OIKOS 55: 75–81. Copenhagen 1989

Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments

Tormod Vaaland Burkey

Burkey, T. V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. – Oikos 55: 75–81.

Is a single large or several small reserves (SLOSS) the optimal reserve strategy? A stochastic simulation model of extinction in nature reserves is presented. The model yields clear guidelines for minimizing the probability of stochastic extinction in reserves.
Simulation time is crucial to how the risk of extinction changes with fragmentation. For short to moderate time spans the probability of extinction increases exponentially with the degree of fragmentation. When the time span considered is long enough relative to the size of the reserve, the relationship is sigmoidal. With increasing time span or decreasing reserve size the curve gets steeper. Eventually only the sheer incline and ensuing plateau of a truncated sigmoidal curve remains. Consistently, a species is more likely to survive in a continuous tract of natural habitat than in one that is subdivided into isolated parcels. Migration can greatly reduce the extinction probability of species in fragmented reserves.
The persistent disagreement in the SLOSS debate is discussed, and an attempt is made to explain why conflicting recommendations have emerged.

T. V. Burkey, Div. of Zoology, Dept of Biology, Univ. of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo 3, Norway.

Introduction

The question of whether a single large or several small reserves (SLOSS) is the best strategy for refuge design was first posed by Diamond (1975) and Wilson and Willis (1975), and has since become a matter of considerable controversy.

SLOSS has been formulated alternately in terms of maximizing species richness or in terms of minimizing extinction rates. Diamond (1976), Järvinen (1982), and Hubbell and Wright (1983) have all questioned the appropriateness of species richness as a measure of conservation success. "Species must be weighted, not just counted; the question is not which refuge system contains more total species, but which contains more species that would be doomed to extinction in the absence of refuges." (Diamond 1976). Consonantly, I present a viability analysis of a single, hypothetical species, and I will briefly discuss the utility of this approach in regard to different conservation goals.

I have developed a simulation model with density dependent reproduction and survival to study the probability of a species going extinct in reserves with different degrees of fragmentation but the same total area. The model deals only with extinction due to demographic stochasticity – the changes in population size brought about by random mortality and reproduction. It was my objective to determine whether species are more prone to stochastic extinction in patchy or continuous reserves, to describe the probability of extinction as a function of fragmentation, and to suggest an explanation for the relationships discovered. The model allows individuals in fragmented reserve systems to migrate between patches, and I describe the effects of inter-patch migration on extinction rates.

The model

The model is a stochastic analog to the discrete logistic growth model. It simulates the dynamics of a population

---

Accepted 31 October 1988

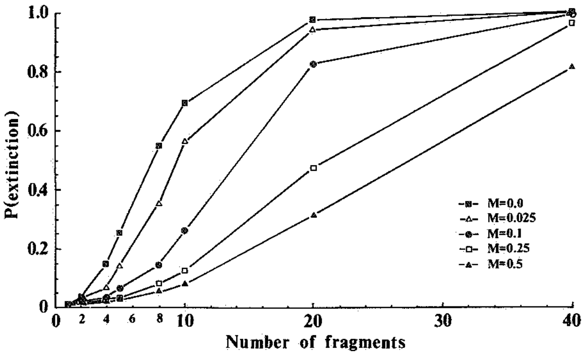

Fig. 1. The probability of extinction as a function of habitat fragmentation, ε(f), for different inter-patch migration rates, M. Each point represents the number of extinctions in 100 reserve systems (i.e. all patches extinct), averaged over 5 replicate simulations. In order to reduce simulation time, all simulations are of relatively small populations run for 50 time steps. The population parameters $B(N) = 0.8e^{-0.0005N}$, $S_1(N) = 0.8e^{-0.0052N}$, and $S_2(N) = 0.5e^{-0.0005N}$ yield an overall carrying capacity $K = N_0 = 40$ for all systems, regardless of fragmentation.

of N_0 individuals (initially) that are evenly distributed in a habitat mosaic consisting of one or more identical patches. The total size of the reserve system is given by its overall carrying capacity, K (defined as the population size for which the expected population growth rate is 1.0).

Expected birth rate, B(N), first-year survival, $S_1(N)$, and adult survival, $S_2(N)$, are all density-dependent negative exponential functions of the form $P(N) = P_0e^{-k_fN}$, where k_f is a constant determining how quickly the value of each parameter decreases with N – in a reserve consisting of f fragments. P_0 is a constant in the interval (0,1). Each reserve fragment has a carrying capacity of its own, $K_f = K/f$, implemented by setting $k_f = k_1f$, were k_1 is the k_f for an unfragmented reserve. The expected population growth-rate $R(N) = B(N)S_1(N) + S_2(N)$ is also a negative exponential function. The actual growth rates, survival rates, and birth rates are stochastic around their expected values at the actual population size N.

Migration between patches in a reserve system is also stochastic, albeit density independent. Migration rate, M, is defined as the the probability, per time unit, that an individual will migrate to one of the other patches in the reserve system. The unit of time is equivalent to the time from one "reproductive season" to another. At every time step, each surviving adult individual may give birth to another individual, and it may migrate to a connected patch. For every animal in a reserve, a random number $s \in (0,1)$ is generated. If $s > S_i(N)$, where $i = 1$ for subadults and $i = 2$ for adults, the animal dies. For survivors, the test is repeated for reproduction $(b < B(N))$ and for migration $(m < M)$. For each animal that migrates, a random integer is drawn to determine to which patch it will migrate. Hence fragments in a reserve are effectively equidistant. There is no immigration into or emigration out of a reserve system.

Note that this is not a model to estimate the actual probability of extinction in either type of reserve, but to study the *differences* between extinction probabilities in the different reserve systems. With this in mind, it is clear that factors normally considered to influence species viability – sex ratio, age structure, age at first reproduction, reproductive rate, etc. – are of primary importance to us only in so far as they affect fragmented reserves differently than unfragmented reserves.

Results

Extinction in a model of this kind, as in the real world, is inevitable, so extinction probabilities are only meaningful within a particular time-frame. By manipulating simulation times we can arrive at any extinction probability from zero to unity, regardless of fragmentation or migration. At either end of this continuum the actual size of the reserve becomes all-important and the question of SLOSS is irrelevant.

Except for the trivial cases where simulation times are extremely long or short relative to the size of the reserve, the probability of extinction increases exponentially with the degree of fragmentation (Fig. 1). Since the extinction probability can not exceed 1.0 the graph of ε(f) – the probability of extinction as a function of fragmentation – eventually flattens out, becoming sigmoidal when the time span considered is sufficiently long relative to the reserve size. As simulation time is increased or reserve size decreased, differences in extinction probability are exacerbated and the graph gets steeper (Fig. 2). Eventually it gets so steep that the

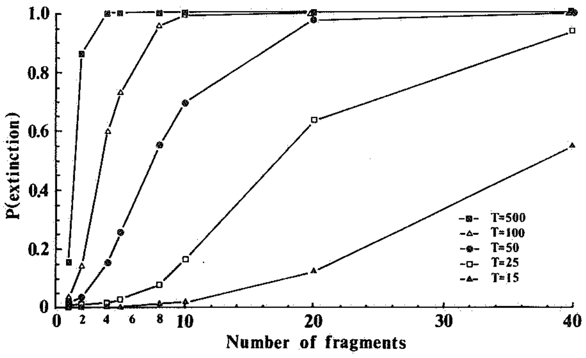

Fig. 2. The probability of extinction as a function of habitat fragmentation for different simulation times, T. In part, the difference in steepness is attributable to the way the arithmetic scale exaggerates the differences in degree of fragmentation as the number of fragments, f, increases. (The transition from 20 to 40 fragments is "stretched" relative to that from 1 to 2 fragments, although both represent a doubling of f). A similar plot on a $\log_2$ scale yields steep almost parallel curves, showing even more clearly the great impact a single doubling of f can have on population viability. This figure can also give some idea of how species persistence changes with degree of fragmentation. Plotting ε(f) for different reserve sizes with simulation time constant, yields similar graphs.

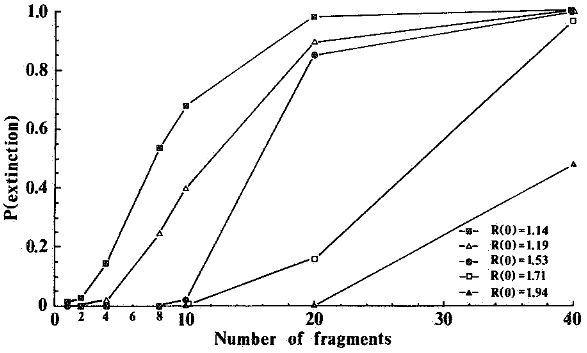

Fig. 3. The probability of extinction as a function of habitat fragmentation, for populations with different expected growth rates, R(N). R(N) is the expected population growth rate, around which the actual growth rate fluctuates on account of stochastic reproduction and mortality. The different growth rates are all negative exponential functions, distinguished by their value for N = 0. All the functions considered intersect at R(K) = 1, where K = 40.

characteristic sigmoidal shape is lost, leaving only the abrupt incline and subsequent levelling off of the upper part of the 'S'.

These results are robust in that they persist regardless of changes in population parameters. No doubt, different population parameters, such as fecundity, longevity, age structure, sex ratio, etc., have an impact on extinction rates in a reserve. They do not, however, change the conclusion that fragmented reserves are more exposed to species losses than are continuous reserves. Only factors that are somehow correlated with fragmentation are relevant in the SLOSS debate. Fig. 3 shows how ε(f) changes for different R(N). Experimenting with environmental stochasticity, by varying the carrying capacity of the reserves randomly over time, it was found that extinction rates increased somewhat, but the characteristic shape of ε(f) persisted. The only factor in the model that can confer some advantage to fragmented reserves, is the occurrence of "natural catastrophes" (The "don't-put-all-your-eggs-in-one-basket" effect).

The graph of ε(f) implies that there are ranges in the degree of fragmentation that are more critical than others. The increase in extinction probability incurred when going from 4 fragments to 8 for instance, may be more severe than from 1 to 2 fragments. The precise location of the steeper section of ε(f) depends, of course, on the species concerned.

Inter-patch migration does not essentially change the shape of ε(f), but it does reduce the slope of the curve. For all practical purposes, a higher inter-patch migration rate yields lower extinction probabilities in fragmented reserves, and hence a shallower slope of ε(f) (Fig. 1). Within any particular reserve system, extinction rate as a function of migration decreases sharply at first, but eventually levels off (Fig. 4). As the migration rate approaches unity the probability of extinction increases somewhat. If we incorporate a cost of migration this effect is magnified. These results are also robust.

A system of 8 patches with a high inter-patch migration rate may suffer fewer extinctions than a system of 5 patches with little or no migration (Fig. 4). Detailed empirical studies will be necessary to determine if similar relationships exist for particular real populations.

Discussion

Modelling fragmentation

No population can grow indefinitely. This is essential in explaining the higher extinction rate in fragmented reserves. Density dependence is a prerequisite for differential extinction between a single large and two (or more) small reserves. Without it, the life and death of each individual is independent of that of its compatriots. Since they are independent, they might as well be isolated from each other. That is, they might as well be in different reserve fragments. Without density dependence, fragmentation has no impact on population viability whatsoever (given an asexual organism that is not particular about its social structure, as long as edge effects and genetic effects are disregarded, and all fragments are subject to the same environmental conditions), and a population in a small reserve will have the exact same growth potential as a similar population in a large reserve.

Järvinen (1982) uses a density-independent model proposed by Pielou (1977) to show that it is "not obvious a priori whether one large or several small populations can be maintained more securely". Had he instead used a density-dependent model, clear predictions in this matter would have emerged.

With density dependence, as in the logistic growth model, a population will every now and then butt against the limits imposed on its growth by the environment. Dividing a population into different subpopu-

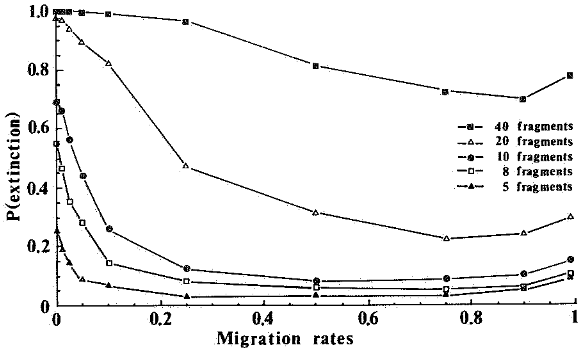

Fig. 4. The probability of extinction as a function of inter-patch migration rates, for reserves that are subdivided into different numbers of fragments. The increase in extinction probability observed in reserves with very high migration rates is due, at least in part, to the fact that "rescue effect" is reduced when the individuals are continuously being moved around between patches. Population parameters are the same as in Figs 1 and 2.

lations in isolated reserve fragments amounts to imposing separate growth limits on each portion of the population. Thus, even when the population as a whole is below carrying capacity, portions of the population may be near their local growth limits and experiencing little or no growth. A particularly illustrative example is when one of two patches has gone extinct while the other is at carrying capacity. This reserve system would have $R(K/2) = 1$, while a continuous reserve at $N = K/2$ would be in a state of maximum population growth.

The essence of this is that fragmented reserves experience periods with low growth rates more often than unfragmented reserves. $N = 0$ and $N = K$ are both such points of non-growth which reduce the viability of a fragmented population relative to that of an unfragmented one. The more fragmented a reserve is, the higher the probability of *single patches* going extinct, since population size in each patch will be smaller. When a patch is extinct it will have zero population growth until recolonization. Thus population growth in the reserve as a whole is reduced, further increasing the probability of global extinction. The lower the migration rate, the longer the average time from local extinction to recolonization, and the higher the probability of overall extinction. In this model, where edge effects and genetics are ignored, fragmentation affects a reserve only when, due to stochastic birth and death, the individuals are unevenly distributed over the different fragments. With density-dependent migration, individuals would leave densely populated fragments in favour of those more sparsely inhabited. Any uneven distribution would thus be more effectively counteracted than in the present model, where the migration rate is independent of population size.

My results are consistent with empirical findings of Fahrig and Merriam (1985), which showed that population growth in white-footed mice (*Peromyscus leucopus*) was lower in isolated woodlots than in connected woodlots. Models by Reddingius and den Boer (1970), and Roff (1974a,b) have also shown that dispersal may have a positive effect on persistence of subdivided populations.

Computer simulation can be a valuable asset in resolving the controversy over SLOSS. Confounding variables, such as habitat differences and edge effects, are easily controlled, and sample sizes and time scales can be chosen at will. I suspect that many of the empirical studies undertaken with reference to the SLOSS debate have been hampered by such factors beyond the control of the researcher. Better than any empirical study, models can uphold the premise of all else equal.

The model presented in this paper does not incorporate genetic effects, whose importance in the SLOSS debate still appears unresolved (see Soulé 1980, Järvinen 1982). Nor does it consider interference from outside the reserve (one of many edge effects), a function of reserve size and fragmentation, as discussed by Janzen (1983). Janzen's argument supports the contention that large, unfragmented reserves are the best conservation strategy. It appears to me that edge effects are likely to have mostly negative effects on the viability of endangered species (but see Stamps et al. 1987, who show that increased edge-to-size ratio stimulates migration). Some species, of course, do well in habitat edges, but these are often second growth species and pioneer species which are not usually the species we are most anxious to conserve, species which would do well even in the absence of reserves (Diamond 1976, Terborgh 1976, Whitcomb et al. 1976).

Factors omitted in our study of the SLOSS question are only critical if their effects correlate in some way with fragmentation. Only factors that favour fragmented reserves can counteract the phenomena I have described in this paper. Incorporating variable sex ratios or a more complicated age structure, for instance, can only reduce species viability in fragmented reserves further, since small populations are more highly exposed to random changes in these parameters.

The SLOSS debate revisited

Several studies (Simberloff and Abele 1976, 1982, Abele and Connor 1979, Gilpin and Diamond 1980, Higgs and Usher 1980, Higgs 1981, Järvinen 1982, Margules et al. 1982) conclude that two or more islands together can hold more species than a single island of the same total size. This conclusion has been based upon either the species-area relationship (e.g. Simberloff and Abele 1976, 1982, Higgs and Usher 1980, Higgs 1981) or on actual species counts on islands (e.g. Gilpin and Diamond 1980, Järvinen 1982). Thus the contention by Diamond (1975) and Wilson and Willis (1975), that a large, unfragmented reserve is the better conservation strategy, has become a matter of controversy.

The design principles suggested by Diamond (1975) and Wilson and Willis (1975), were aimed at minimizing species extinction *after* isolation. This is not necessarily equivalent to maximizing species richness, the focus of the other authors mentioned above (Simberloff and Abele 1976, 1982, Abele and Connor 1979, Higgs and Usher 1980, etc.). The difference is particularly evident when these only consider species richness at the time that the reserve is first established. Higgs and Usher (1980) and Higgs (1981) recognize that their predictions pertain only to total number of species at isolation, and not to future trends due to extinction and migration.

It is interesting to observe that those contributors in the SLOSS debate that focus on minimizing extinction rates (e.g., Wilson and Willis 1975, Diamond 1975, 1976, Terborgh 1976, Fahrig and Merriam 1985) generally come out in favour of large unfragmented reserves. Their opponents are those focussing on maximizing species richness (e.g., Simberloff and Abele 1976, 1982, Järvinen 1982, Margules et al. 1982), claiming that it is sometimes possible to pack more species into a set of smaller reserves (with the exception of Cole (1981)). It seems to me that most of the disagreement in the SLOSS debate emerges because the participants adopt different conservation goals, and concentrate on different stages of the reserves' lifetimes. Once we realize this, the task of finding our way through the SLOSS jungle seems less overwhelming, and it should be easier to coordinate the conflicting recommendations into a comprehensive strategy for reserve design.

The finding that several small reserves can hold more species might be reversed if the patches were completely isolated from other (larger) species pools. Undoubtedly, there are numerous cases where species are only retained in a reserve because it neighbors on large tracts of suitable habitats. Cole (1981) concludes that multiple small reserves may hold more species than a single large only if faunal exchange with a "mainland" source pool is possible. This effect is likely to have played a role in empirical studies in the SLOSS debate. In a world where human activity makes vast tracts of land increasingly inhospitable to other species, such an exchange may eventually be impossible for many species.

There will always be habitat differences in the "real world". Empirical studies (e.g., Gilpin and Diamond 1980, Higgs and Usher 1980, Järvinen 1982) will never be able to exclude habitat differences as the cause of differential species diversity. Theoretical studies based on the species-area relationship and species overlap (Simberloff and Abele 1976, 1982, Higgs and Usher 1980, Higgs 1981) assume either habitat differences, or equal extinction probability for all species. The latter assumption has been forcefully countered by Diamond (1975, 1976), Terborgh (1976), Whitcomb et al. (1976), and Faaborg (1979). I think it will be easier for us to choose the correct strategy in any concrete management situation if we keep fragmentation and habitat differences apart.

Assuming for the moment that different habitat fragments experience relatively similar environmental conditions (see below), if our goal is survival of a particular species, fragmentation of reserves should be as limited as possible; if reserves are patchy, inter-patch migration should be facilitated by means of corridors. If our goal is preservation of an entire community, I suggest that we take the same approach, focusing our viability analysis on particular keystone species and "area sensitive" species with low population densities, such as the top predators. If, on the other hand, our main goal is to maximize species diversity in a reserve, we must consider both the advantage of capturing more species in the system containing highest habitat diversity, and the higher extinction rate after isolation in the most fragmented reserve. If in particular case it will be possible to gather more species in a fragmented reserve system, this should be weighed against the higher extinction rate following such a design choice.

Conclusion – implications for refuge design

Given that our goal is to minimize the risk of stochastic extinction, the presented model shows that random birth, death and migration processes alone yield clear recommendations for reserve design. It shows that a population with density dependent dynamics will experience random fluctuations in population size that may lead to extinction, and that the risk of such extinction is greater if the area in question is discontinuous than if it is not. Even if we manage to eliminate human encroachment and interference, poaching, introduction of "alien" species and the host of other anthropogenous threats to species in fragmented habitats, and even if genetic effects and microclimate changes were unimportant, habitat fragmentation would have severe effects on population viability. As it is, all these factors are superimposed on and magnify the effects of demographic stochasticity. Migration between reserve fragments can do much to delay the inevitable extinction. Hence, reserves should be large enough that the probability of extinction is acceptably low, as unfragmented as possible, and the "designer" should take step to facilitate inter-patch migration where fragmentation is inevitable. The proposed model vindicates the main refuge design principle suggested by Diamond (1975) and Wilson and Willis (1975). Bear in mind, however, that the model (at least as far as it has been employed in this paper) pertains only to extinction due to demographic stochasticity.

Corridors of similar habitats have been suggested as a way of enhancing migration between reserve fragments (Diamond 1975, Wilson and Willis 1975). The design of corridors is virgin territory in conservation biology – empirical studies are needed, and autecological studies will be essential. Edge effects in corridors merit special attention.

Extinction rates fall sharply to begin with as migration is increased from zero, but stabilize at higher migration rates. The indication is that inter-patch corridors can be very useful, but that there comes a point when additional corridors avail us little, so that our efforts should be put towards other ends. However, it is evident that, as fragmentation increases, higher dispersal rates are required to maximize survival (Fig. 4).

Granted, such results from a computer model are insufficient to prove that the same holds true for real species in the wild. Margules et al. (1982) state that "there is little evidence on the effect of immigration and isolation in maintaining species number in reserves". Although we cannot refute such a claim, the model has shown that there is good reason to suspect that insularization has real effects on species viability.

Sadly, in today's world the ultimate causes of extinction, such as persecution and habitat alterations, are still of overwhelming importance – even in nature reserves. Thus, demographic stochasticity may be far less important than other factors affecting survival probabilities in fragmented landscapes (Leigh 1981, Simberloff 1986, Järvinen, pers. comm.). For small populations, however, there is no getting around the impact of demographic stochasticity on species persistence – whether this small population size is initially due to human activity or not (cf. Figs. 2 and 3, and see for example Shaffer and Samson 1985).

In real world management situations the optimal design choice depends on the relative importance of outside interference (Janzen 1983, 1986), microclimate changes (Lovejoy et al. 1983, 1984, 1986, Janzen 1986), social dysfunction (Simberloff 1986) and demographic stochasticity on one side, and environmental stochasticity on the other (see Roughgarden 1979, Soulé 1980, Järvinen 1982, and Simberloff 1986 for deliberations on the effects of genetic stochasticity).

The model proposed by Goodman (1987) indicates that environmental stochasticity may have a drastic effect on population persistence in reserves. This is shown for one rather high value of environmental variance. Goodman concludes that "multiple reserves are preferable to the single large reserve, provided the environmental variation in the separate multiple reserves is at least partially independent, and provided there is at least a small rate of natural or managed recolonization of reserves which experience local extinction". This is equivalent to the results I have seen with the present model when I have incorporated sufficiently high probabilities of "natural catastrophes" (similar to inflicting an environmental source of variance on the population growth rate). With a high rate of natural catastrophes (with at least some inter-patch independence), the spread of risk in a fragmented reserve may be enough to counterbalance the effects of demographic stochasticity. This is not surprising. The question is whether or not the environmental variability in a given habitat is large enough and the inter-patch environmental correlation small enough in the real world. This is an empirical matter which must be investigated thoroughly, and which must probably be assessed in each particular management situation.

In practice, the SLOSS question must always be supplemented with detailed population viability analysis. Discussions of population viability aspects are found in Shaffer (1981), Hubbell and Wright (1983), Shaffer and Samson (1985), Soulé and Simberloff (1986), and Soulé (1987).

It does not follow from my discussion that small reserves are worthless. Small and fragmented reserves may play an important role in conserving local endemics (Terborgh 1974, Terborgh and Winter 1983), especially species with low area requirements (if these are not heavily dependent upon more area sensitive species). Other assets of small reserves are listed in Whitcomb et al. (1976).

Although I feel that general principles for reserve design, based on solid knowledge of population dynamics, are crucial in our struggle to preserve endangered species, I agree whole-heartedly with Simberloff and Abele (1976) that a comprehensive autecological consideration must play an important role in specific management situations. More important than any research, however, is the task of ensuring that refuges in the wild actually get established while there is still time. We all *know* that vast natural refuges are paramount to the future existence of life on earth. It is imperative that we all take active part in safeguarding the species for whose demise we will otherwise be responsible.

Acknowledgements – I thank N. C. Stenseth, R. A. Ims, L. Kirkendall, T. F. Hansen and H. Steen for reading and commenting on numerous drafts of this paper.

References

Abele, L. G. and Connor, E. F. 1979. Application of island biogeography theory to refuge design: Making the right decision for the wrong reasons. – In: Linn, R. M. (ed.), Proc. First Conf. on Sci. Res. in the National Parks. Vol. 1. U.S. Dept of the Interior, Washington, DC, pp. 89–94.

Cole, B. J. 1981. Colonization abilities, island size, and the number of species on archipelagoes. – Am. Nat. 117: 629–638.

Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. – Biol. Conserv. 7: 129–145.

– 1976. Island biogeography and conservation: Strategy and limitations. – Science 193: 1027–1029.

Faaborg, J. 1979. Qualitative patterns of avian extinction on neotropical land-bridge islands: Lessons for conservation. – J. Appl. Ecol. 16: 99–107.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. – Ecology 66: 1762–1768.

Gilpin, M. E. and Diamond, J. M. 1980. Subdivision of nature reserves and the maintenance of species diversity. – Nature, Lond. 285: 567–568.

Goodman, D. 1987. The demography of chance extinction. – In: Soulé, M. E. (ed.), Viable populations for conservation. Cambridge Univ. Press, Cambridge, pp. 11–34.

Higgs, A. J. 1981. Island biogeography theory and nature reserve design. – J. Biogeogr. 8: 117–124.

– and Usher, M. B. 1980. Should nature reserves be large or small? – Nature, Lond. 285: 568–569.

Hubbell, S. P. and Wright, S. J. 1983. Stochastic extinction and reserve size: A focal species approach. – Oikos 41: 466–476.

Janzen, D. H. 1983. No park is an island: Increase in interference from outside as park size decreases. – Oikos 41: 402–410.

– 1986. The eternal external threat. – In: Soulé, M. E. (ed.), Conservation biology: The science of scarcity and diversity. Sinauer, Sunderland, MA, pp. 286–303.

Järvinen, O. 1982. Conservation of endangered plant populations: Single large or several small reserves. – Oikos 38: 301–307.

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. – J. Theor. Biol. 90: 213–239.

Lovejoy, T. E., Bierregaard, R. O., Rankin, J. M. and Schubart, H. O. R. 1983. Ecological dynamics of forest fragments. – In: Sutton, S. L., Whitemore, T. C. and Chadwich, A. C. (eds), Tropical rain forests: Ecology and management. Blackwell, Oxford, pp. 377–384.

– , Rankin, J. M., Bierregaard, R. O., Brown, K. S., Emmons, L. H. and Van der Voort, M. E. 1984. Ecosystem decay of Amazon forest remnants. – In: Nitecki, M. H. (ed.), Extinctions. Univ. of Chicago Press, Chicago, pp. 295–325.

– , Bierregaard, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown, K. S., Powell, A. H., Powell, G. V. N., Schubart, H. O. R. and Hays, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. – In: Soulé, M. E. (ed.), Conservation biology: The science of scarcity and diversity. Sinauer, Sunderland, MA, pp. 257–285.

Margules, C., Higgs, A. J. and Rafe, R. W. 1982. Modern biogeographic theory: Are there any lessons for nature reserve design? – Biol. Conserv. 24: 115–128.

Pielou, E. C. 1977. Mathematical ecology. – Wiley, New York.

Reddingius, J. and den Boer, P. J. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. – Oecologia (Berl.) 5: 240–284.

Roff, D. A. 1974a. Spatial heterogeneity and the persistence of populations. – Oecologia (Berl.) 15: 245–258.

– 1974b. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. – Oecologia (Berl.) 15: 259–275.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: An introduction. – Macmillan, New York.

Shaffer, M. L. 1981. Minimal population sizes for species conservation. – BioScience 31: 131–134.

– and Samson, F. B. 1985. Population size and extinction: A note on determining critical population sizes. – Am. Nat. 125: 144–152.

Simberloff, D. S. 1986. The proximate causes of extinction. – In: Raup, D. M. and Jablonski, D. (eds), Patterns and processes in the history of life. Springer, Berlin, pp. 259–276.

– and Abele, L. G. 1976. Island biogeography theory and conservation practice. – Science 191: 285–286.

– and Abele, L. G. 1982. Refuge design and island biogeographic theory: Effects of fragmentation. – Am. Nat. 120: 41–50.

Soulé, M. E. 1980. Threshold for survival: Maintaining fitness and evolutionary potential. – In: Soulé, M. E. and Wilcox, B. A. (eds.), Conservation Biology. An evolutionary-ecological perspective. Sinauer, Sunderland, MA, pp. 151–169.

– 1987. Viable populations for conservation. Cambridge Univ. Press, Cambridge.

– and Simberloff, D. S. 1986. What do genetics and ecology tell us about the design of nature reserves? – Biol. Conserv. 35: 19–40.

Stamps, J. A., Buechner, M. and Krishnan, V. V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. – Am. Nat. 129: 533–552.

Terborgh, J. W. 1974. Preservation of natural diversity: The problem of extinction prone species. – BioScience 24: 715–722.

– 1976. Island biogeography and conservation: Strategy and limitations. – Science 193: 1029–1030.

– and Winter, B. 1983. A method for citing parks and reserves with special reference to Colombia and Ecuador. – Biol. Conserv. 27: 45–58.

Whitcomb, R. F., Lynch, J. F., Opler, P. A. and Robbins, C. S. 1976. Island biogeography and conservation: Strategy and limitations. – Science 193: 1030–1032.

Wilson, E. O. and Willis, E. O. 1975. Applied biogeography. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Belknap Press of Harvard Univ., Cambridge, MA, pp. 523–534.