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Source: *Evolution*, Vol. 17, No. 4 (Dec., 1963), pp. 373-387
Published by: Society for the Study of Evolution
Stable URL: http://www.jstor.org/stable/2407089
Accessed: 12-11-2015 20:56 UTC

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY

THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. 17 DECEMBER, 1963 No. 4

AN EQUILIBRIUM THEORY OF INSULAR ZOOGEOGRAPHY

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Received March 1, 1963

THE FAUNA-AREA CURVE

As the area of sampling A increases in an ecologically uniform area, the number of plant and animal species s increases in an approximately logarithmic manner, or

$$s = bA^k, \tag{1}$$

where $k < 1$, as shown most recently in in the detailed analysis of Preston (1962). The same relationship holds for islands, where, as one of us has noted (Wilson, 1961), the parameters b and k vary among taxa. Thus, in the ponerine ants of Melanesia and the Moluccas, k (which might be called the *faunal coefficient*) is approximately 0.5 where area is measured in square miles; in the Carabidae and herpetofauna of the Greater Antilles and associated islands, 0.3; in the land and freshwater birds of Indonesia, 0.4; and in the islands of the Sahul Shelf (New Guinea and environs), 0.5.

THE DISTANCE EFFECT IN PACIFIC BIRDS

The relation of number of land and freshwater bird species to area is very orderly in the closely grouped Sunda Islands (fig. 1), but somewhat less so in the islands of Melanesia, Micronesia, and Polynesia taken together (fig. 2). The greater variance of the latter group is attributable primarily to one variable, distance between the islands. In particular, the distance effect can be illustrated by taking the distance from the primary faunal "source area" of Melanesia and relating it to faunal number in the following manner. From fig. 2, take the line connecting New Guinea and the nearby Kei Islands as a "saturation curve" (other lines would be adequate but less suitable to the purpose), calculate the predicted range of "saturation" values among "saturated" islands of varying area from the curve, then take calculated "percentage saturation" as $s_i \times 100/B_i$, where s_i is the real number of species on any island and B_i the saturation number for islands of that area. As shown in fig. 3, the percentage saturation is nicely correlated in an inverse manner with distance from New Guinea. This allows quantification of the rule expressed qualitatively by past authors (see Mayr, 1940) that island faunas become progressively "impoverished" with distance from the nearest land mass.

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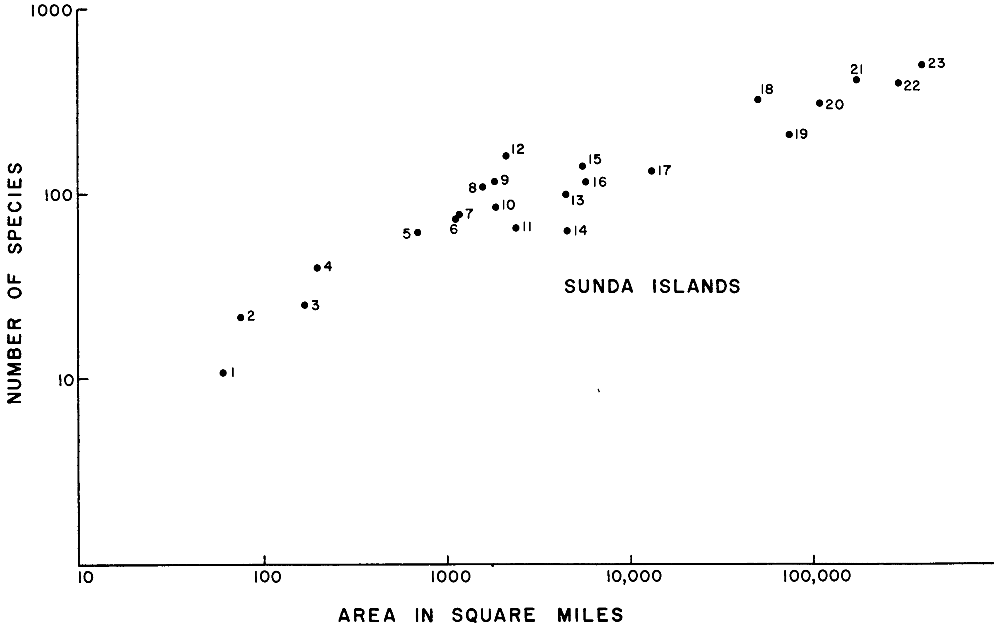

FIG. 1. The numbers of land and freshwater bird species on various islands of the Sunda group, together with the Philippines and New Guinea. The islands are grouped close to one another and to the Asian continent and Greater Sunda group, where most of the species live; and the distance effect is not apparent. (1) Christmas, (2) Bawean, (3) Engano, (4) Savu, (5) Simalur, (6) Alors, (7) Wetar, (8) Nias, (9) Lombok, (10) Billiton, (11) Mentawei, (12) Bali, (13) Sumba, (14) Bangka, (15) Flores, (16) Sumbawa, (17) Timor, (18) Java, (19) Celebes, (20) Philippines, (21) Sumatra, (22) Borneo, (23) New Guinea. Based on data from Delacour and Mayr (1946), Mayr (1940, 1944), Rensch (1936), and Stresemann (1934, 1939).

AN EQUILIBRIUM MODEL

The impoverishment of the species on remote islands is usually explained, if at all, in terms of the length of time species have been able to colonize and their chances of reaching the remote island in that time. According to this explanation, the number of species on islands grows with time and, given enough time, remote islands will have the same number of species as comparable islands nearer to the source of colonization. The following alternative explanation may often be nearer the truth. Fig. 4 shows how the number of new species entering an island may be balanced by the number of species becoming extinct on that island. The descending curve is the rate at which *new* species enter the island by colonization. This rate does indeed fall as the number of species on the islands increases, because the chance that an immigrant be a new species, not already on the island, falls. Furthermore, the curve falls more steeply at first. This is a consequence of the fact that some species are commoner immigrants than others and that these rapid immigrants are likely, on typical islands, to be the first species present. When there are no species on the island ($N = 0$), the height of the curve represents the number of species arriving per unit of time. Thus the intercept, I, is the rate of immigration of species, new or already present, onto the island. The curve falls to zero at the point $N = P$ where all of the immigrating species are already present so that no new ones are arriving. P is thus the number of species in the "species pool" of immigrants. The shape of the rising curve in the same figure, which represents the

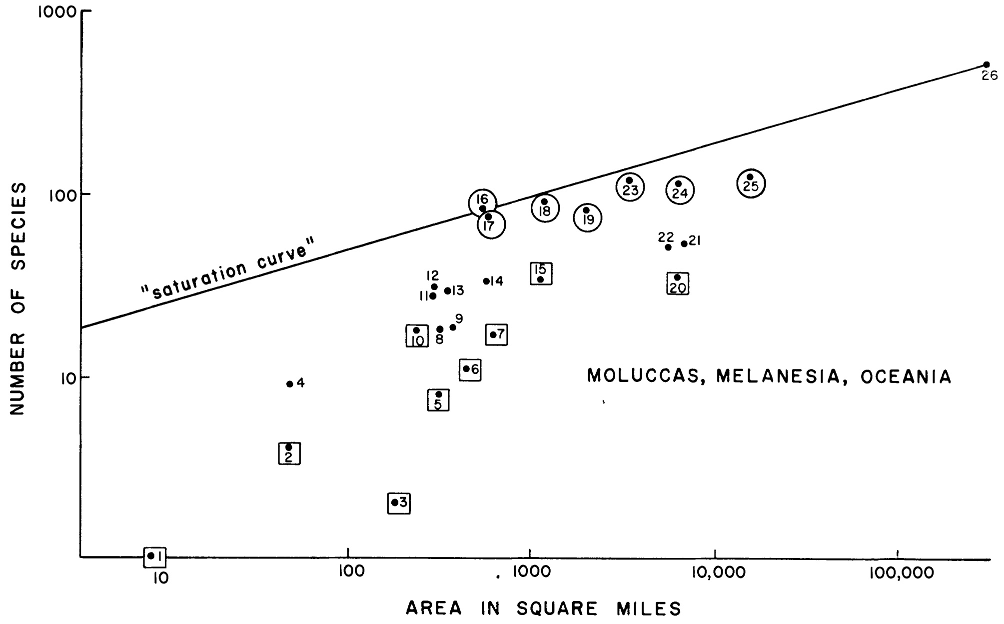

FIG. 2. The numbers of land and freshwater bird species on various islands of the Moluccas, Melanesia, Micronesia, and Polynesia. Here the archiplagoes are widely scattered, and the distance effect is apparent in the greater variance. Hawaii is included even though its fauna is derived mostly from the New World (Mayr, 1943). "Near" islands (less than 500 miles from New Guinea) are enclosed in circles, "far" islands (greater than 2,000 miles) in squares, and islands at intermediate distances are left unenclosed. The saturation curve is drawn through large and small islands at source of colonization. (1) Wake, (2) Henderson, (3) Line, (4) Kusaie, (5) Tuamotu, (6) Marquesas, (7) Society, (8) Ponape, (9) Marianas, (10) Tonga, (11) Carolines, (12) Palau, (13) Santa Cruz, (14) Rennell, (15) Samoa, (16) Kei, (17) Louisiade, (18) D'Entrecasteaux, (19) Tanimbar, (20) Hawaii, (21) Fiji, (22) New Hebrides, (23) Buru, (24) Ceram, (25) Solomons, (26) New Guinea. Based on data from Mayr (1933, 1940, 1943) and Greenway (1958).

rate at which species are becoming extinct on the island, can also be determined roughly. In case all of the species are equally likely to die out and this probability is independent of the number of other species present, the number of species becoming extinct in a unit of time is proportional to the number of species present, so that the curve would rise linearly with N. More realistically, some species die out more readily than others and the more species there are, the rarer each is, and hence an increased number of species increases the likelihood of any given species dying out. Under normal conditions both of these corrections would tend to increase the slope of the extinction curve for large values of N. (In the rare situation in which the species which enter most often as immigrants are the ones which die out most readily—presumably because the island is atypical so that species which are common elsewhere cannot survive well—the curve of extinction may have a steeper slope for small N.) If N is the number of species present at the start, then $E(N)/N$ is the fraction dying out, which can also be interpreted crudely as the probability that any given species will die out. Since this fraction cannot exceed 1, the extinction curve cannot rise higher than the straight line of a 45° angle rising from the origin of the coordinates.

It is clear that the rising and falling curves must intersect and we will denote by $\hat{s}$ the value of N for which the rate of immigration of new species is balanced by

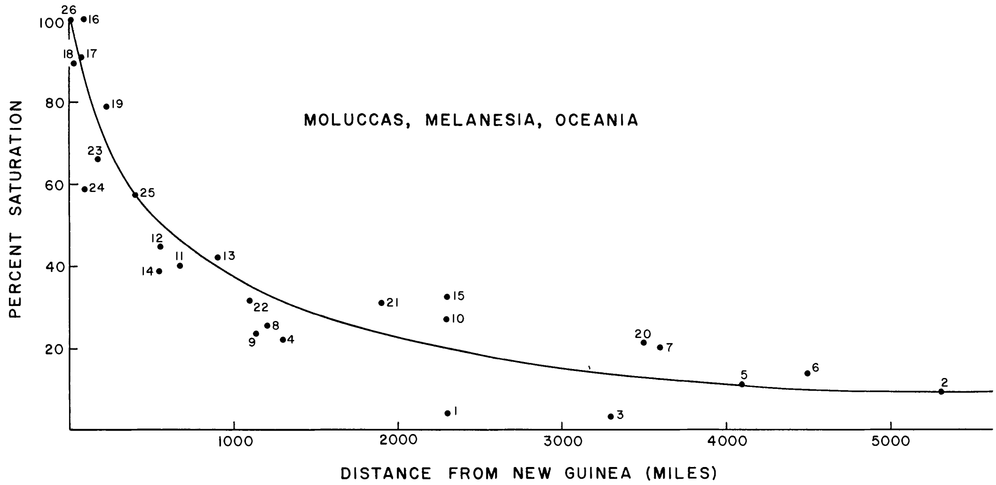

FIG. 3. Per cent saturation, based on the "saturation curve" of fig. 2, as a function of distance from New Guinea. The numbers refer to the same islands identified in the caption of fig. 2. Note that from equation (4) it is an oversimplification to take distances solely from New Guinea. The abscissa should give a more complex function of distances from all the surrounding islands, with the result that far islands would appear less "distant." But this representation expresses the distance effect adequately for the conclusions drawn.

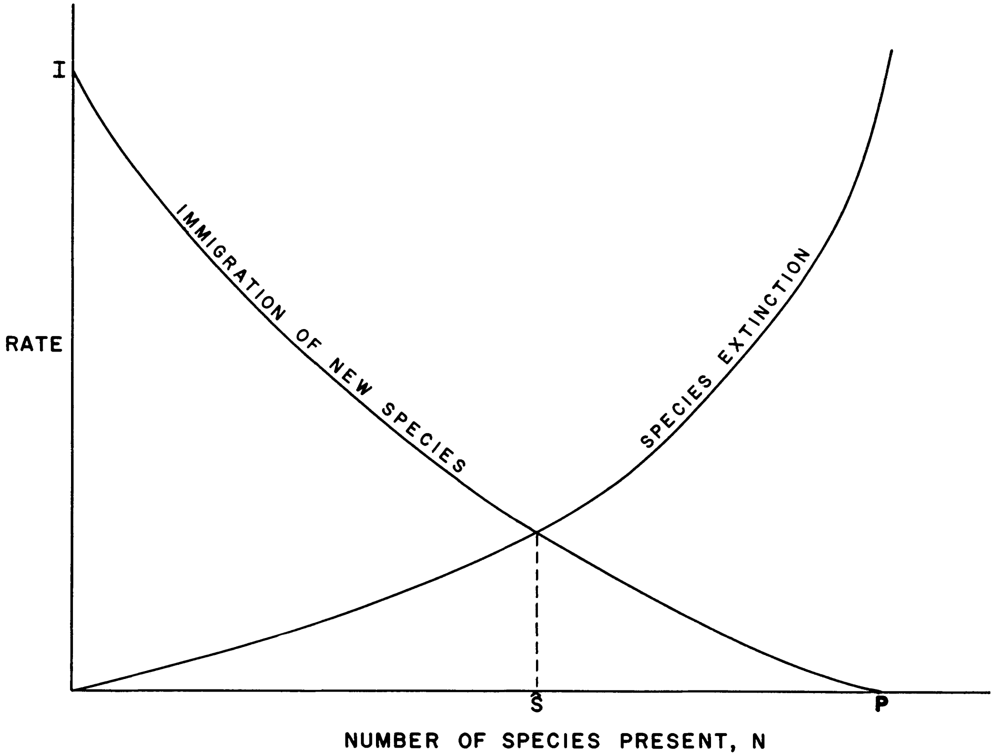

FIG. 4. Equilibrium model of a fauna of a single island. See explanation in the text.

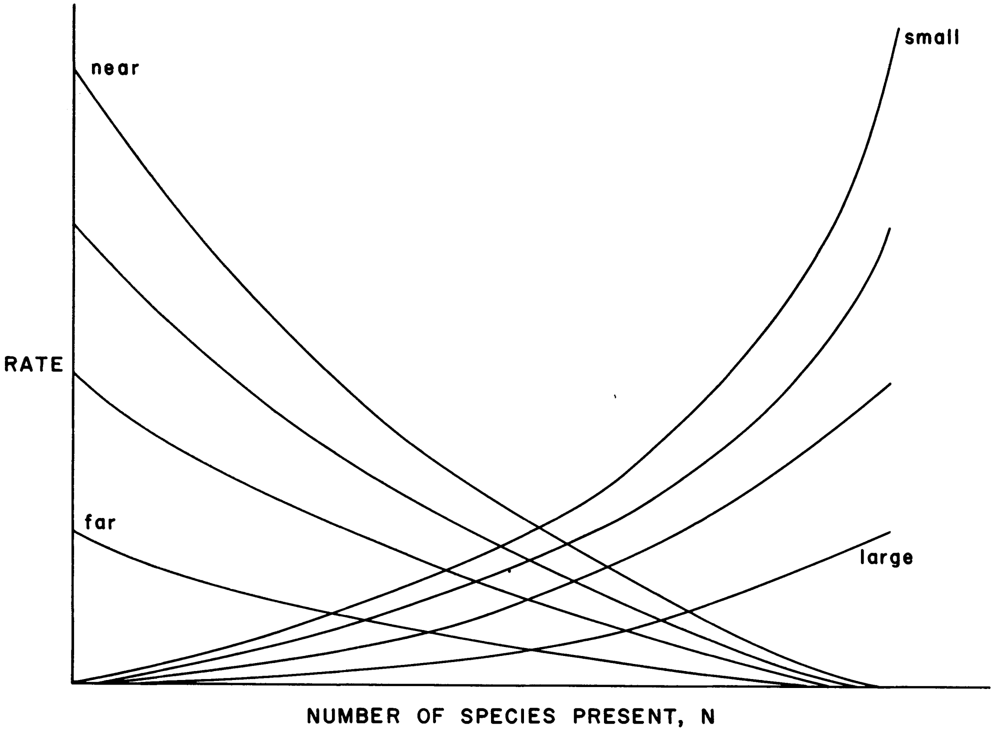

FIG. 5. Equilibrium model of faunas of several islands of varying distances from the source area and varying size. Note that the effect shown by the data of fig. 2, of faunas of far islands increasing with size more rapidly than those of near islands, is predicted by this model. Further explanation in text.

the rate of extinction. The number of species on the island will be stabilized at $\hat{s}$, for a glance at the figure shows that when N is greater than $\hat{s}$, extinction exceeds immigration of new species so that N decreases, and when N is less than $\hat{s}$, immigration of new species exceeds extinction so that N will increase. Therefore, in order to predict the number of species on an island we need only construct these two curves and see where they intersect. We shall make a somewhat oversimplified attempt to do this in later paragraphs. First, however, there are several interesting qualitative predictions which we can make without committing ourselves to any specific shape of the immigration and extinction curves.

A. An island which is farther from the source of colonization (or for any other reason has a smaller value of I) will, other things being equal, have fewer species, because the immigration curve will be lower and hence intersect the mortality curve farther to the left (see fig. 5).

B. Reduction of the "species pool" of immigrants, P, will reduce the number of species on the island (for the same reason as in A).

C. If an island has smaller area, more severe climate (or for any other reason has a greater extinction rate), the mortality curve will rise and the number of species will decrease (see fig. 5).

D. If we have two islands with the same immigration curve but different extinction curves, any given species on the one with the higher extinction curve is more likely to die out, because $E(N)/N$ can be seen to be higher [$E(N)/N$ is the slope of the line joining the intersection point to the origin].

E. The number of species found on islands far from the source of colonization will grow more rapidly with island area than will the number on near islands. More precisely, if the area of the island is denoted by A, and $\hat{s}$ is the equilibrium number of species, then d^2s/dA^2 is greater for far islands than for near ones. This can be verified empirically by plotting points or by noticing that the change in the angle of intersection is greater for far islands.

F. The number of species on large islands decreases with distance from source of colonization faster than does the number of species on small islands. (This is merely another way of writing E and is verified similarly.)

Further, as will be shown later, the variance in $\hat{s}$ (due to randomness in immigrations and extinctions) will be lower than that expected if the "classical" explanation holds. In the classical explanation most of those species will be found which have at any time succeeded in immigrating. At least for distant islands this number would have an approximately Poisson distribution so that the variance would be approximately equal to the mean. Our model predicts a reduced variance, so that if the observed variance is significantly smaller than the mean for distant islands, it is evidence for the equilibrium explanation.

The evidence in fig. 2, relating to the insular bird faunas east of Weber's Line, is consistent with all of these predictions. To see this for the non-obvious prediction E, notice that a greater slope on this log-log plot corresponds to a greater second derivative, since A becomes sufficiently large.

THE FORM OF THE IMMIGRATION AND EXTINCTION CURVES

If the equilibrium model we have presented is correct, it should be possible eventually to derive some quantitative generalizations concerning rates of immigration and extinction. In the section to follow we have deduced an equilibrium equation which is adequate as a first approximation, in that it yields the general form of the empirically derived fauna–area curves without contradicting (for the moment) our intuitive ideas of the underlying biological processes. This attempt to produce a formal equation is subject to indefinite future improvements and does not affect the validity of the graphically derived equilibrium theory. We start with the statement that

$$\Delta s = M + G - D, \qquad (2)$$

where s is the number of species on an island, M is the number of species successfully immigrating to the island per year, G is the number of new species being added per year by local speciation (not including immigrant species that merely diverge to species level without multiplying), and D is the number of species dying out per year. At equilibrium,

$$M + G = D.$$

The immigration rate M must be determined by at least two independent values: (1) the rate at which propagules reach the island, which is dependent on the size of the island and its distance from the source of the propagules, as well as the nature of the source area, but not on the condition of the recipient island's fauna; and (2) as noted already, the number of species already resident on the island. Propagules are defined here as the minimum number of individuals of a given species needed to achieve colonization; a more exact explication is given in the Appendix. Consider first the source region. If it is climatically and faunistically similar to other potential source regions, the number of propagules passing beyond its shores per year is likely to be closely related to the size of the population of the taxon living on it, which in turn is approximately a linear function of its area. This notion is supported by the evidence from Indo-Australian ant zoogeography, which indicates that the ratio of faunal exchange is about equal to the ratio of the areas of the source regions (Wilson, 1961). On the other hand, the number of propagules reaching the recipient island probably varies linearly with the angle it subtends with reference to the center of the source region. Only near islands will vary much because of this factor. Finally, the number of propagules reaching the recipient island is most likely to be an exponential function of its distance from the source region. In the simplest case, if the probability that a given propagule ceases its overseas voyage (e.g., it falls into the sea and dies) at any given instant in time remains constant, then the fraction of propagules reaching a given distance fits an exponential holding-time distribution. If these assumptions are correct, the number of propagules reaching an island from a given source region per year can be approximated as

$$\alpha A_i \frac{\text{diam}_i\, e^{-\lambda d_i}}{2\pi d_i}, \qquad (3)$$

where A_i is the area of the source region, d_i is the mean distance between the source region and recipient island, diam_i is the diameter of the recipient island taken at a right angle to the direction of d_i, and α is a coefficient relating area to the number of propagules produced. More generally, where more than one source region is in position, the rate of propagule arrival would be

$$\frac{\alpha}{2\pi}\sum_i \frac{\text{diam}_i}{d_i} A_i e^{-\lambda d_i}, \qquad (4)$$

where the summation is of contributions from each of the ith source regions. Again, note that a propagule is defined as the minimum number of individuals required to achieve colonization.

Only a certain fraction of arriving propagules will add a new species to the fauna, however, because except for "empty" islands at least some ecological positions will be filled. As indicated in fig. 4, the rate of immigration (i.e., rate of propagule arrival times the fraction colonizing) declines to zero as the number of resident species (s) approaches the limit P. The curve relating the immigration rate to degree of unsaturation is probably a concave one, as indicated in fig. 4, for two reasons: (1) the more abundant immigrants reach the island earlier, and (2) we would expect otherwise randomly arriving elements to settle into available positions according to a simple occupancy model where one and only one object is allowed to occupy each randomly placed position (Feller, 1958). These circumstances would result in the rate of successful occupation decelerating as positions are filled. While these are interesting subjects in themselves, a reasonable approximation is obtained if it is assumed that the rate of occupation is an inverse linear function of the number of occupied positions, or

$$\left(1 - \frac{s}{P}\right). \qquad (5)$$

Then

$$M = \frac{\alpha(1 - s/P)}{2\pi}\sum_i \frac{\text{diam}_i}{d_i} A_i e^{-\lambda d_i}. \qquad (6)$$

We know the immigration line in fig. 4 is not straight; to take this into account we must modify formula 5 by adding a term in s^2. However, this will not be necessary for our immediate purposes.

Now let us consider G, the rate of new productions on the island by local speciation. Note that this rate does not include the mere divergence of an island endemic to a specific level with reference to the stock species in the source area; that species is still counted as contributing to M, the immigration rate, no matter how far it evolves. Only new species generated from it and in addition to it are counted in G. First, consider an archipelago as a unit and the increase of s by divergence of species on the various islands to the level of allopatric species, i.e., the production of a local archipelagic superspecies. If this is the case, and no exchange of endemics is yet achieved among the islands of the archipelago, the number of species in the archipelago is limited to

$$\sum_{i=1}^{\infty} n_i \hat{s}_i, \qquad (7)$$

where n_i is the number of islands in the archipelago of ith area and $\hat{s}_i$ is the number of species occurring at equilibrium on islands of *i*th area. But the generation of allopatric species in superspecies does not multiply species on single islands or greatly change the fauna of the archipelago as a whole from the value predicted by the fauna–area curve, as can be readily seen in figs. 2 and 3. G, the increase of s by local speciation on single islands and exchange of autochthonous species between islands, probably becomes significant only in the oldest, largest, and most isolated archipelagoes, such as Hawaii and the Galápagos. Where it occurs, the exchange among the islands can be predicted from (6), with individual islands in the archipelago serving as both source regions and recipient islands. However, for most cases it is probably safe to omit G from the model, i.e., consider only source regions outside the archipelago, and hence

$$\Delta s = M - D. \qquad (8)$$

The extinction rate D would seem intuitively to depend in some simple manner on (1) the mean size of the species populations, which in turn is determined by the size of the island and the number of species belonging to the taxon that occur on it; and (2) the yearly mortality rate of the organisms. Let us suppose that the probability of extinction of a species is merely the probability that all the individuals of a given species will die in one year. If the deaths of individuals are unrelated to each other and the population sizes of the species are equal and nonfluctuating,

$$D = sP^{N_r/s}, \qquad (9)$$

where N_r is the total number of individuals in the taxon on the recipient island and P is their annual mortality rate. More realistically, the species of a taxon, such as the birds, vary in abundance in a manner approximating a Barton–Davis distribution (MacArthur, 1957) although the approximation is probably not good for a whole island. In s nonfluctuating species ordered according to their rank (K) in relative rareness,

$$D = \sum_{i=1}^{s} p^{(N_r/s)\sum_{1=i}^{K} 1/(s-i+1)}. \qquad (10)$$

This is still an oversimplification, if for no other reason than the fact that populations do fluctuate, and with increased fluctuation D will increase. However, both models, as well as elaborations of them to account for fluctuation, predict an exponential increase of D with restriction of island area. The increase of D which accompanies an increase in number of resident species is more complicated but is shown in fig. 4.

MODEL OF IMMIGRATION AND EXTINCTION PROCESS ON A SINGLE ISLAND

Let $P_s(t)$ be the probability that, at time t, our island has s species, λ_s be the rate of immigration of new species onto the island, when s are present, μ_s be the rate of extinction of species on the island when s are present; and λ_s and μ_s then represent the intersecting curves in fig. 4. This is a "birth and death process" only slightly different from the kind most familiar to mathematicians (cf. Feller, 1958, last chapter). By the rules of probability

$$\begin{aligned} P_s(t+h) = {} & P_s(t)(1-\lambda_s h-\mu_s h) \\ & + P_{s-1}(t)\lambda_{s-1}h \\ & + P_{s+1}(t)\mu_{s+1}h\,, \end{aligned}$$

since to have s at time $t+h$ requires that at a short time preceding one of the following conditions held: (1) there were s and that no immigration or extinction took place, or (2) that there were $s-1$ and one species immigrated, or (3) that there $s+1$ and one species became extinct. We take h to be small enough that probabilities of two or more extinctions and/or immigrations can be ignored. Bringing $P_s(t)$ to the left-hand side, dividing by h, and passing to the limit as $h \rightarrow 0$

$$\begin{aligned} \frac{\mathrm{d}P_s(t)}{\mathrm{d}t} = {} & -(\lambda_s+\mu_s)P_s(t) + \lambda_{s-1}P_{s-1}(t) \\ & + \mu_{s+1}P_{s+1}(t). \qquad (11) \end{aligned}$$

For this formula to be true in the case where $s = 0$, we must require that $\lambda_{-1} = 0$ and $\mu_0 = 0$. In principle we could solve

(11) for $P_s(t)$; for our purposes it is more useful to find the mean, $M(t)$, and the variance, $\mathrm{var}(t)$, of the number of species at time t. These can be estimated in nature by measuring the mean and variance in numbers of species on a series of islands of about the same distance and area and hence of the same λ_s and μ_s. To find the mean, $M(t)$, from (11) we multiply both sides of (11) by s and then sum from $s =$ 0 to $s = \infty$. Since $\sum_{s=0}^{\infty} sP_s(t) = M(t)$, this gives us

$$\frac{\mathrm{d}M(t)}{\mathrm{d}t} = -\sum_{s=0}^{\infty} (\lambda_s + \mu_s) sP_s(t) + \sum_{s-1=0}^{\infty} \lambda_{s-1}[(s-1)+1]P_{s-1}(t) + \sum_{s+1=0}^{\infty} \mu_{s+1}[(s+1)-1]P_{s+1}(t).$$

(Here terms $\lambda_{-1} \cdot 0 \cdot P_{-1}(t) = 0$ and $\mu_0 \cdot (-1) P_0(t) = 0$ have been subtracted or added without altering values.) This reduces to

$$\frac{\mathrm{d}M(t)}{\mathrm{d}t} = \sum_{s=0}^{\infty} \lambda_s P_s(t) - \sum_{s=0}^{\infty} \mu_s P_s(t) = \overline{\lambda_s(t)} - \overline{\mu_s(t)}. \qquad (12)$$

But, since λ_s and μ_s are, at least locally, approximately straight, the mean value of λ_s at time t is about equal to $\lambda_{M(t)}$ and similarly $\overline{\mu_s(t)} \sim \mu_{M(t)}$. Hence, approximately

$$\frac{\mathrm{d}M(t)}{\mathrm{d}t} = \lambda_{M(t)} - \mu_{M(t)}, \qquad (13)$$

or the expected number of species in Fig. 4 moves toward $\hat{s}$ at a rate equal to the difference in height of the immigration and extinction curves. In fact, if $\mathrm{d}\mu/\mathrm{d}s - \mathrm{d}\lambda/\mathrm{d}s$, evaluated near $s = \hat{s}$ is abbreviated by F, then, approximately $\mathrm{d}M(t)/\mathrm{d}t = F(\hat{s} - M(t))$ whose solution is $M(t) = \hat{s}(1 - e^{-Ft})$. Finally, we can compute the time required to reach 90% (say) of the saturation value $\hat{s}$ so that $M(t)/\hat{s} = 0.9$ or $e^{-Ft} = 0.1$.
Therefore,

$$t = \frac{2.303}{F}. \qquad (13a)$$

A similar formula for the variance is obtained by multiplying both sides of (11) by $(s - M(t))^2$ and summing from $s = 0$ to $s = \infty$. As before, since $\mathrm{var}(t) = \sum_{s=0}^{\infty} (s - M(t))^2 P_s(t)$, this results in

$$\begin{aligned}\frac{\mathrm{d}\,\mathrm{var}(t)}{\mathrm{d}t} &= -\sum_{s=0}^{\infty} (\lambda_s + \mu_s)(s - M(t))^2 P_s(t) \\ &\quad + \sum_{s-1=0}^{\infty} \lambda_{s-1}[(s-1-M(t))+1]^2 P_{s+1}(t) \\ &\quad + \sum_{s+1=0}^{\infty} \mu_{s+1}[(s+1-M(t))-1]^2 P_{s+1}(t) \\ &= 2\sum_{s=0}^{\infty} \lambda_s (s - M(t)) P_s(t) \\ &\quad - 2\sum_{s=0}^{\infty} \mu_s (s - M(t)) P_s(t) \\ &\quad + \sum_{s=0}^{\infty} \lambda_s P_s(t) + \sum_{s=0}^{\infty} \mu_s P_s(t). \qquad (14)\end{aligned}$$

Again we can simplify this by noting that the λ_s and μ_s curves are only slowly curving and hence in any local region are approximately straight. Hence, where derivatives are now evaluated near the point $s = M(t)$,

$$\lambda_s = \lambda_{M(t)} + [s - M(t)]\frac{\mathrm{d}\lambda}{\mathrm{d}s}$$

$$\mu_s = \mu_{M(t)} + [s - M(t)]\frac{\mathrm{d}\mu}{\mathrm{d}s}. \qquad (15)$$

Substituting (15) into (14) we get

$$\begin{aligned}\frac{\mathrm{d}\,\mathrm{var}(t)}{\mathrm{d}t} &= 2(\lambda_{M(t)} - \mu_{M(t)}) \sum_{s=0}^{\infty} (s - M(t)) P_s(t) \\ &\quad + 2\left(\frac{\mathrm{d}\lambda}{\mathrm{d}s} - \frac{\mathrm{d}\mu}{\mathrm{d}s}\right) \sum_{s=0}^{\infty} (s - M(t))^2 P_s(t) \\ &\quad + [\lambda_{m(t)} + \mu_{M(t)}] \sum_{s=0}^{\infty} P_s(t) \\ &\quad + \left(\frac{\mathrm{d}\lambda}{\mathrm{d}s} + \frac{\mathrm{d}\mu}{\mathrm{d}s}\right) \sum_{s=0}^{\infty} (s - M(t)) P_s(t),\end{aligned}$$

which, since $\sum_{s=0}^{\infty} P_s(t) = 1$ and

$\sum (s - M(t))P_s(t) = M(t) - M(t) = 0$,
becomes,

$$\frac{\mathrm{d}\,\mathrm{var}(t)}{\mathrm{d}t} = -2\left(\frac{\mathrm{d}\mu}{\mathrm{d}s} - \frac{\mathrm{d}\lambda}{\mathrm{d}s}\right)\mathrm{var}(t) + \lambda_{M(t)} + \mu_{M(t)} \,. \qquad (16)$$

This is readily solved for var(t):

$$\mathrm{var}(t) = e^{-2[(\mathrm{d}\mu/\mathrm{d}s)-(\mathrm{d}\lambda/\mathrm{d}s)]t} \times \int_0^t (\lambda_{M(t)} + \mu_{M(t)})e^{2[(\mathrm{d}\mu/\mathrm{d}s)-(\mathrm{d}\lambda/\mathrm{d}s)]t}\,\mathrm{d}t \,. \qquad (16a)$$

However, it is more instructive to compare mean and variance for the extreme situations of saturation and complete unsaturation, or equivalently of $t =$ near ∞ and t = near zero.

At equilibrium, $\frac{\mathrm{d}\,\mathrm{var}(t)}{\mathrm{d}t} = 0$, so by (16) ·

$$\mathrm{var}(t) = \frac{\lambda_{\hat{s}} + \mu_{\hat{s}}}{2\left(\frac{\mathrm{d}\mu}{\mathrm{d}s} - \frac{\mathrm{d}\lambda}{\mathrm{d}s}\right)} \,. \qquad (17)$$

At equilibrium $\lambda_{\hat{s}} = \mu_{\hat{s}} = x$ say and we have already symbolized the difference of the derivatives at $s = \hat{s}$ by F (cf. eq. [13a]). Hence, at equilibrium

$$\mathrm{var} = \frac{X}{F} \,. \qquad (17a)$$

Now since μ_s has non-decreasing slope $X/s \leqslant \mathrm{d}\mu/\mathrm{d}s \,|_{s=\hat{s}}$ or $X \leqslant \hat{s}\,\mathrm{d}\mu/\mathrm{d}s \,|_{\hat{s}}$.

Therefore, variance $\leqslant \frac{\hat{s}\,\mathrm{d}\mu/\mathrm{d}s}{\mathrm{d}\mu/\mathrm{d}s - \mathrm{d}\lambda/\mathrm{d}s}$ or, at equilibrium

$$\frac{\text{variance}}{\text{mean}} \leqslant \frac{\mathrm{d}\mu/\mathrm{d}s}{\mathrm{d}\mu/\mathrm{d}s - \mathrm{d}\lambda/\mathrm{d}s} \,. \qquad (18)$$

In particular, if the extinction and immigration curves have slopes about equal in absolute value, (variance/mean) $\leqslant$ ½. On the other hand, when t is near zero, equation (16) shows that var$(t) \sim \lambda_0 t$. Similarly, when t is near zero, equations (13) or (14) show that $M(t) \sim \lambda_0 t$. Hence, in a very unsaturated situation, approximately,

$$\frac{\text{variance}}{\text{mean}} = 1 \,. \qquad (19)$$

Therefore, we would expect the variance/mean to rise from somewhere around ½ to 1, as we proceed from saturated islands to extremely unsaturated islands farthest from the source of colonization.

Finally, if the number of species dying out per year, X (at equilibrium), is known, we can estimate the time required to 90% saturation from equations (13a) and (17a):

$$\frac{2.303}{t} = \frac{X}{\text{variance}}$$

$$t = \frac{2.303 \text{ variance}}{X} \doteq \frac{2.303}{2}\,\frac{\text{mean}}{X} \,. \qquad (19a)$$

The above model was developed independently from an equilibrium hypothesis just published by Preston (1962). After providing massive documentation of the subject that will be of valuable assistance to future biogeographers, Preston draws the following particular conclusion about continental versus insular biotas: "[The depauperate insular biotas] are not depauperate in any absolute sense. They have the correct number of species for their area, provided that each area is an isolate, but they have far fewer than do equal areas on a mainland, because a mainland area is merely a 'sample' and hence is greatly enriched in the Species/Individuals ratio." To illustrate, "in a sample, such as the breeding birds of a hundred acres, we get many species represented by a single pair. Such species would be marked for extinction with one or two seasons' failure of their nests were it not for the fact that such local extirpation can be made good from outside the 'quadrat,' which is not the case with the isolate." This point of view agrees with our own. However, the author apparently missed the precise distance effect and his model is consequently not predictive in the direction we are attempting. His model is, however, more accurate in its account of

TABLE 1. *Number of species of land and freshwater birds on Krakatau and Verlaten during three collection periods together with losses in the two intervals (from Dammerman, 1948)*

	1908			1919–1921			1932–1934			Number "lost"	
	Non-migrant	Migrant	Total	Non-migrant	Migrant	Total	Non-migrant	Migrant	Total	1908 to 1919–1921	1919–1921 to 1932–1934
Krakatau	13	0	13	27	4	31	27	3	30	2	5
Verlaten	1	0	1	27	2	29	29	5	34	0	2

relative abundance, corresponding to our equation (10).

THE CASE OF THE KRAKATAU FAUNAS

The data on the growth of the bird faunas of the Krakatau Islands, summarized by Dammerman (1948), provide a rare opportunity to test the foregoing model of the immigration and extinction process on a single island. As is well known, the island of Krakatau proper exploded in August, 1883, after a three-month period of repeated eruptions. Half of Krakatau disappeared entirely and the remainder, together with the neighboring islands of Verlaten and Lang, was buried beneath a layer of glowing hot pumice and ash from 30 to 60 meters thick. Almost certainly the entire flora and fauna were destroyed. The repopulation proceeded rapidly thereafter. Collections and sight records of birds, made mostly in 1908, 1919–1921, and 1932–1934, show that the number of species of land and freshwater birds on both Krakatau and Verlaten climbed rapidly between 1908 and 1919–1921 and did not alter significantly by 1932–1934 (see table 1). Further, the number of non-migrant land and freshwater species on both islands in 1919–1921 and 1932–1934, i.e., 27–29, fall very close to the extrapolated fauna–area curve of our fig. 1. Both lines of evidence suggest that the Krakatau faunas had approached equilibrium within only 25 to 36 years after the explosion.

Depending on the exact form of the immigration and extinction curves (see fig. 4), the ratio of variance to mean of numbers of species on similar islands at or near saturation can be expected to vary between about ¼ and ¾. If the slopes of the two curves are equal at the point of intersection, the ratio would be near ½. Then the variance of faunas of Krakatau-like islands (same area and isolation) can be expected to fall between 7 and 21 species. Applying this estimate to equation (19a) and taking t (the time required to reach 90% of the equilibrium number) as 30 years, X, the annual extinction rate, is estimated to lie between 0.5 and 1.6 species per year.

This estimate of annual extinction rate (and hence of the acquisition rate) in an equilibrium fauna is surprisingly high; it is of the magnitude of 2 to 6% of the standing fauna. Yet it seems to be supported by the collection data. On Krakatau proper, 5 non-migrant land and freshwater species recorded in 1919–1921 were not recorded in 1932–1934, but 5 other species were recorded for the first time in 1932–1934. On Verlaten 2 species were "lost" and 4 were "gained." This balance sheet cannot easily be dismissed as an artifact of collecting technique. Dammerman notes that during this period, "The most remarkable thing is that now for the first time true fly catchers, *Muscicapidae,* appeared on the islands, and that there were no less than four species: *Cyornis rufigastra, Gerygone modigliani, Alseonax latirostris* and *Zanthopygia narcissina*. The two last species are migratory and were therefore only accidental visitors, but the sudden appearance of the *Cyornis* species in great numbers is noteworthy. These birds, first observed in May 1929, had already colonized three islands and may now be called common there. Moreover the *Gerygone,* unmistakable from his gentle note and common along the coast and in the mangrove forest, is certainly a new acquisition." Extinctions are less susceptible of proof but the following evidence is suggestive. "On the other hand two species mentioned by Jacobson (1908) were not found in 1921 and have not been observed since, namely the small kingfisher *Alcedo coerulescens* and the familiar bulbul *Pycnonotus aurigaster*." Between 1919–1921 and 1932–1934 the conspicuous *Demiegretta s. sacra* and *Accipter* sp. were "lost," although these species may not have been truly established as breeding populations. But "the well-known grey-backed shrike (*Lanius schach bentet*), a bird conspicuous in the open field, recorded in 1908 and found breeding in 1919, was not seen in 1933. Whether the species had really completely disappeared or only diminished so much in numbers that it was not noticed, the future must show." Future research on the Krakatau fauna would indeed be of great interest, in view of the very dynamic equilibrium suggested by the model we have presented. If the "losses" in the data represent true extinctions, the rate of extinction would be 0.2 to 0.4 species per year, closely approaching the predicted rate of 0.5 to 1.6. This must be regarded as a minimum figure, since it is likely that species could easily be lost and regained all in one 12-year period.

Such might be the situation in the early history of the equilibrium fauna. It is not possible to predict whether the rate of turnover would change through time. As other taxa reached saturation and more species of birds had a chance at colonization, it is conceivable that more "harmonic" species systems would accumulate within which the turnover rate would decline.

Prediction of a "Radiation Zone"

On islands holding equilibrium faunas, the ratio of the number of species arriving from other islands in the same archipelago (G in equation no. 2) to the number arriving from outside the archipelago (M in no. 2) can be expected to increase with distance from the major extra-archipelagic source area. Where the archipelagoes are of approximately similar area and configuration, G/M should increase in an orderly fashion with distance. Note that G provides the best available measure of what is loosely referred to in the literature as adaptive radiation. Specifically, adaptive radiation takes place as species are generated within archipelagoes, disperse between islands, and, most importantly, accumulate on individual islands to form diversified associations of sympatric species. In equilibrium faunas, then, the following prediction is possible: adaptive radiation, measured by G/M, will increase with distance from the major source region and after corrections for area and climate, reach a maximum on archipelagoes and large islands located in a circular zone close to the outermost range of the taxon. This might be referred to as the "radiation zone" of taxa with equilibrium faunas. Many examples possibly conforming to such a rule can be cited: the birds of Hawaii and the Galápagos, the murid rodents of Luzon, the cyprinid fish of Mindanao, the frogs of the Seychelles, the gekkonid lizards of New Caledonia, the Drosophilidae of Hawaii, the ants of Fiji and New Caledonia, and many others (see especially in Darlington, 1957; and Zimmerman, 1948). But there are conspicuous exceptions: the frogs just reach New Zealand but have not radiated there; the same is true of the insectivores of the Greater Antilles, the terrestrial mammals of the Solomons, the snakes of Fiji, and the lizards of Fiji and Samoa. To say that the latter taxa have only recently reached the islands in question, or that they are not in equilibrium, would be a premature if not facile explanation. But it is worth considering as a working hypothesis.

Estimating the Mean Dispersal Distance

A possible application of the equilibrium model in the indirect estimation of the mean dispersal distance, or λ in equation

(3). Note that if similar parameters of dispersal occur within archipelagoes as well as between them,

$$\frac{G}{M} = \frac{A_1 \,\mathrm{diam}_1\, d_2}{A_2 \,\mathrm{diam}_2\, d_1} e^{\lambda(d_2 - d_1)}, \qquad (20)$$

and

$$\lambda = \ln \frac{A_2 \,\mathrm{diam}_2\, d_1 G}{A_1 \,\mathrm{diam}_1\, d_2 M} \bigg/ (d_2 - d_1), \qquad (21)$$

where, in a simple case, A_1, diam_1, and d_1 refer to the relation between the recipient island and some single major source island within the same archipelago; and A_2, diam_2, and d_2 refer to the relation between the recipient island and the major source region outside the archipelago.

Consider the case of the Geospizinae of the Galápagos. On the assumption that a single stock colonized the Galápagos (Lack, 1947), G/M for each island can be taken as equal to G, or the number of geospizine species. In particular, the peripherally located Chatham Island, with seven species, is worth evaluating. South America is the source of M and Indefatigable Island can probably be regarded as the principal source of G for Chatham. Given G/M as seven and assuming that the Geospizinae are in equilibrium, λ for the Geospizinae can be calculated from (21) as 0.018 mile. For birds as a whole, where G/M is approximately unity, λ is about 0.014 mile.

But there are at least three major sources of error in making an estimate in this way:

1. Whereas M is based from the start on propagules from an equilibrium fauna in South America, G increased gradually in the early history of the Galápagos through speciation of the Geospizinae on islands other than Chatham. Hence, G/M on Chatham is actually higher than the ratio of species drawn from the Galápagos to those drawn from outside the archipelago, which is our only way of computing G/M directly. Since λ increases with G/M, the estimates of λ given would be too low, if all other parameters were correct.

2. Most species of birds probably do not disperse according to a simple exponential holding-time distribution. Rather, they probably fly a single direction for considerable periods of time and cease flying at distances that can be approximated by the normal distribution. For this reason also, λ as estimated above would probably be too low.

3. We are using $\hat{S}_G/\hat{S}_M$ for G/M, which is only approximate.

These considerations lead us to believe that 0.01 mile can safely be set as the lower limit of λ for birds leaving the eastern South American coast. Using equation no. 12 in another case, we have attempted to calculate λ for birds moving through the Lesser Sunda chain of Indonesia. The Alor group was chosen as being conveniently located for the analysis, with Flores regarded as the principal source of western species and Timor as the principal source of eastern species. From the data of Mayr (1944) on the relationships of the Alor fauna, and assuming arbitrarily an exponential holding-time dispersal, λ can be calculated as approximately 0.3 mile. In this case the first source of error mentioned above with reference to the Galápagos fauna is removed but the second remains. Hence, the estimate is still probably a lower limit.

Of course these estimates are in themselves neither very surprising nor otherwise illuminating. We cite them primarily to show the possibilities of using zoogeographic data to set boundary conditions on population ecological phenomena that would otherwise be very difficult to assess.

Finally, while we believe the evidence favors the hypothesis that Indo-Australian insular bird faunas are at or near equilibrium, we do not intend to extend this conclusion carelessly to other taxa or even other bird faunas. Our purpose has been to deal with general equilibrium criteria, which might be applied to other faunas, together with some of the biological implications of the equilibrium condition.

SUMMARY

A graphical equilibrium model, balancing immigration and extinction rates of species, has been developed which appears fully consistent with the fauna–area curves and the distance effect seen in land and freshwater bird faunas of the Indo-Australian islands. The establishment of the equilibrium condition allows the development of a more precise zoogeographic theory than hitherto possible.

One new and non-obvious prediction can be made from the model which is immediately verifiable from existing data, that the number of species increases with area more rapidly on far islands than on near ones. Similarly, the number of species on large islands decreases with distance faster than does the number of species on small islands.

As groups of islands pass from the unsaturated to saturated conditions, the variance-to-mean ratio should change from unity to about one-half. When the faunal buildup reaches 90% of the equilibrium number, the extinction rate in species/year should equal 2.303 times the variance divided by the time (in years) required to reach the 90% level. The implications of this relation are discussed with reference to the Krakatau faunas, where the buildup rate is known.

A "radiation zone," in which the rate of intra-archipelagic exchange of autochthonous species approaches or exceeds extra-archipelagic immigration toward the outer limits of the taxon's range, is predicted as still another consequence of the equilibrium condition. This condition seems to be fulfilled by conventional information but cannot be rigorously tested with the existing data.

Where faunas are at or near equilibrium, it should be possible to devise indirect estimates of the actual immigration and extinction rates, as well as of the times required to reach equilibrium. It should also be possible to estimate the mean dispersal distance of propagules overseas from the zoogeographic data. Mathematical models have been constructed to these ends and certain applications suggested.

The main purpose of the paper is to express the criteria and implications of the equilibrium condition, without extending them for the present beyond the Indo-Australian bird faunas.

ACKNOWLEDGMENTS

We are grateful to Dr. W. H. Bossert, Prof. P. J. Darlington, Prof. E. Mayr, and Prof. G. G. Simpson for material aid and advice during the course of the study. Special acknowledgment must be made to the published works of K. W. Dammerman, E. Mayr, B. Rensch, and E. Stresemann, whose remarkably thorough faunistic data provided both the initial stimulus and the principal working material of our analysis. The work was supported by NSF Grant G-11575.

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APPENDIX: MEASUREMENT OF A PROPAGULE

A rudimentary account of how many immigrants are required to constitute a propagule may be constructed as follows. Let η be the average number of individuals next generation per individual this generation. Thus, for instance, if $\eta = 1.03$, the population is increasing at 3% interest rate.

Let us now suppose that the number of descendants per individual has a Poisson distribution. If it has not, due to small birth rate, the figures do not change appreciably. Then, due to chance alone, the population descended from immigrants may vanish. This subject is well known in probability theory as "Extinction probabilities in branching processes" (cf. Feller 1958, p. 274). The usual equation for the probability ζ of eventual extinction (Feller's equation 5.2 with $P(\zeta) = e^{-\eta(1-\zeta)}$, for a Poisson distribution), gives

$$\zeta = e^{-\eta(1-\zeta)}.$$

Solving this by trial and error for the probability of eventual extinction ζ, given a variety of values of η, we get the array shown in table 2. From this we can calculate how large a number of simultaneous immigrants would stand probability just one-half of becoming extinct during the initial stages of population growth following the introduction. In fact, if r pairs immigrate simultaneously, the probability that all will eventually be without descendants is ζ^r. Solving $\zeta^R = 0.5$ we find the number, R, of pairs of immigrants necessary to stand half a chance of not becoming extinct as given in table 3. From this it is clear that when η is 1, the propagule has infinite size, but that as η increases, the propagule size decreases rapidly, until, for a species which increases at 38.5% interest rate, one pair is sufficient to stand probability 1.2 of effecting a colonization. With sexual species which hunt for mates, η may be very nearly 1 initially.

TABLE 2. *Relation of replacement rate (η) of immigrants to probability of extinction (ζ)*

η	1	1.01	1.1	1.385
ζ	1	0.98	0.825	0.5

TABLE 3. *Relation of replacement rate (η) to the number of pairs (R) of immigrants required to give the population a 50% chance of survival*

η	1	1.01	1.1	1.385
R	∞	34	3.6	1