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Calculation of immigration and extinction curves from the species-area-distance relation

(biogeography/islands/models/birds/Solomon Archipelago)

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ABSTRACT Quantitative models of the species-area-distance relation, based on equilibria between immigration and extinction rates, have been tested against data for birds on 52 Solomon islands. Biologically reasonable models account for 98% of the variance in species number. The data are adequate to permit determination of immigration and extinction curves and the values of seven associated parameters. The resulting curves are very concave. Extinction rates vary almost exactly as the reciprocal of area, but the effect of area on immigration rates is slight. Recognition of major differences among species in immigration and extinction rates and in dispersal distances proves essential to a successful model.

In 1963 MacArthur and Wilson (1, 2) showed by graphical methods that the well-known dependence of island species number S on island area A and distance D can be qualitatively predicted by considering equilibria between area-dependent extinction rates (E) and distance-dependent immigration rates (I) (see Fig. 2 of the present paper). This insight raised the obvious prospect that quantitative analysis of S-A-D relations observed in nature might permit detailed reconstruction of how immigration and extinction rates vary with S, A, and D. To date, however, only limited progress has been made towards this goal. Observations of S as a function of A have generally been fitted to empirical equations, mainly $S \propto A^z$ or $\log S \propto \log A$, rather than to equations derived from theoretical models of immigration and extinction. Few attempts have made to fit the whole S-A-D relation even by empirical equations.

A reason for this slow development of theoretical models of the S-A-D relation has been the lack of an adequate data base against which to test such models. Since the simplest reasonable models require fitting three to seven parameters (see below), a suitable data base must fulfill three criteria: (*i*) it must include many islands spanning a wide range of A and D values; (*ii*) values of S must be accurate; and (*iii*) almost all variation in S must be related to variation in A and D, and effects of the three next most important variables—altitude, history, and habitat variation independent of variation in area—must either be negligible or else separable by analysis. These conditions are met by recently published values (3, 4), depicted in Fig. 1, for number of lowland bird species on 52 islands of the Solomon Archipelago in the tropical Southwest Pacific. Island area ranges from about 0.003–3000 square miles (0.0078–7800 km^2), distance up to 384 miles (614 km). We shall show that variation in A and D explains 98% of the variation in S. The effect of altitude can be separated by analysis (3, 5), while effects on S of history (e.g., of Pleistocene land bridges) and of habitat variation independent of area variation are negligible.

We begin by discussing the minimum number of parameters, and the general form, that functions modelling I and E should have. Next, the particular functions that best fit S-A-D values of Solomon birds are determined. The biological conclusions emerging from this model-fitting are summarized. Finally, we show how the empirical equations usually invoked to fit the S-A relation relate to our model. This is the fourth paper in a series on ecology and evolution of Northern Melanesian birds, the three previous papers having considered the S-A relation (3), montane avifauna (4), and S-D relation (5).

Phenomenological models

Of the 52 Solomon islands for which bird species number is accurately known, 37 are considered "central" because they are closely grouped and their S values[‡] are correlated with A alone, not with their low D values (3, 4). Diamond and Mayr (3) showed by a two-parameter phenomenological equation, $S = a + b \log A$, that variation in A explains 98% of the variance in S on the 37 central islands. We have used a five-parameter phenomenological equation,

$$S = (a + b\log A)\exp(-D^c/dA^e) \qquad [1]$$

with best-fit values $a = 34.7$, $b = 12.08$, $c = 0.67$, $d = 12.41$ and $e = 0.28$, to show that variation in A and D explains 98% of the variance in S on all 52 Solomon islands, the 37 central ones plus the 15 "remote" ones. Because Eq. 1 has not been derived from theoretical considerations, its five parameters lack biological meaning. Its good fit simply shows that the data are cleanly related to A and D. The theoretical models that we develop below also relate S to A and D, but use biologically meaningful parameters that describe the dependence of I and E on S, A, and D.

What forms may the functions E, I, and S take?

Let S represent the number of species on an island and $\hat{S}$ the equilibrium number. If the total species number in the available colonist pool is P, then $0 \leq S, \hat{S} \leq P$. E and I, whose units are species per unit time, must depend on S. In addition, E will decrease with island area A; I will decrease with island distance D from the source of colonists; and I might increase with A.

Assume that $E(S, A)$ and $I(S, A, D)$ each behave as a product of two functions:

$$E(S,A) = e(A)g(S) \qquad [2a]$$

$$I(S,A,D) = i(A,D)h(S) \qquad [2b]$$

$g(S)$ must be 0 for $S = 0$ and positive for $S > 0$, while $h(S)$ must be 0 for $S = P$ and positive for $0 \leq S < P$. *If* all species had identical extinction probabilities and identical immigration

Abbreviations: S-A-D relation, species-area-distance relation; I, distance-dependent immigration rates; E, area-dependent extinction rates.

[‡] Throughout this paper S is taken as the number of lowland bird populations on each island, symbolized by S_{low} in ref. 2. Ref. 5 discusses the number of montane bird populations.

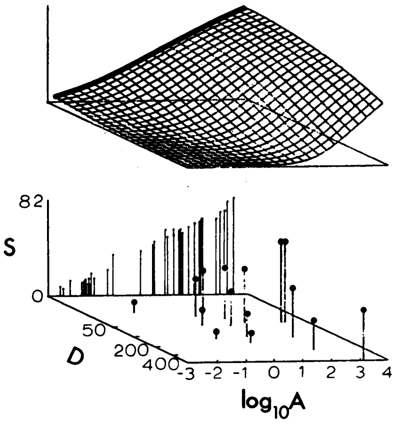

FIG. 1. (Bottom) Values of S, A, and D for 52 Solomon islands plotted in three-dimensional space. Axes are chosen as S, log A, and $\sqrt[3]{D}$ for convenience of scaling. Small dots on light stalks at $D = 0$ refer to 37 central islands, large dots on heavy stalks to 15 remote islands. (Top) The surface determined by Eq. 7, the equation based on immigration–extinction equilibria that best fits the values depicted on the left, using the same axes. The heavy line is the S-A relation at $D = 0$, which is approximately but not strictly linear over a considerable range on S-log A axes.

probabilities, and *if* there were no interactions between species, the extinction and immigration probabilities *per species* would be independent of S, and E would increase and I decrease linearly with S: $g(S) = E_oS$, $h(S) = I_o(1 - S/P)$, where E_o and I_o are constants. Neither assumption is reasonable. Species differ in their extinction probabilities and in their colonizing abilities. The most extinction-prone species will tend to disappear first with decreasing S, while the best colonists will tend to arrive first with increasing S. In addition, competitive interactions between species will cause extinction and immigration probabilities per species, respectively, to increase and decrease with S. Both effects (species differences, and competition) suggest for the signs of the derivatives of $g(S)$ and $h(S)$ that $g'(S) > 0$, $g''(S) > 0$, $h'(S) < 0$, and $h''(S) > 0$ ("concave" extinction and immigration curves). However, these trends could be reversed over some range of S by strong facilitatory interactions among species such as are unlikely for birds but could be significant for plants, insects, and sessile marine invertebrates, since one species could be favored by the shade, substrate, or food supplied by another species. The result could be $g''(S) < 0$, $h''(S) < 0$ [and, in extreme cases, $g'(S) < 0$, $h'(S) > 0$] over some range of S. Functions accounting for these possibilities are

$$g(S) = E_oS^n; h(S) = I_o(1 - S/P)^m \qquad [3]$$

where E_o and I_o are constants, and $m, n > 1$ in most cases of biological interest.

With decreasing A, population sizes decrease and hence extinction probabilities per species increase: $e'(A) < 0$. If carrying capacity is proportional to A, and if extinctions are solely the result of demographic fluctuations (i.e., stochastic birth and death processes), $e(A)$ should go as $\exp(1/A)$ or as A^{-x}, where x is greater than 1 (ref. 2).

For the decrease in I with D, one possible functional form is the equation for diffusion or a two-dimensional random walk, $i(D) = [\exp(-D^2/D_o)]/D$, where D_o is a constant. This form would arise if a dispersing individual randomly changed its compass bearing at intervals, causing i to decline steeply with D (because repeated random choice of bearing is unlikely to yield the same choice many successive times). As a second alternative, constant compass bearing and constant risk of death per unit distance covered would yield $i(D) = \exp(-D/D_o)$.

But, in addition, species differ greatly in the distances they fly overwater (4), implying dispersion in the parameter D_o. We have tested two ways of modelling this dispersion: a rectangular distribution of $1/D_o$, and the equation $i(D) = \exp(-D^y/D_o)$, where $y < 1$. This last form has an effect equivalent to introducing dispersion, because i on distant islands relative to close islands will be higher than if $y = 1$, reflecting the contribution of species with higher-than-average values of D_o. For the rectangular distribution of $1/\overline{D}_o$, assume that the distribution has width $2w$, where $w \leq 1/\overline{D}_o$ and where $1/\overline{D}_o$ is the mean value of the distribution. The probability that $1/D_o$ lies between $1/D_o$ and $(1/D_o) + \delta(1/D_o)$ is $\delta/2w\overline{D}_o$. Integration over the whole width of the distribution then yields

$$i(D) = (1/2w)\int_{(1/\overline{D}_o - w)}^{(1/\overline{D}_o + w)} [\exp(-D/D_o)]d(1/D_o) \qquad [4]$$

The analogous rectangular distribution for D_o cannot be integrated in closed form.

i might also increase with A for at least two reasons. First, with increasing diameter of "target area" an island is increasingly likely to be seen by, or to intercept the flight path of, a dispersing bird. This effect might make i proportional to A^v, where $v \sim 0.5$ or > 0.5, depending on whether effects of island altitude in increasing island visibility are insignificant or significant. Second, with increasing A the probability increases that a colonist will find a suitable site on the island, or a "hot spot" of locally high resource production (Fig. 16 of ref. 6). These area effects could be expressed by the functions $i(A, D) = \exp(-D^y/D_oA^v)$ or $A^v[\exp(-D^y/D_o)]$.

The rate of change of species number is given by $\delta S/\delta t = I - E = i(A, D)\, h(S) - e(A)\, g(S)$. At equilibrium,

$$0 = i(A,D)h(\hat{S}) - e(A)g(\hat{S}) \qquad [5]$$

In some cases Eq. 5 may be solved to obtain $\hat{S}$ as some explicit function $\hat{S} = f(A, D)$. In other cases, however, including the case of the best model for Solomon birds, an explicit general solution $f(A, D)$ cannot be written, and $\hat{S}$ is an implicit function of A and D that must be solved by iteration techniques.

Substitution of Eqs. 3 into Eq. 5 shows that the solution for $\hat{S}$ will involve only the ratio of g to h, not the absolute values of these functions. We can therefore multiply Eqs. 3 by $(1/I_o)$ to yield new definitions of g and h with one less fitted parameter:

$$g(S) = RS^n, \text{where } R \equiv E_o/I_o \qquad [6a]$$

$$h(S) = (1 - S/P)^m \qquad [6b]$$

Thus, a realistic model of immigration and extinction involves at least seven parameters: R, m, n, x, D_o, y or w, and v, or their equivalents.

Expressed negatively, testing of a realistic immigration-extinction model is impossible without a data base adequate to permit extraction of at least seven parameters. Otherwise, calculation of model parameters would be a meaningless exercise, and it is often with justice that biologists deprecate multi-parameter models for an assumed ability to fit even a tail-wagging elephant. Expressed positively, if one has an adequate data base, one can hope to extract at least seven numbers describing processes of fundamental biological interest, namely, how I and E vary with S, A, and D. We shall demonstrate statistically that the Solomon data base does permit extraction of these seven parameters.

Fitting theory to data

To evaluate the fit of alternative models to Solomon bird data by regression techniques, we obtain the set of model parameter

Table 1. Fits of theoretical models to *S-A-D* values for Solomon island birds

Model	*I*	*E*	*S*	Parameters	e.v. (%)	*H*
1	$(1 - S/P_o)\exp(-D/D_o)$	RS/A	Explicit	2	0	
2	$(1 - S/P_o)^n \exp(-D/D_o)$	RS^n/A	Explicit	3	78.2	$H_1 = 2.145$**
3	$(1 - S/P_o)^n \exp(-D/D_o)$	$RS^n \exp(1/A)$	Explicit	3	0	
4	$(1 - S/P_o)^n \exp(-\sqrt{D}/D_o)$	RS^n/A	Explicit	3	84.8	$H_2 = 1.197$**
5	$(1 - S/P_o)^{2n} \exp(-\sqrt{D}/D_o)$	RS^n/A	Explicit	3	96.8	$H_4 = 2.180$**
6	$(1 - S/P_o)^m \exp(-D/D_o)$	RS^n/A	Implicit	4	89.8	$H_2 = 1.467$**
7	$(1 - S/P_o)^m [\exp(-D^2/D_o]/D$	RS^n/A	Implicit	4	28.0	
8	$(1 - S/P_o)^m \exp(-D^y/D_o)$	RS^n/A	Implicit	5	96.8	$H_6 = 1.780$**
9	$(1 - S/P_o)^m (1/2w) \int_{(1/\bar{D}_o - w)}^{(1/\bar{D}_o + w)} [\exp(-D/D_o)]\, d(1/D_o)$	RS^n/A	Implicit	5	94.9	$H_6 = 1.414$**
10	$(1 - S/P_o)^m \exp(-D^y/D_oA^v)$	RS^n/A	Implicit	6	97.9	$H_8 = 1.235$*
11	$(1 - S/P_o)^m A^v \exp(-D^y/D_o)$	RS^n/A	Implicit	6	96.8	$H_8 = 1.000$
12	$(1 - S/P)^m \exp(-D^y/D_oA^v)$	RS^n/A	Implicit	7	98.0	$H_{10} = 1.017$
13	$(1 - S/P_o)^m \exp(-D^y/D_oA^v)$	RS^n/A^x	Implicit	7	98.0	$H_{10} = 1.015$

Regression fits for 13 models to *S-A-D* values for 52 Solomon islands. $\hat{S}$, the expected equilibrium number of species on an island, is obtained as an explicit or implicit function (column 4) by equating an immigration function (column 2) and an extinction function (column 3). For example, model 4 yields the explicit solution $\hat{S} = 1/\{(1/P_o) + [R\exp(\sqrt{D}/D_o)]^{1/n}/A^{1/n}\}$. Column 5 gives the fitted number of parameters. e.v. is the explained variance of S, in %. H_n is the Hamilton statistic relative to model n; see *text* for correspondence of H_n values and significance levels. ** or * mean that the added parameter by which the given model differs from the simpler model n is significant at the $P < 0.005$ or $P < 0.05$ level, respectively. Nonasterisked models are not significant even by the $P < 0.25$ criterion. P_o (= 106 species), the known pool of Solomon lowland birds, is specified in all models except model 12, where P is a fitted parameter. In model 9, w is constrained as $\leq (1/\bar{D}_o)$. The *S-A-D* values are those for the 15 "remote" islands in Table 1 of ref. 4, plus those for 37 "central" islands in Table 1 of ref. 3 (comprising all islands of that table except Malaita, San Cristobal, and the 11 islands for which the table gave D values; D for these 37 islands is taken as 0, and S as the S_{low} values of the table).

values k_j that minimizes the sum $Q = \Sigma_i[S_o(A_i, D_i) - S_p(A_i, D_i; k_j)]^2$, where D_i and A_i are distance and area of the ith island, and subscripts o and p refer, respectively, to the observed S value and to the value predicted by the model. As a goodness-of-fit statistic we use the percent explained variance (e.v.), defined as e.v. $= 100\{1 - Q/\Sigma_i[\bar{S} - S_o(A_i, D_i)]^2\}$, where $\bar{S}$ is the mean of all S_o values. A perfect fit would yield e.v. of 100%, while e.v. for a bad fit is low. Most of the models we tested were sufficiently complex to require nonlinear regression programs, which obtain the local slope of the terrain in the j-dimensional parameter space and then move uphill until they reach the point in parameter space where Q is optimized. We checked for suboptimal peaks by starting from different points in parameter space, and we found none. We tried adding parameters to models in various sequences, and found that the statistical significance and best-fit values of the parameters are insensitive to the order in which they are added. Our explained variance estimates are believed to be accurate to at least 0.1%.

Naturally, the addition of any randomly chosen, adjustable parameter may improve the fit of a model to a data base. To determine whether the improved fit is in fact significant or is no more than expected by chance, one needs a statistical test that takes into account the amount of improvement and also the number of data points as expressed in the degrees of freedom. We have used the so-called Hamilton statistic (7) to determine whether addition of each parameter is statistically warranted. For a model x being compared to a model y which has one fewer parameter, this statistic is defined as $H_y = [(100 - \text{e.v.}_y)/(100 - \text{e.v.}_x)]^{1/2}$. For 40 degrees of freedom (most of our fitted models had between 44 and 50 degrees of freedom) H must exceed 1.050, 1.105, or 1.166 for model x to be a significant improvement over model y at the $P < 0.05$, 0.005, or 0.0005 level, respectively. For 12–13 degrees of freedom (models 8–11 of Table 1, which fit the parameters y, w, and v to data for the 15 isolated islands), an improvement significant at the $P < 0.05$ or $P < 0.005$ level requires $H > 1.18$ or 1.41, respectively. Table 1 will show that H is 1.235–2.145 for each added parameter as we proceed from a two- to a six-parameter model (models 1 → 2 → 6 → 8 → 10): i.e., these added parameters are all highly significant.

Biological significance

Table 1 presents fits to 13 models. Comparison of these fits yields the following conclusions:

(*i*) In all models except model 13, the species pool size P is not taken as a fitted parameter but is fixed at P_o = 106 species, the known pool of lowland bird species in the Solomons. In model 12, where P is taken as a variable to be fitted by our regression analysis, the resulting best-fit value is 109 species, which does not differ statistically from the value of 106 independently known to be the true one ($H_{10} = 1.017$, $P > 0.25$). This agreement illustrates that the model-fitting analysis is realistic.

(*ii*) Both the immigration curve $h(S)$ and extinction curve $g(S)$ are very concave, the immigration curve more so (see discussion of Eq. 2 for biological significance of concavity). A model of linear immigration and extinction curves, which assumes that all species are identical and noncompeting, is literally worthless (model 1: e.v. 0%!). If the respective exponents m and n of these curves are assumed equal, the fitted estimate (model 2) is 3.13. If m and n are fitted separately (model 10), their respective values are 7.23 and 2.37. Direct independent confirmation of this pronounced concavity comes from determination of the curves by studies of species fluctuations around equilibrium (Diamond and Jones, unpublished). Other corroborating evidence comes, for the extinction curve, from so-called relaxation studies on supersaturated islands (8, 9), from fitting models to bird species numbers on many archipelagoes (10), and from observation of great differences among species in proneness to extinction (6, 9, 11); for the immigration curve, from relaxation studies on defaunated islands (8) and from observation of great differences among species in overwater dispersal ability (4, 6).

(*iii*) Comparison of models 2 and 3 shows that extinction rates vary as $1/A$, not as $\exp(1/A)$. In model 13, when the extinction function $e(A) = 1/A^x$ was tested, the best-fit value of x was 1.02, which does not differ significantly from 1.00 ($H_{10} = 1.015$, $P > 0.25$). Thus, we have the pleasingly simple result that extinction rates vary as the reciprocal of area, and one of the seven model parameters can be dropped.

(*iv*) Comparison of models 10 and 11 with model 8 shows that immigration rates increase with area if $i(A, D)$ is taken as $\exp(-D^y/D_oA^v)$, but not if $i(A, D)$ is taken as $A^v \exp(-D^yD_o)$. Even with the former function the best-fit value of the exponent v is only 0.087 ($v = 0$ would mean no area dependence at all), and an immigration function independent of A (model 8) still yields an e.v. of 96.8%. That is, area affects species number much more importantly through extinction than through immigration.

(*v*) As a model for bird dispersal, a random walk is much worse than dispersal in a straight line (compare e.v. values of models 6 and 7). This conclusion corresponds to our field experience (ref. 6, pp. 376–377) that bird colonists dispersing overwater tend to fly more or less in one direction and do not randomly change bearings at intervals. But is an exponential function, as we assumed, the most realistic form for the distance dependence of immigration of a single species?

(*vi*) Species differences in mean dispersal distance are important to the *S-A-D* relation, as reflected in the considerable improvement in e.v. associated with two alternative ways of introducing dispersion into D_o (compare model 8 or 9 with model 6). The form $\exp(-D^y/D_o)$ works better than rectangular dispersion in $1/D_o$. Model 6, which ignores species differences in dispersal distance, not only gives a poorer fit but also a systematic misfit: it greatly underestimates S on the most remote islands, which in reality are reached mainly by a few "long-distance colonists." In fitting model 9 we constrained the half-width w of a rectangular distribution in $(1/D_o)$ to $\leq (1/\overline{D}_o)$ (where $1/\overline{D}_o$ is the mean of $1/D_o$), and we obtained $w = 1/\overline{D}_o$ as the best-fit value. This again implies that some species are long-distance colonists ($1/D_o \rightarrow 0$, $D_o \rightarrow \infty$). Examination of species distribution patterns directly confirms these conclusions (4). When the constraint $w \leq (1/\overline{D}_o)$ is removed in fitting model 9, the fit is improved (e.v. 95.7% instead of 94.9%), but the best-fit w somewhat exceeds $1/\overline{D}_o$ and cannot be assigned biological meaning, as it implies $D_o < 0$ for some species. The actual form of the dispersion in D_o, i.e., the distribution of mean dispersion distances of different species, remains an unsolved problem. A rectangular distribution in $1/\overline{D}_o$ is unrealistic in that it assumes an upper limit to $1/D_o$, of $2/\overline{D}_o$, hence a lower limit to D_o of half the mean. In reality, some Solomon species fail to cross water gaps whose width is a small fraction of the calculated mean D_o value of 23 miles for the Solomons (4). A Poisson or lognormal distribution of D_o values would be more realistic.

To understand the fundamentally different types of species differences underlying the immigration-curve exponent m and dispersion in D_o, recall that dispersion of a given species may be modelled by the equation $I = I_o \exp(-D/D')$, where I is the rate at which colonists reach a distance D from the source, I_o is the species-specific product of source population size times *per capita* rate of production of dispersing colonists, and D' is a second species-specific constant describing the mean dispersal distance of the colonists (4). Then species differences in I (i.e., in I_o as well as in D') and in D' alone underlie the exponent m and dispersion in D_o, respectively.

(*vii*) Species number at equilibrium depends only on the ratio of extinction rate to immigration rate (i.e., on $R = E_o/I_o$), not on their absolute values, which become relevant to S only during relaxation from a nonequilibrial value.

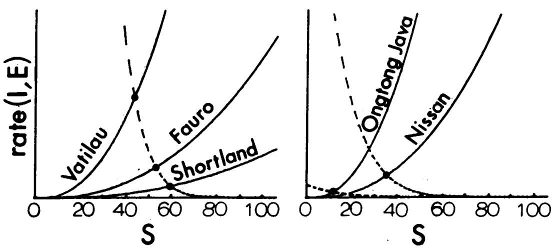

FIG. 2. Examples of immigration curves (dashed lines) and extinction curves (solid lines) for avifaunas of particular Solomon islands. The curves were calculated by inserting the islands' A and D values into Eq. 7. Ordinate, I or E (species per unit time, in arbitrary units); abscissa, S. Abscissa values of intersections between immigration and extinction curves, marked by dots, are $\hat{S}$, the predicted equilibrium species number for the island. (Left), Vatilau (A = 5.4 square miles, D = 0 miles, actual S = 41 species), Fauro (27.4, 0, 51), and Shortland (89.5, 0, 58); these three islands share the same immigration curve, since D = 0. (Right) Ongtong Java (A = 3.69 square miles, D = 147 miles, actual S = 9 species) and Nissan (14.3, 38.9, 29).

(*viii*) A model based on immigration-extinction equilibria accounts for the dependence of S on A and D, not only qualitatively, as shown by MacArthur and Wilson, but also quantitatively. Since our best model (model 10) has six fitted constants and may conjure up suspicions of tail-wagging elephants, it is worth summarizing why the model is realistic, simple, and general. Each of the parameters has a simple biological meaning and is essential to a realistic understanding of species equilibria: ratio of extinction and immigration coefficients $R = E_o/I_o$, mean dispersal distance D_o, species differences in D_o (expressed in the D exponent y or else in the dispersion half-width w), exponents m and n reflecting species differences in immigration and extinction rates and also species interactions, and area dependence of immigration (exponent v). These parameters prove to be significant at the <0.005 level. Omission of parameters is associated with readily interpreted systematic misfits of the data (see discussion of the misfit of model 6, caused by ignoring species differences in D_o). Many alternative multiparameter models that we tested and discarded yield poor fits to the data. In the case of one parameter, P, whose value is known independently of our regression procedure, the best-fit value (109 species: model 12) is very close to the true value (106 species).

The best phenomenological equation (Eq. 1) and the best biological model (model 10) yield the same explained variance within 0.1%, namely, 98%, an expression of how close the correlation is between S and A and D for the Solomon bird data. The remaining 2% of unexplained variance may reflect a combination of measuring errors, effects of habitat variation independent of area variation, statistical fluctuations in S at equilibrium, and the fact that S_o must be an integer while S_p need not be.

The best model for Solomon birds, model 10, with best-fit parameters, is:

$$I = (1 - S/P)^m \exp(-D^y/D_oA^v); E = RS^n/A \qquad [\mathbf{7a}]$$

$$m = 7.23; n = 2.37; y = 0.553; v = 0.083; \qquad [\mathbf{7b}]$$

$$R = 1.49 \times 10^{-5}; \mathrm{P} = 106 (\text{specified}); D_o = 2.11$$

Fig. 1 (top) depicts the function $\hat{S} = f(A, D)$ that is the implicit solution of Eq. 7 for comparison with the actual *S-A-D* values of Fig. 1 (bottom). Fig. 2 depicts calculated immigration and

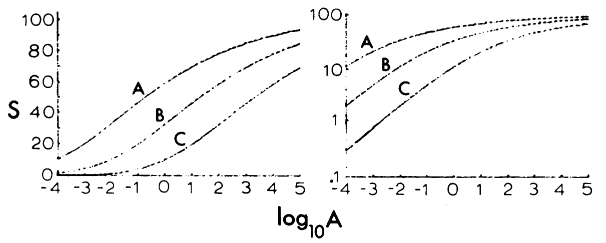

FIG. 3. Species-area relations calculated from Eqs. 7, and plotted either as S against log A (left) or as log S against log A (right). Parameter values are as in Eq. **7b**, except that R_o is 1.49×10^{-7} (A), 1.49×10^{-5} (B), or 1.49×10^{-3} (C), as indicated beside the curve. Note that no curve on either graph is truly linear, though each curve is approximately linear over a certain range on one or the other graph.

extinction curves for some actual Solomon islands, obtained by inserting the islands' A and D values into Eq. 7. Fig. 2 illustrates how the intersection of the reconstructed I and E curves determines species number for each island. Naturally, a fauna or flora other than Solomon birds will certainly require parameter values, and may require functional forms, different from those of Eqs. **7b** and **7a**, respectively.

It is still obvious that biologists faced with the practical problem of fitting S values for a data base much smaller than the Solomon set of 52 islands cannot use the six-parameter model, Eq. 7 (model 10). However, model 5 explains 97% of variance in S for Solomon birds with only three parameters. The simplifications introduced by this model are 3-fold: it neglects the slight area dependence of immigration; it accepts that $m > n$, as found for Solomon birds, but specifically assumes $m = 2n$ because this yields an explicit solution for $\hat{S}$; and it assumes a square root form $\exp(-\sqrt{D}/D_o)$ for dispersion in D_o, close to the best-fit form $\exp(-D^{0.55}/D_o)$ for Solomon birds, although we can think of no theoretical reason for a square root. For fitting small data bases, we therefore suggest that the following model, with three fitted parameters (n, D_o, and R) and with P specified from the archipelago species list, may involve only a moderate loss in accuracy: $I = (1 - S/\mathrm{P})^{2n} \exp(-\sqrt{D}/D_o)$; $E = RS^n/A$. An alternative, suggested by the good fit of model 9 with the finding that the best-fit value of w is simply $1/\overline{D}_o$, is to replace $\exp(-\overline{D}/D_o)$ in model 5 by $(\frac{1}{2}w) \int_0^{2/\overline{D}_o} [exp(-D/D_o)]\, d(1/D_o)$.

Relation to traditional *S-A* plots

Biologists have usually graphed actual S-A data in either of two ways: as S or else log S against log A, which would yield a linear graph if the data fitted an exponential function ($\exp S \propto A^z$) or a power function ($S \propto A^z$), respectively. There has been much discussion as to the respective merits of these two graphs, e.g., whether one is more appropriate to plants and the other to animals, or each to a community with a particular type of species-abundance relation (see refs. 3 and 10 for summary). Fig. 3, which depicts both types of graphs for Eq. 7, the equation derived from our best immigration-extinction model, for three sets of parameter choices, suggests a simpler explanation. For a sufficiently wide range of S and A values, Eq. 7 is linear on *neither* graph. However, over a moderate range of A values Eq. 7 may look more linear on one graph or the other depending on the particular parameter values and on which segment of the S-A relation is being observed. For example, comparison of the left and right halves of Fig. 3 shows that, for the parameter values (curves labeled B) and area range (mostly 10^{-2}–10^3 square miles) of our Solomon bird data, an S-log A graph looks linear, while a log S − log A graph looks sublinear, as noted previously (3).

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1. MacArthur, R. H. & Wilson, E. O. (1963) *Evolution* **17,** 373–387.
2. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton University Press, Princeton, N.J.).
3. Diamond, J. M. & Mayr, E. (1976) *Proc. Natl. Acad. Sci. USA* **73,** 262–266.
4. Diamond, J. M., Gilpin, M. E. & Mayr, E. (1976) *Proc. Natl. Acad. Sci. USA* **73,** 2160–2164.
5. Mayr, E. & Diamond, J. M. (1976) *Proc. Natl. Acad. Sci. USA* **73,** 1765–1/69.
6. Diamond, J. M. (1975) in *Ecology and Evolution of Communities*, eds. Cody, M. L. & Diamond, J. M. (Harvard University Press, Cambridge, Mass.), pp. 342–444.
7. Hamilton, W. C. (1964) *Statistics in Physical Science* (Ronald Press, New York).
8. Diamond, J. M. (1972) *Proc. Natl. Acad. Sci. USA* **69,** 3199–3203.
9. Terborgh, J. W. (1974) *BioScience* **24,** 715–722.
10. Schoener, T. W. (1976) *Proc. 16th Intern. Ornith. Congr.*, in press.
11. Diamond, J. M. (1976) *Proc. 16th Intern. Ornith. Congr.*, in press.