

# Conservation Strategies: Island Biogeography And the Design of Nature Reserves

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**Editor's Note:** Following is a longer than usual article, describing the work of five scientists to determine optimum park size where the main objective is to maximize species diversity. They describe some preliminary findings and the research plan for next year. According to Dr. Quinn, "The controversy we deal with is presently one of the hottest topics in conservation biology and our findings will no doubt add more fuel to the fire."

With the recognition that some large fraction of the world's species is threatened with extinction through development and habitat destruction, the maintenance of the biological and genetic diversity of natural communities is becoming an increasingly important part of conservation strategies. Although zoos and "gene banks" will have a role to play, parks and nature reserves will continue to be the most important tool for managing and preserving the declining number of species and genetic pools.

The logistical difficulties of adequately surveying all of the biota of all potential reserve areas, so that informed choices can be made on purely empirical data, appear insurmountable. Consequently, ecological theory is likely to assume an important role in assessing opportunities for land and species preservation. One of the more promising applications of basic ecology to conservation strategies may be in the analysis discerning between the effectiveness of preserving a few large areas versus utilizing the same resources to acquire a number of smaller tracts, equal in area to the larger ones.

One of the more predictable patterns in nature is a regular relationship between the areas of islands, or other isolated patches of habitat such as mountaintops, and the number of species that they harbor. Typically, the species count increases in proportion to roughly the fourth root of island area. To explain this observation, theorists have developed the "Theory of Island Biogeography", proposing that island biotas may be viewed as persisting in a dynamic equilibrium in which species extinctions are balanced by immigration of new species.

Insofar as parks and refuges can be viewed as "islands" of pristine habitat, separated by areas that are usually unsuitable to threatened species, this research provides a tool for estimating the number of target species that might persist within a park of a particular size, and the rate at which species might be expected to disappear due to unforeseen random environmental or demographic fluctuations in the future.

It does not follow from an increasing species-area curve that a single contiguous area will harbor more species than the same amount of land set aside as a number of smaller reserves. On the contrary, mathematical models and empirical studies in the field and laboratory have often found that subdivided habitats promote regional coexistence of species that would be unable to cohabit single homogeneous areas. On the other hand, it is well established that some populations, often of conspicuous species such as grizzly bears, condors, and other large vertebrate predators, require enormous areas to protect a viable

population, and would not be expected to persist in a fragmented collection of small reserves. Such species are often of special importance in conservation strategies.

As a result, there is no clear agreement among researchers whether a diversity of target species is best protected by emphasizing large acquisitions, necessarily few in number, or emphasizing the number of parks and refuges, at the expense of individual reserve size.

More fundamentally, it is not known, as a matter of ecological principle, whether fragmented habitats are generally richer than comparable contiguous areas, because some populations are always protected by isolation from predators, diseases, competitors, or other species-wide calamities, or whether the large contiguous areas are richer because more complex ecosystems are intact, and particularly susceptible species are buffered from chance extinction.

Our project attempts to provide explicit tests of the effects of subdivision of habitats – size versus number – in several quite different settings. **We are conducting two experiments, one with grassland plants and insects, and another with marine intertidal invertebrates.** We explicitly test in a controllable field setting, whether single large areas contain more species than identical areas subdivided to various degrees. While the tests are admittedly artificial when applied to actual parks, they constitute, as far as we know, the most thorough experiments yet attempted on the possible ecological principles involved.

As a second approach, we have reexamined data from island censuses. Although there are shortcomings in using islands as models for parks, the models provide much of the data and motivation for current ideas on these topics. As habitats have been isolated for long periods of time, they also may provide a better model to patterns expected in the future, than do the still-changing communities of recently isolated parks.

Finally, we have assembled a database of censused species, mostly vertebrates and vascular plants, from National Parks in California, which we will use to examine real-world patterns of diversity as a function of park size and location.

## Does "Island Biogeography" Suggest That Effective Parks Must Be Large?

The regularity of species-area relations in nature has led a number of workers to conclude that parks, like islands, must be large to maximize diversity. While it requires no theory to say that a large park in any given location will be better than a small one, it is not obvious that a single large park is better than two parks each half the size, or 100 one percent the size.

A hypothetical example will illustrate this point. Figure 1 depicts three "island" systems with identical species-area curves (shown in Fig. 1D). The letters denote individual species. The habitat in each archipelago consists, by area, of  $\frac{1}{3}$  small islands,  $\frac{1}{3}$  medium, and  $\frac{1}{3}$  large. By inspection, the agency with the resources to acquire  $\frac{1}{3}$  of the area to maximize existing diversity might choose the large island in Figure 1A, or perhaps the small islands in Figure 1B,

and would have no clearcut choice in Figure 1C.

The "Diamond Isles" (Fig. 1A) represent a situation similar to that suggested by UCLA biologist Jared Diamond for birds of South Pacific islands. The large islands' greater environmental stability, larger population sizes, and diversity provides greater opportunities for specialization. As a result, a few "weedy" species (Diamond's "supertramps") with generalist habits and high dispersal abilities will predominate on the small islands, and the more specialized, unique, and competitively dominant species will be limited to large islands. In this scenario, a collection of reserves chosen from the largest islands will generally yield the most species.

In the "Lack Archipelago" (Fig. 1B – named after the great British ornithologist David Lack) similar species exclude one another, with the winner generally being the species which, by chance, colonizes the island first. The mechanism could be either a "priority effect", in which more abundant species compete more effectively, or perhaps modification of the habitat or ecological community by the first invader, making it less suitable for later species. Here, most of the species are restricted to small islands.

The "Tallahassee Archipelago" (Fig. 1C) is inspired by Daniel Simberloff and his colleagues at Florida State University, who have argued that patterns in island faunas generally do not differ from those expected from chance colonization. If the probability of a species successfully colonizing an island is proportional to its area, the small islands, in aggregate will harbor the same diversity as the same area on a single larger island. [Simberloff and Abele have recently observed that many real islands do not fit this "null" model, generally with departures in the direction of greater diversity on small islands.]

In our experiments we will look at each of the above 3 situations in an effort to discern which choices managers might make to most efficiently utilize their limited financial resources when purchasing and managing preserves. We will present several lines of evidence that, if the manager is interested in maximizing species diversity, his most effective option is generally to invest in a number of smaller land areas rather than one large preserve. With today's limited funds available for land purchases, and with the extensive subdivision and diverse ownership of available habitats, the acquisition of smaller preserves becomes an even more desirable option.

## Methods

1) **Experimental Investigations.** We have designed and initiated an experiment to directly compare species found in large artificial "parks", compared to numbers harbored in equal areas in multiple small "parks". The experimental system consists of fenced plots of three sizes in a field near the University of California's Davis campus. Plot numbers are adjusted to keep the total area in any given plot size constant (i.e. we have 32 plots of 2 m<sup>2</sup>, 8 of 8 m<sup>2</sup>, and 2 plots of 32 m<sup>2</sup>, for a total of 64 m<sup>2</sup> per treatment). We have also established half this number of control plots, how-

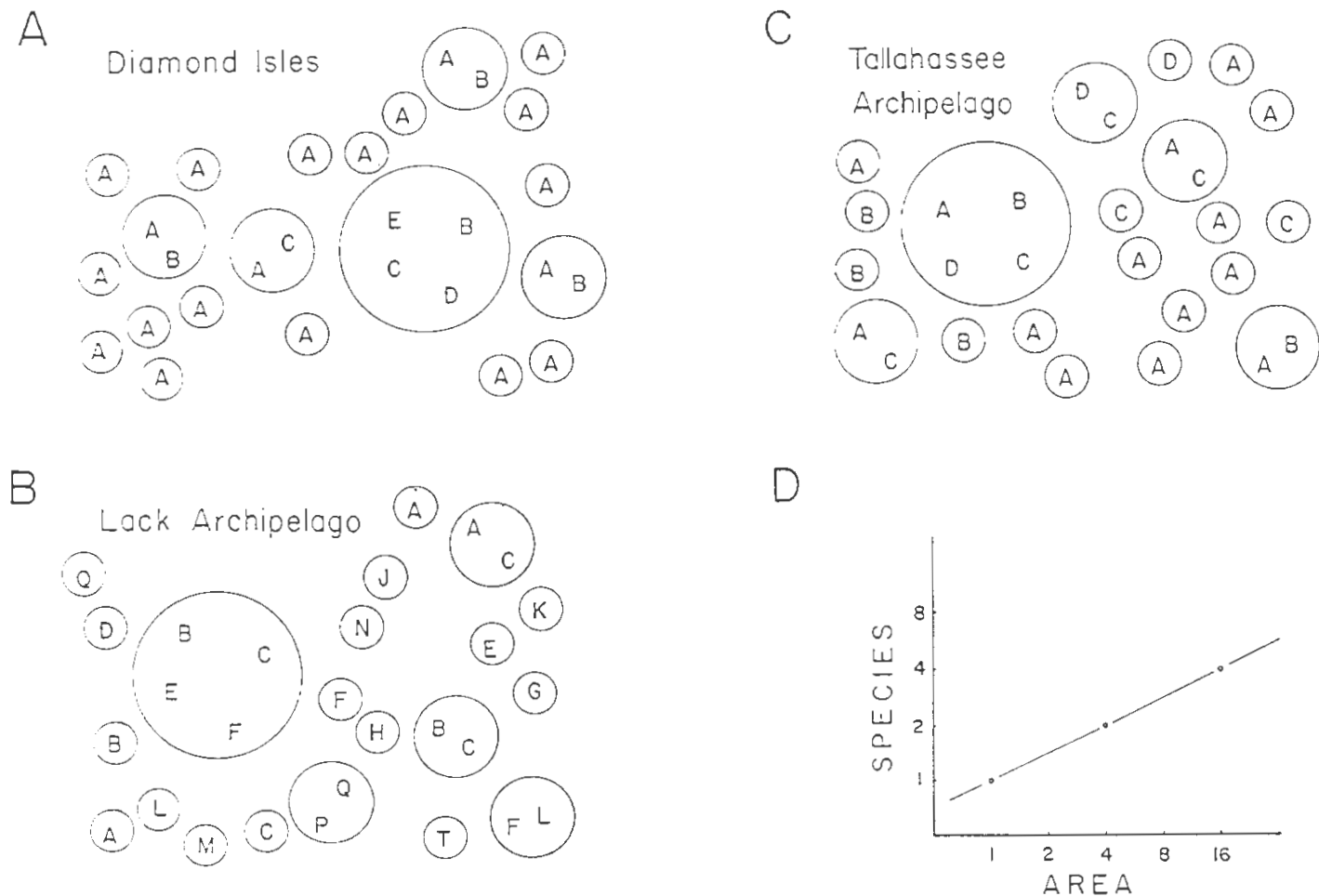


**Figure 1.** Hypothetical archipelagos with identical species-area curves (D) but favoring different acquisition strategies. In A, acquisition of large units would be favored. In B, the small units, in aggregate contain more species. In C, there is no clear advantage to single large, versus multiple small reserves.

ever these were not fenced. The areas between the plots are grazed intensively by sheep.

We are monitoring each plot for all plants and insects in this grasslands experiment. Using this design, we can test directly whether a single large unit contains more of the target species than the same area subdivided into smaller plots, as claimed. While this system is admittedly artificial, insects and annual plants found in plots isolated by grazing may be reasonably analogous to birds and trees in parks isolated by farmland, but on a spatial and temporal scale (and expense) amenable to experimentation.

We have just begun a second experiment of identical design in a marine community. Hard substrate settlement surfaces have been set in a sandflat area in the Bodega Marine Reserve, and the characteristic mussel-barnacle-limpet-starfish community is beginning to develop. Plate sizes range from  $1/64$  to  $1 \text{ m}^2$ . In this community, even the smallest size may harbor in excess of 20 species and thousands of individuals.

2) Patterns on islands. We have analysed all censuses of species on oceanic islands or terrestrial "habitat islands" (e.g. forest plots and mountaintops) that we have been able to find published or cited in the modern biogeography literature. To date, we have located roughly 35 data sets sufficiently complete to be reliable.

3) Park censuses. For all National Parks, State Parks, and refuges in California for which information is available, we will assemble data on area, habitat type and species richness. Initially, we have concentrated on National Park Service lands in California.

Because of the availability of reliable records from many locations, we have nearly completed the initial database of birds, mammals, trees, and wildflower species. Later we hope to expand the database to include all State Parks and Wildlife Refuges, and, as available, more taxa from NPS areas.

These data have been assembled in a way that should make them useful to managers and other researchers for a variety of uses. The data are stored in the Division of Environmental Studies computer facility on the University of California Davis campus. This is the first time that a centralized list of plant and animal species for California's parks has been assembled at one location. Any manager or researcher can now, with a short written request, receive a rapid response to what groups of plants or animals are presently known to occur in any park in the data base. We will continually update these lists as new information becomes available.

4) Data Analysis. Ideally, one would like to compare the species in a collection of small parks to those in a large park in the same geographical area. Since actual parks (and natural islands) do not generally have enough smaller units to allow the direct comparison, we have developed a technique to compare accumulated diversity for any given acreage under particular land acquisition strategies (i.e. small parks vs. large parks). These may be compared for effectiveness using cumulative species-area curves with relatively standard statistical techniques. We are examining patterns in both total species counts, and certain sets of rare and endangered species.

### Preliminary Results

All of this research is still ongoing, but the preliminary results show an unexpected consistency among studies. In virtually all cases, collections of smaller areas harbor more species than single larger areas. We were surprised by this finding, given the diversity of data analysed and the divergence of opinion on this topic among conservation and ecological researchers. The areas considered vary from a few square meters to hundreds of thousands of square kilometers, the animal and plant groups studied include everything from annual weeds and ephemeral insects to redwoods and giant tortoises, and the locations range from equatorial islands to desert mountaintops.

### Experimental Studies

The results of our grasslands experiment in 1984 are shown in Table 1 (next page). Over a 16-fold plot size difference, the most subdivided area contains roughly 78% more plant species and 53% more insect species than the undivided large plots. Early season patterns from 1985 appear similar. It is too early to assess the results of the marine experiment.

### Natural Islands

In 31 of the 35 data sets that we have examined to date, collections of small islands consistently harbored more species than did the largest islands. Typical cases are provided by the Galapagos archipelago (most of which is an Ecuadorian national park), and the Hawaiian islands. Isabela, at  $4607 \text{ km}^2$  is the single largest Galapagos island, comprising roughly 59% of the total land area of the archipelago. It also

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# Island Biogeography (Continued from page 7)

**Table 1.** Species diversity as a function of plot size in a California grassland community. All species observed during the summer of 1984.

## EXPERIMENTAL ENCLOSURES

| Plot Size                  | Plant Species Number | Insect Species Number | Sample Size (# of plots) |
|----------------------------|----------------------|-----------------------|--------------------------|
| Small (2 m <sup>2</sup> )  | 16                   | 75                    | 32                       |
| Medium (8 m <sup>2</sup> ) | 13                   | 62                    | 8                        |
| Large (32 m <sup>2</sup> ) | 9                    | 49                    | 2                        |

contains much of the archipelago's montane and cloud forest habitat, for which some groups, such as ferns, are especially adapted. Nevertheless, only 344 of the 655 reported land plant species are reported from Isabela, including 59 of the 86 ferns.

In comparison, the collection of smaller islands harbors 609 plant species, including 78 ferns. Just 204 of the 625 known Galapagos insect species are found on Isabela, versus 578 on the smaller islands. Twenty of 26 land birds, including 10 of the 13 Darwin's finches, breed on Isabela. All land birds are found elsewhere in the islands. Twenty-five of the land bird species can be found on the 14 smallest islands surveyed, totalling only 1042 km<sup>2</sup>. Similarly, the island of Hawaii represents 63% of the land area of the Hawaiian archipelago, and is inhabited by 30 of the 70 extant native land bird species. The smaller islands together harbor 51 species.

Thus, most island groups seem to best resemble the "Lack Archipelago" scenario. The only exception we have found to date on actual islands are ground beetles from the Faroes Islands. Birds and mammals from mountaintops in the Great Basin, and alpine plants in the Adirondacks also depart from the general pattern. In all of these cases subdivision appears to have little effect on species diversity (the "Tallahassee Archipelago" scenario).

We have not yet found any data sets showing large islands or habitat patches containing significantly more species than a comparable-sized collection of small islands or patches (as in the "Diamond Isles"). Unfortunately, we have been unable to find any suitable data from tropical rainforests, in which this issue seems most controversial.

### National Parks

The data from existing National Parks are still being

corrected for taxonomic uncertainty and incompleteness, but overall the patterns are similar to what we have found in our grasslands experiment, and from the analysis of natural islands. Far more species are listed in the relatively small area of half a dozen dispersed small parks than in the largest parks in the system. For example, the combination of Redwood, North Cascades, and Big Bend National Parks, totalling some 5100 km<sup>2</sup>, harbors 14 species of large mammals. Yellowstone is the largest park in the continental United States, and has the richest large mammal fauna. Yet with almost twice the area (9000 km<sup>2</sup>), it has two fewer species.

The differences are far more dramatic in plants. Because the habitat diversity among small parks, compared to that within large parks, is considerable, this comparison may be somewhat misleading, and it is not obvious that the populations in all of the small parks will ultimately be self-sustaining. We plan analyses of habitat diversity to explore this subject further. Nevertheless, the data from American parks do not suggest from species counts alone that small reserves are less effective as conservation tools than large reserves.

### Summary

It has been long-recognized that the sizes and spatial distributions of parks and refuges strongly influence their success in preserving natural species diversity and in preventing the decline or extinction of particular endangered populations. It is currently widely accepted that managers should dedicate available resources to establishing a small number of very large reserves. The proposition that this represents the most effective conservation strategy for maximizing species diversity does not follow logically from

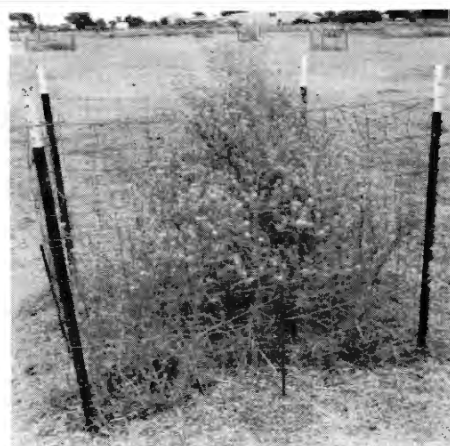


**Figure 3.** A small enclosure.

known species-area relationships in either "island biogeography" or existing reserves, and is empirically poorly tested.

Our preliminary investigations of data from natural islands, National Parks, and a field experiment constructing artificial "parks" in a grassland and insect community suggest that acquiring larger numbers of (necessarily smaller) parks may be a substantially more effective strategy for conserving maximum biological diversity than is tying up available resources in a few very large units.

We do not suggest that these observations provide any particular policy prescription. Maximizing diversity is just one of the many goals of park formation. Feasibility of alternate strategies may be much more limited by political or aesthetic considerations than capital costs of land acquisition. In any case, both natural islands and our experimental plots provide imperfect analogs of parks and refuges, and are somewhat special examples of subdivided habitats.

Isolated island groups have biotas biased toward species with exceptional dispersal abilities, and many groups show considerable endemism. Nearshore islands, by contrast, may be recolonized by mainland species that would not persist if the island were isolated, and thus be a poor model for self-sustaining reserves. The ecology of tractable experimental species may not be representative of that of rare and endangered species.

Particular target species (e.g. California condors, grizzly bears) may be threatened because large size and high trophic status keep populations sparse under the best of conditions. Such species undoubtedly require large refuge areas because of extensive home ranges, migratory patterns, or the need to maintain genetic diversity. Consequently, the minimum refuge size in many cases may be quite different from that suggested by species counts alone.

Nevertheless, we can assess the claim that ecological principles favor very large parks to maximize diversity. On the basis of our preliminary findings, such a claim seems suspect, although the value of large parks is certainly justified on other grounds.

At present, there is no way to assess conclusively the processes promoting diversity in collections of parks, islands, or even experimental plots. Their relative importance undoubtedly varies among locations and taxa. However, although the mechanistic basis for species-area effects is little understood, empirical observations suggest that greater species diversity is maintained on multiple "islands", whether real islands, isolated habitat patches, or plots, than on a comparable land area of a single large "island."

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**Figure 2.** The study area from the air.

Insofar as the "islands" we have examined provide valid models for parks and refuges, and a principal objective of conservation is the maintenance of overall species diversity, the number of refuges appears to be of equal or greater importance than the size of individual reserves. Policy prescriptions based on this observation should be approached with caution. It would be unfortunate, however, if exclusive emphasis on minimizing extinction rates in single large parks or islands caused planners to overlook the potential effectiveness of numerous and dispersed tracts in preserving a greater variety of species, habitats, and functioning ecological communities.

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**Figure 4.** In the service of science.