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## *Introduction*

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*And of every living thing of all flesh, two of every sort shalt thou bring into the ark. Genesis*

### **Definition: How much is enough?**

Given biblical precedence, it is not surprising that for millennia, a pair (male and female) has been deemed sufficient to initiate, if not perpetuate, a population. In fact, there is more than scriptural authority behind this myth. With luck, two can indeed be a sufficient number of founders.

What is luck? Without going into theories of randomness and probability, luck implies a fortunate or unusual circumstance leading to a good result. The result of interest in this book is the survival of a population in a state that maintains its vigor and its potential for evolutionary adaptation. Such a population is a viable population. Legend does not question Noah's success with each of his multitudinous experiments. He must have been very lucky indeed. He also had some advantages over us, not the least of which was a fresh, well-watered planet.

The problem that we address in this book is 'How much is enough?'. Put more concretely, it is: What are the minimum\* conditions for the long-term† persistence and adaptation of a species or population in a given place? This is one of the most difficult and challenging intellectual problems in conservation biology. Arguably, it is the quintessential issue

\* See the following section for a discussion of the 'minimum' issue.

† We are not concerned here with short-term survival criteria or rules such as 'the rule of 50' discussed in Frankel and Soulé (1981, Chapter 6). Such short-term guidelines apply only to captive breeding and similar 'holding operations,' although they have often been misapplied to populations in nature. For example, the short-term rule of 50 does not protect the population against the loss of most of its genetic variation (Franklin, 1980; Soulé, 1980).

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in population biology, because it requires a prediction based on a synthesis of all the biotic and abiotic factors in the spatial-temporal continuum.

Returning to the definition, we must define ‘long-term persistence,’ and ‘adaptation.’ The former phrase means the capacity of the group to maintain itself without significant demographic or genetic manipulation for the foreseeable ecological future (usually centuries) with a certain, agreed on, degree of certitude, say 95%. The probabilistic qualification is necessary (Shaffer, Chapter 5), because it would be impossible to guarantee absolutely the survival of a group. The qualifying phrase ‘without significant demographic or genetic manipulation’ is meant to imply that we are concerned with the ability of populations to maintain themselves in nature, given sufficient habitat and other elements of benign neglect, including freedom from excessive harvesting.

The term ‘adaptation’ implies that the group maintains a normal level of immediate fitness (individual vigor, fertility, fecundity), and has sufficient genetic variation to adapt by natural selection to changing environmental conditions within the predicted range of frequency and amplitude of disturbance and change.

If the entire history of our planet were condensed into one hour, it is only in the last few fractions of a second that mankind and its technology has spread across the globe – with devastating results for other species. For this reason, viability is now a *cause célèbre*. The last time a similar degree of disturbance occurred (during the Pleistocene glaciations), the pace of change was slow enough for vegetation belts to be compressed towards the equator or to shift in accordance with the changing distribution of rainfall. Such shifts are now impossible because of the geographic distribution of anthropogenic habitat destruction, and because the rate of change and destruction today is measured in years and decades rather than in centuries and millennia. Therefore, termination rates are now expected to be much greater.

Major extinctions have occurred before, and many species did go extinct in the Pleistocene. The difference is that now it is our species that is responsible, and countermeasures are therefore feasible. Presumably, glacial and interglacial humans could have prevented the Pleistocene extinctions if they had had our values, our knowledge of genetics, ecology, biogeography, and our level of technology.

### **History of the viable population concept**

The following sketch of the history of the population viability idea is incomplete and assuredly biased. I must leave it to others to correct the account. My personal view is that the subject of population viability

has a very short history, although its roots attenuate to a distant past. As described below, I distinguish *population* viability from *system* viability, although the two subjects are interdependent in most cases.

Conservationists (including preservationists) wish to maintain the health and diversity of natural systems – ecosystems, communities, habitats, as well as species. Until recently, however, most of the emphasis has been on the protection of whole systems. The favored technique, since the early decades of this century, has been the setting aside of areas for this purpose. The management of such ‘set asides’ is becoming increasingly difficult and sophisticated, in part because of the growing numbers of humans.

These difficulties (see Soulé, 1986a for reviews) have led biologists to ask ‘What are the (minimum) conditions for the viability of natural systems?’ The quest for answers has generally followed two somewhat independent tracks. First, community ecologists have focused on minimum areas (e.g., Moore, 1962; Lovejoy, 1980) for system viability, with seminal contributions from island biogeography (Diamond, 1975; Terborgh, 1975; see Wilcox, 1980). Population biologists have focused on the minimum population sizes (e.g., Franklin, 1980; Frankel and Soulé, 1981; Shaffer, 1981) or densities (e.g., Hubbell and Foster, 1986) for target species. These two tracks are now coming together because of the realization that often the most pragmatic way to define system viability is to do so in terms of the viability of critical or keystone species within the system (Frankel and Soulé, 1981; Shaffer, 1981; Wilcox and Murphy, 1985; Soulé and Simberloff, 1986). This is not to say that other, more holistic criteria, such as preserving entire watersheds, are not equally or more important in some circumstances.

During the last few decades, there has been an exponential increase in the estimates of population sizes that ensure viability. One reason for this is the changing interpretation of the term ‘viability.’ In the early days it meant short-term persistence in a constant environment, or resilience. In other words, the time scale of concern (Frankel and Soulé, 1981) was short. Since 1980, the time scale has increased because biologists started to consider threats such as epidemics, catastrophes, and genetic drift.

The first systematic attacks on the problem considered only *population dynamics*, or, more strictly, the birth-and-death branching process (Feller, 1939; MacArthur, 1972; MacArthur and Wilson, 1967; Richter-Dyn and Goel, 1972). As more factors have been introduced into the analysis, the estimates have increased. These factors are *environmental variation* (randomness, stochasticity) (Leigh, 1981; Ginzburg, *et al.*, 1982; Shaffer, 1983; Goodman, Chapter 2; Belovsky, Chapter 3), *genetics* (Frankel, 1974; Franklin, 1980; Soulé, 1980; Frankel and Soulé, 1981; Lande and

Barrowclough, Chapter 6), *catastrophe* (Shaffer, 1981; Ewens *et al.*, Chapter 4), and *metapopulation structure and fragmentation* (Shaffer, 1985; Gilpin, Chapter 7).

The preceding paragraph might give the impression that these factors interact in a simple, additive fashion, an impression laid to rest by Shaffer (1981) who encouraged an overall systems approach to the problem, emphasizing the interaction of factors, and the probabilistic nature of viability estimates. This theme was picked up by Schonewald-Cox (1983), who tabulated degrees of risk associated with different population levels. More recently Gilpin and Soulé (1986) portray perturbed populations as a system of interacting extinction vortices that can exacerbate themselves and each other by positive feedback loops.

The moral of this tale is that the closer we approach reality, the more complex the problem appears. This should come as no surprise.

#### **Minimum viable populations**

Until now, I have avoided using the term ‘minimum viable population’ or MVP, even though the term and acronym are in common use in conservation biology. Indeed, many of the chapters in this book use the term. Nonetheless, it is controversial. Some conservationists argue that the term is tactically self-defeating and ethically offensive. Their reasoning is that the job of conservation biologists should be to recommend or provide for more than just the minimum number or distribution of a species. Just as a compassionate physician ought to prescribe the optimum conditions for health, they would say, a conservation biologist should avoid a garrison mentality. They should prescribe to managers and policy makers the conditions for robust and bountiful populations.

The dilemma is that such recommendations would be swept aside as impossibly idealistic. For example, say that each nation has a national policy to maintain viable populations of all native vertebrate predators. Now consider the timber wolf (*Canis lupus*). Some would say that an optimum population of the wolf might be its pre-human or pre-agricultural density and range, including the places where Moscow, Oslo, and Chicago now exist. This definition of ‘optimum’ would obviously expose conservationists to ridicule. Any other definition of ‘optimum’ would be arbitrary.

But the underlying point is important. It is that MVP estimates should include built-in margins of safety. That is, MVPs should, in a sense, be ‘bountiful.’ This is already inherent in the definition of MVP in the preceding section – one simply adjusts the level of risk (probability of persistence) to suit society’s requirements, including one’s definition of

bountiful. For example, certain groups in society might be content with a 50% probability of persistence for 100 years, while other groups would settle for nothing less than a 99% probability of persistence for 1000 years.

Some people have suggested that we retain the term MVP, but change its meaning from ‘minimum viable population’ to ‘managing for viable populations.’ Although no one can dictate such conventions, my preference is to retain the original, more precise meaning.

As discussed elsewhere (Gilpin and Soulé, 1986) an MVP can be thought of as a set of estimates that are the product of a systematic process for estimating species-, location-, and time-specific criteria for persistence; the process itself is referred to as population vulnerability (or viability) analysis, PVA. But whatever jargon we choose to adopt, the point is that *there is no single value or ‘magic number’ that has universal validity*. Not only is each situation unique, but the acceptable level of risk determines the numbers, densities, and distribution in space of the MVP (Schonewald-Cox, 1983).

On the other hand, there are some components of viability analysis that establish relatively fixed floors below which MVPs should not drop. Genetic criteria, particularly, may yield such thresholds (Franklin, 1980; Soulé, 1980; Lande and Barrowclough, Chapter 6). It is a grave mistake, however, to substitute such relatively ‘hard’ components of viability analysis for the MVP itself. This is discussed further in Chapter 10.

### Issues of scale and dimensionality

The viable population problem involves several kinds of scale, and it is essential to consider the kinds and degrees of scalar phenomena that affect a particular viability analysis. These scale phenomena include the range (areal extent) of the species, and the patchiness/uniformity of its distribution in space. A related issue is the temporal dynamics (rate of turnover) of the patchiness. These issues come to light when examining the meaning of ‘population,’ because scale phenomena are related to population structure and dynamics.

‘Population’ means different things to different people. To the non-biologist it means the people in a certain place or in the whole world. Biologists usually use the term to mean the individuals of a particular species in a particular group or in a definable place. Thus we may speak of the world’s population of sperm whales (*Physeter catodon*), or a particular patch of *Delphinium barbeyi* in a particular meadow in the Rocky Mountains. Michael Gilpin (Chapter 7) illustrates this diversity of population structure in his discussion of patchiness and metapopulations.

In the case of certain endangered species, one patch may comprise the

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entire species, and the extinction of such a patch is then the extinction of the species. In most cases, however, managers will not be dealing with the last remaining patch or subpopulation, but rather with one of several populations or with a group that is thinly dispersed over a large area (such as many predators).

Therefore, a population may be a very real, functional group of individuals (as with a herd of ungulates, a nesting colony of geese, or a pack of wolves), or it may be a completely arbitrary designation (motivated by administrative regulations), such as the peregrine falcons (*Falco peregrinus*) that reside in a particular national park, or the sperm whales that happen to be within 200 miles of the coast of Argentina on January 17.

The biologist/manager must be mindful of these distinctions throughout the course of a viability analysis. One of the pitfalls of viability analysis is confusion about the population size of a particular group being managed, and the ultimate viability of the 'population' to which it belongs. For example, the wolves in the Appennini Mountains of Italy, and grizzly bears (*Ursus arctos horribilis*) in and around Yellowstone National Park, may never be viable if considered in isolation from conspecific groups in other places. On the other hand, such isolated groups may be important for the viability of the species as a whole. But even if they are not essential for the health of the species, they may still be 'viable,' if they are managed as part of the species as a whole, assuming that natural or assisted movement of individuals between groups (and other management interventions) is possible.

The consideration of this kind of viability, that of component groups, raises other questions. For example, some component populations are more critical than others. The Canadian grizzly population, which numbers in the thousands, is more critical, for example, than is the US population, which numbers in the low hundreds (Gilpin, Chapter 7). On the other hand, the viability of a species may sometimes depend on the viability of a relatively small subgroup that occupies a transitional isthmus. This may be the situation with some of the Appalachian groups of black bear (*Ursus americanus*); if one of the linking populations disappears, the entire population could be at risk.

Managers are often faced with the situation of managing a component population of a large vertebrate or a migratory species. In such cases viability may depend on joint, cooperative actions of two or more jurisdictions (Salwasser *et al.*, Chapter 9): no single jurisdiction can contain a population that is large enough to be viable in the sense defined above. At the same time, each subpopulation must be managed so as to benefit the entire population, and so as not to cause problems for the other jurisdictions.

Another related issue is the rate of turnover (extinction and recolonization) of populations in patches of habitat. This is because the turnover rate determines whether one is going to analyze and manage single populations, with unbroken genetic and temporal continuity, or whether one is dealing with a dynamic metapopulation structure in which the individual subpopulations (patch populations) come and go in ecological time (decades or less). Where persistence times are relatively long, the genetics and dynamics of the target population are the paramount concern, along with, perhaps, the possible interchange of individuals and genetic material between these relatively stable entities.

In the latter (turnover) case, however, it would be folly to bet heavily on the viability of individual patch populations, because each of these has a high probability of extinction. Rather, one's focus shifts upward in the spatial-temporal hierarchy to the metapopulation – the paramount concern is the persistence of the unit or set of populations, which depends on the rates of extinction and colonization of patches (Ewens *et al.*, Chapter 4, and Gilpin, Chapter 7).

There are some obvious, if rough, indicators of a species' position on this turnover continuum. These indicators are morphological or life history traits that correlate with persistence in absolute time (Belovsky, Chapter 3). Among them are body size, age at first reproduction, birth interval (Andy Dobson, pers. comm.), and susceptibility to catastrophe. At the high turnover end of the spectrum are small, short-lived or annual species. At the low turnover end are large-bodied, long-lived species. Subpopulations of the latter kind of species, e.g., redwoods (*Sequoia*), probably have a natural turnover rate that is geological in temporal scale.

### **Viability is not the only issue**

Just because we have put together a whole book on the subject of population viability should not lead anyone to the conclusion that we believe that viability analysis is the beginning and end of conservation and conservation biology. By analogy, a book on electro-magnetism admits the existence of other forces. There are other issues and problems in conservation biology that are just as challenging and important (Soulé, 1986b).

In most cases, population viability will be seen in a larger ecological context. Viability, in the strict sense, will be impossible for some populations in certain situations, but wise management may still be able to insure the persistence of a relatively 'natural' community or system. Probably the majority of nature reserves in the world are too small to contain more than a few family groups of primates or herds of large

ungulates. Such tiny groups in vest pocket reserves may contribute virtually nothing to the viability of the species as a whole, but their survival may be important, nonetheless, for ecological and social reasons, including the maintenance of certain successional habitats, and the educational experiences that such animals afford visitors. When such groups die out, therefore, they should simply be replaced from whatever source is available.

Purists might object that this kind of management is ‘unnatural,’ but this argument lacks force in today’s world. (An implied norm behind this criticism is the existence of a natural law that forbids the artificial maintenance of community and ecological structure where anthropogenic factors have led to the imminent extinction of some species within the system.) The subject of such difficult or ‘hopeless’ situations is dealt with in Chapters 8 and 10.

#### **Candidates for viability analysis**

Earlier in this chapter I mentioned that viability analysis of critical or keystone species may be an efficient way to begin to cope with the issue of whole system viability (Soulé and Simberloff, 1985). This may appear to be an overly naive approach to the problem of defining the minimum viable size of nature reserves, but it may be the most practical. We cannot ignore the simple fact that no methodology has been proposed that permits us to determine the minimum areas of reserves with reference only to ecological or system processes. Other guidelines, such as ‘protect entire watersheds’ are too vague to be of much use in areas with too little or too much topographic relief.

As ecologists, we may be reluctant to place the responsibility for the viability of hundreds or thousands of species – an entire ecosystem – on the shoulders of just a handful of ‘indicator’ or keystone species. It seems too simple, too non-ecological. But there do not appear to be good alternatives.

On the other hand, one of the oldest ecological principles is Liebig’s Law of the Minimum – the limiting factor for system viability is the one in shortest supply. In a very real sense, keystone species are often the critical limiting factors in systems (Gilbert, 1980; Terborgh, 1986). Therefore, the MVP approach to system viability is more ‘ecological’ than it may appear at first sight. At the very least it is a convenient, identifiable handle to a problem that has been intractable for too long.

Implicit in much of the preceding discussion are some of the rules for choosing the candidates for viability analysis. I shall end this chapter by listing some of the obvious ones:



- (1) species whose activities create critical habitat for several other species;
- (2) mutualist species whose behaviors enhance the fitness (e.g., reproduction, dispersal) of other species;
- (3) predatory or parasitic species that regulate the populations of other species, and whose absence would ultimately lead to a decrease in species diversity;
- (4) species that have spiritual, aesthetic, recreational, or economic value to humans;
- (5) rare or endangered species.

Note that the origins of these rules are diverse. All of them rest on the normative axiom that diversity is good (Soulé, 1985), although the first three rules depend on conventional ecological knowledge. The basis of the fourth rule is at least partly instrumentalist – nature is a valuable source of commodities and experiences, although spiritual and aesthetic uses of nature are often non-consumptive and unselfish. The last rule is fundamentally ethical, because it implies that other species have intrinsic value.

### References

- Diamond, J. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7: 129–46.
- Feller, W. 1939. Die Grundlagen der Volterraschen Theorie des Kampfes ums dasein in wahrscheinlichkeitstheoretischer Behandlung. *Acta Biotheoretica* 5: 11–40.
- Frankel, O. H. 1974. Genetic conservation: our evolutionary responsibility. *Genetics* 78: 53–65.
- Frankel, O. H. and Soulé, M. E. 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge.
- Franklin, I. A. 1980. Evolutionary change in small populations. Pp. 135–49 in M. E. Soulé and B. A. Wilcox (eds.) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Mass.
- Gilbert, L. E. 1980. Food web organization and the conservation of Neotropical diversity. Pp. 11–13 in M. E. Soulé and B. A. Wilcox (eds.) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Mass.
- Gilpin, M. E. and Soulé, M. E. 1986. Minimum Viable Populations: the processes of species extinctions. Pp. 13–34 in M. E. Soulé (ed.) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Mass.
- Ginzburg, L., Slobodkin, L. B., Johnson, K., and Bindman, A. G. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* 2: 171–81.
- Hubbell, S. P. and Foster, R. B. 1986. Commonness and rarity in a Neotropical forest. Pp. 205–32 in M. E. Soulé (ed.) *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Mass.

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- Leigh, E. G. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* **90**: 213–39.
- Lovejoy, T. E. 1980. Discontinuous wilderness: minimum areas for conservation. *Parks* **5**(2): 13–15.
- MacArthur, R. H. 1972. *Geographical Ecology*. Harper and Row, New York.
- MacArthur, R. H. and Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Moore, N. W. 1962. The heaths of Dorset and their conservation. *J. Ecology* **50**: 369–91.
- Richter-Dyn, N. and Goel, N. S. 1972. On the extinction of a colonizing species. *Theor. Pop. Biol.* **3**: 406–23.
- Schonewald-Cox, C. M. 1983. Guidelines to management: A beginning attempt. Pp. 414–45 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas (eds.) *Genetics and Conservation*. Benjamin Cummings, Menlo Park, Calif.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *Bioscience* **31**: 131–4.
- Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. *Int. Conf. Bear Res. Manage.* **5**: 133–9.
- Shaffer, M. L. 1985. The metapopulation and species conservation: The special case of the Northern Spotted Owl. Pp. 86–99 in R. J. Gutierrez and A. B. Carey (eds.) *Ecological and Management of the Spotted Owl in the Pacific Northwest*. Gen. Tech. Rep. PNW-185. Portland, Or: USDA, Forest Service, Pacific Northwest Forest and Range, Expt. Stn.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pp. 151–69 in M. E. Soulé and B. A. Wilcox (eds.) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Mass.
- Soulé, M. E. 1985. What is conservation biology? *Bioscience* **35**: 727–34.
- Soulé, M. E. 1986a. *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Mass.
- Soulé, M. E. 1986b. Conservation biology and the 'real world.' Pp. 1–12 in M. E. Soulé (ed.) *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Mass.
- Soulé, M. E. and Simberloff, D. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* **35**: 19–40.
- Terborgh, J. 1975. Faunal equilibria and the design of wildlife preserves. Pp. 369–80 in F. Golley and E. Medina (eds.) *Trends in Terrestrial and Aquatic Research*. Springer, New York.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pp. 330–44 in M. E. Soulé (ed.) *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Mass.
- Wilcox, B. A. 1980. Insular ecology and conservation. Pp. 95–117 in M. E. Soulé and B. A. Wilcox (eds.) *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Mass.
- Wilcox, B. A. and Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. *Amer. Natur.* **125**: 879–87.