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IN THE DARWIN FINCHES

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In this paper we use multiple-regression analysis to consider the general evolutionary problem of the relative importance of the various factors governing the proliferation of related subspecies or species on member islands of an archipelago. From this quantitative analysis of the relation of isolation to endemism and sympatry¹ in the Darwin finches, deductions are made concerning (i) the location within the Galápagos Archipelago of insular sites of origin of the species and (ii) whether or not these sites are also the ones where the remarkable, external morphological divergences characteristic of the group occurred. Together these considerations constitute a reinvestigation of factors underlying the processes of species multiplication and differentiation within an archipelago, and it is hoped that this will encourage students of other groups of organisms to make comparable comparisons and determine if our generalizations are universally applicable.

For the Darwin finches (Geospizinae), which have undergone a moderate, adaptive radiation² within the strongly isolated complex of the Galápagos Islands, we have found it useful to ask the question: Why, in this bird group of restricted distribution,

is there a tendency for many species and few endemic subspecies to occur on some islands, and for few species but more endemics to occur on other islands (see fig. 1)? Explanation of the negative relation (correlation coefficient or $r = -0.60$) between insular numbers of species and insular numbers of endemic subspecies relates to the evolutionary problem cited. Under various guises, the problem has been taken up by others, with Ridgeway (1896), Swarth (1931, 1934), Lack (1947), and Bowman (1961) being major references to the topic.

We seek in the present study of the Darwin finches an evaluation that is more statistically oriented than is usual for such problems (cf., however, Kramer and Mertens, 1938). Our determination of partial-regression coefficients by the method of least squares involves estimation of the "partial" influences on total insular numbers of either species or endemic subspecies of the following four factors: insular area; insular numbers of land plant species; insular isolation as measured by distance from nearest island; and insular isolation as measured by distance from Indefatigable Island located in the central archipelago area.

PRESUPPOSITIONS

In dealing with determinants of endemism and sympatry for land-dwelling groups radiating within an archipelago, there are undoubtedly many theoretical approaches; it is obvious that numerous factors (historic, geographic, topographic, ecologic, genetic, accidental, etc.) need to be taken into consideration. Among these, the fundamental importance of geographic or extrinsic isolation as a prerequisite for differentiation to the level of the endemic

¹ The term sympatry (*sensu stricto*) refers to geographic overlap of breeding distributions of members of the same genus (Mayr, 1942). Since our study demands numerous references to numbers of related species (i.e., consubfamilial but not necessarily congeneric species) on individual islands, we use, for sake of brevity in the present paper only, sympatry as a general term to denote the occurrence on an island of more than one presumably phylogenetically related species.

² Presumably from one species there have arisen 13 or 14 species of divers ecological specializations (cf. Darwin, 1859; Lack, 1947).

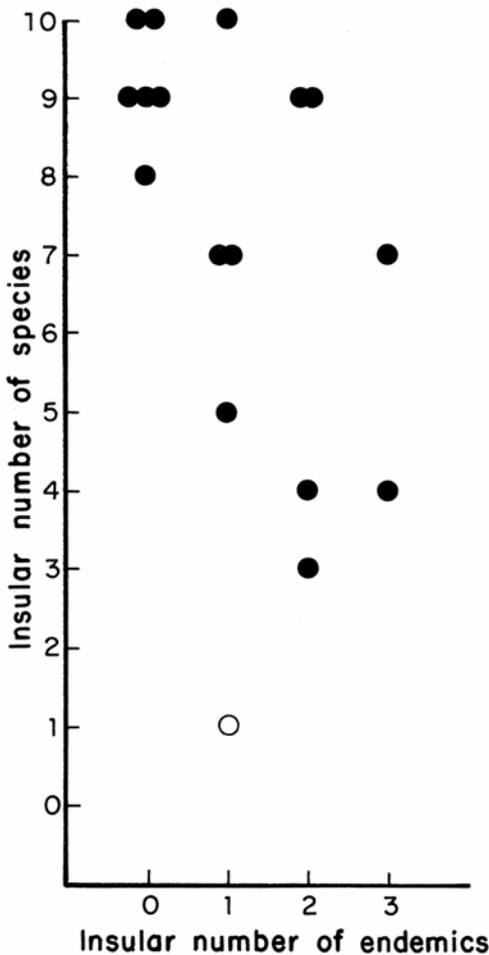


FIG. 1. Inverse relation between insular numbers of species and endemic subspecies for the Darwin finch faunas of 16 islands in the Galápagos Archipelago. The open circle represents the single endemic species found on Cocos Island some 600 miles to the northeast of the archipelago.

subspecies or species is now well understood (cf. Mayr, 1959, 1963). Furthermore, it is generally recognized that a common conceptual difficulty for such analyses involves the weighting and assessing of the relative importances of the independent or interdependent factors which contribute to the dependent variables studied—in our case, insular numbers of species and endemic subspecies. The results here reported indicate that multiple-regression analysis is a valuable

technique for avoiding such a difficulty (cf., e.g., Kramer and Mertens, *op. cit.*; Huntington, 1952; Moreau, 1957; MacArthur and MacArthur, 1961).

For clarity in presentation only, we divide our views on the importance of geographic isolation for regulation of insular endemism and sympatry into two inferential generalizations. These constitute the major theoretical presuppositions of our study; they are common knowledge to students of zoogeography and speciation theory.

First, normal biological dispersal tendencies account for and permit both the establishment of new isolates and the expansion of breeding distributions. In terms of distance from parental sources and of utilization of adjacent but discontinuously connected areas (e.g., island chains), it seems likely that geographic isolation favors endemism but retards extension of breeding ranges. In other words, chances for colonization of one island from another may be expected to decrease as the distance between the islands increases; at the same time, chances for the colonizers to differentiate as endemics are expected to increase as the isolation distance increases (see fig. 2).

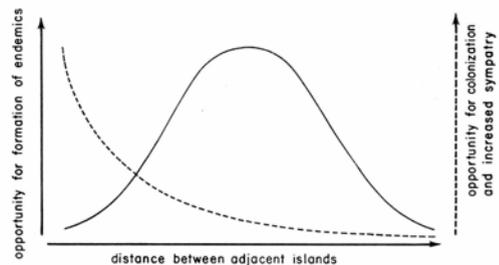


FIG. 2. Schematic diagram for the hypothesized interrelations of opportunity for colonization and opportunity for formation of endemic subspecies in relation to varying distances between two imaginary islands between which dispersal and species formation is occurring. Here it is assumed (i) that the dispersal curve is one representing the random occurrence of isolated events in a continuum as predicted by a Poisson distribution and (ii) that the curve for production of endemics is estimated by a Gaussian distribution.

Second, it seems safe to generalize qualitatively that on the average the greater the exchange of individuals between two islands, the greater the opportunity for genetic swamping between them, and thus the less likely the differentiation of isolates, even though here there are potentially greater chances for insular interchanges of species (hence, increased sympatry or numbers of related species on islands close to one another). Finally, if the distance between two islands is too great, no colonization, and hence no endemism, will occur.

On these grounds, our presuppositions predict for the Darwin finches radiating within the Galápagos Archipelago the observed negative association (fig. 1) between insular numbers of species and insular numbers of endemic subspecies. Such an association, then, might be considered a *result* of a pattern of dispersal and isolation wherein (i) more isolated islands are in a situation favoring increased endemism and reduced sympatry because of decreased dispersal (hence reduced swamping) and (ii) less isolated islands are in a situation favoring increased sympatry and decreased endemism because of greater dispersal and the resulting operation of the swamping effect (see Mayr, 1954).

Thus, we hypothesize that opportunity for colonization among islands is a reflection of the organisms' dispersal curves following a one-sided unimodal curve (a Poisson distribution curve?; cf., however, Johnston, 1956, 1961), and that opportunity for formation of endemics is a reflection of geographic isolation following a two-sided unimodal curve (a Gaussian curve?). Such ideas are graphed semi-quantitatively in fig. 2. They represent only one of several models which satisfy the two presuppositions noted above, and it is clear that the matter is in need of a more rigorous, analytical treatment.

METHODOLOGY AND SELECTION OF FACTORS

In selecting factors which might influence degrees of sympatry and endemism in

the Galápagos Archipelago, we have tried to select (table 1), from the limited data available for each of the islands, that which can be expected to test evolutionary generalizations or speculations currently available. About this we are reminded of Slobodkin's suggestion (1961) for the development of a predictive general theory for community ecology: that is, that seemingly plausible, alternate hypotheses be tested for their respective powers to predict known generalizations, and that the less valuable ones then be discarded or de-emphasized. Similar comments should hold true for attempts to establish predictive theories in zoogeography and speciation theory (see Hamilton and Rubinoff, 1963).

Noting, nevertheless, that our analysis can provide results of no greater meaning than that with which the variables or factors are selected and measured, our chosen factors are described as follows:

Insular area in square miles (X_1).—If the data (Preston, 1962) for this variable for the Galápagos Islands are plotted in a scatter diagram against insular numbers of geospizid species, a positive association ($r = +0.38$) is observed. Essentially no association ($r = -0.09$) is observed for the relation between the variable and insular numbers of endemic subspecies. It is generally accepted that an increase in insular area reflects directly increases in amplitudes of topographic, plant, and habitat variations, and thus directly indexes biotic diversity. Also, the greater the size of an island, the greater the "target surface" for dispersing pioneers, and this may be another aspect of increased insular area which promotes the likelihood of colonization and increase in numbers of sympatric species. Furthermore, insofar as numbers of related species per island are concerned, one might argue that larger islands, with greater topographic diversity, offer greater opportunities for isolation and speciation within islands than do smaller islands. This, then, might also result in a positive association between area of island and numbers of related species

TABLE 1. Basic data† for a multiple-regression analysis of insular numbers of geospizid species and endemics

Island	Number of geospizid species		Number of endemics		Area of island		Number of land plant species		Isolation		Predicted values‡ for the Y 's	
	$-Y_1$	$(\hat{Y}_1)^*$	$-Y_2$	$(\hat{Y}_2)^*$	$-X_1-$	$-X_2-$	$-X_3-$	$-X_4-$	$-\hat{Y}_1-$	$-\hat{Y}_2-$		
Culpepper	4	(4)	2	(2)	0.9 sq. mi.	7 species	21 mi.	162 mi.	4.3	1.6 (1.7)		
Wenman	5	(5)	1	(2)	1.8	14	21	139	4.9	1.6 (1.7)		
Abingdon	9	(7)	2	(1)	20.0	119	18	75	6.5	1.4 (1.4)		
Bindloe	7	(7)	1	(1)	45.0	47	18	54	7.0	1.4 (1.4)		
Narborough	9	(7)	0	(0)	245.0	80	3	59	7.1	0.1 (0.1)		
Albemarle	10	(9)	1	(0)	2,249.0	325	3	17	9.2	0.2 (0.1)		
Tower	4	(6)	3	(2)	4.4	22	29	58	5.8	2.4 (2.4)		
Hood	3	(6)	2	(2)	18.0	79	28	55	5.9	2.3 (2.3)		
Chatham	7	(6)	3	(2)	195.0	306	28	42	6.2	2.4 (2.3)		
Charles	9	(6)	2	(3)	64.0	319	30	31	6.2	2.5 (2.5)		
Jervis	9	(9)	0	(0)	1.9	42	3	15	9.2	0.2 (0.1)		
James	10	(9)	0	(0)	203.0	224	3	12	9.3	0.2 (0.1)		
Barrington	7	(8)	1	(1)	7.5	48	11	10	8.4	0.9 (0.8)		
Duncan	9	(9)	0	(1)	7.1	103	7	6	9.0	0.5 (0.4)		
Indefatigable	10	(10)	0	(0)	389.0	193	1	0	9.7	0.0 (0.1)		
Seymour	8	(10)	0	(0)	1.0	52	1	1	9.7	0.0 (0.1)		

† Y_1, Y_2, X_4 from Bowman (1961); X_1, X_2 from Preston (1961); X_3 computed from map in Bowman (*op. cit.*). For background of X_2 , see also Stewart (1911), Kroeber (1916), and Svenson (1946).

* In parentheses, after the observed Y 's, are given for comparison the rounded, predicted values (\hat{Y}).
 ‡ Calculated from multiple-regression equations (table 3) which utilize only X_3 and X_4 (see text). For \hat{Y}_2 , values are given by the equation $-0.1 + 0.089X_3 - 0.001X_4$ and then, in parentheses, by $-0.2 + 0.09X_3$ (see table 3).

(cf., Dobzhansky, 1957; Preston, *op. cit.*).

Floristic diversity as measured by number of plant species (X_2).—The influences of this factor would seem to be comparable in part to those postulated for the preceding, and the association (data from Preston, *op. cit.*) between this factor and numbers of species is a positive one ($r = +0.55$); the association between the variable and numbers of endemics is negative ($r = -0.18$). For birds, on an *a priori* basis, the influence of floristic diversity might be considered to be an important factor in the "environmental opportunity" favoring establishment of pioneer populations. While number of plant species is probably a poor index of that to which birds respond in their immediate environments (Pitelka, 1941; MacArthur and MacArthur, *op. cit.*), it is the best such measure available to us at present.

Isolation as measured in terms of shore-to-shore distance between nearest island (X_3).—We select this factor (measure-

ments taken from Bowman's 1961 map) because it seems the best measure of geographic isolation according to our presuppositions (see above and fig. 2). This factor is moderately, negatively associated ($r = -0.69$) with numbers of species and strongly, positively associated ($r = +0.91$) with numbers of endemics.

We discovered the strong correlation between variation in insular number of endemic subspecies and variation in distance from the nearest geospizid-inhabited island while investigating the factual basis for Bowman's criticism (1961) of Lack's thesis (1947) that the more isolated islands of the archipelago tend to have a greater percentage of endemic geospizid subspecies (i.e., "peculiar forms") than the less isolated ones. The bearing of our findings on this argument is presented below (see p. 395 and p. 398).

Isolation as measured by shore-to-shore distance from Indefatigable (X_4).—This factor is negatively associated ($r = -0.65$)

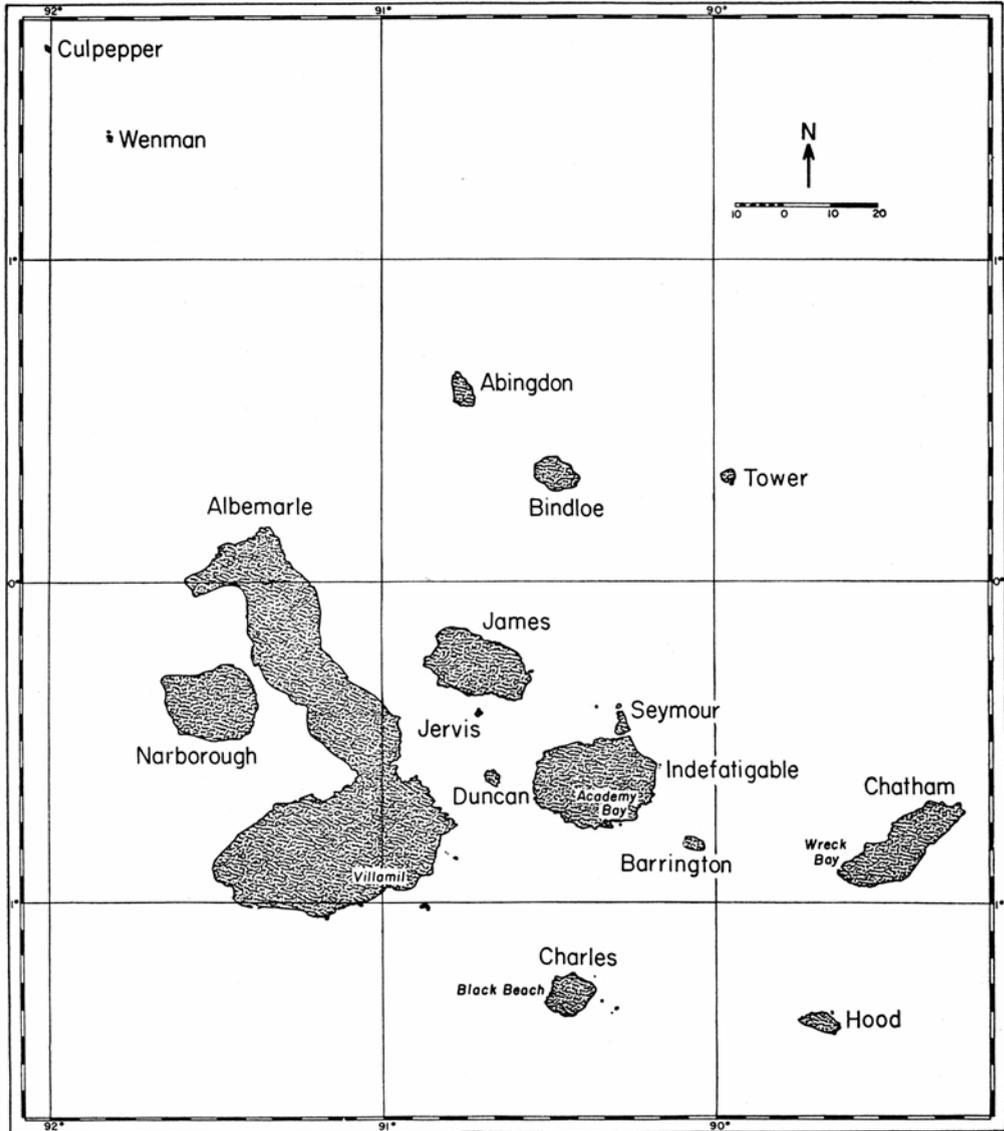


FIG. 3. Map of the Galápagos Archipelago, showing the major islands inhabited by the Darwin finches (from Bowman, 1961).

with insular numbers of species. We use it here for two reasons: First, it was used by Bowman (*op. cit.*) to criticize Lack's thesis cited above. It is unfortunate that Bowman presented his data for the relation between this measure of isolation and numbers of endemics in a table and not by a scatter diagram. There is a weak, posi-

tive association ($r = +0.44$) between Y_2 and X_4 . Accordingly, we suggest that Bowman's data alone might be considered as supporting Lack's less quantitatively based contention. By multiple-regression analysis, we thus test the value of Bowman's measure (X_4) of isolation against ours (X_3) for predicting insular numbers

TABLE 2. Initial calculations for regression coefficients listed in table 3*

$\Sigma Y_1 = 120.0$	$\bar{y}_1 = 7.5$	$\Sigma Y_1^2 = 982.0$
$\Sigma Y_2 = 18.0$	$\bar{y}_2 = 1.1$	$\Sigma Y_2^2 = 38.0$
$\Sigma X_1 = 3,451.6$	$\bar{x}_1 = 215.8$	$\Sigma X_1^2 = 5,355,558.08$
$\Sigma X_2 = 1,980.0$	$\bar{x}_2 = 123.8$	$\Sigma X_2^2 = 435,560.7$
$\Sigma X_3 = 225.0$	$\bar{x}_3 = 14.1$	$\Sigma X_3^2 = 5,047.0$
$\Sigma X_4 = 736.0$	$\bar{x}_4 = 46.0$	$\Sigma X_4^2 = 67,496.0$
$\Sigma Y_1 X_1 = 33,276.7$	$\Sigma Y_2 X_3 = 418.0$	$\Sigma X_3 X_4 = 14,433.0$
$\Sigma Y_1 X_2 = 17,033.0$	$\Sigma Y_2 X_4 = 1,166.0$	$\Sigma y_1^2 = 82.0$
$\Sigma Y_1 X_3 = 1,415.0$	$\Sigma X_1 X_2 = 958,428.4$	$\Sigma y_2^2 = 17.8$
$\Sigma Y_1 X_4 = 4,454.0$	$\Sigma X_1 X_3 = 17,857.2$	$\Sigma x_1^2 = 4,610,532.8$
$\Sigma Y_1 Y_2 = 112.0$	$\Sigma X_1 X_4 = 71,016.3$	$\Sigma x_2^2 = 190,543.0$
$\Sigma Y_2 X_1 = 3,107.3$	$\Sigma X_2 X_3 = 27,924.0$	$\Sigma x_3^2 = 1,882.9$
$\Sigma Y_2 X_2 = 2,466.0$	$\Sigma X_2 X_4 = 57,618.0$	$\Sigma x_4^2 = 33,640.0$
$\Sigma y_1 x_1 = 7,382.2$	$\Sigma y_2 x_1 = -776.9$	$\Sigma x_1 x_3 = -30,695.0$
$\Sigma y_1 x_2 = 2,183.0$	$\Sigma y_2 x_2 = -339.7$	$\Sigma x_1 x_4 = -87,803.3$
$\Sigma y_1 x_3 = -272.5$	$\Sigma y_2 x_3 = 164.9$	$\Sigma x_2 x_3 = 80.3$
$\Sigma y_1 x_4 = -1,066.0$	$\Sigma y_2 x_4 = 338.0$	$\Sigma x_2 x_4 = -33,462.0$
$\Sigma y_1 y_2 = -23.0$	$\Sigma x_1 x_2 = 531,169.1$	$\Sigma x_3 x_4 = 4,083.0$
$\Sigma y^2 = \Sigma Y^2 - \frac{(\Sigma Y)^2}{n}$ $\Sigma yx = \Sigma YX - \frac{(\Sigma Y)(\Sigma X)}{n}$		

* $n = 16$; for units of measurement and basic data see table 1.

of species and endemic subspecies. Second, the central area of the archipelago is an area of large islands, of relatively large numbers of finch and plant species, and of relatively small distances between islands. Thus, Bowman's measure of isolation conceivably could be associated in a positive manner with biotic diversity.

These then are our X 's or variables thought to be useful in predicting numbers of species (Y_1) or endemic subspecies (Y_2) for the Darwin finches in the Galápagos Archipelago. Insular numbers of species and endemic subspecies are taken from Bowman (*op. cit.*), who follows Swarth's taxonomic conclusions (1931). Since both Lack (*op. cit.*) and Bowman agree in most cases with Swarth's judgments on which insular populations have diverged sufficiently from their conspecific counterparts on other islands to merit designation as endemic subspecies, we believe the data for Y_2 to represent a good index to intraspecific divergences toward endemism. Incidentally, if the reader, following Wilson and Brown (1953), ob-

jects to the expression endemic subspecies, then the substantives, endemic segment or endemically differentiated population, may be used.

RESULTS

Assuming a model of fixed X 's for available data (tables 1 and 2), our results from multiple-regression analyses are summarized in table 3. Analyses of variance are given in table 4, and deviations from regression ($d_{x,y}$), representing $Y - \hat{Y}$, where \hat{Y} is set by the multiple-regression equation, are plotted against X_3 and X_4 in figs. 4 and 5.

Prediction of insular numbers of species (Y_1).—Partial-regression coefficients (p.r.c.) for the relation of the four X 's to Y_1 are $b_{y1.234} = 0$, $b_{y2.134} = 0$, $b_{y3.124} = -0.11$, and $b_{y4.123} = -0.01$. Isolation as measured by shore-to-shore distance between nearest islands (X_3) accounts (F test being significant at a probability level of 0.01) for the largest component of the variance for insular number of geospizid species, and isolation as measured by shore-to-

TABLE 3. *Partial-regression coefficients and multiple-regression equations for analysis of variance for insular numbers of geospizid species and endemics*†‡*

	For number of species (Y_1)	For number of endemics (Y_2)
Relations of X_1, X_2, X_3, X_4 to Y	$b_y 1.234 = +0.00019 = 0.$ $b_y 2.134 = +0.00351 = 0.$ $b_y 3.124 = -0.11094 = -0.11$ $b_y 4.123 = -0.01424 = -0.01$	$b_y 1.234 = +0.00010 = 0.$ $b_y 2.134 = +0.00029 = 0.$ $b_y 3.124 = +0.08201 = +0.08$ $b_y 4.123 = +0.00327 = 0.$
Relation of X_3, X_4 to Y	$b_y 3.4 = -0.10316 = -0.10$ $b_y 4.3 = -0.01917 = -0.02$ $\hat{Y}_1 = +9.8 - 0.10X_3 - 0.02X_4$	$b_y 3.4 = +0.08929 = +0.089$ $b_y 4.3 = -0.00079 = -0.001$ $\hat{Y}_2 = -0.1 + 0.089X_3 - 0.001X_4$ $= -0.2 + 0.09X_3$

* For data for the X 's and Y 's, see tables 1 and 2.

† Y_1 = no. of species; Y_2 = no. of endemics; X_1 = insular area in sq. miles; X_2 = no. of land plant species; X_3 = distance from a given island to nearest neighboring island; X_4 = distance from a given island to Indefatigable (see methods).

‡ For $b_{y3.4}$ (i.e., partial-regression coefficient calculated by least-squares estimates) read regression of Y on X_3 independent of X_4 .

shore distance from Indefatigable Island (X_4) accounts for a smaller, but also significant part of the variance for Y_1 . Insular area (X_1) and insular number of plant species (X_2), having zero p.r.c. values, account for none of the variance of Y_1 , and thus these factors *per se* may be excluded as factors of value in predicting insular numbers of the finch species. The finding of zero partial-regression coefficients for insular area and insular floristic diversity as measured only by number of land plant species indicates that no influence of either, or no interaction between the two, accounts statistically for

the variation of Y_1 . When it is noted that that the r value for Y_1 and X_1 is $+0.38$, it is probably not surprising that insular area fails to predict insular numbers of geospizid species. However, the correlation value of $+0.55$ for Y_1 and number of plant species (X_2) is moderately high, and the lack of an influence of Y_2 on X_1 is perhaps unexpected, although it appears analogous to a comparable finding by MacArthur and MacArthur (1961) in their analysis of determinants of continental variations in bird species diversity. Actually, our findings, as such, do not negate the hypothesis considered; rather,

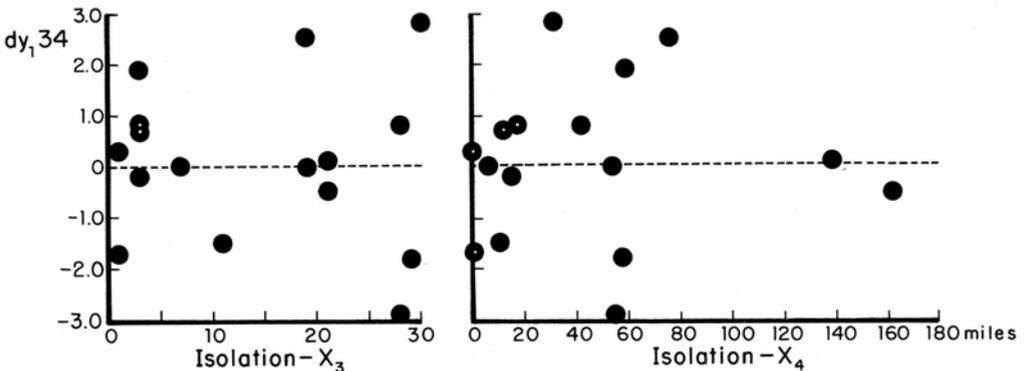


FIG. 4. Deviations from regression ($d_{y_1,34}$). Closed circles, denoting the difference between observed and predicted values (where $\hat{Y}_1 = 9.8 - 0.10X_3 - 0.02X_4$; see table 3) for insular numbers of species, are plotted against two measures of geographic isolation (X_3 and X_4 ; see text) to show the apparent linearity for the regression Y_1 on the X 's.

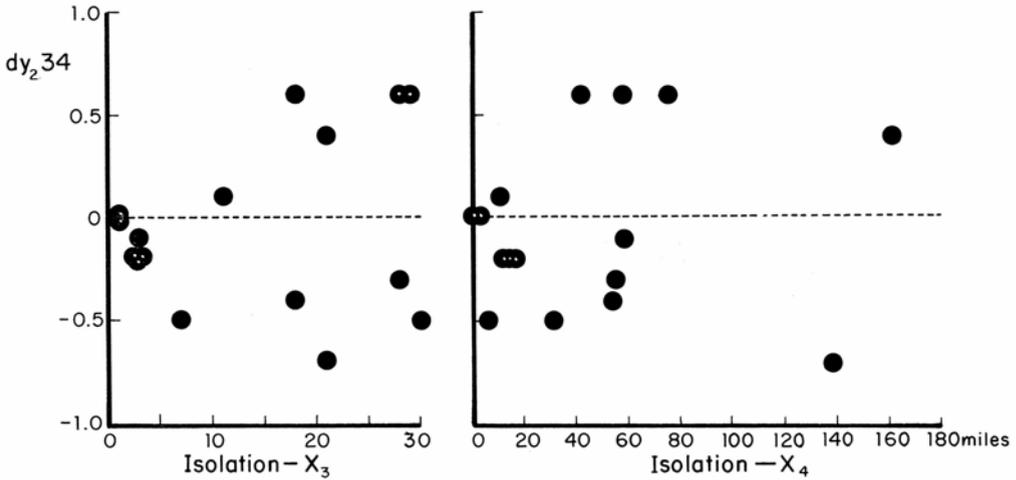


FIG. 5. Deviations from regression (d_{y_234}). Closed circles, denoting difference between observed and predicted values (where $\hat{Y}_2 = 0.089X_3 - 0.001X_4 - 0.1$; see table 3) for insular numbers of endemics, are plotted against the two measures of geographic isolation (X_3 and X_4) to show the apparent linearity for the regression of Y_2 on the X 's.

they help to narrow down the list of ways that floristic diversity is to be measured and tested.

Since all partial-regression coefficients calculated by least-squares estimates are interrelated in a way that inclusion of an unnecessary X alters the values of the other X 's, and since we find zero p.r.c. values for X_1 and X_2 , such values were determined using only X_3 and X_4 . This slightly reduced the p.r.c. value for X_3 , slightly increased the same for X_4 , and resulted in the following multiple-regression equation:

$$\begin{aligned} &\text{insular number} \\ &\text{of geospizid species} \\ &= 9.8 - 0.10 X_3 - 0.02 X_4. \end{aligned}$$

From this equation, predicted values (\hat{Y}_1) were estimated (table 1), and such permitted calculation of the deviations from regression ($d_{y,x} = Y - \hat{Y}$). These values for each island were then plotted (fig. 4) against X_3 and X_4 to see if any information could be gotten on linearity or nonlinearity for relations of X_3 and X_4 to Y_1 . As no obvious curving was noted for the spread of $d_{y,x}$ points, linearity for predictive influences of the two X 's is here assumed. Analysis of the variance of

Y_1 , using only the $b_{y3.4}$ and $b_{y4.3}$ values, reveals (i) that the two combined ($\sum \hat{y}_{34}^2$) account for a highly significant ($P < 0.01$ by F test) component of the variance of insular numbers of species, and (ii) that, when considered separately, each accounts for a component of the variance which is significant only at probability levels of 0.05 to 0.01. The significance of the separate contributions of X_3 and X_4 to the variance of Y_1 is considered below (see p. 396).

Prediction of insular number of endemics (Y_2).—The small, insular numbers of endemics for the Darwin finches (ranging from 0 to 3 endemics per island) present special problems (e.g., in rounding errors and significant figures) to an attempt to estimate their "predicted" values. Nevertheless, we have treated the data for Y_2 in the same manner as described above for Y_1 . For relations to Y_2 of X_1 , X_2 , X_3 , and X_4 , the following p.r.c. values were calculated: $b_{y1.234} = 0$; $b_{y2.134} = 0$; $b_{y3.124} = +0.08$; and $b_{y4.123} = 0$. Since bird systematists often assume that endemism is associated with some kind of ecological specialization, the finding of no relation between insular area or number of land plant species and number of en-

TABLE 4. Analyses of variance for insular numbers of geospizid species and endemics

Partition of the variance for insular numbers of species (Y_1)			
	Degrees of freedom	Sum of squares	Mean squares
Total variation	15	$\Sigma y_{34}^2 = 82.0$	
Variation due to regression*	2	$\Sigma \hat{y}_{34}^2 = 48.6$	24.3
Deviation from regression	13	$\Sigma d_{Y34}^2 = 33.4$	2.6
Test of the null hypothesis		$F \ddagger = 24.3/2.6 = 9.3$;	$P \leq 0.01$
Variation due only to X_3 †		$\Sigma y_{34}^2 - \Sigma \hat{y}_4^2 = 48.6 - 33.7 = 14.9$;	$F = 8.28$;
Variation due only to X_4		$\Sigma y_{43}^2 - \Sigma \hat{y}_3^2 = 48.6 - 39.4 = 9.2$;	$F = 5.11$;
			$P = 0.02 - 0.01$
			$P = 0.05 - 0.04$
		$b_{y_{3.4}} = -0.10$; $b_{y_{4.3}} = -0.02$	
Partition of the variance for insular numbers of endemics (Y_2)			
	Degrees of freedom	Sum of squares	Mean squares
Total variation	15	$\Sigma y_{34}^2 = 17.8$	
Variation due to regression	2	$\Sigma \hat{y}_{34}^2 = 15.0$	7.5
Deviation from regression	13	$\Sigma d_{Y34}^2 = 2.8$	0.2
Test of the null hypothesis		$F = 37.5$	$P \leq 0.01$
Variation due only to X_3		$= 15.0 - 3.4 = 11.6$;	$F = 58.0$
Variation due only to X_4		$= 15.0 - 14.4 = 0.6$;	$F = 3.0$
			$P \leq 0.01$
			$P \geq 0.05$
		$b_{y_{3.4}} = +0.089$; $b_{y_{4.3}} = +0.001$	

* $\Sigma \hat{y}_{34}^2 = b_{y_{3.4}} (\Sigma yx_3) + b_{y_{4.3}} (\Sigma yx_4)$.

† $\Sigma \hat{y}_3^2 = (\Sigma yx_3)^2 / \Sigma x_3^2$.

‡ F = variance ratio.

demic subspecies is unexpected. Again, p.r.c. values were calculated utilizing only X_3 and X_4 (the latter's $b_{y_{4.123}}$ value, although small, still being "higher" than those determined for X_1 and X_2). It is of value to note here that in shifting from four to two X 's the p.r.c. values of X_3 and X_4 increased (see Snedecor, 1957, p. 438). These values ($b_{y_{3.4}} = +0.089$ and $b_{y_{4.3}} = -0.001$) give the following multiple-regression equation:

$$\begin{aligned} \text{Insular number of endemics} \\ &= -0.1 + 0.089X_3 - 0.001X_4 \\ &= -0.2 + 0.09X_3. \end{aligned}$$

Using both equations, predicted insular numbers of endemic subspecies were estimated (table 1) for comparative purposes, and, using only the first equation, the deviations from regression ($d_{y,x}$) are plotted in fig. 4 against isolation as measured by X_3 and X_4 . Linearity of regression is again assumed for Y_2 on X_3 and X_4 , although there is some evidence, from visual examination of the spread of the $d_{y,x}$

points, that X_3 is predicting Y_2 values closer to the observed Y_2 at smaller rather than at greater isolation distances. As only a few islands comprise this "visual estimate," our conclusions on this point must be indecisive.

The relative usefulness of geographic isolation as measured by X_3 and X_4 for predicting insular numbers of species and endemics.—Since scatter diagrams show negative associations for the relation between insular number of species (Y_1) and either X_3 ($r = -0.69$) or X_4 ($r = -0.65$), the question may arise, "why is X_3 a better predictor of Y_1 than is X_4 ?" The answer seems to lie in the different functions for correlation and regression analysis. Most of us who attempt to get at speciation theory from the approach of comparative systematics tend to interpret scatter diagrams of (say) species numbers plotted against environmental data from the viewpoint of correlation theory rather than of regression or partial-regression theory. For example, although Y_1 and X_3

and Y_1 and X_4 have respective r values of -0.69 and -0.65 , their respective regression coefficients are $b_{y_3} = -0.09$ and $b_{y_4} = -0.01$,³ and it will be noted that the union of the latter two X 's in partial-regression analysis causes no further changes in their b values. The fact that X_3 and X_4 , when considered separately, have approximately equal correlation values but different regression values probably bears out what is well known in statistical theory—*viz.*, that in the seeking of factors for purposes of predicting the observed variation of another factor, it is not the correlation coefficient (i.e., $r =$ geometric mean of b_{yx} and of b_{xy} —where neither X nor Y is considered dependent on the other) which is of prime usefulness, but the regression or partial-regression coefficient (i.e., b_{yx} —where Y is considered dependent on X and not *vice versa*).

By strict standards (calculation of F or variance ratio values; see table 4), *separated* contributions of $b_{y_{3.4}}$ and $b_{y_{4.3}}$ to the variance of Y_1 are each significant, but only at probabilities of 0.05 to 0.01. The component ($\Sigma \hat{y}_3^2 = 14.9$) of the variance of Y_1 attributed to X_3 is significant for an F value probability of 0.02 to 0.01, and accordingly, X_4 , with an F value significant at the 0.05 to 0.04 level, may be considered to account ($\Sigma \hat{y}_4^2 = 9.2$) for less of the variation in insular numbers of species than does X_3 .

Thus we conclude that isolation measured by distance between nearest islands accounts negatively for a relatively large component of the variation in insular numbers of species, that isolation measured by distance from Indefatigable Island accounts negatively, but separately,

³ Unlike the correlation coefficient (r), the regression or partial-regression coefficient is not limited to values from -1 to $+1$. Also, a small value for a regression coefficient (b_{yx}) does not necessarily mean a lack of a significant, or real, regression of Y on a given X . If the observed values for the X are large in number (e.g., for our X_3 and X_4 : $\Sigma X_3 = 225.0$ and $\Sigma X_4 = 736.0$), a small b_y value for the larger might be important; decisions about this come from analyses of the variance of the Y 's (see table 4).

for a somewhat smaller part of the insular variation in species numbers, and that another part of the variation of these numbers is "unexplained." This may be due to the error inherent in our analysis, to environmental variables not considered here, or to both.

A different picture exists for the relative values of X_3 and X_4 in predicting insular numbers of endemic subspecies (Y_2). Correlation and regression coefficients here are, respectively, $r = +0.91$, with $b_{y_3} = +0.09$, and $r = +0.44$, with $b_{y_4} = +0.01$. Uniting only X_3 and X_4 , the partial-regression coefficients are $b_{y_{3.4}} = +0.089$ and $b_{y_{4.3}} = -0.001$. Going from regression to partial-regression analysis, the value for the regression of Y_2 on X_3 , independent of X_4 , stays about the same, but the value for the regression of Y_2 on X_4 , independent of X_3 , becomes reduced (table 3). This is indicated by the analysis of the variance of Y_2 (table 4), where it is found that the greater part of the variance of Y_2 is attributed to regression on X_3 and that no significant part (according to results of the F test) can be attributed to regression on X_4 .

For insular variation in number of endemics, the component ($\Sigma d_{Y_{34}}^2$) of variation unexplained by variation in X_3 and X_4 (more accurately, by variation only in X_3) is small and insignificant. For the X 's tested for the Darwin finches, therefore, variation in isolation, measured by distance between nearest geospizid-inhabited islands, accounts positively and almost completely for insular variation in numbers of endemic subspecies.

DISCUSSION

The above results are based on the hypothesis that, among four *a priori*-selected factors of the external environment of the Darwin finches, the factor or set of factors which predicts most closely observed values is the one or set which should be weighted most strongly in deductions about the evolutionary problem concerned. As such, the results suggest that geographic isolation is of overriding

importance as a factor regulating degrees of endemism and sympatry for a monophyletic group evolving within an isolated archipelago. Furthermore, the strong predictive power of geographic isolation (X_3) hints at the remarkable possibility that the production of endemic subspecies is positively related to the normal distribution of inter-island distances or to degree of insular separation. While there are a variety of conclusions or ideas which might be drawn from the results of our analysis, we believe that the following three considerations are of particular interest in the light of recent studies by others:

1. *Isolation as a factor regulating endemism.*—Lack (1947: 119) raised the possibility for these finches that a correlation exists between degree of isolation and the tendency to produce peculiar forms (= endemic subspecies). On the basis of shore-to-shore distances from each island to Indefatigable Island, Bowman (1961: 282–283) concludes that Lack is wrong on the point. Bowman's measure of isolation (our X_4) is of interest since the way it is calculated may help to explain why it gives such a poor prediction ($r = +0.44$) of insular numbers of endemics when compared to the predictive power ($r = +0.91$) of our preferred measure (X_3) of isolation. In choosing Indefatigable as a "point of reference," Bowman states (p. 281) "Indefatigable Island was chosen . . . because of its relatively large size, the numerous species of finch present, the occurrence of all vegetation zones, and its central location in the archipelago. By using this method I do not mean to imply that this or any other central island has been a center of dispersal for the finches." His sentences here quoted seem to lean more on a description of the archipelago than on the problem of defining isolation for the Darwin finches.

Isolation as here employed refers to the separation by extrinsic barriers of an isolate from its parental source in ways such that potentially inbreeding individuals are prevented from arriving frequently enough,

or in numbers sufficient, to swamp the reorganization of the isolate's gene pool (cf. Hamilton, 1962: 46–50). By Bowman's measure of isolation, Narborough (3 miles west of Albemarle) has an isolation value of 59 miles from Indefatigable, while Albemarle has an isolation value of only 17 miles from Indefatigable Island. It is apparent that Bowman's measure of isolation (our X_4) for the finches does not achieve its purpose (see Selander, 1962).

Ideally, our own measure of isolation—even though it predicts fairly accurately (table 1) insular numbers of endemic subspecies—leaves much to be desired. It fails to take into account many other factors which promote or retard the dispersal of individuals. While we believe our findings are at least qualitatively, if not quantitatively, indicative of reality insofar as such can be determined with the data now available, here is one flaw in our measure of isolation: Given a large island and a small one, the two isolated as a unit but separated from one another by a distance sufficient for species multiplication, one can reason that there is greater dispersal from the larger island to the small one than from the smaller to the larger. More individuals or potential dispersors on the larger island are here assumed. To assign each of the islands the same isolation value simply because of a common distance between them would seem to bias one island at the expense of the other. One might, however, argue that these discrepancies cancel each other out because the dispersors from the small island to the large one have a greater "target surface" than those going from the large to the small.

We believe that any attempt to quantify by linear measurements the relation between extrinsic isolation and insular numbers of endemic subspecies, for Darwin finches, must account for a component of the variance ($\Sigma_y^2 = 17.8$) of the insular numbers of endemic subspecies which is equal to, or larger, than that ($\Sigma_{y_3}^2 = 11.6$) we have found by mea-

suring isolation according to distance between nearest islands.

Our findings, then, neatly confirm Lack's 1947 contention that the more isolated islands of the archipelago tend to have greater numbers of endemic subspecies, and our statistical estimate (table 1) of this tendency results from the equation: $0.09(\text{distance to nearest neighboring island possessing a geospizid fauna}) - 0.2$. This suggests that there exists a simple relation between geographic isolation and the formation of endemics which is manifested as a normal distribution (see fig. 2).

2. *Insular sites of origin and divergence for the Darwin finches.*—Defined in terms of discovery and measurement of the causes (intraspecific, interspecific, environmental selection pressures) of the differences between contemporary members of the group, the problem of adaptive radiation in the Darwin finches is outside the scope of our study. We have instead tried to determine the factors causing and regulating multiplication of species and of endemic subspecies. The conclusion that isolation is of overriding importance makes it possible to guess when and where the species arose.

Since endemism is reduced in the central area of the archipelago, where the islands are weakly isolated, and since we argue that interbreeding and swamping resulting from increased interchanges of individuals among these islands is a major factor retarding the divergence of their populations towards endemism, we cannot defend the thesis that the species arose for the most part in the central area where the majority of their contemporary forms occur.

The species may thus be thought to have arisen in the smaller islands on the periphery of the archipelago, and to have dispersed to the central area where population sizes (and genetic variability?; see Mayr, 1954, p. 172–174) would increase in space and time and where conditions favor divergence via ecological specialization. Presumably, subsequent dispersal would in time result in reinvasion of the peripheral



FIG. 6. Proposed cycle for multiplication of species and adaptive radiation of the Darwin finches in the Galápagos Archipelago. As presented it represents the first stage, or the time period when member islands of the archipelago have vacant ecological niches and habitats available for dispersing colonizers. In later or more recent stages, colonization of outer islands would presumably be less likely because of decreased availability of niches and habitats therein. Species are thought to originate on the outer islands, where increased geographic isolation would apparently retard swamping and interbreeding. Divergence is considered to occur for the most part in the inner islands where buildup of species numbers is presumably promoted by increased rates of colonization made possible by the decreased isolation of the islands (cf., figs. 1 and 2).

islands by immigrants from the central area, and the adaptive radiation cycle would continue in a manner schematically diagrammed in fig. 6. As to sites of divergence, if one favors Lack's 1947 view that interspecific interactions associated with competition exert ultimate roles in the ecological specializations of individual species, the central area would be designated as the region of divergence, as here is where the number of species is the greatest. Moreover, if one favors Bowman's 1961 view (following ideas of Andrewartha and Birch, 1954) that ecological specializations result from intraspecific adjustments to respective insular environments, again the central area would seem to provide optimum conditions for divergence. Greater biotic diversity on larger islands and greater chances for recovery of genetic variability would be, theoretically, of prime consideration here.

This speculative scheme for the adaptive radiation of the Darwin finches needs amplification and is presented with the assumption that the stem stock of the Darwin finches first reached some single island of the archipelago. Here, we might think of the original stock passing through a "genetic bottleneck of reduced variability" (Mayr, *op. cit.*, p. 174). Whether the

stock colonized first a central island or a peripheral island is relatively unimportant. Eventually, dispersing individuals or pioneers would reach other islands and the stage would be set for the cycle of adaptive radiation, which cannot occur without multiplication of species. The first stage of the cycle (see fig. 6) would be a buildup of the insular numbers of species and of endemics, with more of the former occurring in the central Galápagos area and more of the latter being formed in the outer areas.

How far this process might continue is a question we cannot approach. We think it likely because of lack of floristic diversity that the outer islands will (or did, as the case may be) reach a saturation point for maximum numbers of breeding species before the larger, inner islands. This, if true, would necessitate modification of the radiation cycle as visualized in fig. 6, because at some later stage dispersors from the inner islands would tend not to find available habitats or niches on the outer islands.

3. *Evolutionary opportunity in relation to requirements for species multiplication and adaptive radiation.*—It is interesting to examine fig. 1 from the side (or the right-hand view), with numbers of species thus being indicated by the horizontal axis and numbers of endemics by the vertical axis. A distribution of points for insular numbers of species and of endemics is then seen in a manner which appears unimodal. We suggest that an archipelago like the Galápagos would be expected to exhibit such a distribution of points if a sufficient number of inhabited islands is available to test the point for a monophyletic group. Referring again to the side view of fig. 1, we believe that as the insular number of species increases to the left the number of endemics will tend to decrease as a result of interbreeding and swamping. The latter must be occurring to some extent if repeated colonizations (made possible by small isolation values)

are increasing insular numbers of species.⁴ Going to the other side of the figure, or the right-hand view, here, with increased isolation values, colonizations are considered to be infrequent, resulting finally in fewer species, but permitting established colonizers to become endemic subspecies as a result of freedom from genetic swamping. These trends are expected to be manifested for the most part by monophyletic groups multiplying in what we term the first stage of the adaptive radiation cycle.

The above discussion centers around the question, "what are the ideal conditions for species multiplication and adaptive radiation within an archipelago?" Although dispersal rates vary from group to group (cf. Mayr, 1942; Miller, 1942), and even though we consider such problems in the Darwin finches only from the most qualitative and speculative standpoint, our findings allow us to state that "evolutionary opportunity" for adaptive radiation is manifested when a group of organisms radiates under conditions which relate to the intersection of the two curves on the left side of fig. 2. That is, at about this point optimum conditions both for proliferation of species and the development of endemics exist because of the relation of the group's dispersal rates and the distances between various islands. For Cocos Island, away from the Galápagos Archipelago and having a geospizid fauna of only one endemic species, "evolutionary opportunity" for the group is indicated on the right side of fig. 2. Here the single species has, so to speak, the opportunity to adapt, but not to speciate. The number and arrangement of islands are other modifying factors which need to be considered, and we hope that others will take up this problem on a more quantitative basis.

⁴ That an appreciable amount of interchange of individuals is in fact occurring (or has occurred) between the Galápagos Islands is evident since not a single island known to be inhabited by the finches has less than three sympatric species (see table 1).

SUMMARY

1. Directing attention to the inverse association between insular numbers of species and endemic subspecies, the problem of the factors governing insular increases in these numbers is outlined for the Darwin finches in the Galápagos Archipelago. By the method of least squares, partial-regression coefficients and multiple-regression equations are calculated for four factors which conceivably might control insular variations in these numbers. Factors evaluated for their independent or interdependent predictive powers are: (a) insular area, (b) floristic diversity as measured by numbers of land plant species, (c) isolation as measured by distance between nearest islands, and (d) isolation as measured by distance from Indefatigable Island, located near the center of the archipelago.

2. Insular area and insular number of land plant species are found to account (p.r.c. values = 0) for none of the variation in insular numbers of species or endemic subspecies, and geographic isolation seems an overriding factor accounting for such variations. The first observation is surprising; however, numbers of plant species may be a poor index to floristic diversity. About the lack of influence of area, little can be said. The influence of insular area may be different for a monophyletic assemblage than for the total insular fauna of an archipelago.

3. For prediction of insular numbers of endemic subspecies, only geographic isolation (p.r.c. = +0.09) as measured by distance between nearest neighboring islands is of major value. An analysis of variance indicates that variation in this factor may be considered to account positively, and independently of the other factors tested, for the majority of the variation in insular numbers of endemic subspecies. This confirms Lack's conclusion (1947) and negates Bowman's differing conclusion (1961), that the more isolated islands tend to produce more endemics than the less isolated ones. The multiple-regression

equation for predicting the number of geospizid endemic subspecies on a given island is 0.09 times the distance from nearest neighboring island minus 0.2.

4. Variation in insular numbers of species is negatively accounted for by variation in geographic isolation (p.r.c. = -0.10) as measured by distance between nearest adjacent islands and, independently of the preceding, by geographic isolation (p.r.c. = -0.02) as measured by distance from Indefatigable Island. The equation predicting numbers of geospizid species for a given island is 9.8 minus 0.10 times the distances from nearest neighboring island minus 0.02 times the distance from Indefatigable. The two measures of geographic isolation leave unexplained a good-sized part of the variation in insular numbers of species, and this is provisionally attributed either to error in a statistical sense or to unknown factors not considered by this analysis.

5. The findings demonstrate the fundamental importance of geographic isolation as a factor which regulates endemism and, to a lesser degree, variations in the size of insular faunae for a presumably monophyletic bird group radiating within an isolated archipelago. Multiple-regression analysis reveals that isolation, measured as linear distance between nearest islands, is the environmental factor which predicts best the empirical observation that the inner islands of the Galápagos Archipelago tend to have more species and fewer endemics, while the outer islands tend to have fewer species but more endemics. The classic explanation for the observation would be that conditions for formation of endemics are unfavorable in the inner islands of the archipelago because of increased dispersal and colonization, interbreeding, and swamping, permitted by the decreased isolation of the islands.

6. If the explanation cited is valid, then the species of the Darwin finches are expected, for the most part, to have their respective origins in the peripheral, or non-central, islands where reduced swamping would not retard incipient speciation. This

hints at the possibility of an adaptive radiation cycle for the Geospizinae: that is, the species originate mostly in the peripheral, more isolated islands, and then disperse to the inner, less isolated islands. Here, where insular sympatry and environmental diversity are maximal, species divergences and specializations might achieve their final manifestations, either in response to related species or to particular insular environments. During the early stages of the cycle, individuals are expected to disperse repeatedly from inner to outer islands, and *vice versa*. The cycle might thus continue until the outer islands have reached ecological saturation for numbers of species.

7. On general theoretical grounds, it is *assumed* that, other things equal, opportunity for formation of endemics or incipient species is predicted by a Gaussian distribution for geographic isolation measured by the linear distance between nearest islands, and that opportunity for colonization by dispersors is predicted by such distances varying according to a Poisson distribution. The present analysis of the Darwin finches seems to support this theory, which is not new but classic. Thus, for multiplication of species and the development of endemics, the quantitative differences in geographic isolation assume an importance for individual isolates and species complementing that of the importance of geographical isolation *per se*.

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Several readers of the typescript have suggested that it might be appropriate to list the literature which—though not bearing directly on our analysis—is historically

of interest concerning the evolutionary role of geographic isolation. Thus we note our indebtedness to the previous literature, as perhaps all of our ideas on the importance and meaning of isolation have their antecedents in the writings of others. Arguments about the role of extrinsic isolation in regard to the speciation process are, of course, classic, and for a review of this we refer the reader to Mayr's discussion (1959) of the great emphasis placed on isolation as a prerequisite for speciation by M. Wagner, H. Seebohm, E. B. Poulton, and K. Jordan. In addition to those cited elsewhere in our paper, the writings of Dobzhansky (1937), Stresemann (1939), Timofeeff-Ressovsky (1939), Huxley (1942), Miller (1947), Grinnell (1943), Wright (1943), Ford (1944), Amadon (1947), Blair (1950, 1955), Stebbins (1950), Brown (1958), Carson (1959), Darlington (1959), White (1959), and Keast (1961) might be mentioned as having influenced in various degrees our thinking on the evolutionary interrelations of dispersal, colonization, and geographic isolation.

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