



CHICAGO JOURNALS



Conservation Strategy: The Effects of Fragmentation on Extinction

Author(s): Bruce A. Wilcox and Dennis D. Murphy

Reviewed work(s):

Source: *The American Naturalist*, Vol. 125, No. 6 (Jun., 1985), pp. 879-887

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2461453>

Accessed: 15/03/2012 11:24

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

CONSERVATION STRATEGY: THE EFFECTS OF FRAGMENTATION ON EXTINCTION

A recurring topic in the application of population biology theory to conservation is whether a single large nature reserve or several small reserves will protect more species (referred to by the acronym SLOSS; e.g., Simberloff and Abele 1976; Gilpin and Diamond 1980; Higgs and Usher 1980; Higgs 1981; Cole 1981). One of a variety of approaches to this problem recently explored by Simberloff and Abele (1982) considers how subdividing a population affects its probability of extinction or, more precisely, the extinction of newly created, smaller subpopulations. Simberloff and Abele discuss additional considerations bearing on SLOSS, but they only draw specific conclusions using this approach. They conclude that the probability of population extinction is not necessarily greater in several small reserves than in a single large reserve, and they also imply that fragmentation of a single large reserve should not affect extinction rates.

Our purpose is not to reexamine the SLOSS issue *per se*, but to discuss the assertion that effectively states that habitat fragmentation should be innocuous to most species, and therefore need not be a consideration in reserve design. This conclusion runs counter to the prevailing view that habitat fragmentation negatively affects population survival, and thus biological diversity, and therefore should be a prime consideration in conservation strategy (e.g., Janzen 1974; Pictou 1979; Soulé and Wilcox 1980; Lovejoy and Oren 1981; Whitcomb et al. 1981). In view of the increasing interest in the application of biological theory to conservation and the reliance on the scientific literature for guidance in conservation decisions, we feel that this contradiction warrants examination.

This apparent contradiction arises from three sources: (1) the SLOSS problem is not equivalent to, or is at very best a special case of, the problem of habitat fragmentation; (2) the population model Simberloff and Abele (1982) employ is inadequate because it ignores key factors affecting population survival; and (3) Simberloff and Abele's treatment does not consider how the disposition of one species may affect the survival of others, because it is limited to single-species population phenomena and ignores interspecific interactions or community-level phenomena.

HABITAT FRAGMENTATION VERSUS SLOSS

The expansion of land use that accompanies human population growth results in the fragmentation of natural habitat. As fragmentation proceeds, average fragment size and total fragment area decrease and insularity of fragments increases (Moore 1962; Webb and Haskins 1980; Burgess and Sharpe 1981). Habitat fragmentation thus can be described as having two components, habitat loss and insularization, both of which contribute to a decline in biological diversity (Wilcox

1980). This "collapse" of a biota has a temporal component which, judging from studies of land-bridge island faunas (Brown 1971, 1978; Diamond 1972; Terborgh 1975; Wilcox 1978, 1980), ranges from virtually instantaneous to 10^4 years, depending on island size and the taxon (Wilcox 1980; Diamond 1984). Not surprisingly, habitat fragmentation is rapidly becoming a central issue in conservation policy, prompting legislative and regulatory action aimed at mitigating its impacts on biotic diversity (e.g., Cooley and Cooley 1984; Harris 1984), as well as prompting long-term research on its effects (e.g., Lovejoy et al. 1983).

The SLOSS problem implicitly addresses fragmentation from a static perspective; that is, it is limited to systems of existing habitat islands supporting biotas presumed to be at equilibrium. A valid comparison of the species diversity or composition of a set of small "reserves" with that of a large "reserve" requires that the biotas either are not supersaturated as a consequence of prior fragmentation, or will not sustain what amounts to further fragmentation by additional conversion of surrounding habitat. Thus, the conservation problem posed by habitat fragmentation is understanding the collapse process that it precipitates, while the problem posed by SLOSS is determining which of two reserve configurations of equal area supports more species after the collapse. SLOSS is therefore a special case of habitat fragmentation and conclusions from its analysis have limited applicability to the more general problem of habitat fragmentation.

The appearance of "fragmentation" in the title of Simberloff and Abele (1982) and the terminology used in the text cloud this distinction between SLOSS and habitat fragmentation. Particularly misleading are the predictions about the effects of fragmenting intact habitat. These predictions are based on a theoretical analysis of a subdivided population, but the analysis fails to consider the overall reduction in population size that is a result of habitat loss. As Simberloff and Abele (1984, p. 399) correctly pointed out more recently: "subdividing an existing refuge by cutting swaths out of it simultaneously decreases its area."

EFFECTS OF POPULATION SUBDIVISION ON EXTINCTION PROBABILITY

Simberloff and Abele's 1982 analysis, even if applied only to SLOSS as a special case of habitat fragmentation (i.e., no loss of habitat area), nonetheless presents major difficulties concerning how subdivision of a population affects its likelihood of extinction. They consider how the probability of extinction is related to population size by employing a stochastic population model (RDG) developed by Richter-Dyn and Goel (1972). RDG examines the relationship between the ratio of per capita birth and death rates (λ/μ) and the time to extinction for a population. The model shows that when λ/μ is greater than about 1.5, there is a critical population size, $N_c \geq 20$, which, if exceeded, will allow persistence of a population for an immensely long time.

Citing this result, Simberloff and Abele (1982, p. 43) contended that "for most species λ/u [$\equiv \lambda/\mu$] will exceed 1.5 at low population sizes, so if a subdivided refuge had all or even one of its subrefuges with greater than a critical population size N_c for most species, the expected times to extinction for the species in both the archipelago of refuges and the original single refuge would be so large that this

need not be a consideration in planning refuge configuration.” They also list, independently of this, additional considerations not accounted for in the RDG model, but draw no general conclusions except that reserve design ultimately depends upon the idiosyncrasies of the particular natural system under consideration.

Population extinction can occur for at least four basic reasons: demographic stochasticity, environmental variation, genetic stochasticity, and natural catastrophes (Shaffer 1981). Demographic stochasticity, upon which RDG is based, is the main cause of extinction only for very small populations. Leigh (1981) has shown that for larger populations, environmental variation is the main cause of fluctuations in size that lead to extinction. Since RDG overlooks the main cause of extinction for population sizes greater than 20, its conclusion that the survival time for a population is independent of its size when it exceeds 20, in effect, is meaningless from a practical standpoint. Even if it is otherwise correct, RDG alone is insufficient to assess the effects of reduced population size on extinction probability in terms of either SLOSS or habitat fragmentation. Shaffer and Sampson (1985) discussed additional shortcomings of the Richter-Dyn and Goel model and presented empirical evidence that suggests that the above values of λ/μ and N_c may not be applicable even for small populations.

The above application of RDG assumed that the survival of each subpopulation is entirely independent of others. Yet for any population or previously occupied habitat patch there is some probability of either recruitment or reestablishment via migration from other populations (if they exist). Richter-Dyn and Goel (1972) extended their model to incorporate this probability. Simberloff and Abele also cited these results, pointing out that, depending on the migration rate between the subpopulations, the probability of survival “might well be increased by subdivision” of a population (Simberloff and Abele 1982, p. 43).

Unfortunately, this is an inappropriate application of Richter-Dyn and Goel’s subdivided-population model. Their unsubdivided population relates the average time to extinction, T_1 , to the carrying capacity, K^* (see their fig. 3); they do not, however, extend this constraint to their model of an ensemble of populations. Thus, Richter-Dyn and Goel’s analysis does not (nor was it apparently intended to) realistically describe alternative conservation strategies when habitat area is constrained, or even an issue.

To our knowledge, only Wright and Hubbell (1983) have developed a model that specifically addresses this problem. Their results show that a single area supports more species than two smaller areas of the same total size, in the presence or absence of migration. This approach is especially promising in that it avoids uncertainty about the value of λ/μ and is supported by data on the frequency of extinction in some insular bird populations. (Also promising from a practical standpoint is that critical population sizes may be estimated from year-to-year abundance data without resorting to speculation about λ and μ .)

An additional difficulty with the practical application of RDG is the model’s assumption of the lack of complexity in population structure or habitat. Most populations are naturally subdivided, consisting of “populations of populations,” or “metapopulations” (Levins 1970). Furthermore, environmental heterogeneity

normally exists within and among suites of habitat patches supporting metapopulations. This consideration renders the development and application of realistic theoretical models more problematical yet. That these factors increase the risk of extinction from fragmentation, however, is both logical and supported by empirical evidence.

Consider, for example, the currently endangered checkerspot butterfly *Euphydryas editha bayensis*, whose populations have been monitored for 25 yr by P. R. Ehrlich and colleagues. During this time, population structure, dynamics, and regulation have been described and extinctions observed (Ehrlich et al. 1975; Ehrlich et al. 1980). Ehrlich (1965) showed that a purported population supported by three nearly contiguous habitat patches on Jasper Ridge Preserve actually consisted of three demographic units whose sizes fluctuated independently in response to annual changes in rainfall. One of these demographic units became extinct, was reestablished by immigration, and again became extinct several years later. A second is now on the verge of extinction. Meanwhile, populations within dispersal distance (Murphy and Ehrlich 1980) have been increasingly isolated or extirpated by habitat fragmentation.

The case for regarding such local extinctions as "normal" ecological events is strengthened by mounting empirical evidence (e.g., den Boer 1981; Blaustein 1981; Parker and Root 1981; Schoener 1983; Diamond 1984). Natural populations of many species are therefore frequently at a "critical size," even though they may consist of hundreds or thousands of individuals during the years prior to extinction, as in the case of *Euphydryas*. Metapopulations of such species undoubtedly persist via interpatch migration which offsets local extinction. Yet, the apparent capacity of even relatively sedentary species to disperse among habitat patches does not suggest that habitat fragmentation will be inconsequential. Metapopulation survival requires a mean extinction rate less than the immigration rate (Levins 1970). The modification or conversion of natural habitat will more probably impede dispersal than will isolation caused by unsuitable natural habitat.

The risk of fragmentation is thus threefold: (1) demographic units may be destroyed outright, reduced in size, or subdivided (thus increasing their rate of extinction); (2) potential sources of immigrants may be lost (as a consequence of risk 1); and (3) immigration may be impeded by conversion of natural habitat between habitat patches. Note that even though risk 3 occurs without a loss of critical habitat per se, the probability of extinction is potentially increased.

The existence of habitat heterogeneity within and among habitat patches casts further doubt on the validity of predictions concerning the effects of fragmentation based solely on conventional population models. Many workers have shown that within-habitat (microhabitat) heterogeneity has a significant effect on the population dynamics of insects (Andrewartha and Birch 1954; Birch 1957; Ehrlich et al. 1975, 1980; Singer and Ehrlich 1979; den Boer 1981; Murphy et al. 1983) and mammals (Anderson 1970; Birney et al. 1976; Stenseth et al. 1977; Rosenzweig and Abramsky 1980; Cockburn and Lidicker 1983). *Euphydryas* butterflies again provide an apt illustration. Local population extinction, particularly in response to drought, is a rather common occurrence in coastal California habitats of *Euphydryas editha* (Ehrlich et al. 1980; Murphy and Ehrlich 1980). Especially dry years

result in high larval mortality in microhabitats with southern exposures where host plants senesce relatively early. Survival occurs exclusively in north-facing microhabitats under such conditions. The pattern of survival, however, is effectively reversed in particularly wet years. Thus, only habitat patches consisting of a variety of microhabitat exposures sustain populations for more than a few years.

The relationship between the size or number of habitat patches and the probability of extinction for their associated species therefore is not a simple matter of relating population density to habitat area, even accounting for within-habitat differences in carrying capacity. The risk of extinction from habitat fragmentation (or mere subdivision) may not be linearly proportional to the associated reduction in habitat or fragment area and may well increase disproportionately, particularly on the geographic scale at which remedial conservation action is taken.

Simberloff and Abele touch on the genetic implications of population subdivision. We concur that assessing the role of genetic stochasticity is problematic; what was not pointed out, however, is the inconsistency between N_e as predicted by RDG and as predicted by population genetic theory. Along with environmental variation, genetic stochasticity can increase the probability of extinction for populations of far greater size than estimated by RDG on the basis of the effect of demographic stochasticity. An order of magnitude larger could be required to maintain genetic variability and, hence, the capacity of populations to adapt to extreme environmental changes. By the most conservative genetic criteria (Franklin 1980), the effective population size, N_e , must be > 50 , which probably translates to an actual population size in the hundreds for most species. Several different approaches currently produce estimates of N_e in this range and higher (Franklin 1980; Soulé 1980; Shaffer 1981).

COMMUNITY-LEVEL EFFECTS AND SECONDARY EXTINCTIONS

The potential effects of habitat fragmentation on extinction go beyond the sole consideration of population-level phenomena. Even if survival of relatively few species is directly jeopardized by fragmentation, the loss of those species may precipitate multiple extinctions through community-level effects. Terborgh (1976) raised this point previously, arguing that some primary extinctions may represent the loss of species in "keystone" positions in communities. More recently, Gilbert (1980) described cases of elaborate mutualistic relationships in neotropical forests which, if disrupted as a consequence of a single extinction, will result indirectly in a cascade of extinctions amounting to the loss of entire food webs.

Community-level effects caused by the loss of species on land-bridge islands have been demonstrated recently in an extensive study of two mutualistic guilds of hummingbird pollinators and plants (Feinsinger et al. 1982). These workers found that as a result of a decrease in the number of hummingbird species, plants were visited more erratically and with less fidelity. Although further consequences were not documented, Feinsinger et al. suggested, as have Futuyma (1973) and Janzen (1974) previously, that tightly coupled systems would exhibit more drastic effects, including extinctions. Such potentially negative consequences of habitat fragmentation through the disruption of mutualistic guilds are

not limited to tropical forests. Most higher plants, for example, are entirely dependent upon mycorrhizal (root-associated) fungi, which in temperate forests may be in turn largely dependent upon small mammals for their dispersal (Maser et al. 1978). Harris (1984) indicates that the extent to which old-growth forests can sustain further fragmentation without jeopardizing their diversity, functional integrity, and ability to contribute to the regenerative capacity of surrounding logged forests may depend on the minimum habitat sizes and degrees of insularity required for small mammal populations. This and other empirical evidence (see Campbell and Clark 1981; Karr 1982; Lovejoy et al. 1984) suggests that such ripple effects ought to be given serious thought when the effects of habitat fragmentation are considered.

Finally, if there is any doubt that fragmentation of existing nature reserves is not a prudent policy, it is dispelled by empirical data on mammalian population densities in a wide range of national parks and similar protected areas. In separate studies East (1981, 1983) and Schonewald-Cox (1983) have both shown that the sizes of many such populations are less than 100, and more than half are in the range of 100–1000. Thus a substantial proportion of the large-mammal faunas of comparatively large and intact reserves already may be at risk without further fragmentation. These observations lend support to predictions, based on island biogeographic theory, that faunal collapse will occur in (intact) reserves (Soulé et al. 1979; East 1983).

Large mammals might be considered a somewhat biased example since they constitute only a tiny fraction of a biota and are especially vulnerable to fragmentation because of their large body size and trophic needs. The growing list of invertebrates endangered as a result of habitat fragmentation (Wells et al. 1983) suggests otherwise, however. Furthermore, for success, conservation strategy must not be based on *how many* species are maintained given hypothetical reserve strategies; rather, the criterion should be *which* species of those that are rare, threatened, or endangered can be preserved given real options.

When one assesses the risk of extinction associated with fragmentation, one must begin by considering all potentially relevant population-level and community-level factors, as well as physical, or edge, effects (e.g., Brittingham and Temple 1983; Lovejoy et al. 1984; Janzen 1983), whether or not fragments already exist (i.e., SLOSS). That current ecological theory is inadequate for resolving many of the details should not detract from what is obvious and accepted by most ecologists: habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis.

ACKNOWLEDGMENTS

We are grateful to J. Armstrong, J. M. Diamond, D. Dobkin, P. R. Ehrlich, S. Hamburg, R. W. Holm, Y. Iwasa, L. Mueller, J. Roughgarden, M. L. Shaffer, and T. E. Lovejoy for commenting on this manuscript. Support has been provided by the Koret Foundation of San Francisco and by NSF grants DEB 7822414 and DAR 8022413.

LITERATURE CITED

- Anderson, P. K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond. 26:299-325.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Birch, L. C. 1957. The role of weather in determining the distribution and abundance of animals. Cold Spring Harbor Symp. Quant. Biol. 22:203-218.
- Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetation cover to cycles of *Microtus* populations. Ecology 57:1043-1051.
- Blaustein, A. R. 1981. Population fluctuation and extinctions of small rodents in coastal southern California. Oecologia 48:71-78.
- Brittingham, M. C., and S. A. Temple. 1983. How cowbirds have caused forest songbirds to decline. BioScience 33:31-35.
- Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. Am. Nat. 105:467-478.
- . 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Nat. Mem. 2:209-227.
- Burgess, R. L., and D. M. Sharpe. 1981. Introduction. Pages 1-5 in R. L. Burgess and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.
- Campbell, T. M., III, and T. W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. Am. Midl. Nat. 105:269-276.
- Cockburn, A., and W. Z. Lidicker. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, *Microtus californicus*. Oecologia 59:167-177.
- Cole, B. J. 1981. Colonizing abilities, island size, and the number of species on archipelagoes. Am. Nat. 117:629-638.
- Cooley, J. L., and J. H. Cooley, eds. 1984. Natural diversity in forest ecosystems: proceedings of the workshop. Institute of Ecology, Athens, Ga.
- Diamond, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proc. Natl. Acad. Sci. USA 69:3199-3203.
- . 1984. "Normal" extinctions of isolated populations. Pages 191-246 in M. H. Nitecki, ed. Extinctions. University of Chicago Press, Chicago.
- den Boer, P. J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50:39-53.
- East, R. 1981. Species-area curves and populations of large mammals in African savanna reserves. Biol. Conserv. 21:111-126.
- . 1983. Application of species-area curves to African savannah reserves. Afr. J. Ecol. 21:123-128.
- Ehrlich, P. R. 1965. The population biology of the butterfly *Euphydryas editha*. II. The structure of the Jasper Ridge colony. Evolution 19:327-336.
- Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechnie, and L. E. Gilbert. 1975. Checkerspot butterflies: a historical perspective. Science 188:221-228.
- Ehrlich, P. R., D. D. Murphy, M. C. Singer, C. B. Sherwood, R. R. White, and I. L. Brown. 1980. Extinction, reduction, stability and increase: the responses of checkerspot butterflies to the California drought. Oecologia 46:101-105.
- Feinsinger, P., J. A. Wolf, and L. A. Swarm. 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. Ecology 63:494-506.
- Franklin, I. F. 1980. Evolutionary change in small populations. Pages 135-149 in M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Mass.
- Futuyma, D. J. 1973. Community structure and stability in constant environments. Am. Nat. 107:443-446.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11-33 in M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Mass.

- Gilpin, M. E., and J. M. Diamond. 1980. Subdivision of nature reserves and the maintenance of species diversity. *Nature* 285:567–568.
- Harris, L. D. 1984. *The fragmented forest*. University of Chicago Press, Chicago.
- Higgs, A. J. 1981. Island biogeography theory and nature reserve design. *J. Biogeogr.* 8:117–124.
- Higgs, A. J., and M. B. Usher. 1980. Should nature reserves be large or small? *Nature* 285:568–569.
- Janzen, D. H. 1974. The deflowering of Central America. *Nat. Hist.* 21:620–637.
- . 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41:402–410.
- Karr, J. 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. *Am. Nat.* 119:220–239.
- Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* 90:213–239.
- Levins, R. 1970. Extinction. Pages 77–107 in M. Gerstenhaber, ed. *Some mathematical questions in biology*. Vol. II. American Mathematical Society, Providence, R.I.
- Lovejoy, T. E., and D. C. Oren. 1981. The minimum critical size of ecosystems. Pages 8–12 in R. L. Burgess and D. M. Sharpe, eds. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- Lovejoy, T. E., R. O. Bierregaard, J. M. Rankin, and H. O. R. Shubard. 1983. Ecological dynamics of forest fragments. Pages 377–384 in S. C. Sutton, T. C. Whitmore, and A. C. Chadwick, eds. *Tropical rain forests*. Blackwell, Oxford.
- Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, Jr., K. S. Brown, Jr., L. H. Emmons, and M. E. Van der Voort. 1984. Ecosystem decay of Amazon forest fragments. Pages 296–325 in M. H. Nitecki, ed. *Extinctions*. University of Chicago Press, Chicago.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:799–809.
- Moore, N. W. 1962. The heaths of Dorset and their conservation. *J. Ecol.* 50:369–391.
- Murphy, D. D., and P. R. Ehrlich. 1980. Two checkerspot subspecies: one new, one on the verge of extinction. *J. Lepid. Soc.* 34:316–320.
- Murphy, D. D., A. E. Launer, and P. R. Ehrlich. 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia* 56:257–263.
- Parker, M. A., and R. B. Root. 1981. Insect herbivores limit habitat distribution of a native composite, *Machaeranthera canescens*. *Ecology* 62:1390–1392.
- Picton, H. D. 1979. The application of insular biogeographic theory to the conservation of large mammals in the northern Rocky Mountains. *Biol. Conserv.* 15:73–79.
- Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. *Theor. Popul. Biol.* 3:406–433.
- Rosenzweig, M. L., and Z. Abramsky. 1980. Microtine cycles: the role of habitat heterogeneity. *Oikos* 34:141–146.
- Schoener, T. N. 1983. Rate of species turnover decreases from lower to higher organisms: a review of the data. *Oikos* 41:372–377.
- Schonewald-Cox, C. M. 1983. Conclusions: Guidelines to management: a beginning attempt. Pages 414–445 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, Calif.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- Shaffer, M. L., and F. B. Sampson. 1985. Population size and extinction: a note on determining critical population size. *Am. Nat.* 125:144–152.
- Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. *Science* 191:285–286.
- . 1982. Refuge design and island biogeographic theory effects and fragmentation. *Am. Nat.* 120:41–50.
- . 1984. Conservation and obfuscation: subdivision of reserves. *Oikos* 42:399–401.
- Singer, M. C., and P. R. Ehrlich. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. *Fortsch. Zool.* 25:53–60.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–

- 169 in M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Mass.
- Soulé, M. E., and B. A. Wilcox, eds. 1980. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Mass.
- Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect: a model of faunal collapse in the game reserves of East Africa. *Biol. Conserv.* 15:259–272.
- Stenseth, N. C., L. Hansson, A. Myllymaki, M. Andersson, and J. Katila. 1977. General models for the population dynamics of the field vole *Microtus agrestis* in central Scandinavia. *Oikos* 29:53–60.
- Terborgh, J. 1975. Faunal equilibria and the design of wildlife preserves. Pages 369–380 in F. B. Golley and E. Medina, eds. Aquatic research. Springer-Verlag, New York.
- . 1976. Island biogeography and conservation: strategy and limitations. *Science* 193:1029–1030.
- Webb, N. R., and L. E. Haskins. 1980. An ecological survey of the Heathlands in the Poole Basin, Dorset, England. *Biol. Conserv.* 17:281–296.
- Wells, S. M., R. M. Pyle, and N. M. Collins. 1983. The IUCN invertebrate red data book. IUCN, Gland, Switzerland.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Pages 126–205 in R. L. Burgess and D. M. Sharpe, eds. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.
- Wilcox, B. A. 1978. Supersaturated island faunas: a species-age relationship for lizards on post-Pleistocene land-bridge islands. *Science* 199:996–998.
- . 1980. Insular ecology and conservation. Pages 95–118 in M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, Mass.
- Wright, S. J., and S. P. Hubbell. 1983. Stochastic extinction and reserve size: a focal species approach. *Oikos* 41:466–476.

BRUCE A. WILCOX
DENNIS D. MURPHY

CENTER FOR CONSERVATION BIOLOGY
DEPARTMENT OF BIOLOGICAL SCIENCES
STANFORD UNIVERSITY
STANFORD, CALIFORNIA 94305

Submitted December 27, 1983; Revised November 29, 1984; Accepted December 6, 1984