THE ISLAND DILEMMA: LESSONS OF MODERN BIOGEOGRAPHIC STUDIES FOR THE DESIGN OF NATURAL RESERVES

JARED M. DIAMOND

Physiology Department, University of California Medical Center, Los Angeles, California 90024, USA

ABSTRACT

A system of natural reserves, each surrounded by altered habitat, resembles a system of islands from the point of view of species restricted to natural habitats. Recent advances in island biogeography may provide a detailed basis for understanding what to expect of such a system of reserves. The main conclusions are as follows:

The number of species that a reserve can hold at equilibrium is a function of its area and its isolation. Larger reserves, and reserves located close to other reserves, can hold more species.

If most of the area of a habitat is destroyed, and a fraction of the area is saved as a reserve, the reserve will initially contain more species than it can hold at equilibrium. The excess will gradually go extinct. The smaller the reserve, the higher will be the extinction rates. Estimates of these extinction rates for bird and mammal species have recently become available in a few cases.

Different species require different minimum areas to have a reasonable chance of survival.

Some geometric design principles are suggested in order to optimise the function of reserves in saving species.

INTRODUCTION

For terrestrial and freshwater plant and animal species, oceanic islands represent areas where the species can exist, surrounded by an area in which the species can survive poorly or not at all and which consequently represents a distributional barrier. Many situations that do not actually involve oceanic islands nevertheless possess the same distributional significance for many species. Thus, for alpine species a mountain top is a distributional 'island' surrounded by a 'sea' of lowlands;

Biol. Conserv. (7) (1975)— © Applied Science Publishers Ltd, England, 1975
Printed in Great Britain

for an aquatic species a lake or river is a distributional island surrounded by a sea of land; for a forest species a wooded tract is a distributional island surrounded by a sea of non-forest habitat; and for a species of the intertidal or shallow-water zones, these zones represent distributional islands compressed between seas of land and of deep water.

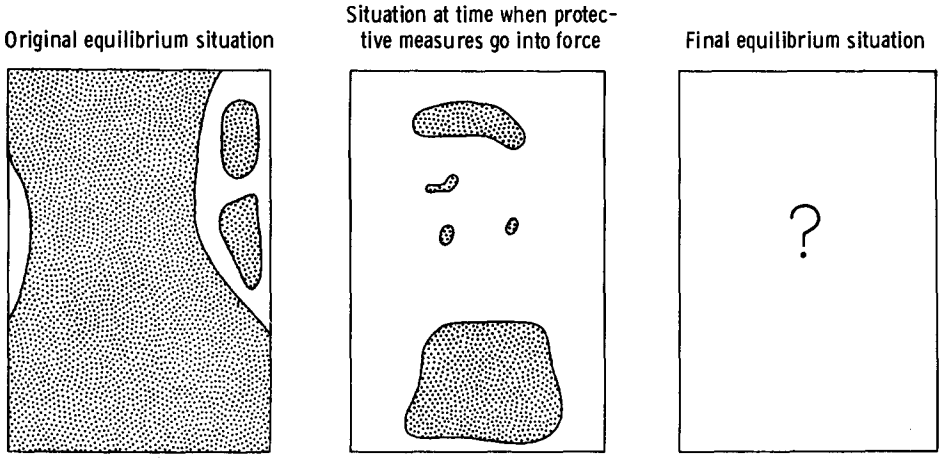

Fig. 1. Illustration of why the problems posed by designing a system of natural reserves are similar to the problems of island biogeography. In the situation before the onset of accelerating habitat destruction by modern man, many natural habitats were present as continuous expanses covering large areas (indicated by shaded areas of sketch on left). Species characteristic of such habitats were similarly distributed over large, relatively continuous expanses. By the time that extensive habitat destruction has occurred and some of the remaining fragments are declared natural reserves, the total area occupied by the habitat and its characteristic species is much reduced (centre sketch). The area is also fragmented into isolated pieces. For many species, such distributions are unstable. Applying the lessons of modern island biogeography to these islands of natural habitat surrounded by a sea of disturbed habitat may help predict their future prospects.

Throughout the world today the areas occupied by many natural habitats, and the distributional areas of many species, are undergoing two types of change (Fig. 1). First, the total area occupied by natural habitats and by species adversely affected by man is shrinking, at the expense of area occupied by man-made habitats and by species benefited by man. Second, formerly continuous natural habitats and distributional ranges of man-intolerant species are being fragmented into disjunctive pieces. If one applies the island metaphor to natural habitats and to man-intolerable species, island areas are shrinking, and large islands are being broken into archipelagos of small islands. These processes have important practical consequences for the future of natural habitats and man-intolerant species (Preston, 1962; Willis, 1974; Diamond, 1972, 1973; Terborgh, in press, *a*, *b*; Wilson & Willis, in press). Ecologists and biogeographers are gaining increasing

understanding of these processes as a result of the recent scientific revolution stemming from the work of MacArthur & Wilson (1963, 1967) and MacArthur (1972). In this paper I shall explore four implications of recent biogeographic work for conservation policies: (1) The ultimate *number* of species that a natural reserve will save is likely to be an increasing function of the reserve's area. (2) The *rate* at which species go extinct in a reserve is likely to be a decreasing function of the reserve's area. (3) The relation between reserved area and probability of a species' survival is characteristically different for different species. (4) Explicit suggestions can be made for the optimal geometric design of reserves.

HOW MANY SPECIES WILL SURVIVE?

Let us first examine the relation between reserve area and the number of species that the reserve can hold at equilibrium. As a practical illustration of this problem, consider the fact that we surely cannot save all the rain forest of the Amazon Basin. What fraction of Amazonia must be left as rain forest to guarantee the survival of half of Amazonia's plant and animal species, and how many species will actually survive if only 1% of Amazonia can be preserved as rain forest? Numerous model

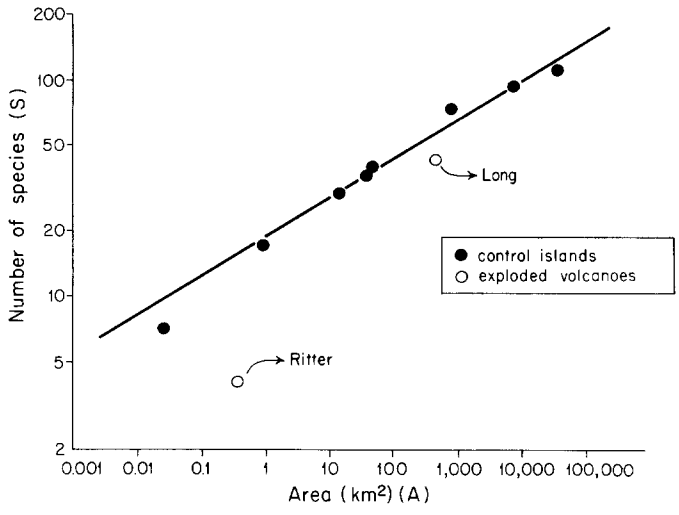

Fig. 2. Example of the relation between species number and island area in an archipelago. The ordinate is the number of resident, non-marine, lowland bird species (S) on the islands of Vitiaz and Dampier Straits near New Guinea in the south-west Pacific Ocean, plotted as a function of island area (A, in km^2) on a double logarithmic scale. The points • represent relatively undisturbed islands. The straight line $S = 18.9A^{0.18}$ was fitted by least mean squares through the points for these islands. Note that species number increases regularly with island area. The two points O refer to Long and Ritter Islands, whose faunas were recently destroyed by volcanic explosions and which have not yet regained their equilibrium species number.

systems to suggest answers to these questions are provided by distributional studies of various plant or animal groups on various archipelagos throughout the world. If one compares islands of different size but with similar habitat and in the same archipelago, the number of species S on an island is usually found to increase with island area A in a double logarithmic relation:

$$S = S_0 A^z \tag{1}$$

where S_0 is a constant for a given species group in a given archipelago, and z usually assumes a value in the range 0.18-0.35 (Preston, 1962; MacArthur & Wilson, 1963, 1967; May, in press). A rough rule of thumb, corresponding to a z value of 0.30, is that a tenfold increase in island area means a twofold increase in the number of species. Figure 2 illustrates the species/area relation for the breeding land and freshwater bird species on the islands of the Bismarck Archipelago near New Guinea and shows that the number of bird species increases regularly with island area. If one compares islands of similar area but at different distances from the continent or large island that serves as the main source of colonisation, then one finds that the number of species on an island decreases with increasing distance. This feature is illustrated by Fig. 3, which shows that the number of bird species on

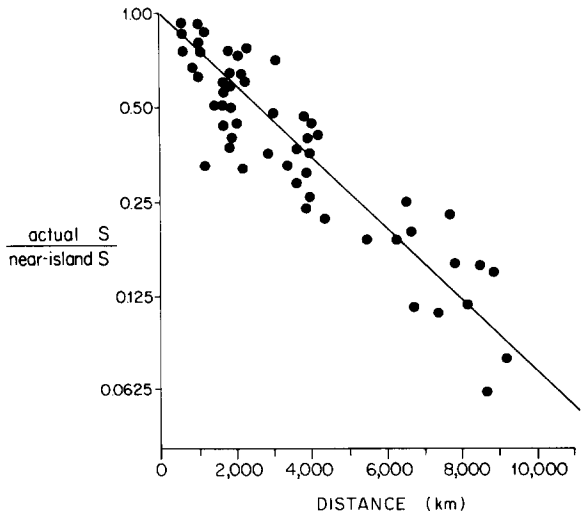

Fig. 3. Example of the relation between species number and island distance from the colonisation source in an island archipelago. The ordinate is the number of resident, non-marine, lowland bird species S on tropical south-west Pacific islands more than 500 km from New Guinea, divided by the number of species expected on an island of equivalent area less than 500 km from New Guinea. The expected near-island S was read off the species/area relation for such islands (Fig. 5). The abscissa is the island distance from New Guinea. Note that S decreases by a factor of 2 per 2600 km distance from New Guinea. (After Diamond, 1972.)

islands of the south-west Pacific decreases by a factor of 2 for each 2600 km of distance from New Guinea. For plants or animals with weaker powers of dispersal than birds, the fall-off in species number with distance is even more rapid.

Similar findings are obtained if, instead of oceanic islands, one compares habitat 'islands' within a continent or large island. For example, isolated as enclaves within the rain forest that covers most of New Guinea are two separate areas of savanna, which received most of their plant and animal species from Australia (Schodde & Calaby, 1972; Schodde & Hitchcock, 1972). The savanna which is larger and also closer to Australia supports twice as many savanna bird species as the smaller and more remote savanna (Fig. 4). Other examples are provided by mountains rising out of the 'sea' of lowlands, such as the isolated mountain ranges of Africa, South America, New Guinea and California. Thus, the number of bird species on each 'island' of alpine vegetation at high elevations in the northern Andes increases with area of alpine habitat and decreases with distance from the large alpine source area in the Andes of Ecuador (Vuilleumier, 1970).

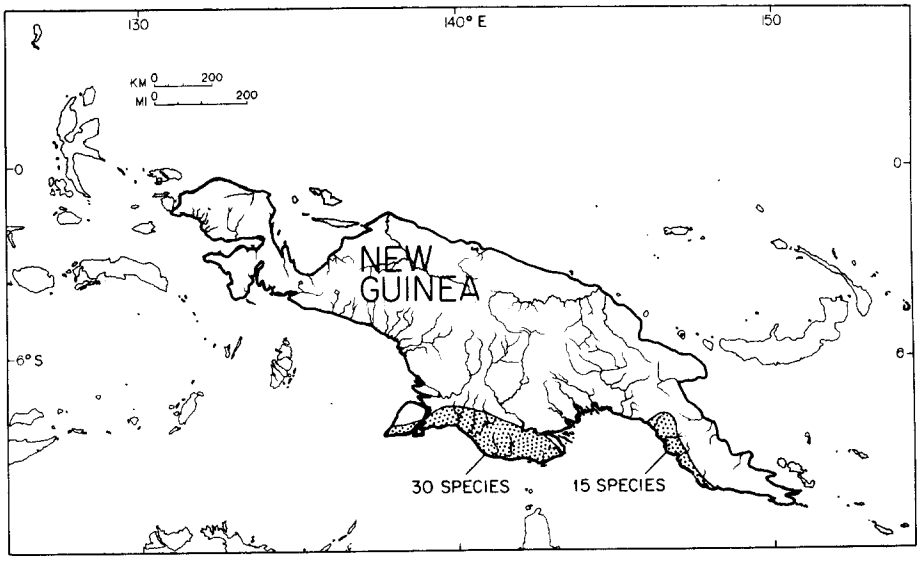

Fig. 4. Example of the relation between area of 'habitat islands' and the number of characteristic species they support. Most of New Guinea is covered by rain forest, but two separate areas on the south coast (shaded in the figure) support savanna woodland. The characteristic bird species of these savannas are mostly derived from Australia (the northern tips of Australia are just visible at the lower border of the figure). The so-called Trans-Fly savanna (left) not only has a larger area than the so-called Port Moresby savanna (right), but is also closer to the colonisation source of Australia. As a result, the Trans-Fly savanna supports twice as many bird species characteristic of savanna woodland (*c.* 30 compared with 15 species) as does the Port Moresby savanna.

Why is it that species number increases with increasing area of habitat but decreases with increasing isolation? In explanation of these findings, Preston (1962) and MacArthur & Wilson (1963, 1967) suggested that species number *S* on an island is set by (or approaches) an equilibrium between immigration rates and extinction rates. Species immigrate into an island as a result of dispersal of colonists from continents or other islands; the more remote the island, the lower is the immigration rate. Species established on an island run the risk of extinction due to fluctuation in population numbers; the smaller the island, the smaller is the population and the higher the extinction rate. Area also affects immigration and extinction rates in several other ways: through its relation to the regional magnitude of spatial and temporal variation in resources; by being correlated with the variety of available habitats as stressed by Lack (1973); and by being correlated with the number of 'hot spots', or sites of locally high utilisable resource production for a particular species (Diamond, in press). On a given island, extinction rates increase, and immigration rates decrease, with increasing *S*. The *S* value on an island in the steady state is the number at which immigration and extinction rates become equal. The larger and less isolated the island, the higher is the species number at which it should equilibrate.

The correctness of this interpretation has been established by several types of study. One has involved observing the increase in species number on an island whose fauna and/or flora have been destroyed. The most famous such study was provided by a 'natural experiment', the colonisation by birds of the vocanic island of Krakatoa after its fauna had been destroyed by an eruption in 1883 (Dammerman, 1948; see MacArthur & Wilson, 1967, pp. 43-51). Similar 'natural experiments' are provided by the birds of Long Island near New Guinea, whose fauna was destroyed by a volcanic eruption two centuries ago (*see* Fig. 2), and by the birds of seven coral islets in the Vitiaz-Dampier group near New Guinea, when a tidal wave destroyed the fauna in 1888 (Diamond, 1974). Simberloff & Wilson (1969) created an analogous 'artificial experiment' by fumigating several mangrove trees standing in the ocean off the coast of Florida and observing the recolonisation of these trees by arthropods. In all these studies, the number of species on the island returned within a relatively short time to the value appropriate to the island's area and isolation, confirming that this value really was an equilibrium value. Naturally, the rate of approach to equilibrium depends on the plant or animal group studied and the island's location: for example, successive surveys have shown the number of plant species on Krakatoa still to be rising and not yet to have reached equilibrium (Docters van Leeuwen, 1936; MacArthur & Wilson, 1967, p. 49).

Another type of test of the MacArthur-Wilson interpretation is provided by turnover studies at equilibrium. According to the MacArthur-Wilson interpretation, although the *number* of species on an island may remain near an equilibrium value, the *identities* of the species need not remain constant, because

new species are continually immigrating and other species are going extinct. Estimates of immigration and extinction rates at equilibrium have been obtained by comparing surveys of an island in separate years. Such studies have been carried out for the birds of the Channel Islands off California (Diamond, 1969; Hunt & Hunt, 1974; Jones & Diamond, in press), Karkar Island off New Guinea (Diamond, 1971), Vuatom Island off New Britain (Diamond, in press), and Mona Island off Puerto Rico (Terborgh & Faaborg, 1973). All these studies found that a certain number of species present in the earlier survey had disappeared by the time of the later survey, but that a similar number of other species immigrated in the intervening years, so that the total number of species remained approximately constant unless there was a major habitat disturbance. As expected from considering the risk of extinction in relation to population size, most of the populations that disappeared had initially consisted of few individuals. The turnover rates per year (immigration or extinction rates) observed in these studies have been in the order of 0.2-6% of the island's bird species for islands of 300-400 km^2 area.

Thus, the number of species that a reserve can 'hold' at equilibrium is likely to be set by a balance between immigration rates and extinction rates. The set-point will be at a larger number of species, the larger the reserve or the closer it is to a source of colonists:

1. If 90% of the area occupied by a habitat is converted by man into another habitat and the remaining 10% is saved as an undivided reserve, one might expect to save roughly about half of the species restricted to the preserved habitat type, while the populations of the remaining half of the species will eventually disappear from the reserve. It should be stressed explicitly that increased habitat diversity is part of the reason, but not the only one (*cf.* p. 134 for others), why larger areas hold more species. Thus, even if a reserve does include some of the type of habitat preferred by a threatened species, the species may still disappear because of population fluctuations, spatial or temporal variation in resources, and too few or too small 'hot spots'.

2. If one saves two reserves, the smaller reserve will retain fewer species if it is remote from the larger reserve than it would if it were near the larger reserve.

3. As the contrast increases between the preserved habitat types and the surrounding habitat types, or between the ecological requirements of a threatened species and the resources actually available in areas lying between reserves, the results of island biogeographic studies become increasingly relevant. The greater this contrast, the lower will be the population density of the threatened species in the area between reserves, and the lower will be the species' dispersal rate between the reserves. To some species the intervening area may be no barrier at all, while to other species it may be as much of a barrier as the ocean is to a flightless mammal.

HOW RAPIDLY WILL SPECIES GO EXTINCT ?

Suppose that 90% of a habitat is destroyed and the remaining 10% is saved as a faunal reserve. The reserve will initially support most, though not all, species restricted to the original expanse of habitat. (The actual proportion of the species present in such a portion of a larger habitat is discussed on pp. 9-10 and 16 of MacArthur & Wilson (1967).) However, we have just seen that at equilibrium the reserve will support only about half the species of the original expanse of habitat. Thus, at the time that the reserve is set aside, it will contain more species than its area can support at equilibrium as an island. Species will go extinct until the new equilibrium number is reached. Such a reserve will constitute the exact converse of an island which has had its fauna destroyed: equilibrium of species number will be approached from above, by an excess of extinction over immigration, rather than from below, by an excess of immigration over extinction. The important practical question thus arises: how rapidly will species number 'relax' to the new equilibrium value? If equilibrium times were of the order of millions of years, these extinctions would not be a matter of practical concern, whereas a reserve that lost half of its species in a decade would be unacceptable.

A natural experiment that permits one to assess 'relaxation rates' as a function of the reserve's area is provided by so-called land-bridge islands (Diamond, 1972, 1973). During the late Pleistocene, when much sea-water was locked up in glaciers, the ocean level was about 100-200 m lower than at present. Consequently, islands separated from continents or from larger islands by water less than 100 m deep formed part of the continents or larger islands, and shared the continental faunas and floras. Examples of such 'land-bridge islands' are Britain off Europe, Aru and other islands off New Guinea, Tasmania off Australia, Trinidad off South America, Borneo and Java off south-east Asia, and Fernando Po off Africa. When rising sea levels severed the land-bridges about 10,000 years ago, these land-bridge islands must have found themselves supersaturated; they initially supported a species-rich continental fauna rather than the smaller number of species appropriate to their area at equilibrium. Gradually, species must have been lost by an excess of extinctions over immigrations. Figure 5 illustrates how far the avifaunas of the satellite land-bridge islands of New Guinea have returned towards equilibrium in 10,000 years. The larger land-bridge islands, with areas of several hundred to several thousand km^2, still have more bird species than predicted for their area from the species/area relation based on islands at equilibrium, though they do have considerably fewer bird species than New Guinea itself. That is, the larger land-bridge islands have lost many but not all of their excess species in 10,000 years. However, land-bridge islands smaller than about 250 km^2 at present have the same number of bird species as similar-sized oceanic islands that never had a land-bridge. Thus, the smaller land-bridge islands have lost their entire excess of bird species in 10,000 years.

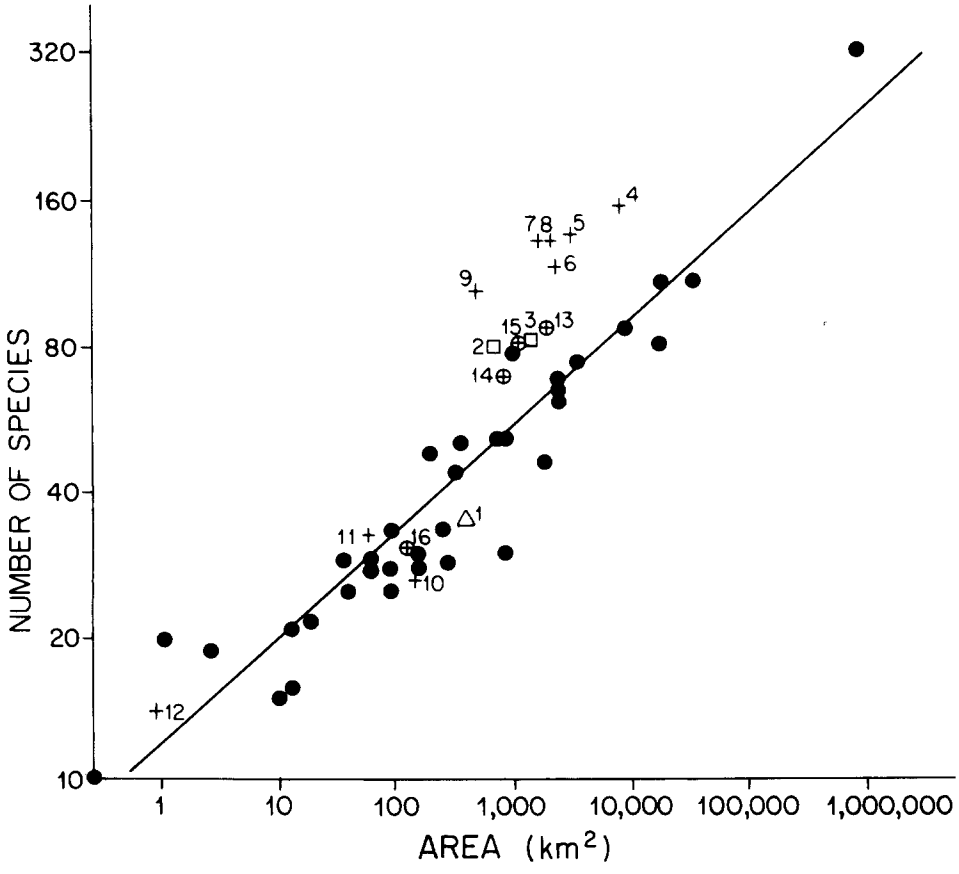

Fig. 5. Example of how one can use land-bridge islands to estimate extinction rates in the faunas of natural reserves. The ordinate is the number of resident, non-marine, lowland bird species on New Guinea satellite islands, plotted as a function of island area on a double logarithmic scale. The points • are islands which have not had a recent land-connection to New Guinea and whose avifaunas are presumed to be at equilibrium. The numbered point △ (1) refers to a recently exploded volcano whose avifauna has not yet returned to equilibrium; points + (4-12), to islands connected to New Guinea by land-bridges at times of lower sea-level 10,000 years ago; points ⊕ (13-16), to islands formerly connected by land-bridges to some other large island but not to New Guinea itself; and points □ (2-3), to islands that lie on a shallow shelf and had a much larger area at times of lower sea-level. Up to the time that the land-bridges were severed by rising sea-level, the New Guinea land-bridge islands (+, 4-12) must have supported nearly the full New Guinea quota of 325 lowland species (point in the upper right-hand corner). At present none of these land-bridge islands supports anything close to 325 species; the larger ones (+, 4-9) do, however, still have more species than expected at equilibrium (as given by points • and the straight line); and the smaller ones (+, 10-12) already have about the number of species expected at equilibrium. The conclusion is that no land-bridge island has been able to hold more than half its initial number of species, but that the larger islands have been able to hold an excess of species for longer. The same conclusion follows from points ⊕ and □. (From Diamond, 1972.)

The re-equilibration of land-bridge islands is the resultant of the extinction rate E (in species/year) exceeding the immigration rate I (in species/year) until an equilibrium species number S_{eq} is attained. Both I and E depend on the instantaneous species number $S(t)$, where t represents time (in years). As a highly simplified model, let us assume constant coefficients K_i and K_e (in year^{-1}) of immigration and extinction, respectively:

$$E = K_e S(t) \tag{2}$$

$$I = K_i[S^* - S(t)] \tag{3}$$

where S^* is the mainland species pool, and $[S^* - S(t)]$ is the number of species in the pool not present on the island at time t, hence available as potential immigrants. At equilibrium, when $dS/dt = I - E = 0$, S_{eq} is given by

$$S_{eq} = K_i S^*/(K_i + K_e) \tag{4}$$

If a land-bridge island initially (at $t = 0$) supports a species number $S(0)$ that exceeds S_{eq}, the rate at which $S(t)$ declines from $S(0)$ towards S_{eq} is obtained by integrating the differential equation

$$dS/dt = I - E = (K_i + K_e)[K_i S^*/(K_i + K_e) - S(t)]$$

with the boundary condition $S(t) = S(0)$ at $t = 0$, to obtain:

$$[S(t) - S_{eq}]/[S(0) - S_{eq}] = \exp(-t/t_r) \tag{5}$$

The relaxation time t_r is the length of time required for the species excess $[S(t) - S_{eq}]$ to relax to $1/e$ or 36.8% of the initial excess $[S(0) - S_{eq}]$, where e is the base of natural logarithms. Relaxation is 90% complete after 2.303 relaxation times.

As an example of the use of this formula, consider the land-bridge island of Misol near New Guinea. At the time 10,000 years ago when it formed part of New Guinea, Misol must have supported nearly the full New Guinea lowlands fauna of 325 bird species. With an area of 2040 km^2, Misol should support only 65 species at equilibrium, by comparison with the species/area relation for islands that lacked land-bridges and are at equilibrium. The present species number on Misol is 135, much less than the initial value of 325 but still in excess of the final equilibrium value. Substituting $S(0) = 325$, $S(t) = 135$, $S_{eq} = 65$, $t = 10{,}000$ years into eqn. (5) yields a relaxation time of 7600 years for the avifauna of Misol.

Similar calculations have been carried out for other land-bridge islands formerly connected to New Guinea, for islands formerly connected to some other large satellite island but not to New Guinea itself, and for islands that lie on a shallow-water shelf and that formerly must have been much larger in area although without

connection to a larger island. A similar analysis in a continental situation was made by Brown (1971), who studied distributions of small non-volant mammals in forests which are now isolated on the tops of mountains rising out of western North American desert basins but which were formerly connected by a continuous forest belt during times of cooler Pleistocene climates. Terborgh (in press, *a, b*) has made a similar analysis of the avifaunas of Caribbean islands and has dramatically confirmed the accuracy of his calculations by showing that they correctly predict the extinction rates observed within the present century on Barro Colorado Island (Willis, 1974). Both Terborgh's analyses of Caribbean birds and mine of New Guinea birds show that relaxation times increase with increasing island area. Both analyses also show that eqns. (2) and (3) are oversimplified: K_i actually increases with $S(t)$, and K_i decreases with $S(t)$.

Thus, the gradual decline of species number from a high initial value to a lower equilibrium value on land-bridge islands may furnish a model for what could happen when a fraction of an expanse of habitat is set aside as a reserve and the remaining habitat is destroyed. A small reserve not only will eventually contain few species but will also initially lose species at a high rate. For reserves of a few km^2, extinction rates of sedentary bird and mammal species unable to colonise from one reserve to another are so high as to be easily measurable in a few decades. Within a few thousand years even a reserve of 1000 km^2 will have lost most such species confined to the reserve habitat. These estimates assume that man's land-use practices do not grossly alter the preserved habitat. More rapid changes in species composition are likely to occur if sylviculture or other human use changes the habitat structure.

WHAT SPECIES WILL SURVIVE?

In the preceding pages we have considered the problem of survival from a statistical point of view: what fraction of its initial fauna will a reserve eventually save, and how rapidly will the remainder go extinct? We have not yet considered the survival probabilities of individual species. If each species had equal probabilities of survival, then it would be a viable conservation strategy to be satisfied with large numbers of small reserves. Each such vest-pocket reserve would lose most of its species before reaching equilibrium, but with enough reserves any given species would be likely to be among the survivors in at least one reserve. In this section we shall examine the flaw in this strategy: different species have very different area requirements for survival.

The survival problem needs to be considered from two points of view: the chance that a reserve where a species has gone extinct will be recolonised from another reserve, and the chance that a species will go extinct in an isolated reserve. Consider the former question first. Suppose that there are many small reserves. Suppose next

that a given species is incapable of dispersing from one reserve to another across the intervening sea of unsuitable habitat. The isolated populations in each reserve run a finite risk of extinction. If there is no possibility of recolonisation, each extinction is irrevocable, and it is only a question of time before the last population of the species disappears. Suppose on the other hand that dispersal from one reserve to another is possible. Then, although a species temporarily goes extinct in one reserve, the species may have recolonised that reserve by the time it goes extinct in another reserve. If there are enough reserves or high enough recolonisation rates or low enough extinction rates, the chances of the species disappearing simultaneously from all reserves are low, and the long-term survival prospects are bright. Dispersal ability obviously differs enormously among plant and animal species. Flying animals tend to disperse better than non-flying ones; plants with wind-borne seeds tend to disperse better than plants with heavy nuts. The more sedentary the species, the more irrevocable is any local extinction, and the more difficult will it be to devise a successful conservation strategy. Thus, conservation problems will be most acute for slowly dispersing species in normally stable habitats, such as tropical rain forest. Even power of flight cannot be assumed to guarantee high dispersal ability. For instance, 134 of the 325 lowland bird species of New Guinea are absent from all oceanic islands more than a few km from New Guinea, and are confined to New Guinea plus islands with recent land-bridge connections to New Guinea. Similarly, many neotropical bird families with dozens of species have not even a single representative on a single New World island lacking a recent land-bridge to South or Central America; and not a single member of many large Asian bird families has been able to cross Wallace's Line separating the Sunda Shelf land-bridge islands from the oceanic islands of Indonesia. Such bird species have insuperable psychological barriers to crossing water gaps, and are generally characteristic of stable forest habitats. Thus, low recolonisation rates may mean either that a species *cannot* cross unsuitable habitats (a mountain forest rodent faced by a desert barrier), or that it *will not* cross unsuitable habitats (some tropical forest birds faced by a water gap).

Having seen that species vary in their ability to recolonise, let us now consider how species vary in extinction rates of local populations. The New Guinea land-bridge islands again offer a convenient test situation (Diamond, 1972, in press). Recall that these islands initially supported most of the New Guinea lowlands fauna, that the land-bridges were severed about 10,000 years ago, that 134 New Guinea lowlands bird species do not cross water gaps, and that any extinctions of populations of these species on the land-bridge islands cannot therefore have been reversed by recolonisation. Virtually all these species are now absent from all land-bridge islands smaller than 50 km^2, because extinction rates on small islands are so high that virtually no isolated population survives 10,000 years. However, these 134 species vary greatly today in their distribution on the seven larger (450-8000 km^2) land-bridge islands. At the one extreme, some species, such as the

frilled monarch flycatcher *(Monarcha telescophthalmus)*, have survived on all seven islands. At the other extreme, 32 species have disappeared from all seven islands, and must be especially prone to extinction in isolated populations. Most of these 32 species fit into one or more of three categories: birds whose initial populations must have numbered few individuals because of very large territory requirements (*e.g.* the New Guinea harpy eagle *(Harpyopsis novaeguineae)*); birds whose initial populations must have numbered few individuals because of specialised habitat requirements (*e.g.* the swamp rail *(Megacrex inepta)*); and birds which are dependent on seasonal or patchy food sources and normally go through drastic population fluctuations (*e.g.* fruit-eaters and flower-feeders).

Another natural experiment in differential extinction is provided by New Hanover, an island of 1200 km^2 in the Bismarck Archipelago near New Guinea. In the late Pleistocene, New Hanover was connected by a land-bridge to the larger island of New Ireland and must then have shared most of New Ireland's species. Today New Hanover has lost about 22% of New Ireland's species, a fractional loss that does not sound serious. However, among these lost species are 19 of the 26 New Ireland species confined to the larger Bismarck islands, including every endemic Bismarck species in this category. That is, New Hanover differentially lost those species most in need of protection. As a faunal reserve, New Hanover would rate as a disaster. Yet its area of 1200 km^2 is not small by the standards of many of the tropical rain forest parks that one can realistically hope for today.

As a further example of a natural experiment in differential extinction, consider the mammals isolated on mountain tops rising from North American desert basins, mentioned in the previous section. Like the bird species restricted to the New Guinea land-bridge islands, the isolated populations of these mammal species have been exposed to the risk of extinction for the past 10,000 years, without opportunity for recolonisation. Today, some of these mammal species are still present on most of the mountains, while other species have disappeared from all but a few mountains. The species with the highest extinction rates are those whose initial populations must have numbered few individuals: either because the species is a carnivore rather than a herbivore, or because it has specialised habitat requirements, or because it is a large animal (Brown, 1971).

A method of quantifying the survival prospects of a species is to determine its so-called incidence function (Diamond, in press). On islands of the New Guinea region one notes that some bird species occur only on the largest and most species-rich islands; other species also occur on medium-sized islands; and others also occur on small islands. To display these patterns graphically, one groups islands into classes containing similar numbers of bird species (*e.g.* 1-4, 5-9, 10-20, 21-35, 36-50, etc.); calculates the *incidence* J or fraction of the islands in a given class on which a particular species occurs; and plots incidence against the total species number S on the island (Fig. 6). Since S is closely correlated with area, in effect these graphs represent the probability that a species will occur on an island of a particular size.

For most species, J goes to zero for S values below some value characteristic of the particular species, meaning that there is no chance of survival on islands below a certain size. These incidence functions can be interpreted in terms of the biology of the particular species (*e.g.* its population density, reproductive strategy, and dispersal ability). From these incidence functions one can estimate what chance a certain species has of surviving on a reserve of a certain size.

Thus, different species have different probabilities of persisting on a reserve of a given size. These probabilities depend on the abundance of the species and the

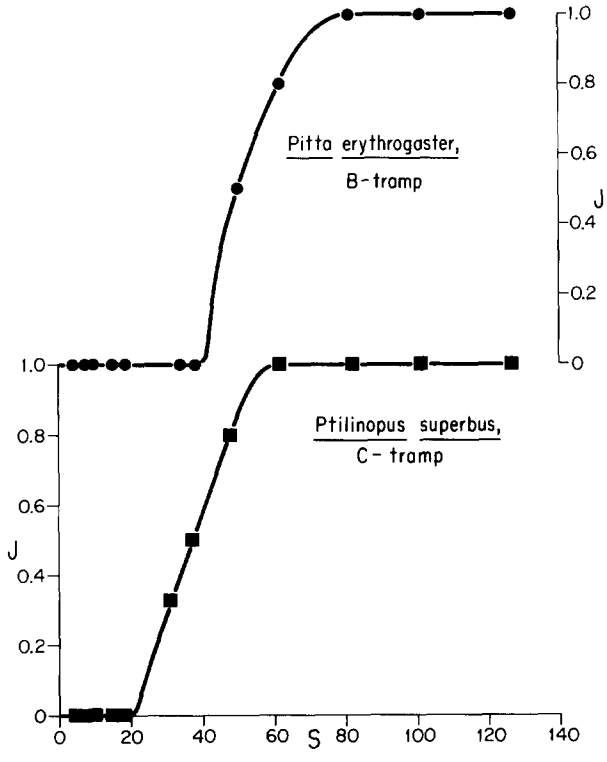

Fig. 6. So-called incidence functions for two bird species of the Bismarck Archipelago near New Guinea. The incidence $J(S)$ is defined as the fraction of the islands with a given total number of bird species S that a given species occurs on. For example, the so-called B-tramp *Pitta erythrogaster* (●) is on all islands (*i.e.* $J = 1.0$) with $S > 80$, on about half of the islands ($J = 0.5$) with S around 55, and on no island ($J = 0$) with $S < 40$. Other bird species of the Bismarck Archipelago have different incidence functions: for example, the so-called C-tramp *Ptilinopus superbus* (■) is on all islands with $S > 60$ and on many islands ($J = 0.3$-0.8) with $S = 30$-50. Since S is mainly a function of island area, the message is that each species requires some characteristic minimum area of island for it to have a reasonable chance of surviving.

magnitude of its population fluctuations, and also on its ability to recolonise a reserve on which it has once gone extinct. Even on reserves as large as 10,000 km^2, some species have negligible prospects of long-term survival. Such species would be doomed by a system of many small reserves, even if the aggregate area of the system were large.

WHAT DESIGN PRINCIPLES WILL MINIMISE EXTINCTION RATES IN NATURAL RESERVES?

In the preceding sections we have examined how the eventual number of species that a reserve can hold is related to area, how extinction rates are related to area, and how area-dependent survival prospects vary among species. Given this background information, let us finally consider what the designer of natural

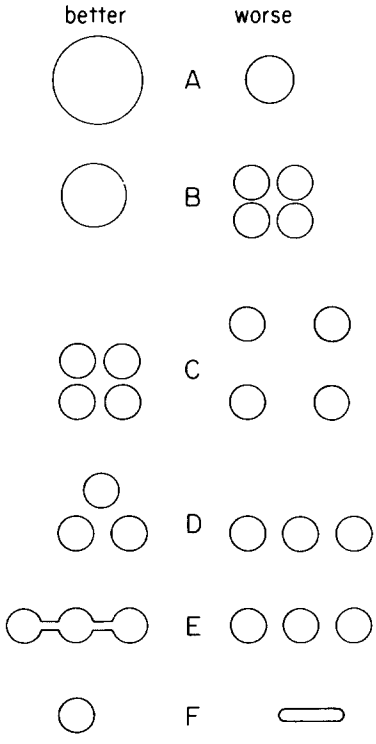

Fig. 7. Suggested geometric principles, derived from island biogeographic studies, for the design of natural reserves. In each of the six cases labelled A to F, species extinction rates will be lower for the reserve design on the left than for the reserve design on the right. See text for discussion.

reserves can do to minimise extinction rates (Diamond, 1972, 1973; Terborgh, in press, *a, b,* Wilson & Willis, in press). Figure 7 (modified from Wilson & Willis, in press) summarises a series of design principles, identified as A, B, C, D, E and F.

A large reserve is better than a small reserve (principle A), for two reasons: the large reserve can hold more species at equilibrium, and it will have lower extinction rates.

In practice, the area available for reserves must represent a compromise between competing social and political interests. Given a certain total area available for reserves in a homogeneous habitat, the reserve should generally be divided into as few disjunctive pieces as possible (principle B), for essentially the reasons underlying principle A. Many species that would have a good chance of surviving in a single large reserve would have their survival chances reduced if the same area were apportioned among several smaller reserves. Many species, especially those of tropical forests, are stopped by narrow dispersal barriers. For such species even a highway swath through a reserve could have the effect of converting one large island into two half-sized islands. Principle B needs to be qualified by the statement that separate reserves in an inhomogeneous region may each favour the survival of a different group of species; and that even in a homogeneous region, separate reserves may save more species of a set of vicariant similar species, one of which would ultimately exclude the others from a single reserve.

If the available area must be broken into several disjunctive reserves, then these reserves should be as close to each other as possible, if the habitat is homogeneous (principle C). Proximity will increase immigration rates between reserves, hence the probability that colonists from one reserve will reach another reserve where the population of the colonist species has gone extinct.

If there are several disjunctive reserves, these should ideally be grouped equidistant from each other rather than grouped linearly (principle D). An equidistant grouping means that populations from each reserve can readily recolonise, or be recolonised from, another reserve. In a linear arrangement, the terminal reserves are relatively remote from each other, reducing exchange of colonists.

If there are several disjunctive reserves, connecting them by strips of the protected habitat (Preston, 1962; Willis, 1974) may significantly improve their conservation function at little further cost in land withdrawn from development (principle E). This is because species of the protected habitat can then disperse between reserves without having to cross a sea of unsuitable habitat. Especially in the case of sedentary species with restricted habitat preferences, such as understorey rain forest species or some bird species of California oak woodland and chaparral, corridors between reserves may dramatically increase dispersal rates over what would otherwise be negligible values.

Any given reserve should be as nearly circular in shape as other considerations permit, to minimise dispersal distances within the reserve (principle F). If the

reserve is too elongate or has dead-end peninsulas, dispersal rates to outlying parts of the reserve from more central parts may be sufficiently low to perpetuate local extinctions by island-like effects.

ACKNOWLEDGEMENTS

Field work in the south-west Pacific was supported by the National Geographic Society, Explorers Club, American Philosophical Society, Chapman Fund and Sanford Trust of the American Museum of Natural History, and Alpha Helix New Guinea Program of the National Science Foundation.

REFERENCES

BROWN, J. H. (1971). Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.*, **105**, 467-78.

DAMMERMAN, K. W. (1948). The fauna of Krakatau 1883-1933. *Verh. Koninkl. Ned. Akad. Wetenschap. Afdel. Natuurk.*, **44**(2), 1-594.

DIAMOND, J. M. (1969). Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc. natn. Acad. Sci. USA*, **64**, 57-63.

DIAMOND, J. M. (1971). Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. *Proc. natn. Acad. Sci. USA*, **68**, 2742-5.

DIAMOND, J. M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. natn. Acad. Sci. USA*, **69**, 3199-203.

DIAMOND, J. M. (1973). Distributional ecology of New Guinea birds. *Science, N.Y.*, **179**, 759-69.

DIAMOND, J. M. (1974). Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science, N.Y.*, **184**, 802-6.

DIAMOND, J. M. (in press). Incidence functions, assembly rules, and resource coupling of New Guinea bird communities. In *Ecological structure of species communities*, ed. by M. L. Cody & J. M. Diamond. Cambridge, Mass., Harvard University Press.

DOCTERS VAN LEEUWEN, W. M. (1936). Krakatau, 1833 to 1933. *Ann. Jard. Bot. Buitenzorg*, **56-57**, 1-506.

HUNT, G. J. Jr & HUNT, M. W. (1974). Trophic levels and turnover rates: the avifauna of Santa Barbara Island, California. *Condor*.

JONES, H. L. & DIAMOND, J. M. (in press). *Species equilibrium and turnover in the avifauna of the California Channel Islands*. Princeton, N.J., Princeton University Press.

LACK, D. (1973). The numbers and species of hummingbirds in the West Indies. *Evolution*, **27**, 326-7.

MACARTHUR, R. H. & WILSON, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373-87.

MACARTHUR, R. H. & WILSON, E. O. (1967). *The theory of island biogeography*. Princeton, N.J., Princeton University Press.

MACARTHUR, R. H. (1972). *Geographical ecology*. New York, Harper & Row.

MAY, R. M. (in press). Patterns of species abundance and diversity. In *Ecological structure of species communities*, ed. by M. L. Cody & J. M. Diamond. Cambridge, Mass., Harvard University Press.

PRESTON, F. W. (1962). The canonical distribution of commonness and rarity. *Ecology*, **43**, 185-215, 410-32.

SCHODDE, R. & CALABY, J. H. (1972). The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. In *Bridge and barrier: the natural and cultural history of Torres Strait*, ed. by D. Walker, 257-300. Canberra, Australian National University.

SCHODDE, R. & HITCHCOCK, W. B. (1972). Birds. In *Encyclopedia of Papua and New Guinea*, **1**, ed. by P. A. Ryan, 67-86. Melbourne, Melbourne University Press.

SIMBERLOFF, D. S. & WILSON, E. O. (1969). Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, **50**, 278-96.

TERBORGH, J. W. (in press, *a*). Faunal equilibria and the design of wildlife preserves. In *Trends in tropical ecology*. New York, Academic Press.

TERBORGH, J. W. (in press, *b*). Preservation of natural diversity: the problem of extinction prone species. *BioScience*.

TERBORGH, J. W. & FAABORG, J. (1973). Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk*, **90**, 759-79.

VUILLEUMIER, F. (1970). Insular biogeography in continental regions. I. The northern Andes of South America. *Am. Nat.*, **104**, 373-88.

WILLIS, E. O. (1974). Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.*, **44**, 153-69.

WILSON, E. O. & WILLIS, E. O. (in press). Applied biogeography. In *Ecological structure of species communities*, ed. by M. L. Cody & J. M. Diamond. Cambridge, Mass., Harvard University Press.