REFUGE DESIGN AND ISLAND BIOGEOGRAPHIC THEORY: EFFECTS OF FRAGMENTATION

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In the extensive literature suggesting application of equilibrium island biogeographic theory (MacArthur and Wilson 1967) to the design of wildlife refuges (references in Simberloff 1982), the most frequent specific recommendation is that a single large refuge will maintain more species than two or more small ones with total area equal to that of the single large one (Wilson and Willis 1975; Diamond and May 1976). Henceforth the question of a single large or several small refuges is represented by the acronym SLOSS. We quickly noted (Simberloff and Abele 1976a) that, in fact, the theory of island biogeography is completely neutral with respect to SLOSS and that, depending on the gradient of colonizing abilities among species in the available pool, the theory can be construed to predict that several small refuges will maintain more species than will one large one of equal area, or vice versa. In short, the theory does not generate a clear recommendation; this is an empirical matter. Abele and Connor (1979), Higgs and Usher (1980), Higgs (1981), and Higgs et al. (1982) all reached the same conclusion on the same basis. Hooper (1971) adumbrated this idea. Preston (1962) did not address conservation issues, but used exactly the same species-area relationship that we did and concluded that number of species on an archipelago as opposed to a single large island is an idiosyncratic matter that does not admit of general laws.

Our observation was criticized (Diamond 1976; Terborgh 1976; Whitcomb et al. 1976) on several grounds; however, as we noted in our rebuttal (Simberloff and Abele 1976b) and as Cole (1981) recently confirmed, none of our critics actually dealt with our argument. Cole (1981) has finally directly addressed our model, and drawn a different conclusion from ours (or rather has placed very different emphasis on the same conclusion). Since there are now abundant data, in addition to theory, relevant to this matter, we wish to return to the question of whether SLOSS has a general answer. At the outset we observe that Cole's (1981) figure 1 and the accompanying text do not bear on this question, because he treats an archipelago of two small islands whose total area is usually much less than that of the one large island. Neither we nor, to our knowledge, anyone else has ever suggested that a smaller total area of any configuration will conserve more species than a larger one, all other things being equal.
Cole suggests that from the standpoint of species richness refuge design is a two-stage process: (1) The colonization stage is the initial decision to preserve specific tracts, with whatever species these contain at the time of preservation. (2) The extinction stage is the subsequent gradual loss of species from these tracts. Cole believes that our argument pertains only to the colonization stage, but we disagree; we explicitly treated both effects.

To study the colonization stage, first we demonstrated that if the species-area relationship were the widely cited $S = kA^z$ ($S =$ number of species, $A =$ area, $k$ and $z$ fitted constants) the total species number for two identical small islands would fall somewhere between $S_s$ (the number of species on one small island), where a well-defined gradient of dispersal and survival capabilities characterized the species pool, and $2S_s$, where no such gradient existed and where competitive interactions prevent many pairs of species from coexisting in the same refuge. If there were no gradient, but competitive interactions were unimportant, we showed the total number of species $S_T$ to be between these two extremes: $S_T = 2S_s - S_s^2/P (P =$ number of species in the pool). Cole repeats the same exercise for the latter case, calculates the same $S_T$, and also agrees with us that the actual total number of species rests on the extent to which a gradient exists in dispersal and survival capabilities. Our strategy was then to compare $S_T$ to $S_s$ ($S_s =$ the number of species in the single large refuge) and our conclusion was that, without the gradient, $S_T$ exceeded $S_s$ for a wide range of conditions, and that whether the gradient for any particular pool would be sufficient to reverse this inequality is an empirical matter for each pool. We drew identical conclusions for archipelagoes of more than two refuges, always maintaining total archipelagic area equal to that of a single large refuge.

Cole (1981) takes a particular gradient of colonizing ability, the geometric series, and finds that an archipelago of two small islands will contain more species than a single large one if and only if both the archipelago and the single large island contain but a small fraction of the species pool. Since such areas are inappropriate as permanent wildlife refuges (p. 637), he concludes that "fragmentation of a potential refuge . . . might be the wrong management strategy." We agree; it might. On the other hand, it might not. As we said in 1976, this is an empirical matter, and must be addressed anew for each taxon and region. What is surprising to us is that, for a majority of cases examined to date, it is the right strategy (see below).

THE EXTINCTION STAGE

Cole says that our 1976 argument addressed only the colonization stage, but we explicitly dealt with extinction as well: "There is a limit beyond which subdivision produces refuges and, therefore, population sizes so small that extinction rates are greatly increased . . . . On demographic grounds one may predict that the increase in extinction rates with decrease in population size will be particularly rapid below some 'critical population size'" (Simberloff and Abele 1976a, p. 286). The details of the model predicting a critical population size are not important in understanding the general implications for SLOSS. MacArthur and Wilson (1967) first pro-
posed the notion of a critical population size, and Richter-Dyn and Goel (1972) produced a more realistic model. Shaffer (1981) reviews the literature. Richter-Dyn and Goel (1972) conclude that there are two general patterns. First, if the per capita birth rate ($\lambda$) and death rate ($\mu$) at small population size are such that $\lambda/\mu \geq 1.5$, there is a critical population size $n_c$ that is not very large (usually $\leq 20$) such that once $n_c$ is achieved extinction is very unlikely and expected persistence time immensely long. For a population with $\lambda/\mu = 1$, there is no such critical size $n_c$, and it is not unlikely that a population will become extinct in a reasonable time even if it has once approached the environmental carrying capacity. Figure 27 of MacArthur and Wilson (1967) provides the clearest depiction of this state of affairs.

We believe that for most species $\lambda/\mu$ 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. The exact expected time to extinction in the two situations requires the entire probability density functions for time to extinction and these are not available, but Richter-Dyn and Goel (1972) explore the case where $\lambda/\mu \geq 1.5$ and there is either one large or several small populations (same total). They conclude (pp. 421–422) that, depending on the migration rate of individuals between the small populations, the expected persistence time for the species as a whole might well be increased by subdivision into several small populations. Other considerations, such as inbreeding, were absent from this exercise.

Whether the Richter-Dyn and Goel model or any other predicting a minimum critical size faithfully models nature is not known. The most straightforward test would be an experiment, but only Crowell (1973) with rodents has attempted such a laborious approach, and he had too few replicates to generate a clear result. An easy but much less convincing demonstration would consist of simply scanning a large list of islands or refuges to see if, for each species, there is some “minimum critical area” below which the species is almost never found and above which it is almost omnipresent. This exercise has been systematically done by Heatwole (1975) for Pacific herpetofauna, Moore and Hooper (1975) for British birds, Forman et al. (1976) for New Jersey birds, and Cole (1982) for Florida mangrove ants. Perhaps only for the latter study is there a sufficient number of islands clearly identical in habitat but different in area for one confidently to ascribe species’ presence or absence to areal and not habitat differences. Diamond (1975a) describes minimum areas for New Guinean birds but has not published the results.

Finally, since extinction as a function of population size is a stochastic event, and since population size depends not only on area but on density as well, one would rather know the average population density (and variance) for each species on islands of different sizes. Haila and Järvinen (1981) call this function a “prevalence function” and construct it for two warblers. Whether the concept of minimum area is sufficient to generate realistic predictions about refuge performance, or whether we must use an elaboration such as a prevalence function, is
irrelevant to our general conclusion: How population size is related to area, and extinction probability to population size, determines whether one large or several small refuges will generate the lower extinction rate. Both of these relationships are species-specific, fundamentally empirical, and very poorly known for virtually all species.

We have now outlined how our original considerations encompass the effects of both colonization and extinction, and have concluded once again that the workings of both processes with respect to SLOSS rest on empirical data that have rarely, if ever, been gathered and brought to bear on the issue. So the reductionist approach has been unable to produce convincing refuge design guidelines. There is, of course, another possible approach to the same question. One could omit the reductionist models completely and simply ask of the data: Does one large site or several small ones of equal total area actually contain more species, for whatever reason? Since we are dealing with a practical as well as theoretical matter here, and have been admonished that the urgency of conservation to some extent obviates the need for scientific rigor in our models (e.g., Soulé 1980, pp. 167–168), perhaps this is the best tack, especially since some data have now been analyzed in this way. Before we turn to them, however, we briefly catalog several factors that neither Cole’s models nor ours treat, but that clearly bear heavily on refuge design (Simberloff 1982).

OTHER RELEVANT CONSIDERATIONS

1. The entire above discussion rests on the view that what one most aims to do is to maximize the number of conserved species. Cole (1981, p. 631) is explicit: “From the standpoint of conservation and the design of wildlife refuges one wishes to preserve as many species as possible.” To us it is not clear that this is usually the conservationists’ goal. We are not addressing whether it should or should not be the goal; we are only observing that other goals are often stated. Frequently the aim seems to be preservation of a specific species, and not maximization of diversity. Some of our opponents in the SLOSS debate have themselves taken this very viewpoint. Diamond (1976, p. 1028), for example, says, “conservation strategy should not treat all species as equal but must focus on species and habitats threatened by human activities,” and (p. 1028) “species must be weighted, not just counted.” To the extent that one is interested in specific species and not just the number of species, dynamic equilibrium theory does not apply directly, though such subsidiary notions as minimum area may still be useful. We suspect that the primary requirement would usually be presence of appropriate habitats for the target species.

2. Diamond (1975b) is explicit that his reasoning applies only to refuges in a homogeneous habitat, but in some sense no habitat is completely homogeneous and no two refuges would ever be identical in habitat (Higgs et al. 1982). It is an ecological maxim that all species are somewhat restricted in habitat requirements (e.g., Connor and McCoy 1979) so that the number of species on an island or in a refuge is probably chiefly determined by the number of habitats (e.g., Watson 1964). Even where area is the best predictor of number of species, the usual
assumption is that increasing area represents increasing subtle habitat diversity (Simberloff 1974; e.g., Game and Peterken 1981). Even if sites were randomly chosen, rather than selected so as to maximize diversity, it is likely that a group of separate sites would encompass more habitats than would one large site of equal area, and thus would contain more species. Game and Peterken (1981) find exactly this situation for plant species in Lincolnshire woods. If one set out deliberately to maximize habitat diversity, the same argument should apply a fortiori; Kitchener et al. (1980) believe that for this very reason a group of small refuges in Australia contain all the lizard species that would be found in a single large refuge of vastly greater total area.

3. Cost of acquisition per unit area may differ systematically with area of sites. To us it seems that it would probably cost more to purchase one large piece of land rather than several small ones of identical habitat, all other things being equal. Game and Peterken (1981) suggest the opposite. For England, Hooper (1971) finds a critical area of 32 ha, below which price is a decreasing function of area and above which price is constant. Certainly if the small sites were specifically selected for their locations and/or habitats, the per unit area price might increase. In any event, it is not likely that these costs will be identical for the two strategies.

4. Genetic considerations would indicate that if the subrefuges in the archipelago were too small, inbreeding depression could become severe. Franklin (1980) suggests that a minimum effective population size of approximately 50 would usually suffice to stanch the dangers of inbreeding depression, but that the amount of genetic variability required to maintain the long-term capacity for rapid major evolutionary change would necessitate perhaps 500 individuals. Whether major evolutionary change is something we are concerned about in conservation is questionable, as Franklin (1980, p. 136) observes. Further, Berry (1971) examined the same problem and concluded (pp. 199–200) that "It is extremely unlikely that any natural management procedures could significantly affect the amount of variation in a local population to the extent of making the population unable to respond to environmental change." To the extent that inbreeding depression were problematic, and if population densities were equal, one large refuge would be better than several small ones. Density increases on small insular habitats are known for both birds and mammals (MacArthur 1972, p. 118) and may counteract this advantage.

5. Management cost, including staffing, would probably be less for one large than for several small refuges.

6. One may generally suppose that catastrophes like epizootic diseases, fires, and introduced predators, parasites, or competitors would pose a lesser threat to the archipelago of small refuges than to the single large one, by virtue of limiting the fraction of the conserved area exposed to the catastrophe. Simberloff (1978) has pointed out that the Seychelles Islands have lost only two of 14 endemic bird species despite two centuries of fires, introduced predators, land-clearing, and other anthropogenous insults. This is probably because the archipelago consists of several small islands instead of one large one, and it is quite possible that with only one island virtually none of the endemic avifauna would have survived. Simon and Géroudet (1970) depict the extinction of the heath hen (Tympanuchus cupido) in
which the population's last 25 yr were spent in one refuge on Martha's Vineyard. Two salient events in this setting that led to its extinction were a fire in 1916 and a disease in 1920; both catastrophes could not have ravaged the population had it been maintained in two or more isolated refuges.

7. Failure to consider economic and social consequences of refuge design suggests a certain arrogance. It is particularly overbearing for North Americans to lament the destruction of the tropics and to plead for the preservation of huge tropical tracts, without careful consideration of what is to be done with the people who inhabit these tracts or depend upon them for their existence. Clear-cutting and slash/burn techniques are undesirable but alternatives may not be apparent to a rural family of 12 in the tropics. Even less apparent to them will be the raging controversy over SLOSS. Any realistic refuge design scheme must incorporate financial compensation and deal also with the social ramifications of sequestering land. Coe (1980) discusses this matter in detail for Africa.

RELEVANT DATA

Whatever the merits of the reductionist arguments summarized in the first part of this paper, one may ask whether actual data on SLOSS generate a pattern. We believe they do.

To our knowledge, the only direct experimental test is that on arthropods of Florida mangrove islands, which is still in progress and which we mentioned in our first paper. The result we reported then was that of two islands, each rendered into archipelagoes by channels cut through them, one (the larger) had the total number of species for the archipelago slightly exceed that for the original island, while the other (the smaller) produced exactly the opposite result. We note that Cole (1981) mentioned only the first of these islands, and that his explanation, that the number of species in the archipelago is but a small fraction of the species pool, is belied by the result on the second (smaller) island. We said (Simberloff and Abele 1976a) that one explanation might center on the minimum population size concept, that the sub-islands of the smaller archipelago might have been sufficiently small that many species fell below their critical population sizes, and that no data exist to test this hypothesis. Except for the ants (Cole 1982), data are still absent.

All other attempts to address SLOSS have been inferential: Lists for both large and small islands are compiled, then the lists for a group of small islands are merged for comparison to the list from a large island of area equal to the total area for the small ones. One assumes habitat diversity is equal for the two configurations, but this is probably not true. However, this assumption is at least as likely to be violated if one is actually designing refuges (Higgs et al. 1982), so if we are interested in the practical consequences of a design criterion, perhaps the inferential studies are useful.

Abele and Patton (1976) find for crustaceans on coral heads that pairs of small coral heads have more species than a single large one, while for larger coral heads ($S_c/P = .175$) there is no consistent difference between pairs and a single still larger one of equal total area.

Forman et al. (1976) conclude that, for New Jersey forest birds, single big forest
patches contain more species than do several small patches of equal total area, but
the data (R. T. T. Forman, personal communication) from which the conclusion is
drawn do not support it; in fact, the null hypothesis of no effect of degree of
habitat fractionation is not falsified (Simberloff 1982). Similarly, Nilsson (1978, p.
26) concludes for birds and plants of Swedish islands that “very large reserves,
instead of several small ones of a similar combined area, are necessary,” while
later (p. 27) conceding that his own data do not support this conclusion. Simberloff
(1982) plots Nilsson’s data and finds for neither taxon any evidence that one large
island supports more species than several small ones. Lynch and Whitcomb (1980)
purport to remedy the shortage of empirical data in the SLOSS controversy, but
never actually address the question. Rather, they report avifaunal change in a
number of small forests near Washington, D.C. All these forest patches are
surrounded by increasingly disturbed nonforest habitats, and Lynch and Whit-
comb concede that they cannot identify the relative contributions of area, isola-
tion, and disturbance to extinction rates. Their only directly pertinent statement
on SLOSS is that certain unidentified species never occur in small forests, while
there are no species precluded from large forests.

Higgs and Margules (1981) use data from Brown (1978) for birds and mammals
on mountaintops in the Great Basin and find that two small mountaintops usually
encompass more species than one large one does. For breeding land birds, mams-
als, and higher plants of Yorkshire, they compare successively larger
groups of 10-km squares and find that either single large areas or two small ones
can contain more species. For plants in Lincolnshire woods, by contrast, Game
and Peterken (1981) find that a single large woods usually contains fewer species
than two or more small ones of equal total area, even if the latter are randomly
chosen. Higgs and Usher (1980) similarly find for plants of Yorkshire limestone
pavements, chalk quarry reserves, and lowland heaths, and Scottish soft coastal
habitats that two or more small sites generally contain more species than one large
one, with total area equal. Malyshev (1980) came to the same conclusion for plants
of several regions.

Kitchener et al. (1980) observe for lizards in the Western Australia wheatbelt
that the most important predictor of species richness is number of vegetation
associations and conclude that the notion of one large refuge rather than several
small ones is wrong: “The signal statement to be made ... is that while scattered
small reserves, totalling 1.78 × 10^6 ha, contain almost all known lizard species in
the central and southern wheatbelt, a single area in this region, having the
characteristics of these reserves, in order to contain the same number of lizard
species would need to be immensely larger—possibly by a factor of 600” (p. 44).
They note the lack of rigor in the response of Whitcomb et al. (1976) to Simberloff
and Abele (1976a), and support our claim that the contention that a single large
reserve is optimal rests on extremely shaky grounds.

Finally, Gilpin and Diamond (1980) study lowland forest birds of the New
Hebrides and report that pairs of islands typically contain 5%–10% more species
than does a single island, with total areas equal. This is particularly gratifying to us
since Diamond (1976, p. 1028) dismissed our arguments (Simberloff and Abele
1976a) on SLOSS as “scarcely relevant”.

CONCLUSIONS

A scan of published data that directly address SLOSS shows not a single case where one large site unequivocally excels several small ones, and many where several small ones clearly contain more species than one large one. Neither does the one reported experiment show one strategy to be better than the other. The taxa treated are arboreal arthropods, marine crustaceans, birds, plants, mammals, and lizards, so we agree with Cole (1981) that our earlier results (Simberloff and Abele 1976a) are not a taxonomic idiosyncrasy of arthropods. The data do not support "the major conclusion of [Cole's] paper . . . that the larger refuges or islands generally will preserve more species than a series of small refuges of equivalent total area" (Cole 1981, p. 637). In fact, they lead to the opposite conclusion. Furthermore, Cole's suggestion that the several small refuges have more species than one large one only when the number of species in the archipelago is a small fraction of the species pool is also wrong. The studies of, inter alia, Kitchener et al. (1980) and Gilpin and Diamond (1980) did not deal with small fractions of the respective species pools, but rather with about as substantial a fraction as one would likely ever be able to attempt to preserve by establishing refuges.

Since conservation is a practical and urgent matter and our contention all along has been that design criteria for refuges are both idiosyncratic and empirical, we suggest that the clear message of the data suffices as an ending to this tale and it is not of great importance to explain why Cole's model led him astray. A promising place to start might be in his assertion (p. 632) that the geometric model on which he bases his conclusion "captures much of the variability of more complicated models." Perhaps it does not capture much of the actual distribution of colonization abilities. Another might be that it does not treat the relationship between population sizes and expected times to extinction. Again, the considerations of habitat diversity and the effects of catastrophes, discussed above, generally militate for several small rather than one large refuge and are not incorporated in Cole's or other models. It is scarcely conceivable that a general model could include all these forces, and it is likely that others that we have not considered will also affect species richness in refuges. So we are led to our original conclusion (Simberloff and Abele 1976a, p. 286): "This is not a plea, then, for a specific conservation regime, but rather for a more comprehensive autecological consideration."

SUMMARY

Cole's theoretical conclusion that one large site generally contains more species than several small ones of equal total area is falsified by data in the literature, as is his contention that exceptions will only occur when the species in the sites are but a small fraction of those in the species pool. For a variety of taxa, for a number of different habitat types, and for a wide range of sizes of the biota as a fraction of the pool, either there is no clear best strategy, or several small sites are better than one large site. Since there are numerous idiosyncratic biological considerations,
plus a number of nonbiological ones that bear heavily on refuge design, it is unlikely that a general reductionist model can generate useful predictions or advice on this matter.

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LITERATURE CITED


