10
Island Biogeography and the Design of Natural Reserves

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10.1 Introduction

The flora and fauna of islands have played a central role in the development of ecological thought, from the early formulations of evolution and biogeography by Darwin and Wallace, through Mayr's demonstration of the role of geographic isolation in speciation, to the analytical theory of island biogeography pioneered by MacArthur and Wilson. Some reasons why islands have been well suited to provoking or testing theoretical ideas are that they have definite boundaries, come in many different sizes and heights and remotenesses, often have relatively simple communities of plants and animals, and serve as ready made evolutionary laboratories offering replicate 'natural experiments' in community assembly.

Islands may be real islands in the ocean, or they may be virtual islands such as hilltops (where for many species the surrounding lowland presents a distributional barrier), lakes, or wooded tracts surrounded by open land. In particular, the natural reserves and wildlife refuges that are set aside from large areas bent to man's purposes may be thought of as islands in a sea of altered habitat. In view of the manifest destiny of much of the world's tropical rain forest, we may ask such questions as: How many species of Amazonian plants and animals will survive if only 1 per cent of the Amazonian rain forest can be preserved? At what rate will species be extinguished? Which species will be likely to survive in the reserve, and which will most likely be lost? These are pressing questions, to which the theory of island biogeography holds at least some of the answers.

This chapter first treats 'static' aspects of the equilibrium biota, discussing empirical and theoretical relationships between the island area, A, and the number of species present, S. Second, 'dynamic' aspects of the equilibrium are examined; equilibrium is seen as a balance

between immigration and extinction, and the rates at which the system approaches the equilibrium configuration from below, from the neighbourhood, and from above are discussed. Next we discuss *which* species tend to be present on a given island at a given stage in its history, and conclude with some speculations as to the emergent principles for the design of natural reserves.

10.2 Species–area relations

10.2.1 *Empirical relations*

There have been many studies which compare the number of species, S, on islands of different area, A, but with similar habitat and in the same archipelago or island group. For both plants and animals, and for a variety of taxonomic groups from birds to beetles and ants, such

Table 10.1. The species–area exponent z.

Organism	Location	z	Source
beetles	West Indies	0.34	Darlington
reptiles and amphibians	West Indies	0.30	Darlington
birds	West Indies	0.24	Hamilton, Barth, Rubinoff
birds	East Indies	0.28	Hamilton, Barth, Rubinoff
birds	East-Central Pacific	0.30	Hamilton, Barth, Rubinoff
ants	Melanesia	0.30	MacArthur and Wilson
land vertebrates	Lake Michigan Islands	0.24	Preston
birds	New Guinea Islands	0.22	Diamond
birds	New Britain Islands	0.18	Diamond
birds	Solomon Islands	0.09	Diamond and Mayr
birds	New Hebrides	0.05	Diamond and Marshall
land plants	Galapagos	0.32	Preston
land plants	Galapagos	0.33	Hamilton, Barth, Rubinoff
land plants	Galapagos	0.31	Johnson and Raven
land plants	World-wide	0.22	Preston
land plants	British Isles	0.21	Johnson and Raven
land plants	Yorkshire nature reserves	0.21	Usher
land plants	California Islands	0.37	Johnson, Mason, Raven

Values of z in eq. (10.1), as deduced from observations on various groups of plants and animals in various archipelagoes. For original references, see May (1975f).

studies commonly lead to a relation of the form

$$S = cA^z \qquad (10.1)$$

The dimensionless parameter z (the slope of the regression line on a $\log S$ versus $\log A$ plot) typically has a value in the range 0·18–0·35; c is a proportionality constant, which depends *inter alia* on the dimensions in which A is measured and on the taxonomic group studied. The data are sometimes better fitted by a relation of the form $S = a + b \log A$: for a fuller discussion see, e.g., Diamond and Mayr (1976).
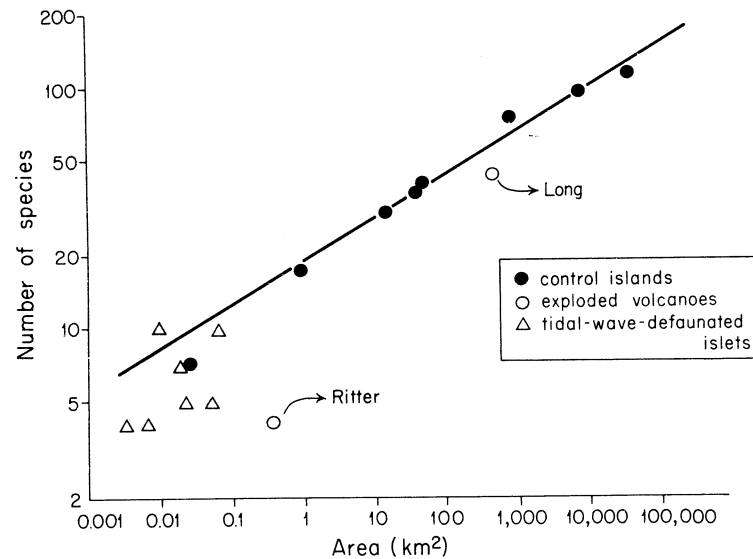

Fig. 10.1. An example of the relation between species number and island area in an archipelago: number of resident, nonmarine, lowland bird species S on islands in the Bismarck Archipelago, plotted as a function of island area on a double logarithmic scale. The solid circles represent relatively undisturbed islands, and the straight line $S = 18\cdot9$ $A^{0\cdot15}$ was fitted by least-mean-squares through the points for the seven largest islands. The open circles refer to the exploded volcanoes, Long and Ritter, where species number is still below equilibrium, especially on Ritter, because of incomplete regeneration of vegetation. The open triangles refer to coral islets inundated by the Ritter tidal wave in 1888. (From Diamond, 1974.)

Table 10.1 gives a list of the values of z in the S–A relation (10.1) for groups of plants and animals in various parts of the world. Figure 10.1 illustrates the relation, for number of bird species on islands of the Bismarck Archipelago near New Guinea.

A rough rule, which summarizes the S–A relation (10.1) with values of z in the range typically observed, is that a tenfold decrease in area corresponds to a halving of the equilibrium number of species present.
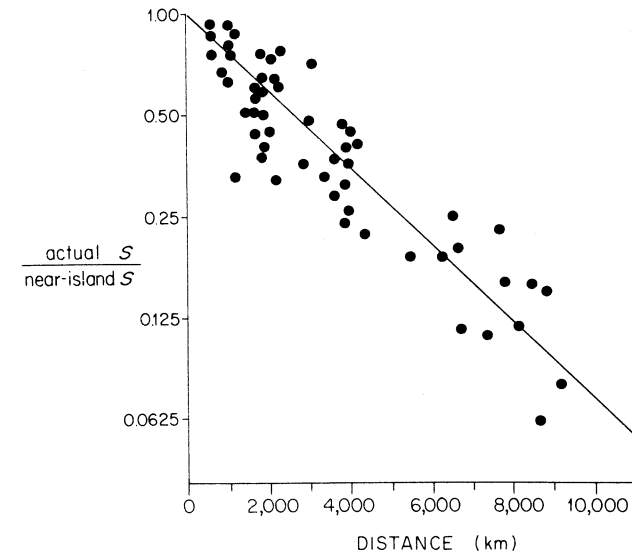

Fig. 10.2. An example of the relation between species number and island distance from the colonization source, for birds on tropical islands of the Southwest Pacific. The ordinate (logarithmic scale) is the number of resident, nonmarine, lowland bird species on islands more than 500 km from the larger source island of New Guinea, divided by the number of species on an island of equivalent area close to New Guinea. The abscissa is island distance from New Guinea. The approximately linear relation means that species number decreases exponentially with distance, by a factor of 2 per 2600 km. (From Diamond, 1972.)

Thus, to answer one of the paradigmatic questions in the introduction, saving 1 per cent of the Amazonian rain forest might correspond, very roughly, to saving 25 per cent of the original species. Such relations are admittedly crude and neglectful of detail, but they provide an informed first guess at the relation between the area of a reserve and the number of species which are eventually likely to be preserved in it.

A further empirical rule is that, if one compares islands of similar area, S decreases with increasing distance D from the colonization source. Figure 10.2 illustrates this trend for birds on tropical Pacific islands colonized from New Guinea.
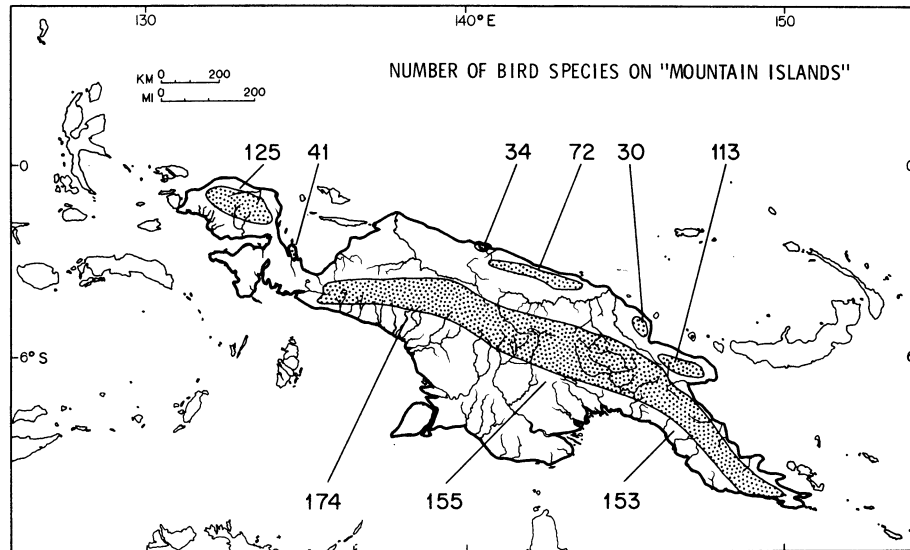

Fig. 10.3. An example of the relation between species number and area of a 'habitat island'. New Guinea consists of a large central mountain range plus about six smaller mountain ranges along the north coast (dotted areas), separated from each other by a 'sea' of intervening lowlands. There are many New Guinea bird species that are confined to higher elevations in the mountains, and for which New Guinea itself therefore behaves as an island archipelago. Numbers on the map give the number of such montane bird species on each small range and at three different locations on the central range. Note that the larger ranges have more montane species. Most of the variation in S not correlated with variation in A is correlated with variation in altitude.

Dependence of S on A is also observed for 'habitat islands' within continents or other islands. Figures 10.3 and 10.4 are two from among the many illustrative examples that could be chosen; see also MacArthur and Wilson (1967), Vuilleumier (1970), Brown (1971), and Diamond (1975a).
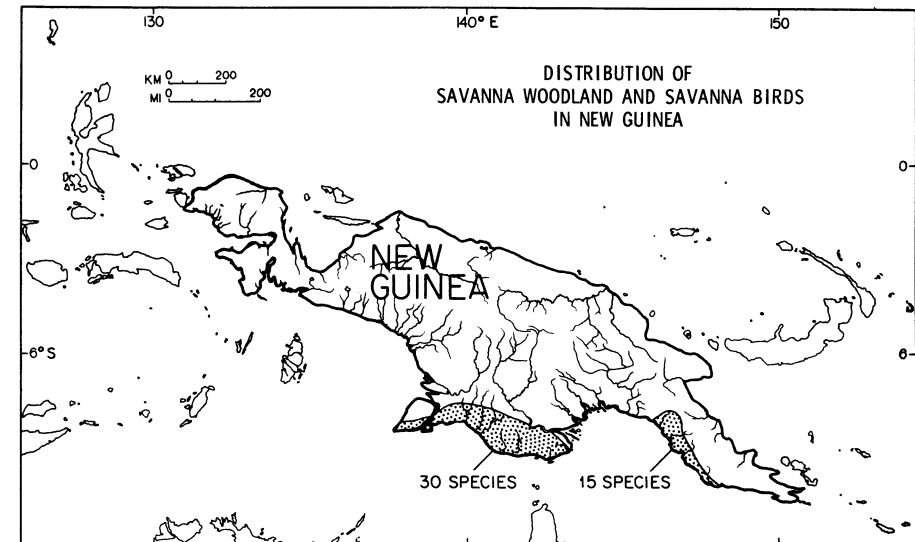
Fig. 10.4. An example of the relation between the area *and* degree of isolation of a habitat island, and the number of species it contains. Most of New Guinea is covered by rain forest, but two separate areas on the south coast (shaded in the figure) support savanna woodland. The characteristic bird species of these savannas are mostly derived from Australia (the northern tips of which are just visible at the lower border of the figure). The Trans-Fly savanna (left) not only has a larger area than the Port Moresby savanna (right), but is also closer to the colonization source of Australia. As a result, the Trans-Fly supports twice as many bird species characteristic of savanna woodland (about 30 compared with 15) as does the Port Moresby savanna. (From Diamond, 1975a.)

10.2.2 Theoretical Explanations

The phenomenological eq. (10.1) is based on observational data, and is useful as such. This section attempts to provide the equation with a theoretical underpinning.

In the preceding chapter, we saw that for any large and fairly heterogeneous assembly of species the distribution of relative abundance is likely to be of lognormal form. Going further, Preston (1962) observed that this lognormal is commonly of 'canonical' form, corresponding to the parameter γ (see section 9.4) having the special value $\gamma = 1$. In this event, there is a unique relation between the number of species, S, and the total number of individuals in the biota, N say. This was

noted by Preston (1962) and by MacArthur and Wilson (1967), who both went on to add a second assumption, namely that there is an approximately linear relationship between the total number of individuals, N, and the island area, A. The underlying implicit biological assumption, that total density of individuals is independent of area (and of S), is not strictly valid, but the deviations do not greatly affect the predicted species–area relation. When put together with the assumption of a canonical lognormal species relative abundance (which relates S to N), the assumption relating N to A leads to a unique relationship between S and A. This mathematical relationship between S and A is complicated (May, 1975f, p. 112), but for large S ($S>20$ or so) it is increasingly well approximated by eq. (10.1) with $z = 0·25$ (May, 1975f; this analytic result is to be compared with the numerical curve-fitting previously employed by Preston, 1962, to get $z = 0·262$ and by MacArthur and Wilson, 1967 to get $z = 0·263$). At low values of S, the exact S–A relation obtained under the above assumptions exhibits a downturn, of just the kind exhibited by the data (solid circles and open triangles) in Fig. 10.1.

The details of these derivations depend on the rather mystical 'canonical' assumption that $\gamma = 1$. More generally, as we explained in section 9.4, we expect some lognormal distribution of species relative abundance, with the parameter γ in the neighbourhood of unity (say 0·6 to 1·7) for a wide range of values of S and N: see May (1975f, Fig. 4). When coupled with the assumption that N is proportional to A, this leads to a 1-parameter family of S–A curves, depending on the explicit value of the parameter γ. As for the special 'canonical' case, these relations are well approximated by eq. (10.1) once S is relatively large, with z now a function of γ. Specifically, $z = 1/(4\gamma)$ for $\gamma > 1$ and $z = (1+\gamma)^{-2}$ for $\gamma < 1$, so that the plausible range of variation of γ leads to eq. (10.1) with values of z in the range 0·39 to 0·15 (May, 1975f).

This provides a detail-independent explanation of the empirical eq. (10.1), based on statistical generalities along with the assumption that biomass is roughly proportional to area. However, as discussed in section 9.4, the statistical arguments which lead to the lognormal distribution and a z value around 0·25 are no more than plausible generalities, and there are many circumstances (e.g., early succession, disturbed habitat, etc.) where those arguments do not apply. Any attempt to explain the systematic differences in z-values among the groups of species listed in Table 10.1, or other fine details of S–A relations, will demand that more attention be paid to biological details. One such

more fundamental approach is to derive the S–A relation from an understanding of extinction and immigration rates (see below): this work has been initiated by Schoener (1976b) and Gilpin and Diamond (1976). It emerges from such a treatment that z decreases with increasing immigration rates, as exemplified by the progressive decrease in z for birds of New Guinea islands, New Britain islands, Solomon islands and the New Hebrides (Table 10.1), and increases with increasing extinction rates.

10.3   Rates of approach to equilibrium

10.3.1   Extinction and immigration

Preston (1962) and MacArthur and Wilson (1963, 1967) have pointed out that the number of species on an island is set by a dynamic balance between immigration and extinction. For any particular island, the nett extinction rate will increase as the total number of species present increases; conversely, the nett rate at which new species are added— the immigration rate—will decrease as S increases. This situation is illustrated schematically in Fig. 10.5 (see also Figs. 10.6 and 10.7). The equilibrium number of species, S^*, is that at which extinction and immigration rates are equal.

This perception gives insight into the relation between an island's size and degree of isolation, and the equilibrium number of species on it. Species immigrate onto an island as a result of dispersal of colonists from continents or other islands: the more remote the island, the lower the immigration rate (i.e., the shallower the dashed curve in Figs. 10.5, 10.6 and 10.7). 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 (i.e., the more steeply rising the solid curve in Figs. 10.5 and 10.7). Area also affects immigration and extinction in several other ways: through its relation to the magnitude of spatial and temporal variability 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 utilizable resource production for a particular species (Diamond, 1975b). All in all, the larger and less isolated the island, the higher is the species number at which it should equilibrate.

To illustrate how these ideas can be elaborated in more quantitative fashion, we consider the unrealistically simple case where all species have the same, constant immigration rate, μ, and extinction rate, λ.
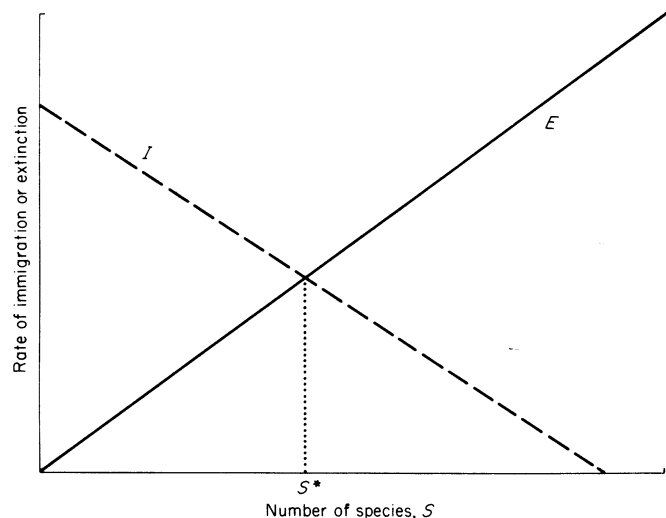

Fig. 10.5. Schematic illustration of an island's extinction curve E (solid line), and immigration curve I (dashed line), as functions of the number of species on the island, S. This figure is for the unlikely case when each species has the same extinction rate and immigration rate, so that the nett rates (expressed as number of species per unit time) are linear functions of S: see eqs. (10.2) and (10.3). The island equilibrium number of species is S^*, where the curves intersect.

Needless to say, this circumstance never prevails in the real world, but it provides a simple model which is useful for exposition; it may also be a sensible approximation to more general nonlinear models (e.g., Fig. 10.7 below) in the neighbourhood of equilibrium. If all species have the same extinction rate, λ, the nett extinction rate, E, expressed as number of species extinguished in unit time, is

$$E = \lambda S. \tag{10.2}$$

Similarly, the nett immigration rate, I, again expressed as number of species newly immigrating in unit time, is

$$I = \mu(S_T - S). \tag{10.3}$$

Here S_T is the total number of potential immigrants in the mainland pool, so that $(S_T - S)$ is the number of candidates for immigration to an

island on which S species are already present. Equations (10.2) and (10.3) give the curves illustrated in Fig. 10.5. At equilibrium $E = I$, which gives the equilibrium species number, S^*, as

$$S^* = [\mu/(\lambda + \mu)] S_T. \tag{10.4}$$

If the island is not in equilibrium, the change in the number of species in unit time is given by the difference between immigration and extinction:

$$dS(t)/dt = I - E. \tag{10.5}$$

That is, from eqs. (10.2) and (10.3),

$$dS(t)/dt = \mu S_T - (\lambda + \mu)S(t). \tag{10.6}$$

Equation (10.6) may be integrated. If the initial number of species on the island is $S(0)$ at $t = 0$, then

$$S(t) = S^* + [S(0) - S^*] \, e^{-(\lambda + \mu)t}. \tag{10.7}$$

This expression describes the rate at which the system approaches the equilibrium value S^*. Setting aside the excessive simplicity of the underlying assumptions, this expression could be fitted to observational data to obtain estimates of λ, μ and S^*.

However, it is grossly unrealistic to assume that all species have the same λ and μ values, hence that extinction and immigration rates vary linearly with S [eqs. (10.2) and (10.3)]. In reality, λ and μ values of the species coexisting in a community range over many orders of magnitude and have an approximately lognormal distribution (Gilpin and Diamond, 1980). There are two major reasons why nett extinction rates should be expected to increase faster than linearly with S, and likewise why nett immigration rates should fall faster than linearly as S increases: species differ greatly in their values of λ or of μ; and competition causes, for each species, μ to decrease and λ to increase with S. An extreme view, which is implicit in some of the writings of Lack (1973, 1976), is that there are a certain number S^* of species permanently resident on the island, and that any other immigrants will fail to breed; there are a particular S^* species that are ecologically appropriate to the island. This situation is illustrated in Fig. 10.6, which shows the corresponding ultimately steep extinction curve: the extinction rates for the S^* species which, as it were, 'belong' on the island are effectively zero; for any other species, the extinction rate is effectively infinite.

The real situation almost invariably lies between the extremes depicted in Figs. 10.5 and 10.6. In general, as more and more species are packed in, the island approaches ecological saturation, and the
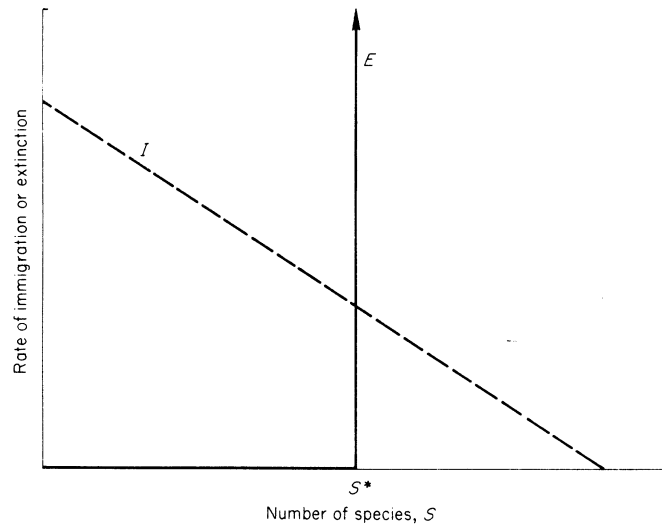

Fig. 10.6. Extinction (solid line) and immigration (dashed line) curves for an island, as functions of S, as in Fig. 10.5. The difference is that here there are S^* species which 'belong' on the island, having effectively zero extinction rate, and *no* other species are capable of breeding on the island. This results in an infinitely steep extinction curve E, as illustrated [i.e., eq. (10.8) in the limit $n \to \infty$].

overall extinction curve, E, steepens rapidly. This may be represented by writing

$$E(S) = \varepsilon(S/S_0)^n, \qquad (10.8)$$

where n is now a parameter which describes the steepness of the curve. The simple case of eq. (10.2), constant extinction rate for species, corresponds to the limit $n = 1$; the opposite extreme of Fig. 10.6 corresponds to the limit $n \to \infty$ (whence $E \to 0$ for $S < S_0$, $E \to \infty$ for $S > S_0$). Observational data for birds on real islands suggests values of n around 2 to 4 (Gilpin and Diamond, 1976; Schoener, 1976b; see also Terborgh's, 1974, work below). Analogous expressions may be used to parameterize the nonlinear behaviour of most curves for nett immigration, $I(S)$, which for birds prove to be even steeper than the extinction curves ($n \sim 6$: Gilpin and Diamond, 1976). Figure 10.7 illustrates such extinction and immigration curves for lowland bird species on a typical island

in the Solomon Archipelago, in the tropical Southwest Pacific (Gilpin and Diamond, 1976).

The comparison between the realistic Fig. 10.7 and the idealized extremes of Figs. 10.5 and 10.6 sheds light on what has sometimes been misperceived as a conflict between the views of MacArthur and Wilson and those of Lack. Species equilibrium is indeed a dynamic thing (as suggested by MacArthur and Wilson). However, as stressed from the start by MacArthur and Wilson (e.g., Fig. 4 of their 1963 paper), the actual extinction and immigration rates which describe species turnover are, in reality, given by curves that are closer in character to Fig. 10.6 (in the spirit of Lack) than to Fig. 10.5.
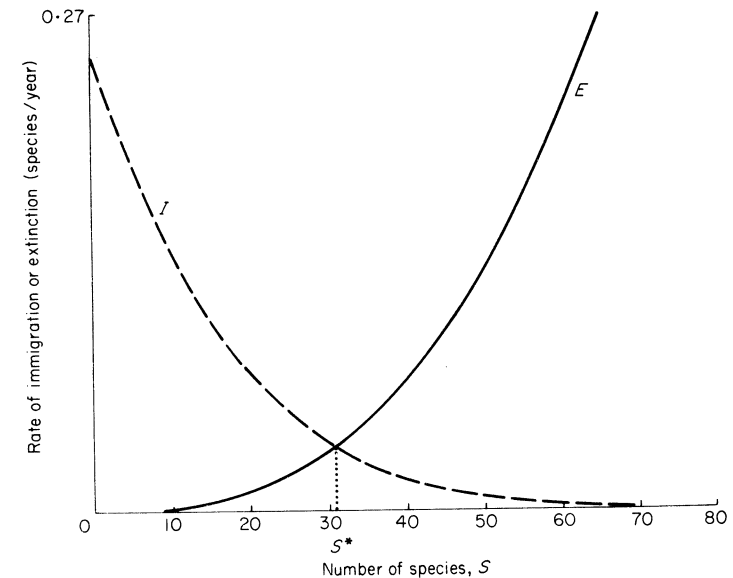

Fig. 10.7. The actual extinction (solid line) and immigration (dashed line) curves for the avifauna on Three Sisters, one of the smaller Solomon islands: the rates are plotted as relative number of species to go extinct, or to immigrate, per year as a function of the number of species on the island. For this island, the extinction curve is of the form of eq. (10.8) with $n = 2 \cdot 75$, and the equilibrium number of species is $S^* = 32$. For further details, see Gilpin and Diamond (1976). These actual curves are to be compared with the idealized extremes depicted in Figs. 10.5 and 10.6.

We now confront these ideas with data on the way the number of species approaches the island equilibrium value from below ($S(0) < S^*$),

in the neighbourhood of equilibrium $(S(0) \sim S^*)$, and from above $(S(0) > S^*)$.

10.3.2 *Species number increasing toward equilibrium*

One type of study involves observing the increase in species number on islands where the flora and/or fauna have been removed either by natural catastrophe or by experimental manipulation. In these situations, the immigration term I is of predominant importance in eq. (10.5), at least in the initial stages.

The most famous such study was provided by a 'natural experiment', the recolonization of the volcanic island of Krakatoa after its biota had been destroyed by an eruption in 1883 (Docters van Leeuwen, 1936; Dammerman, 1948; see MacArthur and Wilson, 1967, pp. 43–51). Here the number of bird species returned in a relatively short time to the value appropriate to the island's area and isolation, whereas the number of plant species is still rising; the rate of approach to equilibrium obviously depends on the plant or animal group under consideration. Similar 'natural experiments' are provided by the birds of Ritter and Long Islands near New Guinea, whose faunas were destroyed by volcanic eruptions in 1888 and about two centuries ago, respectively (see Fig. 10.1); by the birds of seven coral islets in the same area, where the tidal wave following the Ritter eruption destroyed the fauna in 1888 (Diamond, 1974); and by the initial colonization of a newly created volcanic island such as Surtsey, off Iceland.

As discussed in section 9.3, Simberloff and Wilson (1969) created an analogous 'artificial experiment' by fumigating several tiny mangrove islets off the coast of Florida and observing the recolonization by arthropods. Similarly, A. Schoener (1974) suspended plastic sponges and measured the rate at which they were colonized by marine invertebrates.

10.3.3 *Species number around equilibrium*

Another type of test is provided by turnover studies at equilibrium. According to the above 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 for birds have been obtained by comparing surveys of an island in separate years; among such studies are those for the birds of the Channel Islands off California (Diamond, 1969; Hunt and Hunt, 1974; Jones and Diamond, 1976), Karkar Island off New Guinea (Diamond, 1971), Mona Island off Puerto Rico (Terborgh and Faaborg, 1973), islands off the coast of Britain and Germany (data of Jones and Diamond, summarized by Diamond and May, 1977), and European mainland census plots (Järvinen, 1979). Two practical problems in turnover studies are: (a) to estimate man's effect on natural turnover rates (see Jones and Diamond, 1976); and (b) to correct for the precipitous decline in apparent turnover rate with increasing interval between censuses, as a result of extinctions and reimmigrations in the interval remaining unnoticed and cancelling each other's effect (Diamond and May, 1977).

All these turnover 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 (extinction and immigration rates) observed in these bird studies were in the range of 0·2 to 20 per cent of the island's bird species for islands of area ranging from 400 to 0·4 km².

10.3.4 *Species number decreasing towards equilibrium*

The situation of greatest relevance to floral and faunal conservation arises when some fraction of a habitat is set aside as a reserve, and the rest destroyed. Such a reserve will at first be 'supersaturated', containing more species than are appropriate to its area at equilibrium. The situation is the exact converse of an island which has had its biota destroyed (section 10.3.2): equilibrium of species number will be approached from above, and the extinction term E will be of predominant importance in eq. (10.5), at least in the early stages.

A natural experiment of this kind is provided by so-called land-bridge islands. During the most recent ice age, which lasted for an extended period of thousands of years and ended about 10,000 years ago, enough water was locked up in glaciers to make the ocean levels

about 100 m. lower than at present. Consequently islands that are now separated from continents or larger islands by water less than 100 m. deep were once attached, and shared the continental biota. Examples of such land-bridge islands are Britain off Europe, Aru and other islands off New Guinea, Trinidad off South America, Fernando Po off Africa, and Borneo and Japan off Asia. Subsequent to these islands being created by rising sea levels about 10,000 years ago, their continental complement of species has slowly decreased towards the equilibrium value appropriate to an island of their modern area.

Terborgh (1974) has made a quantitative such study for birds on five neotropical land-bridge islands. The number of bird species currently on each island is known, and the number present on each island before it was cut off 10,000 years ago may be estimated from the neighbouring mainland species numbers. Terborgh notes that in this relaxation process extinction is predominant [so that I is neglected in eq. (10.5)], and he chooses to describe the nett extinction rate by eq. (10.8) with $n = 2$; thus he fits the data to

$$dS/dt = kS^2. \qquad (10.9)$$

The extinction parameter k thus deduced is shown, as a function of island area, in Fig. 10.8. Similar results, and in particular the tendency for extinction rates to decrease as island area increases, have been obtained by Diamond (1972, 1973) for birds on land-bridge islands off New Guinea and elsewhere in the southwest Pacific, and by Wilcox (1980) for mammals on islands of the southeast Asian continental shelf. Brown (1971) has made an analogous study of the distribution of small mammals in forests which are now isolated on mountaintop 'islands' rising out of the 'sea' of desert in western North America, but which were connected by a continuous forest belt or 'habitat land-bridge' during times of cooler Pleistocene climates (see Table 10.2).

Terborgh (1974) has made a dramatic application of the calculations summarized in Fig. 10.8, by showing that they correctly predict the extinction rates observed within the present century on Barro Colorado Island. This island was created from a former hilltop by the flooding of adjacent valleys to create Lake Gatun when the Panama Canal was constructed, and since 1923 it has been carefully protected as a wildlife preserve. A meticulous account of the bird species present on the island over the past 50 years has recently been published by Willis (1974). From the k-versus-area patterns for post-Pleistocene relaxation rates on neotropical land-bridge islands, Fig. 10.8, Terborgh makes an
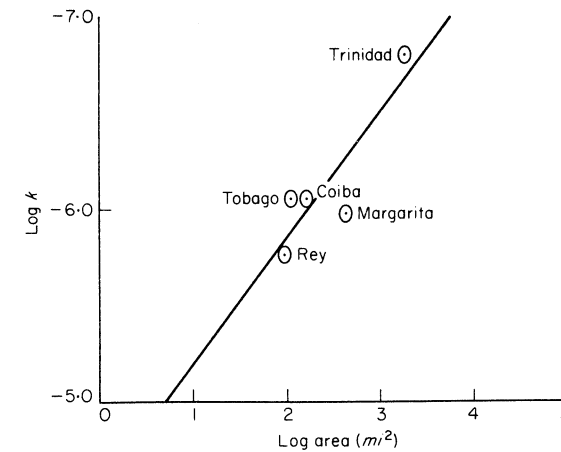
Fig. 10.8. The extinction parameter k of eq. (10.9) as a function of island area, for birds on land-bridge islands in the West Indies. (From Terborgh, 1974.)

estimate of the k value for Barro Colorado Island. Equation (10.9) can then be used to get an estimate of the decline in the island's number of bird species since 1923. This theoretical estimate of 16–17 forest bird species lost is gratifyingly in accord with the actual number of 15.

10.4   Which species survive?

Up to this point the problem of survival has been discussed in statistical terms: what fraction of its initial biota will a reserve eventually save, and how rapidly will the remainder go extinct? We now go on to consider the survival probabilities of individual species.

These considerations bear directly on conservation strategies. If each species had a roughly equal probability of survival, then large numbers of small reserves could be a satisfactory policy: each 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. The flaw in this strategy is that different species usually have very different area requirements for survival, arising from very different rates of immigration and of extinction.

Consider first the question of immigration. Even if there are many small reserves, a species that is incapable of dispersing from one reserve to another across the intervening sea of unsuitable habitat is doomed to

eventual extinction: its lights will wink out, one by one, with no chance of reignition. Conversely, a species capable of dispersing from one reserve to another may persist by virtue of a dynamic balance between local extinction and reimmigration, provided recolonization rates are high enough or extinction rates low enough. 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. These conservation problems will be most acute for the sort of slowly dispersing species found in normally stable habitats, such as tropical rain forest. Even the power of flight cannot be assumed to guarantee high dispersal ability. For example, 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 associated land-bridge islands. Similarly, many neotropical bird families with dozens of species have not one representative on a single New World island lacking a recent land-bridge to the mainland; 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 are generally characteristic of stable forest habitats, and have insuperable psychological barriers to crossing water gaps. In short, low recolonization rates may mean either that a species cannot, or that it will not, cross unsuitable habitats.

Given this variation in ability to recolonize, we turn to consider how species vary in extinction rates of local populations. The New Guinea land-bridge islands alluded to in section 10.3.4 offer a convenient test situation (Diamond, 1972, 1975a). As mentioned in the preceding paragraph, there are 134 New Guinea lowland bird species that do not cross water gaps, and consequently post-Pleistocene extinction of these species on land-bridge islands cannot have been reversed by recolonization. Because extinction rates on relatively small islands are high (cf. Fig. 10.8), virtually all these species are now absent from all land-bridge islands smaller than 50 km². On the other hand, these 134 species vary greatly in their distribution on the seven larger (450–8000 km²) land-bridge islands. At one extreme, some species (e.g., the frilled monarch flycatcher, *Monarcha telescophthalmus*) have survived on all seven islands; at the other extreme, 32 species have disappeared

from all seven islands. Most of these 32 extinction-prone 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 with small initial populations because of specialized habitat requirements (e.g., the swamp rail, *Megacrex inepta*); and birds which are dependent on seasonal or patchy food sources, and which normally go through drastic population fluctuations (e.g., fruit-eaters and flower-feeders). These observations tend to be confirmed by other bird studies, and by the work of Brown (1971), referred to above, on differential extinction rates among mammal species isolated on mountain tops (Table 10.2).

Another natural experiment in differential extinction is provided by New Hanover, a 1200 km² island which in the late Pleistocene was connected by a land-bridge to the larger island of New Ireland in the Bismarck Archipelago. Although today New Hanover has only lost about 22 per cent of New Ireland's species, 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, those species most in need of protection were differentially lost: as a faunal reserve, New Hanover would rate as a disaster. Yet its area of 1200 km² is not small by the standards of many of the tropical rain forest parks that one can realistically hope for.

Just as rising post-Pleistocene sea levels caused area fragmentation and hence population extinctions by dissecting formerly continuous land masses into islands, so (on a shorter time scale) have man's activities caused population extinctions by fragmenting formerly continuous forests into isolated wood-lots. Among bird populations disappearing in fragmented Brazilian forests, the best predictor of extinction is low abundance (data of Willis, analysed by Terborgh and Winter, 1980). A similar conclusion applies to bird extinctions in an isolated Ecuadorean forest (Leck, 1979). Low abundance is also strongly correlated with risk of extinction in turnover studies at equilibrium (Jones and Diamond, 1976).

The survival prospects for a particular species may be quantified by determining its 'incidence function', $J(S)$ (Diamond, 1975b). We have noted, at least for birds and mammals, that some species occur only on the largest and most species-rich islands, other species occur also on medium-sized islands, and others also occur on small islands. These patterns may be displayed graphically by grouping the islands into

Table 10.2. Mammals on mountain islands of the Great Basin.

Species	Habitat and diet	Weight (g)	Number of islands per species	Ruby	Toiyabe	Toquima	White-Inyo	Snake	Schell Creek	Deep Creek	White Pine	Oquirrh	Roberts Creek	Diamond	Stansbury	Grant	Spruce	Spring	Pilot	Panamint
Neotoma cinerea	GH	317	14	×	×	×	×	×	×	×	×	–	–	×	×	–	×	×	×	×
Eutamias umbrinus	GH	57	14	×	×	×	×	×	×	×	×	×	×	×	–	×	×	×	–	–
Spermophilus lateralis	GH	147	13	×	×	×	×	×	×	×	×	–	–	×	–	×	×	×	×	–
Microtus longicaudus	GH	47	12	×	×	×	×	×	×	×	×	×	×	–	×	×	–	–	–	–
Marmota flaviventer	GH	3000	9	×	×	×	×	×	×	×	×	–	–	–	×	–	–	–	–	–
Thomomys talpoides	GH	102	8	×	×	×	×	–	×	–	×	×	–	×	–	–	–	–	–	–
Sorex vagrans	C	6·7	6	×	×	–	–	×	×	×	–	×	–	–	–	–	–	–	–	–
Sorex palustris	C	14	6	×	×	×	×	×	–	–	–	–	×	–	–	–	–	–	–	–
Zapus princeps	SH	33	4	×	×	–	–	–	–	–	–	×	×	–	–	–	–	–	–	–
Ochotona princeps	SH	121	4	–	×	×	×	×	–	–	–	–	–	–	–	–	–	–	–	–
Mustela erminea	C	58	3	×	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–
Spermophilus beldingi	SH	382	3	×	×	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lepus townsendi	SH	2500	1	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Number of species per island				12	12	9	9	8	7	6	6	5	4	4	3	3	3	3	2	1

classes containing similar numbers of species (e.g., 1–4, 5–9, 10–20, 21–35, 36–50, etc.), calculating the incidence J or fraction of the islands in a given class on which a particular species occurs, and plotting J against the total species number S on the island. Some such incidence functions for birds in the Bismarck Archipelago are shown in Fig. 10.9; a much more full discussion is in Diamond (1975b). Since S in the Bismarcks is closely correlated with area, these graphs in effect 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 there is no chance of long-term survival on islands below a certain size. These incidence functions can be interpreted in terms of the 'bionomic strategy' of the species, along the lines of chapter 3. Figure 10.9a is typical of species in the so-called 'super-tramp' category (Diamond, 1974, 1975b); as the figure shows, such birds tend to be found on small islands, but *not* on large ones (because of competitive exclusion from species-rich faunas). Figure 10.9b illustrates the incidence function for an intermediate category of species, while Fig. 10.9c is typical of species found only in

Footnote to Table on facing page.
Out of the Great Basin desert of the western United States rise 17 mountain ranges to elevations above 10,000 ft. Boreal habitats on the summits of these 'mountain islands' are now isolated from each other by the surrounding sea of desert, but were connected to each other and to the source boreal habitats of the much more extensive Rocky Mountains and Sierra Nevada during cooler Pleistocene periods. On these mountaintops live 13 species or superspecies of small flightless mammals, which cannot cross the intervening desert today but which reached the mountain islands over Pleistocene bridges of boreal habitat. Since the Pleistocene these mammal populations have been subject to risk of extinction without opportunity for recolonization. The table illustrates the regular distributional pattern produced by this differential extinction. The presence (×) or absence (–) of each named species is indicated for each named mountain island, along with the total number of islands inhabited by each species (left-most column) and total number of species inhabiting each island (bottom row; this number correlates well with island area). C = carnivore; GH = generalized herbivore (present in most habitats); SH = specialized herbivore (present in only certain habitats); body weight is given in grams. Herbivores can maintain higher population densities than carnivores, small animals higher densities than large animals, and species of generalized habitat preference higher densities than habitat specialists. Thus, the main patterns of differential extinction emerging from the table are that: rare species survive on fewer islands than abundant species; rare species become confined to the larger islands; and different small islands tend to end up with the same group of abundant species. From Brown (1971).
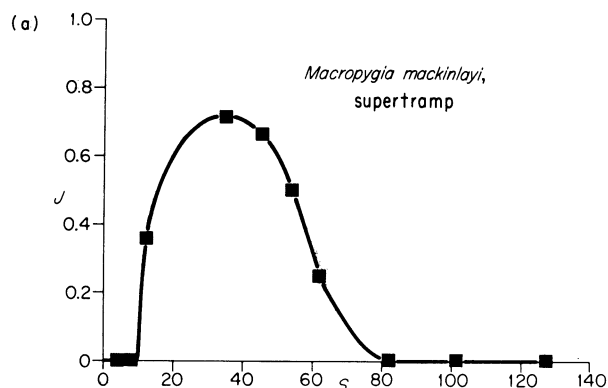
(a)

Fig. 10.9a. The incidence function $J(S)$ for the 'supertramp' pigeon *Macropygia mackinlayi*, in the Bismarck Archipelago. The incidence J represents the fraction of those islands, with S values in a given small range, on which the species occurs, as a function of the number of species S on the island. Each point is typically based on 3–13 islands. For a more detailed discussion, see Diamond (1975b).

the presence of many others (i.e., on large islands). In general terms, one may recognize Figs. 10.9a–c as depicting the spectrum from an extreme r-strategy through to an extreme K-strategy (see chapters 2 and 3); the J-versus-S curves, however, go further to give quantitative substance to these notions.

Incidence represents either the fraction of a set of similar islands which a certain species inhabits at a given time, or else the fraction of time that a certain species inhabits a particular island. These fractions
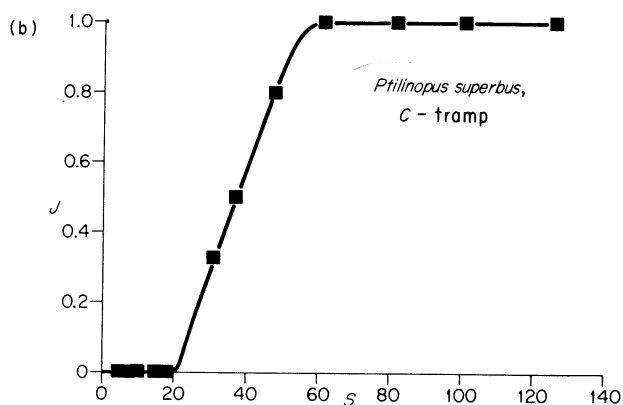
(b)

Fig. 10.9b. The incidence function for the so-called 'C-tramp' pigeon *Ptilinopus superbus*, in the Bismarcks. (From Diamond, 1975b.)

approach equilibrium probabilities determined by a balance between immigration and extinction rates for the particular species, just as total species number approaches an equilibrium value determined by the immigration and extinction rates of all species (section 10.3.1). Hence incidence J equals $\mu/(\mu + \lambda)$, where μ and λ are now the immigration and extinction probabilities of the particular species. This simple model accounts for the bent-S-shaped form of the incidence functions of Figs. 10.9b and 10.9c, as well as for species differences in the abscissa position of the rising portion of the curve (Diamond and Marshall, 1977; Gilpin and Diamond, 1981).
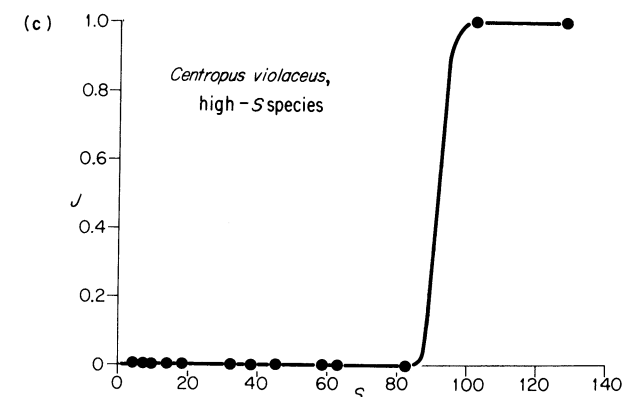
(c)

Fig. 10.9c. Incidence function for the 'high-S' cuckoo *Centropus violaceus*, in the Bismarcks. (From Diamond, 1975b.)

'Assembly rules' furnish additional information as to which species are likely to be present on a given island. These rules (Diamond, 1975b) codify the observation that, of all possible combinations that could be formed from within a group of related species, only certain combinations exist in nature. The rules are evocative of those of the early days of atomic spectroscopy, with its empirical catalogues of allowed and forbidden spectral lines. Thus there are some pairs or groups of species that never coexist; others that form an unstable combination by themselves, but may form part of a stable larger combination; still others constitute stable combinations that resist invaders that would transform them into a forbidden combination; and so on. For the Bismarck avifauna, a detailed account of the assembly rules for such guilds as the cuckoo-dove, the gleaning flycatcher, the myzomelid-sunbird, and the fruit-pigeon guild has been given by Diamond (1975b, pp. 393–411). Faaborg (1976) has made similar detailed studies of the

incidence and assembly of the birds on West Indian islands. In some cases these rules clearly derive from competition for resources, and from harvesting of resources by permitted combinations so as to minimize the unutilized resources available to support potential invaders; other cases are less transparent.

These detailed observations as to the extinction, immigration and overall incidence $J(S)$ of particular species of course provide the underlying explanation for the patterns of curvature in extinction and immigration functions, as illustrated in Fig. 10.7 (Gilpin and Diamond, 1981). Ultimately, the incidence functions and assembly rules are presumably determined by considerations of limits to similarity and niche overlap (see chapters 5, 8) and by the constraints imposed by food web structure (see section 9.3, and in particular the study by Heatwole and Levins, Table 9.3).

The sort of quantitative information that is embodied in incidence functions and assembly rules holds the promise of providing the basis for a predictive science of environmental management.

10.5   Design principles for natural reserves

The work described in this chapter clearly is relevant to questions about the properties of natural reserves: how is the eventual number of species in the reserve related to its area; how do extinction rates vary with area; how do area-dependent survival probabilities vary among species? The answers to these questions prompt the enunciation of certain 'general design principles' for floral and faunal preserves (see, e.g., Willis, 1974; Wilson and Willis, 1975; Diamond, 1975a and 1976a; Terborgh, 1974; May, 1975g; and the chapters in Soulé and Wilcox, 1980, for a book-length treatment). As for most generalities, such design principles are useful, but must be applied with caution in any one specific instance. They are no substitute for a painstaking study of extinction and immigration rates, of incidence functions and assembly rules, for each particular conservation project.

In general, a large reserve is better than a small reserve for two reasons: the large reserve can hold more species at equilibrium, and it will have lower extinction rates. A less straightforward question is whether to prefer one large reserve or else several smaller reserves whose areas add up to the same total as the single large reserve. If one considers only total number of species without regard to how species

differ in their need for protection, either arrangement may have a slight advantage depending on the particular situation (Simberloff and Abele, 1976a). However, recall that different species have different area requirements and that species requiring large areas are often the ones most threatened by man's activities and in need of protection (section 10.4). On these grounds, fragmenting a large reserve into several smaller reserves is a bad rather than a good policy (see Diamond, 1976b, Terborgh, 1976, Whitcomb, Lynch, Opler, and Robbins, 1976, and Simberloff and Abele, 1976b, for various views on this question). Many species, especially those of tropical forests, are stopped by narrow dispersal barriers; for these species, major roads or power lines may effectively fragment a park and hence cause increased risk of extinction.

If one must settle for several smaller parks, a way to raise the equilibrium number of species in any one such park is to raise the immigration rate into it. This can be done by careful juxtaposition of the scattered parks, and by providing corridors or stepping-stones of natural habitat between them.

Any given reserve should be as nearly circular in shape as other circumstances allow. Such maximization of the area-to-perimeter ratio minimizes dispersal distances within the reserve, and avoids 'peninsular effects' whereby dispersal rates to outlying parts of the reserve from more central parts may be so low as to perpetuate local extinctions, thus diminishing the reserve's effective area.

These general design principles are subject to many qualifications and equivocations. *First*, several smaller reserves may have the compensating advantage that in an inhomogeneous region each reserve may favour the survival of a different group of species. 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. *Second*, the above principles ignore epidemiological aspects of park management: many scattered parks are less susceptible to the ravages of an epidemic disease or analogous disaster. *Third*, there is the obvious point that some 'edge' species, that thrive at the interface between habitats, will prefer several smaller parks, or parks with high perimeter-to-area ratios; conversely, edge-intolerant species will be differentially worse off with several smaller areas, and will be unable to survive once the reserves become too small. (However, many edge species will fare well in non-park habitats transformed or dissected by man, while edge-intolerant species will furnish a disproportionate number of the species most dependent on parks

for survival.) *Fourth*, one must consider the dynamical features such as the spatial and temporal patterns of stable oscillation that so frequently characterize populations both in mathematical models and in the real world. The evidence for a roughly 50-year cycle in elephant population eruptions in the area that is today Tsavo National Park in Kenya suggests that such dynamical aspects of natural populations can create management problems when even a very large area is enclosed as reserve.

All these questions need to be illuminated by further research, particularly field work on organisms other than birds. There is clear and present need for the development of techniques to estimate the size and other properties a reserve should possess if it is to fulfil its designated conservation purpose.