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What Do Real Population Dynamics Tell Us About Minimum Viable Population Sizes?

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There is no single "magic" population size that guarantees the persistence of animal populations (e.g., Shaffer 1981; Gilpin & Soulé 1986; Soulé and Simberloff 1986; Lande 1988; Simberloff 1988). This is partly because extinction is probabilistic and partly because each minimum viable population (MVP) must be estimated separately, after considering characteristics of the population and environment under scrutiny. MVP estimates are then used to design and manage reserves for focal species. This approach is exemplified by studies reported in the Special Section on Population Viability Analysis in the March 1990 issue of *Conservation Biology*. The papers by Murphy et al. (1990) and Menges (1990) emphasize aspects of the dynamic nature of the spatial distributions of populations, and they stress the need to conserve what could be termed Minimum Dynamic Areas, often in reserve networks. Yet in the few remote and relatively unmodified regions of the world where reserve design is still possible on a large scale (e.g., parts of Amazonia), many focal species (e.g., large forest eagles) are too poorly known to calculate their MVPs and Minimum Dynamic Areas. Land use decisions will be made before the detailed information necessary to calculate specific MVPs has been obtained and incorporated into appropriate models. It might, however, be feasible to estimate population densities of representative focal species, and measure their home ranges (Thiollay 1989). This less detailed information could then be used to make provisional conservation recommendations, sometimes decades before more accurate MVP and Minimum Dynamic Area estimates could become available. To do this requires MVP guidelines, if not

quite "magic numbers." The purpose of this note is to use empirical data from animal populations to provide rough, interim estimates of population sizes that would be likely to permit medium- to long-term persistence.

Existing Guidelines

Many populations become extinct because the environment changes in a deterministic way. Even in generally suitable environments, however, populations may become extinct as a result of various stochastic events and natural catastrophes (Shaffer 1981; Soulé & Simberloff 1986). These stochastic factors exacerbate one another at low population sizes, leading to what Gilpin and Soulé (1986) term "extinction vortices." MVP values must be set high enough that a population is unlikely to slip into an extinction vortex. The usual approach to the problem has been to build models that predict probabilities of extinction or loss of genetic variation in various circumstances. But however many factors are incorporated in models, some environmental events and natural catastrophes are inherently unpredictable, so there is some question as to whether more complete models will actually produce substantially more robust predictions (cf. Simberloff 1988).

On the basis of existing models and some empirical observations, various generalizations can be made (e.g., see Gilpin & Soulé 1986; Soulé & Simberloff 1986; Soulé 1987; Lande 1988; Simberloff 1988, for reviews). A mean population size of 10 is far too small for many reasons: genetic variation will be lost rapidly, and demographic extinction is likely to be swift. A mean population size of 100 is also too small because genetic variation will still be lost (the effective population size, N_e , will usually be below 50), and because environmen-

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tal variation and natural catastrophes could easily reduce numbers to a level from which the population could not recover. A mean size of 1,000 may often be adequate, provided the population does not inhabit particularly short-lived habitats, and provided the mating system does not result in a small percentage of the population producing most of the offspring. Soulé and Simberloff (1986, p. 19) concluded that "thoughtful estimates of MVPs for many animal species are rarely lower than an effective size of a few hundred," and this lower limit would often correspond to an actual population count of about 1,000. Soulé (1987) guessed that MVPs would often be in the low thousands. A population size of 10,000 should normally be sufficient to permit long-term demographic persistence and to satisfy genetic considerations.

Real Population Dynamics

Some Observed Extinctions

Existing MVP guidelines have been based rather more on theory than on observations of natural population dynamics. Additional information can be gleaned from studies of population persistence and from the dynamics of natural populations. Jones and Diamond (1976) studied extinctions of bird populations from the California Channel Islands. Over an 80-year period, at least 39 percent of populations estimated at fewer than ten pairs became extinct. (Others may have become extinct and been recolonized between census periods.) Of populations numbering 10 to 100 pairs, at least 10 percent became extinct (Fig. 6 in Jones & Diamond 1976). Of populations between 100 and 1,000 pairs, only one became extinct in the same period, and no cases of extinctions of populations of over 1,000 pairs were recorded. Pimm et al. (1988) analyzed extinctions of bird populations from islands around the British coastline. Populations at or below 2 pairs had a mean time to extinction of 1.55 years, populations with a mean size of 2.1 to 5 pairs had a mean time to extinction of 3.48 years, and populations of 5.1 to 12 pairs had a mean time to extinction of 7.52 years.

Populations below 10 pairs survived poorly in both studies. For populations between 10 and 100 pairs, at best there was a 90 percent chance of persistence for 80 years (from Jones & Diamond 1976). This is a lower probability of survival, over a shorter time period, than has been recommended for MVP persistence (Shaffer 1981).

Soulé et al. (1988) studied extinctions of chaparral-requiring birds from habitat islands in and around San Diego, California. Most Wrentit and Bewick's Wren populations in the range of 10 to 50 individuals survived for up to 75 years, but not for longer. In contrast, Rufous-sided Towhee and California Thrasher exhibited

0 percent survival after only 32 years in 10 ha fragments (from Fig. 5B in Soulé et al. 1988); these fragments would have been expected to support average initial population sizes of approximately 50 individuals. Initial population sizes are calculated on the assumption that sites contained 80 percent chaparral at the time of initial isolation (from Fig. 4 in Soulé et al. 1988). In the largest canyon, populations of Rufous-sided Towhee, California Thrasher, and Valley Quail that initially contained approximately 212, 181, and 158 individuals respectively have survived for 50 years (Soulé et al. 1988). For all five species mentioned above, populations that were initially below 50 individuals were very unlikely to persist for longer than 75 years, but populations above 200 would be likely to persist for at least 50 years, and probably for 75 years. For population sizes initially between 50 and 150 individuals, the probability of survival for 75 years depended critically on the species in question.

Observed Population Variability

If population variability can be established, it may be possible to estimate the population size required to produce a negligible probability of extinction over a given period. The longer a population is observed, the greater the range of variation it is seen to exhibit (Pimm & Redfearn 1988). Because measured variability initially increases with time, it is useful to estimate whether variability reaches some asymptote after a certain number of years or generations. Four insect populations reached an asymptote in variability after 8 years (generations), and bird and mammal population variability may have reached an asymptote after 32 to 50 years (Fig. 2 in Pimm & Redfearn 1988). By that time, most of these vertebrates would also have completed eight or more generations. Except for species with generation times longer than very roughly six years, the range of variability observed in population dynamics studies over 50 years may correspond to normal medium-term levels of variability, other than those caused by major natural catastrophes, unusual environmental stochasticity, and unidirectional environmental change. Because increasing numbers of "rare events" and environmental changes are experienced with increasing time, variability will continue to rise gradually with increasing time.

Variability can be expressed as the standard deviation of log (density) (or s.d. of log [population size]), and a value of one is equivalent to population fluctuations through four orders of magnitude (Pimm & Redfearn 1988); more strictly, for a value of one, just over 95 percent of population sizes observed can be expected to be within a range of four orders of magnitude. Over a period of 50 years, four insect species reached a mean variability of roughly 3.4 orders or magnitude, and the most variable population encompassed over four orders of magnitude (reading off Fig. 2 in Pimm & Redfearn

1988). For birds and mammals, mean variability was 1.2 orders of magnitude, and the most variable population covered 3 orders of magnitude in 50 years.

Mean MVP levels should be set so that the minimum population size reached through natural population fluctuations would be unlikely to fall to levels at which populations might enter extinction vortices, below say 100 individuals. I use the MVP criterion that the population should fall to 100 only once in 100 years. Everything being equal, the higher the median population size, the less frequently it will fall to these undesirably low levels (Fig. 1). For birds and mammals, the observed average variability of 1.2 orders of magnitude may be a slight underestimate because the full range of population variation may not have been attained for all species after 50 years. Nonetheless, I have used the observed 50-year population variability in my calculations. On this basis, for a population to fall to 100 only once in 100 years, the geometric mean of population size would

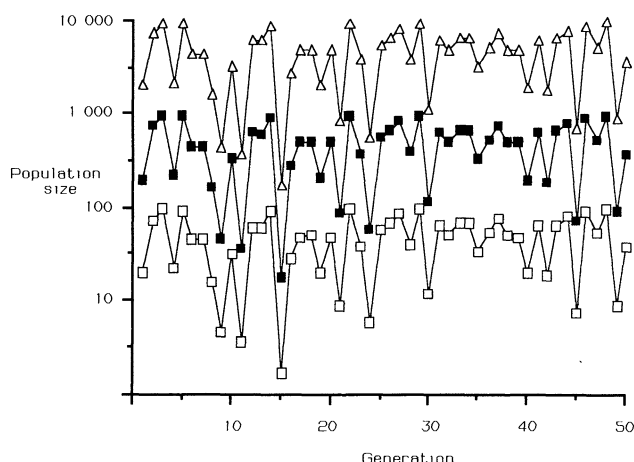


Figure 1. Hypothetical fluctuations of three populations of different size. The largest (open triangles) fluctuates at random between 0 and 9,999 individuals, with a median population size of about 5,000. In this sequence of random population sizes, the minimum population size reached was 172 individuals, and the observed variability was 1.75 orders of magnitude. The other two populations exhibit identical population fluctuations (same percentage change in each generation, and variation over 1.75 orders of magnitude) but scaled to fluctuate between 0 and 999 (solid squares — median 500) and between 0 and 99 (open squares — median 50). The medium-sized population fell below 100 in seven generations, with a minimum of 17. Such a population could easily be trapped by an extinction vortex, although it would not necessarily do so on the first occasion that it fell below 100. The smallest population was always below 100 and below 25 individuals in 14 generations, at which population sizes stochastic events could easily result in extinction.

have to be 500. To make this calculation, I assumed that the values of population size are normally distributed on a log scale. Geometric means are calculated by taking the log of all population sizes, calculating the average of these values, and then taking the antilog of that average. When observed values of population size are normally distributed on a log scale, the geometric mean is close in value to the median population size. On genetic grounds, a geometric mean value, or median, of 500 individuals may still be undesirably low.

The dynamics of particular populations, say over ten or more generations, are rarely known (and if they are, the present coarse estimates can be superseded), so the conservative approach is to assume that a population will exhibit maximum variability: i.e., it will vary by three orders of magnitude. With this variability, a population geometric mean must be 5,500 individuals to drop below 100 at a rate of only once in 100 years.

On the basis of empirical evidence, a population size of 10 is far too small, 100 is usually inadequate, 1,000 is adequate for species of normal variability, and 10,000 should permit medium- to long-term persistence of most of the most variable birds and mammals.

All estimates should be increased by at least one order of magnitude for insects because they usually show greater population variability. In practice environmental effects on insects and aspects of the spatial dynamics of insect populations are usually of overriding importance (e.g., Murphy et al. 1990). Insect conservationists hardly ever find it appropriate to invoke MVP population sizes: they are usually more interested in Minimum Dynamic Areas. The same is true for short-lived plants (Menges 1990) and perhaps also for especially variable vertebrates.

Conclusion

The above findings support Soulé's (1987) contention that theory and empirical observations show general agreement on the orders of magnitude of numbers of individuals required to maintain MVPs of completely isolated populations, in the absence of unidirectional environmental change. In unknown cases, we must be conservative and only reduce MVP size estimates when particular aspects of the population dynamics and genetics of focal species, and the environments they occupy, indicate that this is warranted. The geometric mean value of at least 5,500 may be a useful goal for the preservation of existing populations in undivided habitat (e.g., for reserve design in a few regions), and as a recovery target for smaller populations elsewhere. This empirically derived value is reassuringly close to Soulé's (1987) "low thousands," which he guessed might be needed on the basis of both theory and empirical observation. I would revise Soulé's estimate upwards slightly to say that in unknown cases we should usually

aim for population sizes from several thousand to ten thousand.

This is intended as an initial target population size in unknown cases rather than as a recipe for success or failure. There is no substitute for a thorough knowledge of the species and habitats under consideration (Soulé 1987; Shaffer 1990). Unfortunately, population sizes in the thousands are hard to attain for many vertebrates. Many of these animals now occur only as much smaller populations, even in the largest national parks. This does not mean we should give up, but conservation of these vertebrates will be effective only if all relevant conservation bodies collaborate to ensure an adequate network of smaller populations (with artificial recolonizations and transfers if necessary) (Soulé 1987). Populations that occupy habitat fragments that are far too small to hold thousands of individuals may still possess great conservation potential, particularly when populations are not completely isolated. When populations show average or low population variability and inhabit stable environments, geometric mean values of 500 may be adequate for long-term persistence. For birds, populations above 200 individuals often give high probabilities of survival for periods of at least three quarters of a century (Jones & Diamond 1976; Soulé et al. 1988). Models (see Simberloff 1988) and empirical evidence (Jones & Diamond 1976; Soulé et al. 1988) indicate that *some* populations can persist at even lower levels for many years. Some of the island bird populations studied by Jones and Diamond (1976) may have survived for 80 years despite possessing median numbers of fewer than 10 pairs. Other small populations have survived and prospered: northern elephant seals recovered from about 20 to at least 30,000 individuals over a period of 75 years (Bonnell & Selander 1974). These examples indicate that small populations should certainly not be abandoned as hopeless. It is often easier and less expensive, however, to ensure that a large population does not become small than to ensure that a small population does not become extinct. "There are no hopeless cases, only people without hope and expensive cases" (Soulé 1987, p. 181).

Models have identified many factors likely to be important in conservation biology. Now is the time to re-examine data from wild populations. We need to identify empirically the extent to which population variability is determined by attributes of the organism themselves (e.g., trophic level, taxonomic position) or by variation in the environments they inhabit. Greater use should be made of existing field data on spatial dynamics as well as on the temporal variability of populations to provide generalizations of value to conservation managers.

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