increased catecholamine metabolism) in the central nervous system (10), the hippocampus could be one of the sites of this restoration process.

The electrical activity of the hippocampus is unusual. While the rest of the brain shows a desynchronized EEG pattern during attention, learning, and paradoxical sleep, the hippocampus displays a synchronized electrical activity of four to seven cycles per second (theta rhythm) (11). It is suggested that the hippocampus, through synchronizing influences on the neocortical and subcortical structures, counteracts the effects exerted by the ascending reticular-activating system, and that the functional interplay of the hippocampus and reticular system seems to be of importance with regard to the rhythm of sleep and wakefulness (12). Spontaneous activity of the hippocampal pyramidal cells in cats with permanently implanted electrodes sharply decreased in SWS (13), a phenomenon observed in other brain areas (14). It may be that the electrical activity of specific brain structures during SWS is keyed to local chemical processes. Our data regarding the chemical changes in the hippocampus during SWS indicate that the 5-HT and DA systems become activated at this time. This is of interest because current hypotheses propose an increased activity in the 5-HT system of the raphe nuclei during SWS and an increased activity in the catecholamine system of the nucleus locus coeruleus during paradoxical sleep (3). Because of the reciprocal connection between limbic-forebrain structures (including the hippocampus) and the raphe nuclei, the latter are potentially modulated by limbic-forebrain mechanisms (15). When 80 to 90 percent of the raphe system is destroyed, animals enter a state of permanent arousal that lasts 3 to 4 days; SWS returns partially within a 3-week period (2), and a near normal sleep profile (16) appears by day 30. This indicates that other brain sites functionally compensate for the loss of 5-HT neurons in the raphe. Furthermore, since hippocampectomy was found to reduce significantly both SWS and paradoxical sleep, the hippocampus has been implicated in the facilitation of both SWS and paradoxical sleep (17). Although hibernation differs from normal sleep in many respects (18), it has been reported that when animals are entering hibernation, the concentration of 5-HT increases in the hippocampus several times more than it does in other brain areas (19). Also, when 5-hydroxytryptophan, an immediate precursor of 5-HT, is administered to rats, the highest concentration of 5-HT is found in the hip-

pocampus (20); when administered to rabbits, 5-hydroxytryptophan results in the most marked rate of increase in 5-HT being found in the hippocampus (21). All these findings point to the importance of a serotonergic mechanism in the hippocampus, and a possible role of this area in SWS. The specific increases in the metabolism of 5-HT and the concentration of DA in the hippocampus during SWS indicate that the hippocampus functions as a subsidiary sleep structure to the raphe system and the nucleus locus coeruleus in the brainstem. We also suggest that the obtained decrease in DA metabolism in the striatum and thalamus during SWS may be related to the sleep-generating mechanisms.

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# Island Biogeography and Conservation: Strategy and Limitations

As human destruction of remaining natural habitats accelerates, biologists have felt intuitively that most existing wildlife refuges are too small to avert extinctions of numerous species. However, because there has been no firm basis for even approximately predicting extinctions in refuges, biologists have had difficulty convincing government planners faced with conflicting land-use pressures of the need for large refuges. Recently several workers have recognized that a predictive understanding of extinction might be obtained from island biogeography, since refuges of natural habitat in a sea of human-altered environment behave as islands for species dependent on natural habitat (1–6). All these investigators attempting to understand implications of the "island dilemma" for

conservation strategy have concluded that some large refuges are essential to minimize extinction rates and to ensure certain species any chance of survival at all. These conclusions are based not only on studies of oceanic islands but also of habitat "islands" on mainlands, as well as of refuges themselves.

Simberloff and Abele (7) argue that these applications of biogeographic theory to conservation practice are premature and are based on insufficiently validated theory and possibly also on idiosyncratic results. These authors show that, given certain assumptions, several small refuges may contain more species than a single large refuge of equivalent area. Their reasoning from their assumptions is correct but minimizes or ignores much more important

conservation problems. Because those indifferent to biological conservation may seize on Simberloff and Abele's report as scientific evidence that large refuges are not needed, it is important to understand the flaws in their reasoning.

Human activities threaten some species and habitats more than others. Humans are preferentially destroying some habitats (for example, primary tropical rain forest) and creating others (for example, roadsides and pastures). In addition, species of high dispersal ability and high reproductive potential, living in successional habitats, can survive human-related environmental changes much better than can sedentary species of low reproductive potential that are confined to more mature habitats. Thus, conservation strategy should not treat all species as equal but must focus on species and habitats threatened by human activities. What are the area requirements and dispersal abilities of these extinction-prone species?

First, consider area requirements of species that can disperse among islands or habitat patches. Despite their ability to disperse, such species are often found to be confined to islands or patches much larger than the territory size of a single pair [see (5) for summary]. For example, minimum area requirements of populations of those southwest Pacific land bird species that can colonize islands overwater range up to thousands of square kilometers for species whose territories are measured in hectares (3). Iguanid lizard populations of the Bahamas are confined to islands large enough to support about 100 lizards (8). Similar examples of minimum area requirements have been reported for North American ants, North American birds, and British birds (9). These requirements result from several factors (3, 5). (i) Some habitats exist only on larger islands or patches; (ii) species with seasonally or spatially patchy food supplies must integrate resources over large areas; (iii) species that live at low densities, and hence often become extinct on small islands but rarely recolonize, have low probability of occurrence at equilibrium except on large islands; and (iv) "hot spots" of locally high resource production may be important hedges against extinction but may constitute only a small fraction of breeding territories.

For species capable of dispersal between "islands," extinction of a population in one refuge may possibly be reversed by colonization from another refuge. The island dilemma is posed in more acute form by species that are unable or unwilling to disperse across wa-

ter or alien habitat. Such species include not only flightless organisms but also birds that are strong fliers. For example, many Californian bird species have never been observed on islands or desert oases 20 km from their breeding sites (10); 302 of the 513 breeding land bird species of New Guinea have never been observed on a single oceanic island, not even large islands 8 km from New Guinea (4); and 55 of the 127 breeding land bird species of New Britain never appeared, even as vagrants, on an 8-km² island 6 km offshore during several decades' residence by Meyer, a keen observer (3). Since there are no immigrations to reverse extinction on an island or habitat patch for such species, minimum area requirements are considerably larger than for species capable of dispersal. Thus, New Guinea is surrounded by many "land-bridge islands" that formed part of New Guinea during low sea level of Pleistocene times up to 10,000 years ago. At the present time, 32 of the 134 New Guinea lowland bird species that do not colonize overwater have disappeared from all land-bridge islands, even ones as large as 8000 km². These extinction-prone species with large area requirements include some of the most distinctive New Guinea bird species, such as the vulturine parrot *Psittrichas fulgidus*, harpy eagle *Harpyopsis novaeguineae*, and shovel-billed kingfisher *Clytoceyx rex* (4). Yet few proposed refuges exceed 8000 km² in area.

Similar patterns of differential post-Pleistocene extinction on real land-bridge islands in the ocean, or on virtual ones in seas of alien habitat, have been described for west Australian macropod marsupials, southeast Australian marsupials and rodents, North American montane mammals, neotropical birds, Bismarck Archipelago birds, Solomon Island birds, and Australian lizards (2–5, 11). In all of these studies, most bird and mammal species incapable of interisland dispersal were found to disappear from all islands smaller than a few hundred square kilometers, and some species disappeared even from all islands of many thousand square kilometers. While these patterns are the product of population fluctuations for about 10,000 years, studies in this century on many New Zealand forest reserves (6) and on Panama's Barro Colorado reserve (2) show that many extinctions occur within a few decades, especially in smaller refuges.

As a result of this differential susceptibility of species to extinction in isolated populations, small refuges or islands mainly lose the sedentary species of mature habitats that are most threatened by

human activities, and retain the rapidly dispersing successional and edge species that need no protection. For instance, small forest reserves in New Zealand gradually lose all bird populations belonging to old endemic families and retain a standard quota of birds that are also widespread in suburban gardens, mostly species that recently immigrated or were introduced by Europeans to New Zealand (6).

Simberloff and Abele (7) suggest several reasons that they believe argue for small refuges under some circumstances.

1) Their main argument is that, depending on species pool size and relative areas of refuges, several small refuges sometimes contain somewhat more species than an equivalent area in one large refuge. This argument is scarcely relevant, since species must be weighted, not just counted; the question is not which refuge system contains more total species, but which contains more species that would be doomed to extinction in the absence of refuges. A refuge system that contained many species like starling and house rat while losing only a few species like ivory-billed woodpecker and timber wolf would be a disaster.

2) "For 'fugitive species' adding up to a small fraction of a regional biota a single large refuge could be exactly the wrong strategy" (7). This argument is also usually irrelevant, since fugitive species of high dispersal ability will often survive well in the absence of any refuges.

3) Catastrophes like fire or disease could affect populations in the whole of a large refuge but might not reach some of a network of small refuges. This argument is valid.

4) Implicit in a comment by Simberloff and Abele (their sentence "More realistically, we would hypothesize . . .") is the recognition that each small refuge might save a different member of a set of mutually exclusive competitors, of which one would come to exclude the others from a single large reserve. This argument is also valid.

Against the two valid arguments for multiple refuges must be set the clear message of the island dilemma: different species have different minimum area requirements, while cases of maximum area limits are extremely rare, and the species most in need of refuges are doomed in a system of small refuges. The extinctions in the New Zealand forest reserves and on Barro Colorado warn us how rapidly the ecosystems of undersized reserves can collapse to an inevitable final solution. If the best solution of a system of multiple large refuges cannot

be achieved, the best compromise would be one refuge as large as possible plus some smaller refuges. This recommendation is not based on idiosyncratic taxa but on a variety of taxa on at least four continents. Nor is this recommendation premature, in view of the clear message and the rapid pace of human destruction of natural habitats. In the absence of input from biologists, developers may often prefer small refuges as being easier to create and as leaving more land for development goals of obvious political significance. Biologists should familiarize themselves with the island dilemma so that their arguments for large refuges will be explicit and persuasive.

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Certain interpretations in the report by Simberloff and Abele (*1*), if accepted uncritically, could be detrimental to efforts to protect endangered wildlife.

Following a now well-established practice, Simberloff and Abele use results from island biogeography to draw inferences about the efficacy of isolated parks and refuges as reservoirs of natural diversity. However, some of their conclusions are contrary to those espoused by others who have considered the same problem (*2-4*).

Simberloff and Abele consider an experiment in which very small (<0.05 ha), isolated copses of mangroves were dissected into several lesser units separated by channels wide enough to reduce the dispersal of some of the arthropod species present. After an equilibration period of 3 years, a census was again made of the "archipelago" for its arthropod fauna, with the result that the collection of separate islets contained a few more species (81 as compared to 77) than did the original intact copse. From this they conclude that "the more (and smaller) refuges posited as an alternative to a single large one, the more likely is the archipelago of small refuges to contain more species."

A key feature of their experiment was the presence nearby of large continuous stands of mangroves containing a rich "source" fauna of hundreds of species of arthropods, many of which were capable of invading tiny outlying islets. Indeed, in discussing the experiment, they recognize that "possibly the increased extinction rates on the individual islands in this mangrove archipelago are more than compensated for by the presence of the other islands as nearby sources generating high propagule . . . invasion rates." In contrast, those of us who have argued the essentiality of large preserves have imagined quite a different scenario, one in which most of the landscape has been preempted by agricultural or other human uses, and in which scattered parks remain as the only redoubts for species that are unable to adapt to degraded habitats. The islands considered by Simberloff and Abele were at equilibrium, meaning that extinctions were in balance with recurrent immigrations from a rich external source. However, the dynamics of equilibrial systems are simply not germane to the problem of isolated parks set in an intensively exploited landscape; rather, the appropriate context is that of land-bridge islands in which the source has been removed and only islands remain. Under these circumstances, logic calls for a strategy of minimizing extinctions, and this, I contend, is best accomplished with large preserves. As I shall explain below, there are circumstances in which large preserves are neither necessary nor appropriate, but these are special cases directed toward particular species, rather than toward whole ecosystems.

If it is agreed that the primary objective of a rational conservation policy should be to preserve viable populations of as many as possible of the species that inhabited the pristine landscape, then at least some large reserves are a necessity. This is immediately evident from the fact that species at the top of the trophic ladder (such as wolves, bears, eagles, and mountain lions) require extensive foraging ranges. Population densities of such species are low, typically on the order of one individual per 10 km². To protect representative samples of complete ecosystems, areas of hundreds or thousands of square kilometers are essential.

An optimal system of preserves should be designed to minimize extinctions, a matter that Simberloff and Abele pass over lightly. Much of our knowledge of extinction rates comes from the study of land-bridge islands, islands that were cut off from the adjacent mainland by rising water levels at some known time in the past (frequently the end of the Pleistocene). Kinetic analysis begins with the assumption that land-bridge islands initially contained a species complement equal to that of an equivalent-sized segment of mainland. When dispersal is shut off or severely restricted by the interposition of a water barrier, the high-diversity ecosystem of the newly created island begins to "relax," and eventually converges toward the low-diversity condition of a strictly oceanic island of equivalent size, climate, and remoteness. Several studies of land-bridge islands have been completed, and the results are gratifyingly concordant (*3-5*). The following conclusions appear to be well substantiated.

1) Species loss is area dependent. An island of 250 km² is estimated to lose about 4 percent of its resident bird species during the first century, while one of 5000 km² loses only 0.5 percent (*4*).

2) Extinctions proceed rapidly at first as the most vulnerable species drop out, and then at a diminishing pace as the community approaches equilibrium.

3) Among the first species to expire are those on the highest rungs of the trophic ladder, and the largest members of feeding guilds. The implications of this are uncertain, because the effects of top predators, or even herbivores, on the interactions of species in the lower trophic levels of terrestrial ecosystems are poorly understood. In some aquatic ecosystems, however, it is known that the removal of "keystone" predators can lead to dramatically altered, usually less diverse communities (*6*).

4) Where it has been possible to examine replicated groups of land-bridge islands, the evidence suggests that the order of extinctions is highly consistent. One can infer from this that the individual units of a scattered park system would lose very similar sets of species.

5) As relaxation goes to completion, the character of land-bridge island avian communities is gradually transformed from one typical of the dominant vegeta-

tion (such as primary rain forest) to one typical of successional vegetation (even though the quality of the habitat apparently remains unaltered). In other words, the end point of relaxation is a community composed largely or entirely of widespread "weedy" species which are of negligible interest to conservationists.

In conclusion, I can affirm that extensive areas are needed to preserve examples of intact ecosystems and to forestall the extinction of species having large space requirements. This is not to say, however, that small refuges may not be adequate to serve more limited purposes, such as protecting the habitat of localized endemic forms or the nesting sites of colonial species. In enacting a comprehensive conservation policy we will have to be sensitive to the distinctive features of particular species and ecosystems and intensify the search for ways of protecting wildlife that do not conflict excessively with society's needs for space and resources.

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Simberloff and Abele (*1*) have questioned recent recommendations (*2*) that faunal preservation can best be accomplished by establishing single large reserves. Instead, they conclude that theoretical considerations could in certain circumstances support the sequestering of a series of smaller reserves, and they present experimental evidence in support of this view. However, their proposition depends on biologically unrealistic assumptions and should not be applied to any practical problem of conservation without explicit proof that the assumptions are true.

Simberloff and Abele address themselves mainly to predictions arising from classic mathematical models of the species-area relationship (*3*). According to such models, the equilibrial species num-

ber on a large island is higher than the number on an ecologically similar but smaller island, because the immigration rate of new species is lower and the extinction rate of resident species is higher on smaller islands. In addition, because immigration rates decrease with distance, classical models also predict that more species should be maintained on islands close to continental source areas. Simberloff and Abele accept these predictions but present computations that show that a given refuge area may support more species if it consists of a number of smaller units. To obtain this result, they propose a model in which all of the species in the pool have equal dispersal and survival abilities or in which strong interactions between species make it likely that different sets of species will survive on different islands, or both. However, there is no evidence that such extreme conditions are in fact approached in complex communities (*4*). For example, different reptiles, birds, and mammals require different minimum insular areas for long-term survival (*5*); families of birds differ in their species-area relationships (*6*); extinction rates on land-bridge islands differ among taxa (*7*); forest-interior bird species, especially those nesting on or near the ground, tend to disappear most rapidly from small forested areas in both tropical (*8*) and temperate (*9*) latitudes; and even mangrove arthropods differ in their ability to establish and maintain populations on small islands (*10*). The diversity of species sensitive to effects of area and isolation demonstrates that, contrary to the suggestion of Simberloff and Abele, such sensitivity is not a taxal idiosyncrasy. The inevitable consequence of such diversity in the context of the proposed series of small preserves would be the preferential extinction of the more sensitive species and the emergence on each island of a species assemblage whose members can utilize disturbed habitats and therefore are destined to survive even in the absence of preserves.

A second inadequacy of individual small faunal preserves, or series of such preserves, is their failure to provide a reasonable facsimile of the entire functioning ecological community they are intended to represent. In fact, Simberloff and Abele agree with Sullivan and Shaffer (*11*) that the preservation of entire communities rather than single endangered species is a highly desirable goal. If a functioning community is to be preserved, it must be acknowledged that some species, particularly large ones and those at higher trophic levels, require extensive areas of continuous habitat for survival. For example, no one would

propose that an entire mangrove community, including vertebrates and larger invertebrates, could be preserved in reserves the size of the intact islands (0.02 to 0.05 ha) studied by Simberloff and Abele (*1*), much less in the tinier archipelagos created, even if many islets were involved.

Human impact is often a serious practical problem in natural areas because recreational activity is usually programmed into the reserve from the outset, or if not programmed, is difficult to prevent. The effects of such activity can be severe even in gigantic national parks (*12*). In small reserves, human influences can be disastrous.

Island area, isolation, and human disturbance may interact in complex fashion. Although Simberloff and Abele refer to a critique by Lynch and Johnson (*13*) of reported high avian turnover rates on islands, one of the main points of the critique was that many insular extinctions and colonizations have been related to human disturbance. However, the perturbations that result from habitat alteration and destruction, introduction of nonnative species, use of pesticides, or other stresses are becoming increasingly important determinants of species composition and turnover. These influences will intensify in the future and will have greatest effect on small preserves. Therefore, the most prudent preservation strategies are those that insulate sensitive species from the effects of human disturbance by setting aside large continuous natural areas.

Classical theory (*3*) predicts high turnover rates on small isolated islands. To emphasize the reality of such turnover on mainland "habitat islands" we cite results of Kendeigh's annual censuses of breeding birds (*14, 15*) for Trelease Woods, a 22-ha deciduous forest preserve in Illinois that is surrounded by agricultural land. Several patterns are evident. (i) Annual turnover, computed by the method of Diamond (*16*), was high (mean = 13.6 percent; range = 5.3 to 27.3 percent for the years 1934–1975). Of 62 breeding bird species, only nine (*17*) have been present in each of the 48 censuses since 1927. (ii) Three forest interior specialists characteristic of the Eastern deciduous forest (*14*) have not bred in the woods during the census period; six others (*18*) have bred only sporadically for a year or two at a time. It is reasonable to assume that some or all of these species nested regularly (*19*) in the primordial forest prior to European settlement, but had been extirpated by the time of the first census in the relict woodland. (iii) Ecologically generalized ("weedy") species, many of them per-

manent residents or short distance migrants, now dominate the Trelease Woods avifauna. (iv) Between 1934 and 1953, the mean species richness of the avifauna in Trelease Woods was 23.3 (standard deviation = 4.9). By about 1953 the third most abundant tree, American elm (*Ulmus americana*), had begun to die from Dutch Elm disease. The years 1954 through 1975 then witnessed a highly significant ($P < .01$) increase in avian species richness to an average of 32.5 (standard deviation = 2.8), but predictably (20), the birds that profited were forest-edge species. Thus, an additional inadequacy of small preserves is their sensitivity to destabilization.

Many of the edge species that colonized the interior of Trelease Woods in spectacular fashion during its destabilization also colonize the edges of artificial swaths cut through forest (21). In such cases, the overall avian species richness in an area is increased, but only at the expense of forest-interior species. We therefore hope that the experimental design (4) of Simberloff and Abele, in which such ecotonal effects may have been absent, will not be used to justify disastrous fragmentation of existing forest by roads, pipelines, or similar projects. Our objections to the creation of long strips of edge within a single preserve apply even more strongly to series of small forest preserves. In areas where forest is reduced to isolated woodlots, avian brood parasites, egg predators, and nonnative nest-hole competitors are usually abundant (22) in the surrounding agricultural and urban environments and often invade small tracts. Even acting singly, such species can exert intolerable pressure on other bird species (23), and their combined impact may be a major force in the avifaunal changes that succeed forest fragmentation.

We now wish to apply our general reasoning to preservation of the Eastern deciduous forest, a system with which we have considerable firsthand experience. Simberloff and Abele cite Terborgh's statement (2) that reduction and fragmentation of the forests of Eastern North America caused the extinction of, at most, two bird species. Although it is true that few North American birds have become extinct on a continental scale within historic times, we contend that optimism about the avifauna of the Eastern forest is warranted only as long as extensive areas of homogeneous forest remain standing. In fact, Terborgh pointed out correctly (2) that important factors in avian species survival were (i) the ability of most forest birds to utilize middle successional second growth and (ii) the retention of a total forested area,

which, even at its lowest ebb, was never much below half of the original area. Today the Eastern forest is an archipelago of second growth woodland fragments that vary greatly in size, and it is therefore possible to determine whether subsets of these fragments are in fact acting as preserves on a contemporary basis. Breeding bird censuses and surveys in Eastern North America (24, 25) show that avifaunal composition of forest fragments depends on their size. In extensive forest tracts, up to 92 percent of the breeding individuals are neotropical migrants (26). However, many neotropical migrant species disappear from small isolated forest tracts such as Trelease Woods, and the avifauna of such tracts tend to be dominated by species that are either permanent residents or short distance migrants (9, 25). Extensive census and survey work (27) in central Maryland shows that small (less than 22 ha) tracts have a depleted avifaunal composition also characteristic of suburbs and parks (9), but that deterioration has not occurred in fragments of similar size and vegetational composition adjacent to extensive forest (28). Also, countywide mapping projects (29) have demonstrated that some neotropical migrants apparently no longer breed in agricultural regions where forest fragmentation is most severe. Loss or reduction in breeding densities of neotropical migrant individuals has occurred in a relatively undisturbed mesic forest fragment that is hundreds of years old (20) and in large urban parks of second growth forest (27, 30). For example, in a forest plot within Rock Creek Park in the District of Columbia, the percentage of neotropic migrant breeders declined from 87 percent in 1948 to 35 percent in 1974 (30). The rapidity of decay of the original avifauna in urban parks, in contrast to slower decays (20) in relatively undisturbed forest fragments and lack of perceptible decay in nearby extensive homogeneous forest (28), implicates human perturbation as an important factor contributing to the deterioration. Thus the available data for the Eastern forest, far from demonstrating that large faunal preserves are unnecessary, describe a troubled system in which local and regional extinctions of forest interior specialists are commonplace and in which large series of existing small, isolated forest areas have failed to preserve, even in contemporary time, many of the small avian species that once dominated the forest.

The final argument against fragmentation of our rapidly disappearing large areas of relatively undisturbed habitat is the unhappy fact that the process is, for

all practical purposes, irreversible. Simberloff and Abele's concern about the "cost and irreversibility of large-scale conservation programs" (1) ignores the fact that it is much easier to convert a natural area into a housing development than vice versa. Therefore, the most prudent strategy is to maximize reserve size. If, as Simberloff and Abele propose, an alternate strategy proves more useful in specific instances, we anticipate no shortage of economic interests willing to fragment the preserves at a later date.

We feel some responsibility to suggest orders of size that are relevant to the design of preserves. Optimal size for preserves varies with geography and the kinds of communities involved, but the history of Barro Colorado Island in the Panama Canal Zone is a stern reminder of the irreversible losses that might occur if the size of a preserve is inadequate. In this instance (8, 31) an area of nearly 1500 ha was insufficient to retain the characteristic avifauna of the larger tropical forest from which the island was separated by canal construction in 1914. Our analysis of the Trelease Woods data shows that 22 ha is hopelessly small, even for preservation of small forest-interior birds. We agree with the principle suggested by Sullivan and Shaffer (11) that primary reserves should be of sufficient size to support stable populations of large mammals, and with Terborgh in his estimate that thousands of square kilometers may be required to reduce extinction rates to acceptable levels. If such sizes are involved, there seems to be no need for controversy about the optimal size of forest preserves, since we are unaware of any plans or opportunities to sequester areas that would be inappropriately large.

An acknowledgment of the need for large preserves should not be misconstrued as an argument against smaller ones. Certainly, small reserves are better than none and can accomplish such purposes as (i) preservation of taxa that can survive in small areas, (ii) preservation of unique microhabitats, (iii) provision of "stepping stones" between larger reserves, and (iv) provision of local educational and recreational benefits. We do, therefore, encourage the sequestering of small reserves whenever the establishment of a large reserve is not possible.

In summary, we urge that the size of ecological preserves be maximized because (i) large areas have high immigration rates and low extinction rates; (ii) some taxa require very large areas for survival; (iii) preservation of entire ecological communities, with all trophic levels represented, requires large areas; (iv) large preserves are better buffered

against human perturbation and natural disaster; (v) large areas are necessary to minimize the pressures of predation, parasitism. and competition exerted by species abundant in the disturbed areas surrounding the reserves; (vi) failures of small reserves, originally considered to be adequate. have been amply documented; and (vii) the irreversibility of fragmentation demands a conservative preservation strategy.

Simberloff and Abele have performed a useful service by focusing attention on the potential pitfalls of an oversimplified model. We contend, however, that existing theory corroborated by empirical data is sufficient to validate the general conclusion that refuges should contain as large a contiguous area as possible.

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17. These species were: downy woodpecker (*Dendrocopos pubescens*). great crested flycatcher (*Myiarchus crinitus*), eastern wood pewee (*Contopus virens*), common crow (*Corvus brachyrhynchos*), starling (*Sturnus vulgaris*), red-eyed vireo (*Vireo olivaceus*), brown-headed cowbird (*Molothrus ater*), indigo bunting (*Passerina cyanea*).
18. Species that never bred were: black-and-white warbler (*Mniotilta varia*), worm-eating warbler (*Helmitheros vermivorus*), hooded warbler (*Wilsonia citrina*). Species that bred sporadically were: Acadian flycatcher (*Empidonax virescens*), American redstart (*Setophaga ruticilla*), blue-gray gnatcatcher (*Polioptila caerulea*), ovenbird (*Seiurus aurocapillus*), scarlet tanager (*Piranga olivacea*), yellow-throated vireo (*Vireo flavifrons*).
19. At the time of the studies of R. R. Graber and J. W. Graber [*Ill. Nat. Hist. Surv. Bull.* 28, 383 (1963)], all the missing species were recorded as breeding in Illinois.
20. B. L. Whitcomb, R. F. Whitcomb, D. Bystrak, *Am. Birds*, in press.
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22. The nest predators are: blue jay (*Cyanocitta cristata*). common crow, and common grackle (*Quiscalus quiscula*). Brown-headed cowbird is a brood parasite; house sparrow (*Passer domesticus*) and starling are nest-hole competitors.
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We regret being cast as the bêtes noires of conservation, since our report (1) was designed to strengthen conservation efforts by eliminating reliance on a species-area equation which alone does not support either of two contrasting refuge strategies, and by tailoring conservation efforts to the idiosyncrasies of the taxa in question. We do not agree with Diamond (2) and Terborgh (3) that their data are adequate to support the hypothesis of high extinction rates for birds on islands. With one exception, the "evidence" from land-bridge islands rests not on observation of which species were originally present, but rather on inference from the present source fauna and the species-area equation. Even were habitat differences well quantified, which they are not, the wide variance in fitting data to the standard species-area curve (4) would make such a deductive leap suspect. For Barro Colorado Island at least, the original birds are documented, but the island has undergone major vegetational change in the last century (5) and so can hardly be used as an example of extinction following change in the single variable of area. Perhaps with long-lived animals few appropriate data exist, but this suggests great caution in erecting general theories about extinction.

With respect to the "extreme model," referred to by Whitcomb *et al.*(6), we *did* point out that this would be an "oversimplification," and then cited many of the same references which Whitcomb *et al.* use, to exactly the same end: to indicate how the model might be made more realistic. We did not "pass over lightly" (3) extinctions; our third paragraph from the end addressed exactly this problem.

Our conclusion still stands: the species-area relationship of island biogeography is neutral on the matter of whether one large or several small refuges would be better. We repeat our earlier statement: "This is not a plea, then, for a specific conservation regime, but rather for more comprehensive autecological consideration."

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## Juvenile Hormone and Pest Control

The search for novel chemical pest control agents with improved characteristics, such as increased selectivity for target pests as compared to beneficial arthropods and vertebrates. is a long and difficult process for which the short-term economic incentives are far more elusive than for the development of broad-spectrum pesticides.

The report by McNeil (1) appears to