ISSN 1502-4873 (paper). ISSN 1891-5396 (electronic).
doi: https://doi.org/10.5324/fn.v18i0.6014.

A scientific examination and critique of minimum viable population size

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Henriksen, G. 1997. A scientific examination and critique of minimum viable population size. - Fauna norv. Ser. A 18: 33-41.

A commonly voiced justification for preserving a particular obscure and apparently insignificant species is that species are interconnected in subtle ways, and we are likely to precipitate a cascade of extinction. The focus primarily on minimum viable populations (MVP) of single species carries the potential for suggesting conflicting research programs. If the focus is too heavily on «magic numbers» and rules, this conflict will become intense. Because many species are linked together, there are many cases in which conservation of one species will automatically entail conservation of many others. An understanding of the habitat and biology of the interacting species should allow conservation scientists to make a good estimate of what must be done to save the system, but simply focusing on the numbers that would constitute an MVP of any one interactant would be at best an inefficient approach, at worst extinction would ensure. To derive statistically reliable estimates for MVP is clearly a difficult if not impossible task. But it can be an even tougher task to extrapolate from the MVP into estimating the area of habitat necessary to support such a population, which requires a detailed understanding of a species habitat requirements. Patches of habitat must not only be larger than some critical size, they must also be in a suitable geometric configuration to ensure dispersal among habitat units.

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INTRODUCTION

According to Gilpin and Soulé (1986), the expression «minimum viable population» (MVP) came into vogue, possibly because of an injunction from the Congress of the United States to the U.S. Forest Service to maintain «viable populations» of all native vertebrate species in each National Forest. The term implies that there is some threshold for the number of individuals that will ensure (at some acceptable level of risk) that a population will persist in a viable state for a given interval of time. MVP must be distinguished from the term PVA (population vulnerability analysis). The goal of a PVA is to establish a minimum viable population that reduces the risk of an extinction to an acceptable level. That is, PVA is the process and MVA is the product. The forces that affect population viability and determine MVP's are extremely complex. Thoughtful estimates of MVP's for many animal species are according to Soulé and Simberloff (1986), rarely lower than an effective size of a few hundred.

Soulé (1987) tried to avoid the term MVP, claiming it is controversial. Caughley (1994) find no example of the idea of minimum viable population size in conserving a species in the wild, and argued that it might be just as well because it is a slippery notion, some people thinking of it in terms of the genetics of a population in a stable environment and others considering it in the context of population dynamics in a fluctuating environment. According to Caughley (1994), some conservationists argue that the term is self-defeating and ethically offensive and that the job for conservationist should be to recommend or provide for more than just the minimum number or distribution of a species. Instead, they should describe to managers and policy makers the condition for robust and bountiful populations.

One dilemma is that such recommendations would be swept aside as impossibly idealistic. For example in Norway, where we have decided to maintain viable populations of all native vertebrate predators. Consider the wolf. 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 Oslo and Drammen now exist. This definition of «optimum» would obviously expose conservationists to ridicule, but 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.

Early history

The roots of PVA trace back to MacArthur and Wilsons`s (1967) island biogeography theory. In seeking to explain the relatively low species diversity of island biotas, they proposed that the number of species on an island at any time represented a balance between immigration of species to the island and extinction of species already present. Smaller islands had fewer species, in part, because they could support only smaller populations, and smaller populations should have higher extinction rates.

It did not take long before conservationists saw the similarity between and island and a stand of old-growth timber in a sea of clear-cuts and it was not long before they began to examine the reason why smaller populations should have higher extinction rates (Soulé & Wilcox 1980, Shaffer 1981, Gilpin & Soulé 1986). PVA was born, that is, the process of making an estimate of the MVP size was born.

Earlier investigations of the MVP problem, including MacArthur & Wilson (1967), Richter-Dyn & Goel (1972) and Leigh (1975), emphasised a demographic approach, in which the expected lifetime of the population was the objective. Their work was based on birth and death branching processes, and they found that there were critical «floors» for size, below which the population would quickly go extinct. I will attend to their models later.

In addition to island biogeography, the other key emphasis in the literature of the new conservation science is genetics. Moore (1962) & Hooper (1971) considered the problems of inbreeding depressions that might arise in refuges. Frankel (1970, 1974) and Berry (1971) first raised the spectre that loss of genetic variation through drift might limit subsequent evolution in response to a changing environment.

A paper by Shaffer (1981) appears to have been the first to take an overall systems perspective. He began by distinguishing deterministic extinction from chance or stochastic extinction. Then he distinguished four separate forces, or kinds of variation, that independently contribute to population extinction. The first two were demographic stochasticity and genetic stochasticity. The second two were environmental stochasticity and catastrophes. Despite this comprehensive view, however, Shaffer (1981) used only a combination of demographic and environmental stochasticity in his study of the grizzly bear *Ursus arctos* (Shaffer 1983).

In the following, I will first focus on the genetic aspects, then the demographic approach, including both demographic and environmental stochasticity, and finally I will give some words about the «minimum viable metapopulation size».

Demographic and environmental stochasticity

One might term any random variation in demographic parameters such as birth and death rates or sex ratios, as «demographic stochasticity». By contrast, «environmental stochasticity» would consist of variation in the environment external to a population, e.g. populations of other species (predator, competitors etc.) or the physical environment (weather, fire etc.). May (1973) saw it in another way and by «environmental stochasticity» he meant stochastic variation of «environmental parameters». This led to a confusion, partly because the parameter upon which May (1973) imposed random fluctuation in his example, the intrinsic rate of increase (r), can be viewed as a demographic parameter (e.g. Krebs 1985) rather than a parameter capturing the action of the external environment.

According to Simberloff (1988), the key distinction to draw is this:

- Variation among members of a population in demo-

graphic traits (e.g. whether they live or die, how many offspring they have) is what most workers have interpreted as «demographic stochasticity».
- Variation in the external environment, affecting demographic properties of an entire population, constitutes «environmental stochasticity».

To use other words, variation in the external environment can change demographic traits - weather or food can change the probability of death, for example - and this effect is the most straightforward way to model environmental stochasticity. Therefore, Goodman (1987) argued that no complete distinction exists between demographic and environmental stochasticity and that this is more a question of the level at which one examines the stochastic input.

The effect of demographic stochasticity on population size is greatest in small populations, because the effect of individual variations will be wiped out as the population size increases. Environmental stochasticity is minor or moderate environmental disturbances which affect birth- or death- rates of all individuals in the population equally (May 1974, Goodman 1987, Lande 1993). Environmental stochasticity is important both in small and large populations. Large environmental disturbances are called catastrophes. They will cause a severe reduction in the population size, and, as with environmental disturbances, the effect of catastrophes will depend on the population size (e.g. Pimm 1991, Lande 1993). It may be difficult to distinguished between environmental stochasticity and catastrophes, in particular where the environmental disturbances is severe.

Genetic factors

The magic numbers
Franklin (1980) and Soulé (1980) suggested that a minimum effective population size of 50 would be required to stem inbreeding depression, whereas Franklin (1980) argued that an effective population size of 500 would prevent long-term erosion of genetic viability by drift. They both argued that genetics must be a cornerstone of conservation science. This suggestion was raised to the status of a rule in some management circles. Fifty and 500 are called the «magic numbers» and, though the estimations are based on many suppositions and little data (Lande and Barrowclough 1987), they have already been applied in several management plans (Lande 1988). However, both parts of this rule have been disputed. According to Simberloff (1988), no magic numbers or specific rules are valid, no single MVP is universally applicable to all species. Boyce (1992) argued that if generalisation is possible, it must await the accumulation of case studies and experimental manipulations of population size.

However, criticisms of the 50/500 rule have led to extensive current research, including debates about the SLOSS (single large or several small refuges) concept, corridors, shape of refuges and interests in models for MVP size.

Effective population size
An approach commonly used in trying to determine a genetic basis for MVP is to examine effective population size. The 50/500 rules are purely genetic concepts, and difficult to apply in practice because they assume that a population is composed of N individuals that all have an equal probability of mating and having offspring. However, many individuals in a population do not produce offspring and therefore the effective population size of breeding individuals is often substantially smaller than the actual population size. Because the rate of loss of genetic variability is based on the effective population size, the loss of genetic variability might be quite severe even when population size is high (Kimura and Crow 1963, Franklin 1980). An effective population size that is smaller than the expected can exist when there is an unequal sex ratio in the population, variation in reproductive output or population fluctuations (Primac 1993).

Inbreeding depression
The «magic number» of 50 individuals is based on empirical studies from populations in captivity. The inbreeding coefficient (F) increases by 1/2 N_e per generation, and animal breeders usually find no problem with an increase of 1 % per generation in F. This suggests that N_e =50 is acceptable (Franklin 1980, Soulé 1980). Breeders often allow an increase of 2-3 % per generation in F, but the rule of thumb in conservation should be more conservative because the stakes are higher and wild animals are less likely to tolerate

inbreeding than are domestic ones. Domestic animals have been selected against deleterious alleles for many generations and hence the recommendation of $N_e > 50$.

However, in a wild population, the frequency of deleterious alleles will probably be much higher and therefore inbreeding depression will probably occur faster (Simberloff 1988, Lande 1995, Lynch et al. 1995). There is broad agreement that inbreeding depression can threaten small populations in refuges, particularly completely isolated populations and particularly if the species does not typically inbreed.

Some animal populations, for instance the northern elephant seal *Mirounga angustirostris* (Bonnell and Selander 1974), have very little genetic variation and seem not to suffer inbreeding depression. Despite this loss of genetic viability, the northern elephant seal population has successfully repopulated much of its former range (Riedmann 1990). The species were probably purged of many deleterious alleles by very slow inbreeding and selection, whereas inbreeding depression is likely to arise if outbreeding species are quite suddenly forced to inbreed, as might be the case when habitat is rapidly fragmented.

Genetic drift

According to Simberloff (1988), the 500 part of the rule is even more problematic. Already in 1930, Fisher (1930) stated that the rate of evolution at a single locus by selection is limited by the amount of genetic variation available, and thus there is a reason to be concerned about the evolutionary potential of any population with low genetic variability. The estimate (Franklin 1980) that $N_e=500$ would be required to counteract loss of variation by drift referred to one trait (bristle number) in one species (a fruit fly) in a model that assumed no natural selection; loss of alleles by drift was balanced by gain through mutation.

Recent studies show that several of the earlier generalisations concerning the «magic numbers» were incorrect. Lande (1995) included for instance new estimates of mutation rates in his calculations. New studies of the effects of mutations show that approximately 25 % of the mutations have only a weak negative effect on the phenotype and that they therefore will have a greater chance for fixation in the genotype than a normal mutation. Using these data, Lande (1988) estimated that an effective population size of 5 000 individuals would be necessary to maintain a sufficient genetic variation to secure the possibility for future adaptions. This is 10 times the size of the suggested «magic number» by Franklin (1980) -Soulé (1980). Because the effective population size usually is less than the observed size (Nunney & Elam 1994), this implies that necessary genetic variation for evolutionary change only can be maintained over time in very large populations. Other estimations support these conclusions (Lynch et al. 1995).

This suggests that to maintain a genetically healthy and viable population, it is necessary to secure a much higher population size than the size of the existing populations of most of the endangered species. Already in 1988, Lande (1988) predicted that loss of biological diversity would be due mainly to demographic factors, whereas the reduction in the populations' viability due to unfortunate effects of changes in the genetically composition would be of minor importance. This is supported by analyses of stochastic population models (Leigh 1981, Goodman 1987, Lande 1993) based on basic theory developed by Bartlet (1960) and May (1973, 1974).

MacArthur-Wilson and Richter-Dyn-Goel

In my introduction I mentioned the work of MacArthur & Wilson (1967). The most striking feature of their models is that, for many values of the parameters, a rather sharp inflection exists such that, below some threshold population size, the expected time to extinction is very short, whereas there is long-term persistence above the threshold.

Richter-Dyn & Goel (1972) elaborated this approach with more realistic analytic treatments of birth and death rates. Genetic constitution and age structure were not included. For a wide variety of conditions they found, as had MacArthur & Wilson (1967), a threshold population size with early extinction unlikely above the threshold but very likely below it.

Shaffer & Samson (1985) argued that both models share certain constraints. Each is formulated in continuous time. Neither incorporates sex or age structure nor genetic composition. Both are limited to assessing the effects of environmental stochasticity only with no provision for incorporating the effects of environmental or genetic stochasticity or natural catastrophes. Strictly speaking, these models would apply only to genetically uniform populations with non-overlapping generations that continuously reproduce in a constant environment safe from natural catastrophes.

Given the list of constraints, Shaffer & Samson (1985) questioned the general applicability of these models, and the conclusion drawn from them, to conservation strategy. In their opinion both models are hopelessly misleading. Contending that truly realistic analytic models are likely intractable (Turelli 1977), they called for computer simulations.

Ebenhard (1987), however, argued that the MacArthur-Wilson model was a good predictor of initial survival probabilities (likelihood of growth to threshold size) in experiments with rodents introduced to islands, but criticised it (incorrectly according to Simberloff 1988) on the grounds that it does not predict time to extinction for a propagule of specified size.

In his book «The Balance of Nature?», Pimm (1991) presented a whole section where he wrote why he did not talk about island biogeography, arguing that island biogeography patterns are less helpful in an exploration of the fine details of extinction than they are in suggesting how rapidly species composition changes.

Although the MacArthur-Wilson (MW) and Richter-Dyn-Goel (RDG) models have come under criticism, primary for lack of realism (Shaffer & Samson 1985), they are still used and defended by managers (Groves & Clark 1986).

Graeme Caughley

Recently, the focus on stochasticity has been criticized. In an article in 1994, the Australian ecologist Graeme Caughley (1994) argued that conservation biology is presently advancing on two separate fronts with little overlap and that neither approach alone is likely to achieve its stated purposes. The first set of ideas - the small population paradigm - deals with the risk of extinction inherent in low numbers. This paradigm deals largely with the population genetics and population dynamics problems faced by a population at risk of extinction because its numbers are small and those numbers are capped. This paradigm is well served by theory, in fact this is its strength, but its links to actuality are as yet poorly developed.

The second set, the declining population paradigm, is concerned with the processes by which populations are driven to extinction by agents external to them. It is a population in trouble because something external to it has changed. This alternative approach began earlier and runs parallel with the other. It focuses on ways of detecting, diagnosing and halting a population decline. Its weakness lies in an almost total lack of theoretical underpinning. It comprises mainly case-by-case ecological investigations and recovery operations, often short on scientific rigour, that provide few opportunities for advancing our general understanding of the process of extinction.

Caughley (1994) argued that the small population paradigm has too much influence in conservation biology. The reason for his criticism was the lack of an empirical foundation for several of the conclusions based on theoretical analyses of genetic processes in small populations. Instead, Caughley (1994) suggested an alternative route.

By analysing populations already reduced in size, one could identify common characteristics for the ecological processes that is going on during the decline. Such characteristics will, according to Caughley (1994), form the basis for the development of a new theory for population dynamic characteristics in declining populations. In my opinion, the main point in his critique is that the conservation biologists have been too concerned about the variance in small populations instead of the factors that have made the populations small, that is why the annual rate of increase has been less than 1.

However, Caughley`s (1994) two approaches need not to be alternatives, they might in fact complement each other. We need to understand both the factors that affect the rate of increase and the variance. Though maintenance of genetic variability is important to maintain the potential for evolutionary changes, Lande (1988) focused on demographic processes in small populations, claiming that such knowledge also is necessary to understand changes in the genetic composition of small populations (see also Crow & Denniston 1988, Nunney 1993).

Social dysfunction and the Allee Effect

In their review of animal population dynamics at extremely reduced population levels, Fowler & d Baker (1991) found substantial support for the view that the occurrence of the Allee effect was general; a phenomenon whereby many, if not all, animal populations experience a depression of their capacity for increase at very low population levels. I use the word many (not all), mainly because Sæther et al. (1996) did not find any evidence for the Allee effect in 11 bird species which were reduced to very low population levels.

However, models of genetic, demographic and environmental stochasticity do not take account of the Allee effect. Allee was concerned not with genetic effects, but with physiological and ethological ones, such as difficulties in finding mates (Allee et al. 1949). Some species have characteristic social behaviour, such as group mating, group defense or schooling that increases the risk of extinction from forces like hunting (Soulé 1983). Among others, social behaviours may particularly endanger small populations (Simberloff 1986), such as the requirement for group stimulation for ovarian development or mating.

Many managers have called for consideration of all these factors in management models, rather than simply genetics or demographic stochasticity (e.g. Samson et al. 1985, Shaffer 1985). A similar plea is echoed by theorists (e.g. Ewens et al. 1987, Soulé 1987).

Empirical Evidence

One way to determine MVP sizes and the forces that determine them is empirical. Look at such things as the minimum propagule sizes for successful establishment of introduced species or what happens to very small populations (Allee et al. 1949, Patton 1982, Lehmkuhl 1984). However, there are several problems. Experiments are likely to take too long in most cases of conservation interest (Shaffer 1981) and hence impractical. Furthermore, if the models are correct in predicting a heavy stochastic component to extinction, the scale of experiments would have to be enormous. It is therefore most important that already existing data are made available to population ecologists and that future sampling of information is carried out in a way so they can used in population models.

A less direct empirical approach is examination of biogeographical patterns. One might, for example, scan islands of varying size to see which ones contain a species and which do not. If there is a clear threshold, such that islands larger than some area do contain the species and smaller islands do not, one might then estimate a MVP size from area and density data. Such analyses (Cole 1983, Shoener & Shoener 1983, Simberloff & Levin 1985) demonstrate that many species do show a remarkably predictable sequence of occupancy related to area. However, some species do not conform to these predictions, and other variables (as habitat) may be more important than area.

According to Shaffer (1981), two drawbacks to using biogeographic distributional data to infer MVP size are neglect of critical habitat data and inability to infer rates at which different sized populations go extinct.

Minimum viable Metapopulation size

Finally, I would like to mention the work of Hanski et al. (1996). They define the concept «minimum viable metapopulation size» (MVM) as the minimum number of interacting local populations necessary for the long-term persistence of the metapopulation. In addition, it is useful to consider the minimum amount of suitable habitat (MASH) necessary for metapopulation persistence, because generally not all suitable habitat is occupied simultaneously by a metapopulation persisting in balance between local extinctions and recolonizations. In the metapopulation context, one has to ask questions about extinction due to permanent loss of habitat (-described earlier as the «declining-population paradigm» in Caughley 1994), whereas the concept of MVP is often applied to (small) local populations threatened by extinction for reasons other than systematic environmental change (described earlier as the «-small-population paradigm» in Caughley 1994).

Levin's (1969) metapopulation model suggests that MASH can be estimated by the fraction of empty patches in a network in which the metapopulations occur at a stochastic steady state. Hanski et al. (1996) discussed three reasons why this rule of thumb is likely to give an underestimate, and possibly a severe underestimate, of MASH: the rescue effect, colonization-extinction stochasticity and nonequilibrium (transient) metapopulation dynamics. The assumption that metapopulations occur at a steady state, common to many models, may be frequently violated because of the high rate of habitat loss and fragmentation in many landscapes. Scores of rare and endangered species may already be «living dead», destined to extinction because extinction is the equilibrium toward which their metapopulations is moving in the present fragmented landscape. To conserve these species, we should reverse the process of habitat loss and fragmentation.

CONCLUSION

A commonly voiced justification for preserving a particular obscure and apparently insignificant species is that species are interconnected in subtle ways, and we are likely to precipitate a cascade of extinction (e.g. Vaughn 1983). The focus primarily on MVP of single species obviously carries the potential for suggesting conflicting research programs. If the focus is too heavily on «magic numbers» and rules, this conflict will become intense. However, precisely because many species are linked together, there are many cases in which conservation of one species will automatically entail conservation of many others.

In each instance, an understanding of the habitat and biology of the interacting species should allow conservation scientists to make a good estimate of what must be done to save the system, but simply focusing on the numbers that would constitute an MVP of any one interactant would be at best an inefficient approach, at worst extinction would ensure. Boyce (1992) argued that to derive statistically reliable estimates for MVP is clearly a difficult if not impossible task. But it can be an even tougher task to extrapolate from the MVP into estimating the area of habitat necessary to support such a population, which requires a detailed understanding of a species' habitat requirements (Boecklen & Simberloff 1986). Patches of habitat must not only be larger than some critical size, they must also be in a suitable geometric configuration to ensure dispersal among habitat units (management for spotted owls *Strix occidentalis* (Thomas et al. 1990) provides a complex case study).

Basic ecology is just as challenging and as necessary as systematics for progress in most of the biological areas, including conservation. Sound conservation science must be founded on autecologial studies of individual systems. And just as for systematics, basic ecological studies also need academic scientists and funding agencies to support them, bearing Soulé's (1987) words in mind: There are no hopeless cases, only expensive cases.

ACKNOWLEDGEMENTS

I thank Jon Swenson for correcting the English.

SAMMENDRAG

En kritisk gjennomgang av debatten omkring minimum levedyktig populasjonsstørrelse

Et alminnelig forsvar for å bevare en sjelden eller tilsynelatende ubetydelig art, er å hevde at den er forbundet med andre arter på spissfindige måter slik at vi risikerer en dominoeffekt i utryddelse dersom det skjer arten noe. Fokusering på minste levedyktige bestander (MVP) av enkeltarter, vil derfor kunne ha et potensiale i seg til å foreslå langt mer omfattende forskningsprogrammer. Dersom en fokuserer for mye på «magiske tall» (50/500) og regler, vil denne konflikten kunne bli svært intens. Siden mange arter er nært forbundet, finnes det flere tilfeller hvor bevaring av én art automatisk vil føre til bevaring av mange andre. En forståelse av habitatet og biologien til de arter som virker sammen, burde gi bevaringsbiologer muligheter til å gi gode estimater av hva som må gjøres for å redde systemet. Dersom en bare fokuserer på antall individer som trengs for å opprettholde en minimum levedyktig bestand, vil det i beste fall være en lite egnet tilnærming og i verste fall vil utryddelse bli utfallet. Å utlede statistiske pålitelige estimater for minimum levedyktig bestand er svært vanskelig, kanskje helt umu-

lig, men det vil være enda verre å ekstrapolere fra minimum populasjonsstørrelse til beregninger av hvilket areal som er nødvendig for å forsyne en hel populasjon. Til det kreves det en detaljert forståelse av hvilke krav en art setter til habitatet. Områdene må ikke bare være større enn en viss kritisk størrelse, de må også inneholde en passende geometrisk konfigurasjon slik at utveksling av individer mellom de ulike populasjoner blir sikret.

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