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Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators

(biogeography/islands/Pacific Ocean/speciation)

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ABSTRACT For scattered remote islands and for likely forms of immigration and extinction curves, the equilibrium theory of island biogeography leads to the prediction $\partial^2 \log S/\partial A \partial D > 0$, where S is the number of species on an island, A island area, and D island distance from the colonization source. This prediction is confirmed for birds of the Solomon Archipelago. Bird species can be classified into three types according to how distance affects their distributions: non-water-crossers, which are stopped completely (usually for psychological reasons) by water gaps of even 1 mile; short-distance colonists, successful at colonizing close but not remote islands; and long-distance colonists, successful at colonizing remote as well as close islands. Almost all of the "great speciators", the species for whose inter-island geographic variation the Solomons are famous, prove to be short-distance colonists. Lack's interpretation of the decrease in S with D is shown to rest on incorrect assumptions.

It is a familiar finding of island biogeography that remote islands support fewer species than equal-sized islands close to colonization sources. To model this finding and the equally familiar increase in species number S with island area (A), Preston (1) and MacArthur and Wilson (2, 3) suggested that S on an island may approach an equilibrium value at which the rate of immigration of new species, I, equals the rate of extinction of occupant species, E. By this reasoning, the observed decrease in S with distance D is attributed to the decrease in immigration rates and hence in equilibrium species number with distance.

Assuming that so-called immigration and extinction curves (the dependence of I and E on S) are either linear or else mirror images, MacArthur and Wilson (ref. 2 and ref. 3, pp. 25–28) made three further predictions from the equilibrium hypothesis: (*1*). The *relative* increase in S with A—i.e., $(1/S)\ (\partial S/\partial A)$—should be steeper for remote islands than for close islands. (*2*) The *relative* decrease in S with D—i.e., $(1/S)\ (\partial S/\partial D)$—should be steeper for small islands than for large islands. These two statements are equivalent and reduce to $\partial^2 \log S/\partial A \partial D = \partial^2 \log S/\partial D \partial A > 0$. (*3*) The *absolute* rate of increase of S with A can be more or less steep on remote islands than on close islands (i.e., $\partial^2 S/\partial A \partial D > 0$ or < 0).

In qualitative accord with the first two of these predictions, McArthur and Wilson (ref. 2, Fig. 2; ref. 3, Fig. 10) showed that the S–A relation for birds on islands colonized from New Guinea is steeper for islands more than 2000 miles§ from New Guinea than for closer islands. However, although the S–A relation has been extensively studied for clumped archipelagoes in which D can be neglected as a variable (see ref. 4 for summary), a detailed test of these predictions has not been possible because of the lack of an adequate data base.

The purpose of this paper is to explore the form of dependence of S on D, using accurate, recently published tabulations of bird species numbers on islands of the Solomon Archipelago (4). First, we show theoretically that the inequality $\partial^2 \log S/\partial A \partial D > 0$ should hold for a wide range of likely immigration and extinction curves, not just for linear or mirror-image curves. Next, we test this prediction for Solomon birds. We then show that isolation affects the colonization probability of some species more than of others, and that most of the "great speciators" for which the Solomons are famous belong to one subset of colonists. Finally, we discuss Lack's interpretation of the effect of D on S. A subsequent paper (5) shows how mathematical analysis of the whole S–D–A relation can yield the detailed forms of the immigration and extinction curves.

Under what conditions should $\partial^2 \log S/\partial A \partial D > 0$ hold?

Immigration rates decrease with D and with S, and may increase with A. Extinction rates decrease with A and increase with S. If $I\ (S,D,A)$ and $E\ (S,A)$ behave as products of two functions, general forms of the immigration and extinction curves are

$$E\ (S,A) = e(A)\ g(S) \qquad [1a]$$

$$I\ (S,D,A) = i(D,A)\ h(S) \qquad [1b]$$

where e, g, i, and h are functions to be specified (5). The equilibrium number of species, $\hat{S}$, on an island of area A and isolation D is found by equating the immigration rate, Eq. **1a**, with the extinction rate, Eq. **1b**:

$$0 = i(D,A)\ h(\hat{S}) - e(A)\ g(\hat{S}) \qquad [2]$$

As discussed elsewhere (5), it will always hold that $i \geq 0$, $h \geq 0$, $e \geq 0$, $g \geq 0$, $i_D < 0$, $i_A \geq 0$, $e_A < 0$, and usually that $h_s < 0$, $g_s > 0$, $h_{ss} > 0$, $g_{ss} > 0$ (so-called concave immigration and extinction curves). (Subscripts are used as abbreviations for partial derivatives: e.g., $\partial h/\partial S \equiv h_s$, $\partial^2 h/\partial S^2 \equiv h_{ss}$, $\partial^2 i/\partial A \partial D \equiv i_{AD}$.)

Partial derivatives of $\hat{S}$ may be obtained by differentiating Eq. **2** and solving

$$\partial\hat{S}/\partial A \equiv \hat{S}_A = (i_A h - e_A g)/(eg_S - ih_S) \qquad [3a]$$

$$\partial\hat{S}/\partial D \equiv \hat{S}_D = i_D h/(eg_S - ih_S) \qquad [3b]$$

$$\partial^2\hat{S}/\partial A \partial D \equiv \hat{S}_{AD} = (i_{AD} h + i_D h_S \hat{S}_A + i_A h_S \hat{S}_D + ih_{SS}\hat{S}_A\hat{S}_D - e_A g_S \hat{S}_D - eg_{SS}\hat{S}_A\hat{S}_D)/(eg_S - ih_S) \qquad [3c]$$

The assumptions listed in the previous paragraph about the signs of i, h, e, and g and their derivatives have the consequence that the denominators of Eqs. **3a–3c** and numerator of Eq. **3b** are negative, the numerator of Eq. **3a** positive, so that $\hat{S}_A$ is positive and $\hat{S}_D$ negative. In the numerator of Eq. **3c** the second, third, and sixth terms are positive, the fourth and fifth negative, and the first of indeterminate sign, so that the sign of $\hat{S}_{AD}$ cannot be specified. However, we evaluated this sign in computer

§ Conversion factors: one foot is equal to 0.305 meter; one mile is equal to 1609 meters.

trials, by taking reasonable functions for $e(A)$, $g(S)$, $i(D,A)$, and $h(S)$ (model 10 of ref. 5 plus some alternative functions), and substituting a wide range of values for all parameters of these functions. We found that $\hat{S}_{AD}$ always goes from negative at low $\hat{S}$ to positive at high $\hat{S}$.

Taking the partial derivative of $\log \hat{S}$ with respect to A and D yields

$$\partial^2 \log \hat{S}/\partial A \partial D = (\hat{S}_{AD}/\hat{S}) + (-\hat{S}_A \hat{S}_D/\hat{S}^2) \quad [4]$$

Since the first term of Eq. 4 is positive at high $\hat{S}$ and negative only at low $\hat{S}$, and the second term is always positive and is largest at low $\hat{S}$, $\partial^2 \log \hat{S}/\partial A \partial D$ might be globally positive. In fact, in computer trials using the same functions and parameter values for which we evaluated the sign of $\partial^2 \hat{S}/\partial A \partial D$, we found that $\partial^2 \log \hat{S}/\partial A \partial D$ is always positive.

Thus, the three predictions listed in the second paragraph of this paper follow not only from linear or mirror-image immigration and extinction curves, as MacArthur and Wilson showed, but also for many and perhaps all concave immigration and extinction curves. Since concave curves are the most likely ones on biological grounds (ref. 3, pp. 21–23 and ref. 5), the inequality $\partial^2 \log \hat{S}/\partial A \partial D > 0$ may be the expectation for a wide range of island faunas, provided that they are at equilibrium and that S depends mainly on A and D.¶

Effect of area on the *S–D* relation

Practical requirements for a data base adequate to explore the S–D relation are: accurately known S values for many thoroughly explored islands of varying A and D values; knowledge of which populations are montane on each island, so that elevation can be dropped as an independent variable by restricting consideration to the number of lowland populations S_{low}; tight correlation between lowland habitat diversity and A, so that habitat diversity does not appear as an independent variable; tight correlation between S_{low} and A for close islands, so that small deviations from this relation can be clearly recognized for remote islands; and moderate isolation of remote islands from each other as well as from the source islands (because "clumping" of remote islands confounds the issue by augmenting immigration and shifting the S–A relation in the direction opposite to the shift for scattered islands: see fifth paragraph below and ref. 4, especially footnote on p. 264 of ref. 4).

As discussed previously (4), the land and fresh-water birds of the Solomon Archipelago fulfill most of these requirements well. Among the 39 "central" or "non-isolated" islands of this archipelago, variation in A accounts for 98% of the variation in S_{low}, according to the equation

$$S_{low} = 34.7 + 12.08 \log A \quad [5]$$

where A is in mi^2. The 11 "remote" islands are sufficiently scattered that they have derived most of their bird populations from central islands rather than from each other. Table 1 summarizes S_{low}, D, and A values for these 11 remote islands, defined operationally (for reasons discussed in the second paragraph below) as those islands supporting fewer than 50 species and located more than 6 miles from the nearest island supporting over 50 species. For these 11 islands plus four other islands listed in Table 1 and discussed below, Fig. 1 depicts the isolation effect by plotting a ratio R, defined as the ratio of the actual S_{low} (henceforth symbolized simply by S) to the value predicted by inserting the island's area into Eq. 5 for the central islands:

$$R \equiv S/(34.7 + 12.08 \log A) \quad [6]$$

[MacArthur and Wilson (Fig. 3 of ref. 2) call this ratio "saturation", a term that has caused confusion and is best dropped.] Two conclusions follow from Fig. 1:

(*1*) The ratio R decreases with increasing isolation D, as in numerous other island studies.

(*2*) For a given isolation D, the ratio R decreases with decreasing island area: i.e., the condition $(\partial/\partial A)(\partial \log S/\partial D) = \partial^2 \log S/\partial A \partial D > 0$ does hold. Another expression of this condition is the virtual absence of isolation effects for the larger, species-rich islands with $S_{low} > 50$; this is the reason for considering these islands as "central" and for defining remote islands operationally as we did. Of the 21 islands with $S_{low} > 50$, the seven largest islands ($A > 700$ mi^2) are isolated by gaps of up to 30 mi, while the 14 smaller islands ($13 < A < 272$ mi^2) are isolated by gaps of up to 7 mi. Yet the scatter for these islands on the S–A relation (Figs. 1 and 2 of ref. 4) is small and not clearly related to island isolation, except conceivably for the slight deviation of the points for San Cristobal and Malaita below the regression line (respective R values 0.96 and 0.94, plotted as the two right-most points ● in Figs. 1 and 2 of ref. 4 and as left-most points □ of Fig. 1 of the present paper). Of the islands with $S_{low} > 50$, San Cristobal and Malaita are the two that lie furthest from another island with $S_{low} > 50$ (30 miles in both cases), and they are evidently on the border line of behaving as "remote islands".

If one assumes that the ratio R decreases exponentially with distance [i.e., $R = \exp(-D/D_0)$] and calculates an exponential "space constant" D_0 for each remote island, one finds that D_0 increases from about 9 mi for the smallest remote island, Nugu ($A = 0.0577$ mi^2), to 258 mi for Rennell ($A = 264$ mi^2) and 754 mi for San Cristobal ($A = 1193$ mi^2). Plotted as the two right-most points of Fig. 1 are the values for Ndeni and Espiritu

Table 1. Species number on remote Solomon islands

Island	S	A	D	R
Nugu	9	0.0577	6.7	0.45
Savo	37	11.8	8.4	0.78
Three Sisters	32	4.28	12.2	0.76
Mono	43	28.1	17.8	0.82
Pavuvu and Banika	45	68	28.8	0.79
Borokua	13	1.56	36.4	0.35
Nissan	29	14.3	38.9	0.60
Bellona	20	7.62	97.6	0.44
Rennell	42	264	104.4	0.66
Sikaiana	6	0.502	108.5	0.19
Ongtong Java	9	3.69	147	0.22
Malaita	69	1663	30	0.94
San Cristobal	69	1193	30	0.96
Ndeni	24	169	225	0.39
Espiritu Santo	43	1520	384	0.59

For each island, S is the number of resident land and fresh-water bird species normally occurring near sea-level; A, area in mi^2; D, distance in miles from the nearest island with more than 50 species; R, ratio of actual S to value of $(34.7 + 12.08 \log A)$ predicted for a central island of the same area. Except for Malaita, San Cristobal, and Espiritu Santo, which have elevations of 4200, 3410, and 6200 ft and have 7, 6, and 7 montane species (not included in S values of column 2), respectively, the islands in this table are under 2000 ft, and have no montane species.

¶ We conjecture, but have been unable to show, that analytical proofs of the inequalities $\partial^2 \log \hat{S}/\partial A \partial D > 0$, $\partial^3 \hat{S}/\partial^2 A \partial D > 0$, $\partial^3 \hat{S}/\partial A \partial D^2 > 0$ may be possible, given our assumptions about the signs of i, h, e, and g and their derivatives.

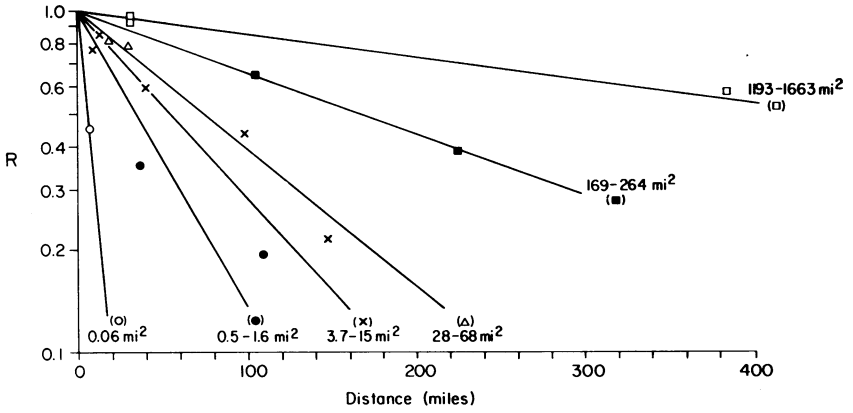

FIG. 1. Effect of isolation on bird species number of Solomon islands. Ordinate: the ratio R, defined as the actual S of a remote island divided by the value expected for a central island of the same area (Eq. 6). Abscissa: distance from nearest island with $S_{low} > 50$. The points are based on the islands listed in Table 1. Different symbols are used for islands of six different size classes, as coded on the graph. Note that species number decreases with isolation, and that this decrease is steeper for smaller islands. The lines are exponentials [$R = \exp(-D/D_0)$] fitted through the points for islands of each size class by calculating the average D_0 value.

Santo, the largest islands of the Santa Cruz Archipelago and the New Hebrides, respectively. These are the nearest archipelagoes to the east and southeast of the Solomons, respectively, and their avifaunas are largely derived from the Solomons. The calculated D_0 value of Ndeni (D_0 = 236 mi) is close to that of the similar-sized Solomon island Rennell (D_0 = 248 mi), while the value of Espiritu Santo (D_0 = 725 mi) is close to that of the similar-sized Malaita (D_0 = 469 mi) or San Cristobal (D_0 = 754 mi). Thus, the impoverishment of the Santa Cruz and New Hebrides avifaunas compared to that of the Solomons can be predicted well by extrapolating the effects of isolation observed within the Solomons themselves.

(3) Since $(\partial/\partial A)(\partial \log S/\partial D) = (\partial/\partial D)(\partial \log S/\partial A)$, Fig. 1 implies that the slope of the species-area relation for *scattered* remote islands *increases* with distance. This pattern contrasts with the pattern for *clumped* remote islands, where the slope of the S–A relation within the clumped archipelago *decreases* with the whole archipelago's isolation (4). For practical purposes, remote islands should be considered as clumped or scattered, depending on whether they have received their immigrants predominantly from each other or from central islands, respectively.

Species differ in their susceptibility to isolation effects

Distribution patterns of individual species show that distance affects colonization probabilities of some species much more than others. As background, recall that the probability of finding a given species on a particular central island (the so-called incidence J of the species) depends strongly on the island's area or total species number according to neat empirical functions $J(A)$ whose form varies characteristically among different types of species (6). Ideally, we should like to construct the whole "incidence surface" $J(A,D)$ for each species, based on the species' distribution on remote as well as on central islands. The Solomons do not contain enough remote islands of many different areas at many different distances to permit this. Calculating J on remote islands solely as a function of D would yield inconsistent patterns, since J depends strongly on A (as well as on D). Instead, we have characterized the shapes of the incidence surfaces crudely, by comparing J on two sets of remote islands [a set of 12 small remote islands ($A \leq 28$ mi^2) and a set of four large remote islands ($A \geq 68$ mi^2)] with J on two control sets of central islands selected so as to provide a similar distribution of areas. Malaita and San Cristobal are omitted from this analysis (because R is so close to 1.0 for them), but three remote islands (Gower, Ulawa, and Ramos) for which ornithological exploration is not quite complete enough to warrant use in the analysis of Table 1 are included, yielding a total of 16 remote islands considered. This analysis reveals three extreme types of overwater colonizing ability in the Solomons:

1. **Non-Water-Crossers.** In the Solomons as in New Guinea (7) and the neotropics (8), some bird species are stopped completely by water gaps of even 1 mile—not because they are flightless, and usually not because they are physically incapable of flying 1 mile, but for psychological reasons. Examples in the Solomons include the hawk *Accipiter imitator*, the owl *Nesasio solomonensis*, and 11 other species confined to the modern fragments of a Pleistocene island, Greater Bukida, which was dissected by the post-Pleistocene rise in sea-level into the present island chain from Buka to the Florida group or Guadalcanal; and six species confined to the island of San Cristobal. If we represent immigration rates I by an expression

$$I = I_0 \exp(-D/D') \qquad [7]$$

where I_0 and D' are species-specific constants and where I_0 represents the product of population size times the *per capita* rate of production of dispersing colonists, then the "mean dispersal distance" D' is virtually zero for these non-water-crossers.

2. **Superior Short-Distance Colonists.** We arbitrarily delineate a set of 32 species by the criteria of presence on at least five of the 27 central control islands, but presence on fractions of the sets of small and large remote islands that are less than 40% of the corresponding fractions for the central island sets, both for the small-island and large-island sets. Most of these 32 species are very widely distributed on the central islands—e.g., 22 of them are C- or D-tramps in Diamond's (6) terminology. The above criteria mean that these species are good at colonizing short distances but poor at colonizing long distances: i.e., in Eq. 7, I_0 is high but D' is low. For example, the *Monarcha* [*barbatus*] superspecies in the Solomons crosses short water gaps so readily that it is on 21 of the 27 central control islands, but it is on not a single one of the 16 remote islands, not even small islands at a distance of 7–8 mi nor a large island at a distance of 29 mi. In all, only four populations of these 32 short-distance colonists occur on the four remote islands beyond 105 mi. Eight of these species have not even reached the large island of San Cristobal at the eastern end of the main Solomon chain, though they are widespread in the rest of the Solomons; and four have not even reached Malaita, the next large island west of San Cristobal.

Recognition of this class of short-distance colonists partly solves the "paradox of the great speciators" (4). The low slope of the *S–A* relation for central Solomon islands implies high inter-island immigration rates. Yet this conclusion is apparently contradicted by the inter-island morphological variation at the subspecies and allospecies level that is the most famous characteristic of the Solomon avifauna and that furnishes textbook examples of the role of geographic variation in speciation (9–12). For instance, the Solomon populations of the *Zosterops* [*griseotincta*] superspecies break up into six allospecies, one of them with three subspecies; the *Myzomela* [*lafargei*] superspecies, into five allospecies, one with three subspecies; *Ninox jacquinoti*, *Rhipidura rufifrons*, and *R. cockerelli*, into seven subspecies each. This degree of differentiation seemingly requires that such species disperse sufficiently well to reach many islands, yet disperse sufficiently poorly that each population can diverge in isolation. How is this paradox to be resolved?

We first note that these "great speciators" are only a small subset of the Solomon avifauna: some species show no geographic variation throughout the Solomons or even through most of the Southwest Pacific (see fourth paragraph below). Defining "great speciators" as species represented by at least five distinct subspecies or allospecies in the Solomons, one finds that only 13 of the 106 widespread lowland species of the Solomons fit this definition. It then turns out that 10 of these 13 great speciators belong to the set of short-distance colonists, although the short-distance colonists constitute only 30% of all widespread lowland species.[‖]

Two alternative interpretations of this correlation can be suggested. First, the great speciators might have colonized many central islands during Pleistocene periods of low sea-level, when inter-island water gaps were narrower than today. When sea-level rose and widened the gaps, the distances even between the central islands would have become too great for these short-distance colonists to cross, and their populations diverged in isolation. The distances to the remote islands were too great for most of these species even at Pleistocene times of low sea-level. Second, some of the great speciators may have gone through colonization cycles (9, 11). That is, they may have had past phases of higher immigration rates and dispersal distances, enabling them to reach many islands. Subsequently they lost much of their dispersal ability, differentiated, and disappeared on small islands that have high faunal turnover and that are too remote to recolonize, given the present dispersal ability of these species. This interpretation is suggested by the fact that several of the great speciators (*Myiagra ferrocyanea*, *Pachycephala pectoralis*, *Rhipidura rufifrons*, and *Halcyon chloris*) are represented on archipelagoes thousands of miles from the Solomons by very distinct subspecies or allospecies, although the first three of these species are absent from most "remote" Solomon islands only 6–147 miles from other Solomon islands. The few remote Solomon islands on which these three species occur are mainly large islands, as expected if faunal turnover had differentially erased their formerly more widespread populations on smaller islands with higher extinction rates. Other indications of greater dispersal in the past are that 11 of the 13 great speciators are widespread in the Bismarck Archipelago, which is separated from the Solomons by a 107 mi water gap that was virtually unchanged in width even at Pleistocene times of low sea-level; and that 10 of the 13 great speciators are on the Admiralty island group, whose distance of 170 miles from the colonization source of New Guinea was only slightly reduced in the Pleistocene.

Two other characteristics of the great speciators besides short-distance colonizing ability may be relevant to their proneness to differentiate. First, survival of an isolated population long enough for it to differentiate requires low probability of extinction, and extinction rates decrease with increasing population size. In agreement with this requirement, all of the great speciators are common birds, and they include almost all of the half-dozen most abundant bird species of the Solomons. If a species colonized rarely (low I_0 in Eq. 7) but went extinct even more rarely, so that a high fraction of islands were occupied at a given time, then the species would tend to be a great speciator regardless of its D' value, because of long population survival and little gene flow from the colonization source. Second, the more readily a species alters its habitat preference and other niche parameters in response to altered competition, the more likely are isolates of the species to diverge morphologically because of the different selective forces associated with different niches. At least half of the great speciators do show conspicuous inter-island niche shifts (13).

3. **Superior Long-Distance Colonists.** We further delineate a set of 18 species by the criterion of presence on fractions of the small and large remote island sets that are greater than 50% of the corresponding fractions for the central island sets, both for the small-island and large-island sets. This criterion means that these species are good at colonizing long distances as well as short distances: i.e., in Eq. 7 I_0 and D' are both high. For example, the heron *Egretta sacra* occurs on every known remote island of the Solomons as well as on almost all other tropical Southwest Pacific islands east to the Pitcairn group, which is 5000 mi east of the Solomons and is the most remote Pacific island group with any land birds at all. Of these 18 long-distance colonists, 12 are widespread on central as well as remote Solomon islands: 10 are *D*-tramps, and two *C*-tramps in Diamond's (6) terminology. The other six are supertramps, species that are even more widespread on remote than on central islands or are even absent from central islands, because of competitive exclusion (6).

Eight of the 18 long-distance colonists reach Samoa or more remote islands of Polynesia, 1700–5000 mi from the Solomons. Correlated with their high inter-island immigration rates, 14 of the 18 long-distance colonists show no geographical variation throughout the Solomons, and four of the eight that reach Samoa are represented even there by the same subspecies as in the Solomons.

Naturally, the ratio of long-distance colonists to short-distance colonists on an island increases with isolation in the Solomons. The ratio also increases with decreasing area, and this increase is steeper for remote than for central islands. That is, $\partial \log S/\partial A$ and $\partial^2 \log S/\partial A \partial D$ are more positive, and $\partial \log S/\partial D$ more negative, for the short-distance colonists than for the long-distance colonists.

Lack's interpretation of the effect of *D* on *S*

Although most biogeographers attribute the decrease in island species number with distance primarily to the decrease in immigration rates with distance, Lack (14–17) has advanced a different interpretation. He noted many cases in which individuals of mainland bird species that do not breed on an island have nevertheless been recorded from the island as vagrants or migrants. From these cases Lack drew two conclusions: (*1*) Since at least some mainland bird species demonstrably can reach the

[‖] The 13 great speciators, with those that are short-distance colonists denoted by asterisks, are * *Accipiter novaehollandiae*, * *Ninox jacquinoti*, * *Ceyx lepidus*, *Halcyon chloris*, * *Coracina lineata*, * *Rhipidura rufifrons*, * *R. cockerelli*, * *Monarcha* [*castaneiventris*], * *M.* [*barbatus*], * *Myiagra* [*ferrocyanea*], *Pachycephala pectoralis*, *Zosterops* [*griseotincta*], *and* * *Myzomela* [*lafargei*].

island, most mainland bird species presumably can reach the island. (2) If a species has been recorded from an island as a vagrant or migrant, this proves that difficulties of reaching the island cannot be the reason why the species fails to establish a breeding population. For example, in discussing the Canary Islands, Madeira, and Azores, which lie in the Atlantic Ocean about 60, 500, and 900 miles from Africa, respectively, Lack points out that respectively 65, 69, and 50 mainland breeding species that do not breed on these islands nevertheless have been recorded from them (as vagrants or migrants). Lack then reasons, "Hence difficulties of dispersal seem excluded for at least most birds" (i.e., as the reason for their failure to have insular breeding populations) (ref. 14, p. 197; cf. also ref. 14, pp. 196, 199, 200, 201, 205, and 207; ref. 15, pp. 238, 241, and 269; ref. 16, pp. 331, 333, 334, 335).

Lack's two conclusions are both wrong for reasons that are fundamental to the understanding of island biogeography. First, inference of adequate dispersal ability of species A from dispersal records for species B involves the tacit assumption that species do not differ greatly in dispersal ability. But species differ enormously in dispersal ability, not only in the Solomon avifauna but also in any other fauna or flora. A water gap that scarcely affects the immigrant flux of one species may reduce the flux of another species to practically zero, depending on the respective dispersal distances D' of the species. Second, Lack's view of immigration is an all-or-none one, in which only an immigration rate of zero suffices to prevent colonization, while any non-zero immigration rate is taken to mean that dispersal barriers are insignificant. But there is in fact a continuous relation between *rate* of immigration and *probability* of successful colonization. When some immigrants of a particular species reach a particular island, their probability of establishing a breeding population depends not only on systematic factors (e.g., ecological suitability and competitive effects as discussed by Lack), but also on innumerable stochastic factors (e.g., whether the immigrants include individuals of different sexes, whether an accident destroys the immigrants while the breeding population is still small, whether conditions at the particular moment and site of immigration are suitable, etc.). For any given set of systematic factors, the cumulative probability that the stochastic difficulties will be overcome increases with the immigration rate. Thus, dispersal records for species B do not prove that dispersal problems are negligible for species B, no less for species A.

As an alternative to the MacArthur-Wilson equilibrium theory of island species number, Lack postulated "ecological impoverishment" to explain the effect of isolation: more remote islands support fewer species because they (supposedly) have fewer types of resources. This may be a significant amplifying factor for taxonomic groups for which a resource consists of a single species of some other taxonomic group: e.g., phytophagous insects, which are often tied to a single plant species and which should for this reason (as well as for the reason of lower immigration rates) be less diverse on more remote islands with fewer plant species. Bird species, however, are rarely confined to a single prey taxon as a resource but instead are "switching" predators that utilize broad resource types, such as insects or fruit within a certain range of sizes and hardness in habitats defined by a certain range of foliage distributions. The diversity of these broad resource types probably decreases much less with distance than does taxonomic diversity of resources, and for many categories of bird resources may not change with distance at all. We therefore doubt that "ecological impoverishment" contributes significantly to isolation effects on bird species number.

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