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Minimum Population Sizes for Species Conservation

Mark L. Shaffer

Many species cannot survive in man-dominated habitats. Reserves of essentially undisturbed habitat are necessary if such species are to survive in the wild. Aside from increased efforts to accelerate habitat acquisition for such species, the most pressing need facing conservationists is development of a predictive understanding of the relationship between a population's size and its chances of extinction.

Biologists have long known that the smaller the population, the more susceptible it is to extinction from various causes. During the current era of heightened competition for use of the world's remaining wildlands, this qualitative understanding is of limited utility to conservation and natural resource planners. The old adage that "the bigger the reserve, the better" must be replaced with more precise prescriptions for how much land is enough to achieve conservation objectives. Efforts at making such determinations have been clouded by inconsistencies in the focus on the unit to be preserved (population, species, community, ecosystem) and lack of an explicit definition of what constitutes successful preservation (persistence for 10, 100, 1000 years, etc.).

The intricate interdependencies of living things dictate that conservation efforts be focused on the community and ecosystem level. Unfortunately, the very magnitude of complexity of these systems makes such efforts difficult. Moreover, certain species are more sensitive than others to changing conditions and begin to decline prior to any noticeable degradation of the community to which they belong. Consequently, conservation efforts have been and, in many cases, will continue to be at the single-species level. Many species currently in jeopardy are large-bodied and/or specialized, two characteristics that usually

lead to low population densities. If we are successful in providing sufficient room for their survival, then other, less space-demanding members of their communities should also survive.

In this paper, I propose tentative criteria for successful preservation at the population level, discuss the various methods available for determining the population sizes and their area requirements to meet these criteria, and relate both to overall conservation strategy.

THE MINIMUM VIABLE POPULATION CONCEPT

Levins (1970) has estimated that, since the beginning of the Cambrian, species have been going extinct at the rate of about one per year (though not uniformly). Extinction thus appears to be a relatively common event. The factors leading to extinction, though varied, can be lumped into two categories: systematic pressures and stochastic perturbations. A necessary first step in the preservation of any species is to identify and, if possible, compensate for any systematic pressures threatening that species. This is not the type of problem of interest here. Rather, the focus is on those stochastic perturbations that may extinguish populations of a species even in an environment that, on average, is favorable for their growth and persistence.

In general, there are four sources of uncertainty to which a population may be subject:

- *demographic stochasticity*, which arises from chance events in the survival and reproductive success of a finite number of individuals (May 1973, Roughgarden 1975);

- *environmental stochasticity* due to temporal variation of habitat parameters and the populations of competitors, predators, parasites, and diseases (May 1973, Roughgarden 1975);

- *natural catastrophes*, such as floods, fires, droughts, etc., which may occur at random intervals through time; and

- *genetic stochasticity* resulting from changes in gene frequencies due to founder effect, random fixation, or inbreeding (Berry 1971, Soulé 1980).

Little is known about the role of any of these factors in any specific case of extinction. Because all of them increase in importance with decreasing population size, assessing the relative importance of each will always prove difficult.

The extinction of the heath hen (*Tympanuchus cupido cupido*) provides an example of the situation (Simon and Géroudet 1970). Once fairly common from New England to Virginia, the species steadily declined as European settlement progressed. By 1876 the species remained only on Martha's Vineyard, and by 1900 there were fewer than 100 survivors. In 1907 a portion of the island was set aside as a refuge for the birds, and a program of predator control was instituted. The population responded to these measures, and by 1916 had reached a size of more than 800 birds. But in that year a fire (natural catastrophe) destroyed most of the remaining nests and habitat, and during the following winter the birds suffered unusually heavy predation (environmental stochasticity) from a high concentration of goshawks (*Accipiter gentilis*). The combined effects of these events reduced the population to 100-150 individuals. In 1920, after the population had increased to about 200, disease (environmental stochasticity) took its toll, and the population was again reduced below 100. Though the species endured awhile longer, by 1932 the last survivor was gone. In the final stages of the population's decline, the birds appeared to become increasingly sterile, and the proportion of males increased (demographic, environmental, or genetic stochasticity). Which of these events, or what combination, was the critical determinant in the species disappearance is unknown.

The net effect of all these types of perturbations on a population's prospects for survival depends to a great extent on

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the population's relationship to other populations of that species—what might be termed its biogeographic context. Any factor depressing the size or growth of a population may be mitigated by immigration of individuals from other populations.

Clearly then, a minimum viable population is not one that can simply maintain itself under average conditions, but one that is of sufficient size to endure the calamities of various perturbations and do so within its particular biogeographic context. Furthermore, survival (and hence, preservation) must be measured relative to some time frame and some set of conditions. Hooper (1971) has already pointed out this fact, but it does not seem to be widely recognized within the conservation field and certainly not in the minds of the general public. The problem of determining minimum viable population sizes and their area requirements is analogous to designing reservoirs to hold flood waters. A reservoir capable of holding the once-in-50-year flood may be grossly inadequate for the once-in-1000-year flood. What time frame to use and the levels of variation and catastrophe to anticipate in determining minimum viable population sizes are very much open questions, but it is critical to view the problem in this way.

Because the dedication of lands to the preservation of biotic diversity increasingly has to compete with investments of that land for the production of other goods and services, reserves should be evaluated on the basis of their utility for meeting the conservation goals set for them over some reasonable time frame. On the other hand, the uncertain nature of the factors that threaten small populations argues against too precise a set of criteria. Given this dilemma, I tentatively and arbitrarily propose the following definition of minimum viable population size: *A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.*

I must stress the tentative nature of this definition. The critical level for survival probabilities might be set at 95%, or 100%, or any other level. Similarly, the time frame of 1000 years might be lengthened to 10,000 or shortened to 100. Such criteria urgently need discussion among conservationists, planners, and natural resource managers. The impor-

tant point is that such a definition is an explicit set of performance criteria for a conservation unit under an explicit set of conditions.

DETERMINING MINIMUM POPULATION SIZES

There are five possible approaches to determining minimum viable population sizes and their area requirements: experiments, biogeographic patterns, theoretical models, simulation models, or genetic considerations. None of these is very sophisticated, and certainly none can be considered failsafe. Nevertheless, most can contribute to a better understanding of population size and survival and to more realistic estimates of the land area required to preserve populations of a particular species.

Experiments

The most straightforward approach to the problem of assessing minimum viable population sizes is simply to create isolated populations and monitor their persistence. This approach is intractable for two reasons: First, we cannot experimentally measure persistence in terms of decades and centuries; institutional abilities or willingness to support research projects are usually limited to a decade or less. Second, in most cases irreversible decisions on land use will be made in the very near term (10 to 20 years). Unless conservationists can provide useful estimates of the location, number, and size of reserves in this time period, the opportunity to do so may be permanently foreclosed. Development interests will not (in some cases, cannot) await the results of research that may take a century to complete. This should not be construed as an argument against long-term population-monitoring studies. Such studies are of great potential value in many areas of biology and ecology, but their utility for solving this particular problem is limited.

Biogeographic Patterns

Examination of the distributional patterns of species that occur in insular or patchy patterns can provide a first approximation of minimum area requirements and, provided some estimate of densities, minimum viable population sizes. This approach requires that species communities occupying such habitat patches are in equilibrium and the approximate length of their isolation is

known. If these conditions are met, such surveys can reveal both the smallest island or patch inhabited by a species and also the percent of islands or patches of a certain class supporting that species, measured either in area or species diversity.

Robbins' (1979) work on the habitat size relationships of the migrant neotropical avifauna of the eastern deciduous forest employs this approach. Although this is probably the most tractable and reliable approach to the problem, it does have its limitations. The most critical is that there is apparently no clear relationship, either theoretical or empirical, between the percent of occupied patches of a certain size and the potential longevity of the populations they support. This is a key research need.

For example, a particular species might be a breeding resident of 95% of islands or patches 50–100 km² in area. Unfortunately, knowing this fact alone reveals nothing about the frequency with which populations on such patches go extinct or recolonize. Suppose populations of this hypothetical species on patches of the given dimensions go extinct, on average, every 20 years. Relying on a single reserve of this size to maintain the species without alternate reserves to provide sources for recolonization will prove ineffective in the long term. To make this approach workable, there must be good information on both the frequency with which species occur on islands or habitat patches of different sizes and species-specific extinction/colonization rates typical of these units. Some information of this type is available for certain avian species (for an overview see Wilcox 1980 or Terborgh and Winter 1980), but much remains to be done.

An additional complication with this approach is that population characteristics (e.g., density, mortality and fecundity rates) of many species show wide variation from one part of their range to another depending on habitat quality or community structure. Two habitat patches of the same size may not support equally large or enduring populations. Such habitat differences are critical to wise conservation planning, and any research efforts employing this approach must recognize and deal with this fact.

Obviously, this approach cannot be used for those species that have contiguous distributions and do not occur either on islands or patchily distributed habitats.

Despite these drawbacks, analysis of biogeographic patterns, when coupled with studies of species-specific turnover rates, is one of the major means of determining minimum viable population sizes and their area requirements. The most valuable research directions to fully utilize this approach are to extend its application to nonavian species, refine analyses to reflect differences in habitat quality as well as quantity, and determine if there is any relationship between the percent occurrence of a species and its characteristic extinction/colonization rates.

Theoretical Models

There are several theoretical models for predicting the probability that a small population will go extinct and the time this will take. There are also numerous models of population growth under stochastic conditions (demographic, environmental, or both). But these models either embody unrealistic assumptions or lead to currently unresolved mathematical problems.

For example, the models of MacArthur and Wilson (1967) and Richter-Dyn and Goel (1972) assume a constant carrying capacity and birth and death rates that change only in response to density. Thus, they deal only with the probability of extinction due to demographic stochasticity. The branching process theory employed by Keiding (1975), though capable of dealing with both demographic and environmental stochasticity, is restricted to exponential growth. Diffusion theory, as employed by various workers (for a review see Shaffer 1978), applies only to a totally unpredictable environment. Moreover, there has been some doubt about the appropriate method of analysis to be applied to diffusion theory equations. Turelli (1977), after a thorough review of analysis methods, emphasized that the diffusion theory models are most appropriately viewed as approximations to more realistic models that are analytically intractable.

The idiosyncratic nature of many species and the great variability inherent in nature probably preclude direct application of any single theoretical model to many real-world situations. Nevertheless, this is an important area of research and deserves increased attention. From a practical standpoint, the most fruitful approach would be the development of a small number of models to fit

various scenarios of population growth and regulation and use these to determine both the relationship of population size to extinction probabilities and the sensitivity of the results to assumptions inherent in the models and key population characteristics. For example, in the classic model of logistic population growth, do survival probabilities depend primarily on mortality or fecundity rates, or carrying capacity? Is the mean or variance of these parameters more important in assessing survival? To what extent is survival affected by introduction of time lags in the density-dependent process of mortality and reproduction? Such models should also facilitate development of effective management strategies for reserves that are too small to assure persistence if left alone.

Simulation Models

Because they are not subject to the various constraints of analytical models, computer simulations employing numerical methods may provide a tractable approach to determining minimum viable population sizes and their area requirements. Aside from their greater realism, such models also provide a flexible tool for assessing the effects of changes in various parameter values (e.g., mortality and fecundity rates, etc.) and/or relationships (density-dependent versus density-independent mortality rates, etc.).

The principle drawbacks of this approach are a lack of generality (i.e., the simulations have to be altered for different species) and demand for extensive data. At a minimum, such models (for vertebrates) require knowledge of the mean and variance of age and sex-specific mortality and fecundity rates, age structure, sex ratios, dispersal, and the relationship of these various parameters to density. Such information should be gathered over a sufficiently long period to assure that it is representative of the full range of conditions the population is subject to, including cyclic behavior. (For some species this may require very long data bases.)

Based on the extensive data of Craighead et al. (1974) for the grizzly bear (*Ursus arctos* L.) in Yellowstone National Park, I (Shaffer 1978) used the simulation approach to assess minimum viable population sizes and area requirements for this species. The simulations could evaluate the effects of either or both demographic and environmental stochasticity. Natural catastrophes appear to be unimportant for the grizzly, and lack of

adequate genetic information precluded testing the effects of genetic stochasticity. The results of this analysis showed that populations of less than 30-70 bears (depending on population characteristics) occupying less than 2500-7400 km² (depending on habitat quality) have less than a 95% chance of surviving for even 100 years. Survival probabilities were most affected by changes in the mean mortality rate, cub sex ratio, and age at first reproduction of females.

This type of approach should be expanded to other species when sufficient data exist. Where possible, future field population studies should be designed to gather the types of information necessary to develop simulation models. Such simulations provide the most tractable and realistic alternative to the analysis of biogeographical patterns and species-specific turnover rates.

Genetic Considerations

Several workers have based minimum population recommendations on genetic and evolutionary arguments. Franklin (1980) has suggested that, simply to maintain short-term fitness (i.e., prevent serious in-breeding and its deleterious effects), the minimum effective population size (in the genetic sense) should be around 50. He further recommended that, to maintain sufficient genetic variability for adaptation to changing environmental conditions, the minimum effective population size should be around 500. Soulé (1980) has pointed out that, above and beyond preserving short-term fitness and genetic adaptability, long-term evolutionary potential (at the species level) may well require a number of substantially larger populations.

These recommendations were based on very general applications of basic genetic principles and, consequently, are somewhat oversimplified. A more detailed approach would involve gathering information on the degree of genetic variability and the breeding structure of the species to be preserved. Given this information, it should then be possible to determine what size population would provide (at some probability level) a representative sample of the genetic diversity typical of the species and what size would be necessary to assure (at some probability level) that none of this variability would be lost due to in-breeding and genetic drift over some specified period of time. Lacking this sort of detailed work, the above recommendations should be viewed as very

rough guidelines rather than specific prescriptions.

SUMMARY

Nature reserves represent the investment of land for the production of a public good—the persistence of populations of various species and the communities they form. The fact that population persistence depends, to a great extent, on population size immediately raises the issue of how persistent society wishes remnant wild populations to be.

This is not a question that can be answered solely on biological grounds. In an expanding human world, competition for use of a finite land base can only intensify. Conservationists will increasingly be pressed on the need to preserve many species and on the efficiency (in terms of land) with which such preservation can be accomplished. In this atmosphere, scientists must develop some consensus on the standards to be applied in determining what constitutes a minimum viable population for successful preservation. I have offered one tentative definition in this paper, but it is not to be taken literally. It is intended as an example for consideration, not a standard for application.

Given some consensus on the standards to be applied, several of the methods outlined here may be used to begin determining minimum viable population sizes and land area requirements for species in jeopardy. The most promising approaches are the extension and refinement of analyses of biogeographic distribution patterns and species-specific turnover rates and the use of available population data in computer simulations designed to test extinction probabilities. Theoretical mathematical models may be useful in revealing which population characteristics or processes are likely to be most important in affecting survival probabilities. Genetic determinants of minimum viable population sizes are still unclear; their resolution hinges primarily on a better knowledge of the breeding structure and genetic variability of particular species and, most importantly, the role of genetic variability in population growth and regulation.

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