to adjustment for unequal sex ratio, age structure and variable population size (Harris and Allendorf 1989). There is no sound basis for selecting one of these basic measures of N_e over another, yet, as Ewens (1990) shows, they can lead to radically different estimates of MVP.

Likewise, there is no solid basis for the often-cited rule of thumb that 500 individuals may be sufficient to maintain long-term viability of a species. Unfortunately, the 50/500 rule does not have a sound genetic or demographic basis (Lande and Barrowclough 1987, Ewens 1990). And there is no theoretical or empirical justification for basing MVP on an estimate of N_e.

Yet, the 50/500 rule is very popular. Clearly such simple guidelines would be very useful as we confront the global extinction crisis. It simply is not feasible to postpone conservation programs while we conduct a detailed PVA for each population of concern. Happily, there is some evidence that we may be able to come up with empirical justification for such rules of thumb. For example, studies of bighorn sheep (*Ovis canadensis*) (Berger 1990) and birds on oceanic or habitat islands (Jones and Diamond 1976, Pimm et al. 1988, Soulé et al. 1988) consistently show that populations less than 50 are insufficient, and the probability of extinction is high for such small populations. Persistence of populations between 50 and 200 is highly variable, whereas populations over 200 are unlikely to go extinct over the time frames of these studies.

Inferences from these few studies should be restricted to particular taxa, and we may require larger numbers for populations that vary more, for example, insect and small mammal populations (Thomas 1990, Tscharntke 1992). Also wise is Soulé's (1987) rule of thumb that one should always attempt to maintain three or more replicate populations. Further empirical evidence urgently is needed to justify the use of rules of thumb for MVP. But until such evidence becomes available, reliance on rules of thumb, such as the 50/500 rule, is arbitrary and capricious.

PVA Lacks Statistical Reliability

Performing a PVA almost always is severely constrained by the availability of data. Securing precise population estimates usually is difficult at best (Seber 1982, Richter and Söndgerath 1990), and for some populations it may not be possible to obtain estimates for many demographic parameters. Furthermore, any realistic population projection model requires knowledge of the population-regulating mechanism (Sinclair 1989) thus requiring estimates of a density-dependent function (McCullough 1990). But absolutely essential is that the model structure be defensible (Grant 1986, *contra* Ginzberg et al. 1990).

Assigning a hard number to a MVP is not possible (Thomas 1990). If the model is sufficiently complex to be realistic, we typically do not have enough data to do a conscientious job of estimating all of the population parameters. When these sampling errors are propagated by stochastic population projection, the confidence intervals surrounding some future probability of extinction are so large that the entire process becomes questionable (Lebreton and Clobert 1991). These problems are particularly severe for threatened and endangered species where the entire living population may be insufficient to yield acceptable levels of precision in estimates of demographic parameters such as survival.

Simulation Approaches

Problems with parameter estimation are indeed serious. But to my mind, the greatest value in PVA is not in the numbers generated by the models but in the identification of a model that formalizes our current understanding of the ecology of a particular population or species. Results from this model constitute testable hypotheses about the behavior of the system.

Software packages for PVA should be used cautiously because each case must be modeled uniquely. Models should be developed that capture the essential ecology of the system, but yet are as simple as possible to reduce the number of parameters that must be estimated. To illustrate the diversity of approaches that may be taken, I will review examples that use a variety of structures and modeling approaches.

The first PVA was Shaffer's (1983) model for grizzly bears (*Ursus arctos horribilis*) in the greater Yellowstone ecosystem. This was a stochastic simulation model that emphasized demographic structure. One approach is to explore the sensitivity of various variables in the model. By so doing, it became clear that adult survival was among the most sensitive elements in the model. PVA thereby offered valuable insight into the management of grizzly bears and contributed to the development of programs to enhance adult bear survival by minimizing conflicts with humans.

In contrast to the demographic approach used for grizzly bears, Foin and Brenchley-Jackson (1991) modeled critical habitat for the endangered light-footed clapper rail (*Rallus longirostris*) in southern California. Reliable demographic details for the rail were unavailable, and the only well-documented connection between the bird and its habitat was a linear relationship between the biomass of Pacific cordgrass (*Spartina foliosa*) and the number of rails. But the salinity, transpiration and soil moisture of salt marshes are essential to the development and maintenance of cordgrass stands used by rails.

For many species, focus on habitat in a PVA model is the correct focus, and I have chosen the light-footed clapper rail example because it does not dwell on the demographic structure of the population. Indeed, such details often are not known and may be best left out of the models. Eberhardt (1987) reviewed data from a number of large mammal populations to show that simple models without age structure could offer quite sufficient descriptions of population dynamics. For many threatened and endangered species, the most fundamental management programs will entail habitat management. Details of demographic structure for these species may be of little value.

The most extensive PVA program has been on the northern spotted owl (*Strix occidentalis caurina*), stimulated by the severe economic consequences of habitat protection for the subspecies (Boyce and Irwin 1990). The first effort included simple Leslie matrix projections with random elements (USDA Forest Service 1986, Marcot and Holthausen 1987). Use of an exponential growth model clearly was inadequate, and the prognosis for the owls was grim irrespective of future habitat management. A more realistic model by Lande (1988) included density dependence via dispersal of young owls. This was subsequently expanded into a dynamic model (Lamberson et al. 1992) and then interfaced with explicit landscapes imported on a geographic information system (McKelvey et al. 1992). Lande's hypothesis regarding population regulation via juvenile dispersal remains untested, but it forms the basis for many of the Interagency Scientific Committee's management recommendations for the northern spotted owl (Thomas et al. 1990).

Adaptive Management

PVA models by themselves usually are weak and cannot be counted on to provide reliable population projections. But when combined with an iterative process of model improvement and validation, the model can provide a progressively more robust understanding of the dynamics of a species and its habitat; and a model developed in such a way can be a powerful tool for management.

How can PVA be incorporated into adaptive management protocols? Adaptive management proposes application of different management tactics in time and space, essentially as experiments, to develop a better understanding of the behavior of the system (Walters 1986). For endangered species applications, it may be possible to implement various management strategies in spatially separated subpopulations. Active management must be part of such a program, and may encompass a variety of activities such as habitat manipulation, predator or disease control, manipulation of potential competitors, winter provisioning of food, transplanting individuals from other subpopulations to sustain genetic variation, and supplementation of population with releases of captive stock. Monitoring of the genetic and population consequences of such manipulations then provides data to validate and/or refine the PVA model.

Management of grizzly bears in the greater Yellowstone ecosystem has proceeded according to an adaptive management protocol. High sensitivity of population growth rate to adult survival suggested the importance of minimizing adult mortality factors. Aggressive programs to eliminate bear/human conflicts focused on areas identified as mortality sinks (i.e., localities where repeated bear mortalities had been documented). As prescribed by an adaptive management program, after the recovery program had been implemented and additional data were obtained, Shaffer's model was updated (Suchy et al. 1985). Preliminary evidence suggests that the program was highly successful. Indeed, federal officials recently have entertained the possibility of delisting grizzly bears and reverting management to respective state and federal agencies (Boyce 1991a). However, extensive wildfires during the summer of 1988 altered habitat for the bears, and further updates to the bear model will need to be incorporated once the demographic response to the fires has been documented.

Another adaptive management program has been proposed for the management of endangered populations of *Banksia cumeata* in Western Australia. Based upon their PVA modeling, Burgman and Lamont (1992) recommended watering seedlings in several subpopulations to enhance seedling survival. Such programs require careful monitoring because watering or other forms of "enrichment" can have community-level effects that could be counter productive (Rosenzweig 1971). For example, it is conceivable that competing species or herbivores might respond more vigorously to watering than the target species.

For the northern spotted owl, the Interagency Scientific Committee (ISC) explicitly acknowledged the importance of adaptive management approaches for evaluating and updating their conservation strategy, posed as an Appendix in the ISC report (Thomas et al. 1990). Adaptive management would require implementation of various timber harvest programs and associated landscape manipulations and then documentation of the consequences for spotted owl populations. Thus far, no such programs have been implemented because litigation has interfered with the ability of management agencies to develop timber harvests.

For several years, the Captive Breeding Specialists Group (CBSG) of the IUCN has been organizing "Population and Habitat Viability Analysis" (PHVA) workshops for various threatened and endangered species. These have been enormously successful at bringing together available data on a species, identifying possible structures for a PVA model and stimulating agency coordination for conservation programs. One cannot place much stock in MVP estimates that emerge from these exercises, but if they help provide structure that will encourage adaptive management approaches, they perform an exceedingly valuable function.

"Adaptive management is learning by doing" (Lee and Lawrence 1986). But agency restrictions may severely limit our ability to actually do management with threatened and endangered species. Naturally, any programs that might pose a risk to a threatened or endangered species will meet strong resistance from agencies charged with protecting the species. Yet, creative manipulations may be allowed if they could only be viewed as enhancing conditions for the species of concern.

In a legal context, PVA probably will face many challenges because of omnipresent biological uncertainty. Given the statistical weakness of population parameter estimates and our inability to generate robust population projections, any PVA will be open to question even though the PVA constitutes our best statement of the expected behavior of a population. Such uncertainty recently was used in court to challenge the proposed adoption of the Interagency Scientific Committee's conservation strategy for the northern spotted owl by the USDA Forest Service. Although Lee and Lawrence (1986) suggest that biological uncertainty may often frustrate attempts to manage by adaptive management, it is through adaptive management that we can hope to resolve some of the uncertainty associated with PVA. It is the best we can do, and we know of no better way to gain "reliable knowledge" about managing our natural resources (Romesburg 1981).

Conclusion

Population viability analysis (PVA) entails evaluation of data and models for a population to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future. Models vary depending upon the availability of data and the particular ecology and life history of the organism. Unfortunately, we have insufficient data to validate PVA models for most endangered species. Seldom, if ever, do replications exist, and small sample sizes typically result in projections bearing large confidence intervals. A great danger exists that resource managers may lend too much credence to a model when they may not fully understand its limitations.

There is too much more to be gained by developing a stronger understanding of the system by modeling, than is lost by shirking modeling for fear of its being misinterpreted. PVA as a process can be an indispensable tool in conservation, and it involves much more than attempts to calculate statistically feeble estimates of minimum viable populations or probabilities of extinction. PVA entails the process of synthesizing information about a species or population and developing the best possible model for the species given the information available. When done properly, this involves working closely with natural resource managers to develop a long-term iterative process of modeling and research that can reveal more about how best to manage a species. Done properly, PVA is a variation on Holling and Walter's notion of adaptive management.

Adaptive management proposes application of different management tactics in time and space to develop a better understanding of the behavior of the system. For application to endangered species problems, implementation of various management strategies may be attempted in spatially separated subpopulations. Active manipulation must be part of such a program. Monitoring of the genetic and population consequences of such manipulations then provides data to validate and/or refine the PVA model.

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