

More Fuel for the Fragmentation Fire: A Reply to Bratton and White

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We welcome the comments of Susan Bratton (*Park Science*, Winter, 1986) and Peter White (Spring issue) on our essay concerning island biogeography theory and its use in the strategy of nature reserve acquisition. We would like to amplify some of their points, and observe that the scientific and policy questions involved are rather different.

The philosopher Karl Popper (1972) has labelled the scientific process as "conjecture and refutation". The conjecture that has been offered to conservation biologists is that a given amount of habitat (in this case, nature reserves) subdivided into a large number of small units ("fragmented") will contain fewer species (Diamond 1975, Sullivan and Shaffer 1975) and will have a greater probability of extinction for susceptible species (Shaffer 1981, Wilcox and Murphy 1985), than will the same total area concentrated into one or a few large units. It is this conjectured principle of nature that we have set out to test.

Although the regular species-area curves observed on islands stimulated the conjecture, it does not actually follow from the resulting theory, as Simberloff and Abele (1982) have pointed out and we illustrated by our hypothetical archipelagos. The general effect of fragmentation (many small units) on diversity is therefore an empirical question.

As far as we know, the experiments that we reported are the first *experimental* tests of the effects of fragmentation on diversity. As Bratton observes, their applicability to parks can be debated on the basis of their size and the choice of species. A variety of "natural experiments," using islands or stands of natural vegetation, is now in the literature (reviewed by McLellan et al. 1986), with species and spatial scales of greater relevance to conservation decisions, but poorer control of other confounding variables. Few tests have been conducted using National Parks or other conservation areas. Bratton, Miller and White's work in the East, and ours in the Western Region, are attempting to fill this gap.

Bratton and White express cautions on interpretation of our work. Most we offered in different language in our essay. However, our main objective was to test the proposed ecological principles involved, not to make predictions for actual management decisions. Nevertheless, it should be remembered that:

1) Choice of scale and species

Our experiments are model systems, conducted on a small scale and using species of limited direct conservation interest. The response of conservation targets to the fragmentation of natural landscapes obviously could be quite different from that of the "weedy" species common in our experiments. The

terrestrial experiment mimics the process of reserve formation in that "parks" were carved out of a continuous landscape, but the marine experiment involves colonization of new areas.

2) **Habitat diversity**

That a collection of small areas generally appears to contain more species than a comparable large area may have a variety of causes, notably habitat diversity, having little to do with reserve or island size alone.

3) **Extinction of conservation targets**

We have analysed the total number of species rather than particular conservation targets, and our results may not hold for the smaller number of species threatened with extinction. In particular, White raises the conjecture that there may be some rather large (circa 500) "minimum viable population size" for large rare animals, below which populations may be rapidly lost from habitat "fragments." It is also possible that inbreeding and loss of genetic diversity could cause long term declines.

4) **"Faunal collapse"**

The results observed in our studies and others like them may not reflect long term diversity patterns because species are more likely to go extinct in "fragmented" habitats during "faunal collapse."

All these processes occur, whether or not they are relevant to the scientific question we set out to address. However, several deserve additional comment.

The use of experimental models is common in science – witness *Drosophila*, *E. coli*, and white laboratory rats. They may be used to reject universal theories, but can not prove generalizations. That is the situation with our study. Experiments with varying National Park system designs and endangered species are infeasible (and probably immoral). Even the ambitious and admirable World Wildlife Fund experiments in Amazonia (Lovejoy et al., 1984) cannot directly answer the question of the least harmful way to clear the forest – the largest experimental plots are too small and the smallest far too poorly replicated. In any case, the results do not necessarily apply to other ecosystems any more than do other models.

So we are left with inadequate information as the only available substitute for no information. We believe simple experiments can be informative, though never definitive, in outlining processes important on the larger scales inaccessible to experimentation. Diversity appears to be correlated with *increased* fragmentation on larger scales also. The challenge is clearly to evaluate the mechanistic effects of scale and taxon that Bratton and White have raised.

The appropriate choice of scale for our experiments is debatable. If grasses and leafhoppers are reasonable models for trees and birds in parks (which they may or may not be), the numbers of individuals, and accessibility of neighboring "parks" is probably not that different from those involved in many real park populations. Conjectures in the literature about fragmentation effects are notably vague about the scale involved, so experimentation on any relevant scale provides at least a partial test.

The ability of collections of small areas to harbor more species than fewer larger areas could have any number of causes beyond area or perimeter effects *per se*. One raised by both Bratton and White is that

a collection of dispersed small areas could incorporate more kinds of habitat than would fewer larger areas. This is clearly an important part of the explanation for the richer terrestrial large mammal fauna in the combination of Big Bend, Redwood and North Cascades than in the larger area of Yellowstone. We raised the example specifically to illustrate that real park systems in practice do effectively conserve important species in consciously dispersed areas. In fact, we think the very nonrandom placement of small parks and reserves is an important reason to reject the island analogy that has been used to dismiss the effectiveness of numerous small conservation areas.

In other cases, the greater species diversity of more fragmented habitats must have some explanation other than habitat diversity. Small oceanic islands have fewer habitats than large islands – they generally lack montane areas, lakes, rivers, etc. – yet in combination they appear virtually always to harbor more species (Quinn and Harrison, unpublished manuscript). The habitats in our experiments are as homogeneous as can be expected in a natural setting, yet they have many more species in the more fragmented treatments.

White notes that small reserves are more subject to losses on the perimeters, and provides several excellent examples. Collections of small reserves are also more likely to be encountered and settled by migrants, and may provide corridors for movement or invasion of new species. The consequences of perimeter effects, corridors, and buffer zones certainly need more attention.

The effects of fragmentation on the viability and population genetics of threatened populations are more problematical – one reason we addressed only overall diversity in our article. Reserves designed for particular species must be large enough to incorporate the range of movement and resources needed to maintain at least a small number of individuals. The fact that for some species the area involved can be enormous speaks to the need for some very large parks in the system. In more general terms, however, the relationship between reserve system fragmentation and population “viability” is not obvious.

Engineers know it is often less expensive to protect against system failure by making redundant copies of failure-prone subsystems than it is to improve the reliability of single units. The mean time to failure is often proportional to the logarithm of the number of redundant backups, and the probability of short term failure may decrease by factors of millions. If global extinction of a species is viewed as a failure of the conservation system, redundancy, in the form of multiple reserves, may decrease the probability of failure more dramatically than would comparable enlargements of a single reserve area. An example: when the extinction mechanism is an epidemic, isolated populations are likely not to become infected, and to be available to restart affected populations, as demonstrated by Carrick (1963). Conversely, of course, a sufficient increase in failure probability of each subsystem may increase the overall rate of failure in the whole system. Mathematical models can be constructed in which fragmentation either increases or decreases the persistence time of species (Wright and Hubbell 1983, Quinn and Hastings, unpublished manuscript.) Our experiments and the empirical evidence that we have found to date are inconclusive.

The relationship between extinction rate and population size is difficult to document. We know of no documentation of an abrupt threshold “minimum via-

ble population size” beyond the obvious one of a single mating pair. California elephant seals, Laysan teals, and rhinoceroses in South African parks and Kenyan game farms would appear to provide counterexamples. The relationship between the loss of genetic information and reserve system fragmentation is equally problematical. As the populations in individual parks become smaller, local inbreeding and the loss of alleles through genetic drift become more rapid. On the other hand, if there are multiple subpopulations, different variants are likely to be fixed by local adaptation or drift in different places, and the genetic variation throughout the species may be better maintained.

White's final caution about the effects of “faunal collapse,” due to the anticipated slow extinction of species from recently isolated parks, is certainly important, but difficult to evaluate. Even on the land bridge islands formed by post-Pleistocene sea level changes, in which faunal collapse is best studied, the estimates of faunal change (Diamond, 1974) come from present distributions, and are subject to many sources of error (see Lynch and Johnson, 1974). As White notes, the “collapse” is thought to have taken many thousands of years, suggesting that present patterns in new parks and reserves can not be used to investigate the process (Soule et al. 1979). The best we can do is to investigate the post-“collapse” biotas of island archipelagos. All of those we have examined have more species (and more endemics) on collections of small islands than on single large ones. It is of course possible to dismiss the island data as irrelevant because of the specialized biology of island species. Doing so, however, makes the whole matter untestable in our lifetimes, and not worthy of scientific debate (Simberloff and Gotelli, 1984).

Policy implications

The effects of park size and number on diversity and extinction rates obviously are relevant to conservation strategies. Equally obviously, they are not the sole, or necessarily even a principal determinant, of the best management approach, for a variety of reasons admirably summarized by White. We believe that a growing weight of evidence rejects the conventional wisdom that diversity considerations *per se* require establishment of very large parks (see also Simberloff and Gotelli, 1984). It does not follow, of course, that many small parks are the best solution – our view is similar to White and Bratton's – that a mixed strategy of some kind will probably be most effective.

While we agree with White that the best conservation strategy would be to have both more and larger parks and reserves, political and economic realities are likely to dictate more stringent choices. In general, the tradeoff is between marginal increases in size of individual reserves, which decreases their individual susceptibility to biological failures of various kinds, and marginal increases in numbers of reserves, which spreads the risk of total failure over a larger number of survivable units. The risks of fire, contamination, or groundwater catastrophes cited by White can in principle be decreased either by enlarging the area, or by setting aside other similar areas not subjected to the same fires, pollution sources, or drainage. Our research does not address these questions.

We did not suggest in our article that multiple small reserves are preferable to fewer larger ones. To the contrary, the policy of concentrating on acquiring unique habitats, scenery, and important landmarks, reflecting multiple and diverse objectives, appears to

have been an effective conservation strategy, and we urge that it not be dramatically shifted to accommodate fashionable ecological generalizations. Endangered species are undoubtedly best preserved by preserving their habitats and resources, and rain-forest conservation is probably better served by effective lobbying than by pure science. We hope that many large parks ultimately will emerge.

There has been a danger in our experience, however, of denigrating the value of small parks simply because they are small. We have repeatedly encountered claims that targeted areas are "below the minimum critical size" used to oppose conservation efforts. Since the opportunities for the establishment of more very large parks seem limited, it is in numerous smaller areas that our best future opportunities may lie. Dubious ecological theory should not be allowed to derail such efforts.

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