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ON PREDICTING INSULAR VARIATION IN ENDEMISM AND
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In previous studies we demonstrated that isolation measured as each island's shore-to-shore distance from the nearest neighboring island predicts the insular variation in number of species or endemic subspecies of Darwin Finches (Geospizinae) in the Galápagos Archipelago (Hamilton and Rubinoff, 1963, 1964). By multiple regression and variance analyses, we showed that if a variety of environmental variables such as insular area, isolation, number of land plant species, and elevation are so tested, nearest-neighbor isolation is the major predictor of the interisland variation in number of finch species or endemic subspecies. The studies cited show that correlation and partial correlation coefficients for nearest-neighbor isolation and number of endemic subspecies are statistically significant and positive in sign, whereas the corresponding coefficients for this measure of isolation and number of species are significant and negative in sign.

Our finding of positive and negative correlations for nearest-neighbor isolation varying respectively with endemics and species numbers for the Darwin Finches is in keeping with a classical conclusion in the field of evolution and speciation theory. This states that spatial isolation (proportionately?) varying with time as well as with distance is necessary for endemic differentiation, incipient speciation, and the formation of *de novo* species (cf. Mayr, 1963). Thus, theory predicts our previously reported findings for these finches: viz., the insular increase in number of endemics and decrease in number of sympatric species with increase in distance between adjacent islands, and the decrease in endemism but increase in sympatry as the water gaps between islands narrow.

In our first paper on this topic (Hamilton and Rubinoff, 1963), we discussed the limitations of our nearest-neighbor measure of isolation. It was observed that the contribution of nearest-neighbor isolation to the variance of endemics numbers is great (81%) relative to that of other environmental variables. The contribution of this measure of isolation to the variance of species numbers is also large (48%), but a sizeable component of the variance remains unaccounted for. We concluded that in predicting interisland variation in endemism or sympatry for the finches it might prove useful to determine and test environmental variables which adjust for both the number and the position of the islands in the archipelago.

It is reasonable to expect within an isolated oceanic archipelago that one island will receive dispersing individuals from the other islands in numbers which decrease in some manner with increase in isolation, and, further, that this insular receipt of dispersors will be modulated by the numbers of islands nearby or far removed (cf. Hamilton et al., 1962). The simplest quantification of this definition of isolation for a given island is the average, shore-to-shore distance to all other islands in the archipelago. We now report the strength of the environmental variable, *average isolation*, in statistical competition with *nearest-neighbor isolation* for ability to predict insular variation of either sympatry or endemism for this monophyletic avian assemblage which has adaptively radiated in the Galápagos Archipelago (Lack, 1947).

A matrix of all possible interisland isolations in statute miles is given for 16 islands of the Galápagos Archipelago in Table 1. The data are taken from a map prepared by the National Geographic Society. The numbers of finch species and endemic subspecies used in the present study are from Lack (1947) and Bowman (1961). Simple correlation and regression analyses (Fig. 1), multiple regression and variance analyses (Table 2), and the testing of significance for the coefficients are by the procedures described by Snedecor (1956). An asterisk * or asterisks ** denote(s) for the coefficients determined significant ($0.05 \geq P > 0.01$) or highly significant ($P < 0.01$) distributions. By convention, the symbol r_{yx} represents the correlation coefficient for two variables (Y, X), where neither X nor Y is designated dependent or independent. The symbol b_{yx} indicates the regression of a dependent variable (Y) on an independent one (X). For either partial correlation or multiple regression, the symbols noted are amended to $r_{yx_1 \cdot x_2 \dots}$ and $b_{yx_1 \cdot x_2 \dots}$ to indicate, respectively, the correlation between Y and X , or the regression of Y on X_1 , independent of variation of other independent variables ($X_2 \dots$). For sake of convenience in this paper, we hereafter designate dependent and independent variables as follows for their insular numbers: endemic subspecies, Y_e ; sympatric species, Y_s ; average isolation, X_a ; and nearest-neighbor isolation X_n .

Fig. 1 shows the correlations and regressions for the numbers of species and endemics respectively paired with nearest-neighbor and average isolation. It is clear that the number of endemic subspecies is more strongly correlated with nearest-neighbor isolation ($r_{en} = +0.90^{**}$) than with average isolation ($r_{ea} = +0.52^*$). The number of insular species, however, is more strongly correlated with average isolation ($r_{sa} = -0.76^{**}$) than with nearest-neighbor isolation ($r_{sn} = -0.69^{**}$). Multiple regression and variance analyses (Table 2) indicate that the major contributor to variance of number of endemics is nearest-neighbor isolation, while the major contributor to variance of species number is average isolation. The multiple regression equations are as follows:

for prediction of insular variation in number of endemics,

$$\hat{Y}_e = -0.04 + 0.002^*X_a + 0.092^{**}X_n; \quad (1)$$

for prediction of insular variation in number of species,

$$\hat{Y}_s = 11.4 - 0.037^{**}X_a - 0.074^*X_n. \quad (2)$$

TABLE 1
Isolation matrix for the 16 islands of the Galápagos Archipelago*

| Island and no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | Avg. isolation |
|----------------|---|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----------------|
| Culpepper | — | 21 | 108 | 133 | 166 | 115 | 135 | 148 | 165 | 177 | 183 | 180 | 212 | 222 | 239 | 255 | 163 |
| Wenman | — | — | 87 | 112 | 145 | 88 | 113 | 124 | 142 | 154 | 160 | 157 | 190 | 220 | 217 | 235 | 143 |
| Abingdon | — | — | — | 18 | 53 | 47 | 73 | 47 | 64 | 78 | 72 | 75 | 101 | 122 | 123 | 147 | 81 |
| Bindloe | — | — | — | — | 22 | 52 | 73 | 34 | 49 | 60 | 48 | 52 | 78 | 102 | 98 | 122 | 70 |
| Tower | — | — | — | — | — | 88 | 107 | 57 | 70 | 79 | 54 | 58 | 75 | 101 | 80 | 114 | 85 |
| Albemarle | — | — | — | — | — | — | 3 | 11 | 16 | 12 | 39 | 18 | 48 | 33 | 81 | 83 | 49 |
| Narborough | — | — | — | — | — | — | — | 35 | 45 | 50 | 76 | 60 | 93 | 82 | 126 | 130 | 80 |
| James | — | — | — | — | — | — | — | — | 3 | 16 | 20 | 12 | 11 | 30 | 75 | 90 | 34 |
| Jervis | — | — | — | — | — | — | — | — | — | 12 | 28 | 5 | 50 | 57 | 82 | 92 | 57 |
| Duncan | — | — | — | — | — | — | — | — | — | — | 27 | 7 | 41 | 42 | 73 | 80 | 61 |
| Seymour | — | — | — | — | — | — | — | — | — | — | — | 1 | 25 | 51 | 52 | 70 | 60 |
| Indefatigable | — | — | — | — | — | — | — | — | — | — | — | — | 11 | 30 | 42 | 54 | 38 |
| Barrington | — | — | — | — | — | — | — | — | — | — | — | — | — | 25 | 22 | 41 | 68 |
| Charles | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 56 | 42 | 80 |
| Chatham | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 28 | 93 |
| Hood | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 101 |

*Isolation in statute miles of each island from the other 15 islands in the archipelago. The average isolation represents the sum of each island's interisland isolations divided by 15.

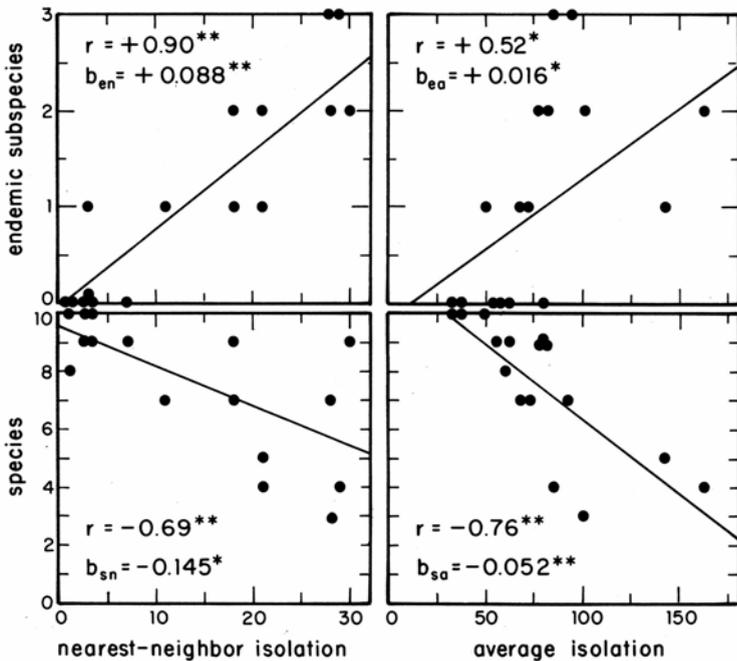


FIG. 1. Relation between insular variation in number of species (Y_s) or endemic subspecies (Y_e) and the variation in statute miles of average isolation (X_a) or nearest-neighbor isolation (X_n) for the Darwin Finches in the Galápagos Archipelago. The correlation (r) and regression (b) coefficients are given for the 16 points in each scatter diagram. The linear regression lines indicated were fitted by the following equations: $\hat{Y}_e = -0.106 + 0.088^{**}X_n$; $\hat{Y}_e = -0.16 + 0.016^{*}X_a$; $\hat{Y}_s = 9.54 - 0.145^{*}X_n$; and $\hat{Y}_s = 11.6 - 0.052^{**}X_a$.

For equation 1, the coefficient of multiple determination ($R_{an}^2 = \Sigma \hat{y}_{e\ an}^2 / \Sigma y_{e\ an}^2 = 14.58/17.75$) is 0.81 (Table 2). Of the observed interisland variation in number of endemic subspecies, 81% can thus be attributed to positive variation in the two measures of isolation. The two-way analysis of variance given in Table 2 shows that nearest-neighbor isolation is the more important contributor to $\Sigma y_{e\ an}^2$, accounting for 67 to 98.5% of this component of variance. Average isolation, however, accounts for only 1.5 to 33% of this "explained" variation. For prediction of the interisland variation in number of species, average isolation rather than nearest-neighbor isolation is the more important variable. R^2 for equation 2 is 0.66, and the two-way analysis of variance given in Table 2 shows the overriding importance of average isolation in estimating insular sympatry for the Darwin Finches.

Fig. 2 illustrates the prediction (\hat{Y}) of insular number of endemic subspecies by nearest-neighbor isolation, and of species by average isolation. The residual variation observed provides little new information, and linearity of regression is assumed. Considering the small values (0-3) manifest for insular endemism, there is little that can be concluded concerning deviations from regression on nearest-neighbor isolation. For the regression of species on average isolation, the deviations from prediction ($\hat{Y} - Y$) are essentially

TABLE 2

Analysis of variance for interisland variation in number of Darwin Finch species or endemic subspecies†

| Source of variation | Degrees of freedom | Sum of squares | Mean squares |
|--|--------------------|---|--------------|
| Total variation | 15 | $\sum y_e^2 = 17.75$ for endemic subspecies | |
| Variation due to regression on X_a and X_n | <u>2</u> | $\sum \hat{y}_{e na}^2 = 14.58$ | 7.29** |
| Unknown | <u>13</u> | $\sum d_{na}^2 = 3.17$ | 0.24 |
| | | [$F = 7.29/0.24 = 30.4$. $P < 0.01$] | |
| X_a and X_n | 2 | $\sum \hat{y}_{e na}^2 = 14.58$ | |
| Variation due to X_n alone | <u>1</u> | $\sum \hat{y}_{e n}^2 = 14.44$ | |
| Variation due to X_a after variation due to X_n is removed | 1 | 0.14 | 0.14 |
| Unknown | 13 | 3.17 | 0.24 |
| | | [$F = 0.58$. $P = > 0.05$] | |
| X_n and X_a | 2 | 14.58 | |
| X_a alone | <u>1</u> | $\sum \hat{y}_{e a}^2 = 4.81$ | |
| X_n after X_a | 1 | 9.77 | 9.77** |
| Unknown | 13 | 3.17 | 0.24 |
| | | [$F = 40.7$. $P < 0.01$] | |
| Total | 15 | $\sum y_s^2 = 82.00$ for species | |
| X_a and X_n | <u>2</u> | 54.38 | 27.19** |
| Unknown | <u>13</u> | 27.63 | 2.13 |
| | | [$F = 12.8$. $P < 0.01$] | |
| X_n and X_a | 2 | 54.37 | |
| X_n alone | <u>1</u> | <u>39.44</u> | |
| X_a after X_n | 1 | 14.93 | 14.93* |
| Unknown | 13 | 27.63 | 2.13 |
| | | [$F = 7.0$. $P = 0.01 - 0.05$] | |
| X_n and X_a | 2 | 54.37 | |
| X_a alone | <u>1</u> | <u>47.88</u> | |
| X_n after X_a | 1 | 6.49 | 6.49 |
| Unknown | 13 | 27.63 | 2.13 |
| | | [$F = 3.0$. $P = > 0.05$] | |

† Y_e = endemic subspecies; Y_s = species; X_n = nearest-neighbor isolation; X_a = average isolation. Calculations from raw data necessary for these analyses are as follows: for equations utilizing Y_e , Y_s , and X_n , alone or in combination, see Hamilton and Rubinoff, 1963, p. 393; for X_a and its combinations with the other variables, the values are $\sum X = 1,263.0$, $\bar{x} = 78.94$, $\sum X^2 = 117,549.0$, $\sum XY_e = 1,714.0$, $\sum XY_s = 8,548.0$, $\sum XX_n = 21,374.0$; $\sum x^2 = 17,850.94$, $\sum y_e x = 293.12$; $\sum y_s x = -924.50$; $\sum xx_n = 3,613.06$.

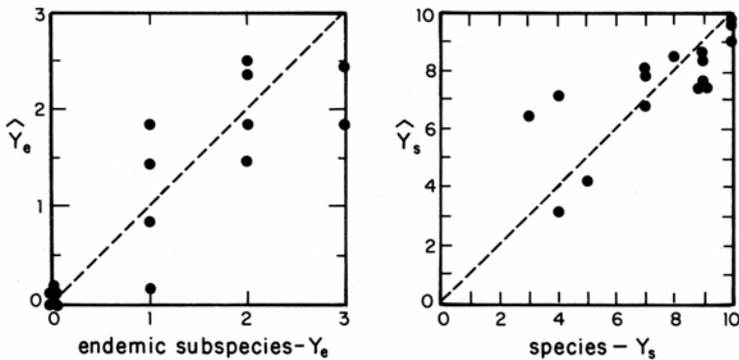


FIG. 2. A comparison of predicted (\hat{Y}) and observed (Y) values for number of endemics regressed on nearest-neighbor isolation, and species number regressed on average isolation. For the regression equation used to predict either \hat{Y}_e or \hat{Y}_s , see Fig. 1. The broken lines denote paths of perfect prediction along which predicted values (\hat{Y}) and observed values (Y) would coincide in equality. For the six values of Y_e given at zero in the left plot, the \hat{Y}_e values vary from -0.016 to 0.156 .

linearly distributed with only two insular avifaunas being overpredicted. Why the islands of Hood and Tower, possessing geospizid faunas of, respectively, 3 and 4 species, should have fewer species in comparison to other islands possessing equivalent values for average isolation is uncertain. This overprediction of Y_s for the two islands also occurs when both measures of isolation are used in multiple regression by equation 2. The reduced number of finch species on Hood and Tower may be a result of greater extinction rates associated with their relatively large average isolations and nearest-neighbor isolations (cf. Table 1), as well as with their small insular areas (see Hamilton and Rubinoff, 1963). If true, this explanation would help to account for the high proportion (0.67 and 0.75) of endemic subspecies to species manifested by their respective finch faunas. This ratio is higher for these two islands than for the other islands in the archipelago. There is now considerable evidence that extinction rates are increased on isolated islands of small size, and, further, that it is the nonendemics or recently arrived species rather than the endemics which are likely to become extinct (Snow, 1950; McArthur and Wilson, 1963; Mayr, 1965a, b; Wilson, 1965). Finally, it should be noted that prediction of number of insular finch species by either average isolation ($R_a^2 = 0.58^{**}$) or both average and nearest-neighbor isolation ($R_{an}^2 = 0.66^{**}$) leaves unexplained a significant component (0.42^{**} or 0.34^*) of the interisland variation in species number. Determination and testing of new environmental variables would be useful in this connection.

DISCUSSION

That one measure of interisland isolation should predict insular variation in endemism, while another predicts variation in sympatry or number of species occurring on individual islands in the Galápagos Archipelago is not surprising. Endemism is expected to be controlled, in part at least, by insular inter-

changes of conspecific individuals "carrying" genes which swamp or dilute the native population's adaptation to the local insular environment as a result of interbreeding of aliens with natives (cf. Mayr, 1954). Surely this interchange of conspecific individuals will be greatest for adjacent islands; and, since the spread of a new species from a single island usually will include at first the adjacent ones, the nearest-neighbor measure of isolation will index to a large degree dispersal at the intraspecific level. Furthermore, dispersal of individuals from many islands—some nearby, some far removed—can be expected to increase the number of species which occur on a given island. Average interisland isolation, then, to a large degree, will index the dispersal of individuals at the interspecific level, and presumably in this way will be useful in predicting insular variations in sympatry for the Darwin Finches.

Neither average nor nearest-neighbor isolation is of significant use in predicting interisland variation in either endemism or sympatry for the avifauna of the Hawaiian Archipelago, the islands in the Gulf of Guinea off West-Equatorial Africa, the East Indies, the islands of the East-Central Pacific, or the West Indies (Hamilton and Rubinoff, in preparation). Both for the honeycreepers (Drepaniidae) and the remaining, land and fresh-water birds in the Hawaiian Archipelago, insular area, elevation, and to a lesser extent distance from Hawaii are the predictors of species numbers and endemics. A minor exception to this is the effect of reduced nearest-neighbor isolation on the islands Molokai, Lanai, and Maui, which are 9 to 10 miles from one another. On this triad of islands there is an expected, significant reduction in endemism for both the honeycreepers and the other land and fresh-water birds (Amadon, 1950). In the Gulf of Guinea, distance from the African mainland is the major determinant of endemism (Amadon, 1953). Amadon's analysis shows that on Fernando Po, 20 miles from the African mainland, endemism is restricted to the subspecific or lower level; while on the islands farther out in the Atlantic, endemism occurs both at the specific and generic level. Among the Pacific islands, with the Hawaiian ones excluded, we find that insular area and isolation measured as distance from the major avifaunal source region (New Guinea) are the significant predictors of species abundance (cf. Mayr, 1940; Zimmerman, 1948; and MacArthur and Wilson, 1963) and endemism; with neither nearest-neighbor nor average isolation being of predictive value (Hamilton, Barth, and Rubinoff, 1964; Hamilton and Rubinoff, in preparation).

It would appear that in studies of insular endemism and sympatry, isolation should be measured separately for each archipelago in accordance with its pattern of island distributions and its particular zoogeographic position. The relative proportion of the total dispersal of individuals which is of an intra- or interarchipelagic nature is obviously a factor to be considered in such measurements. In addition, whether the avifauna considered is mono- or polyphyletic would seem to be of considerable importance. A comparison of the respective contributions of insular area and isolation to variation in species abundance in several archipelagos sheds some light on the latter

topic. Taken together, the data for seven archipelagic avifaunas (noted above) which we have examined by multiple regression analyses indicate in all *but one* that variation in insular area (which presumably indexes variation in habitat or niche diversity; see MacArthur, 1965) is the major predictor of insular number of bird species. The one exception is the Darwin Finches in the Galápagos Archipelago. Here the species numbers vary negatively and significantly with insular isolation (Fig. 1), but fail to vary significantly with insular area (Hamilton and Rubinoff, 1964). This contrasts markedly with the well-known positive species-area relations for other insular avifaunas (cf. Preston, 1962), and we surmise that the absence of a significant species-area variation for the Darwin Finches in the Galápagos Archipelago is a consequence of their monophyletic origin and perhaps recent initiation of adaptive radiation.

We suggest that the members of the original colonizing stock of finches reaching this small cluster of islands isolated in the equatorial region of the eastern Pacific were fortunate in the sense they happened on an archipelago with optimal interisland isolations in relation to their particular intrinsic habits for dispersal or straggling. In such a situation the role of isolation in regulating endemism and sympatry during adaptive radiation would be of paramount importance. Intuitively, we expect this role of isolation to be predominant during the early phase of species multiplication. We conclude that isolation is of increased importance in the regulation of endemism and sympatry in monophyletic bird groups in the initial phase of adaptive radiation, since this is consistent with the generally accepted thesis that spatial isolation of some form or kind is a prerequisite for speciation in most vertebrate organisms. Area, however, is expected to be of more importance in the regulation of such phenomena in polyphyletic avifaunas, or in relative old, monophyletic avifaunas which, having completed the species-multiplication phase of adaptive radiation, are undergoing phyletic specializations in continued adjustment to their niches.

The Hawaiian Honeycreepers are considered here to be an example of a monophyletic group which—compared to the Darwin Finches—is at an older stage of adaptive radiation, with the species-multiplication phase of adaptive radiation essentially complete. As noted above, in this avifauna interisland variations in endemism and sympatry are correlated primarily with area and elevation, and to a lesser extent with distance from Hawaii. If our interpretation of age of the adaptive radiation of the Drepaniidae is incorrect, it can be argued that, in this archipelago, isolation is of some importance in regulating insular sympatry and endemism for the group—provided the honeycreeper fauna of Hawaii is ignored (Hamilton and Rubinoff, in preparation). There, the large increase in number of endemic species on a relatively large island close to several others is probably a partial result of intrainland speciation. Dispersal between the two volcanoes of Hawaii in conjunction with double invasions from the adjacent, but smaller and ecologically less-rich, islands has probably increased endemism on the island (cf. Amadon, 1950). Our discussion emphasizes at the minimum the im-

portance of dissociating inraisland and interisland trends in speciation when analyzing the role of isolation in regulating insular endemism and sympatry.

Archipelagic avifaunas may be provisionally classified as follows: (1) monophyletic and recent (e.g., the Darwin Finches); (2) monophyletic and relatively old or specialized (e.g., the Hawaiian Honeycreepers); and (3) polyphyletic (e.g., the several avifaunas of the islands of the Pacific, the West Indies, and the Gulf of Guinea). Admitting that this classification is abstract and somewhat arbitrary, we conclude that isolation as a causal agent in controlling insular endemism or sympatry is predominant for avifaunas of category (1), of reduced or questionable importance for (2), and of minor importance for (3).

We now consider the natural regulations of endemism and sympatry in either mono- or polyphyletic avifaunas of oceanic archipelagos to be stochastic in their respective manifestations. At least for the Darwin Finches, we have demonstrated that while different measures of isolation are necessary for prediction of insular variation in number of either species or endemics, insular area *per se* is of little importance (Hamilton and Rubinoff, 1964). According to a stochastic hypothesis for such regulations, the relative proportions of chance to deterministic elements would vary from one archipelago to another, as well as from one component of the avifauna to another (e.g., mono- versus polyphyletic groups). For land and fresh-water birds occurring on islands, we visualize the chance elements as being the results of insular isolation, and the deterministic elements as stemming from the availability of insular area, or from an ecological sphere which comprises area, habitat, and niche (Miller, 1949). For the proposed stochastic regulations of production of endemics and of extent of sympatry within archipelagos, we infer from the preceding study that chance elements predominate deterministic ones (i.e., isolation > area) during the initial adaptive radiation of monophyletic groups; whereas, deterministic elements predominate those of chance (i.e., area > isolation) during colonization and speciation by polyphyletic avifaunas or during the postspeciation, phyletic specializations of monophyletic groups. This is not to say that the influences of insular area or ecology on endemism and sympatry or on species abundance are entirely deterministic. On the contrary, as area or ecologic diversity of islands decreases, the stochastically mediated process of rate of species extinction increases (MacArthur and Wilson, 1963; Hamilton and Armstrong, 1964; Mayr, 1965b).

We emphasize that the stochastic hypothesis here used is not demonstrated by our findings. Rather, we have simply assumed an hypothesis which it is hoped will subsequently be tested for its consequences, despite the crude or approximate nature of the initial formulation. The distinction thus made between chance elements associated with dispersal and isolation on the one hand, and deterministic and chance elements associated with colonization and ecology (area, habitat, niche) on the other, is at most a superficial one. For at another level of theorizing, isolation is expected to profoundly in-

fluence the dispersal to islands of the so-called deterministic, ecological elements of habitat and niche (e.g., plant and insect species), which the dispersing birds must find in order to colonize islands and establish self-maintaining populations (Hamilton, Barth, and Rubinoff, 1964; Mayr, 1965a). In conclusion, our assumption of stochastic regulations for avian endemism and sympatry in oceanic archipelagos is compatible with the equilibrium theory of insular zoogeography developed by MacArthur and Wilson (1963), Wilson (1965), and Schoener (in preparation).

SUMMARY

For interisland variation in number of Darwin Finches in the Galápagos Archipelago, endemism is predicted by nearest-neighbor isolation; and species abundance or sympatry is predicted by average isolation. Nearest-neighbor isolation is measured by distance from the nearest island, and average isolation is the average distance to all other islands in the archipelago.

The two measures of isolation are of little predictive value when tested for the avifaunas of six other archipelagos or oceanic island groupings. In these situations, area is a better predictor of species abundance or endemism; and the role of isolation appears only when measured as distance from the major avifaunal source region (e.g., New Guinea for islands of the East-central Pacific; African mainland for islands in the Gulf of Guinea). Insular isolation in these instances is, however, a relatively small contributor to variance of species number when contrasted with the greater contributions made by insular area.

That numbers of insular species and endemics are respectively predicted by average and nearest-neighbor isolation, and not by area, only in the Darwin Finches demonstrates emphatically the importance of isolation in regulating endemism and species abundance (=sympatry) in the adaptive radiation of monophyletic bird groups within archipelagos. This generalization appears valid only when the intra-archipelagic speciations are mostly between islands, and not intransland in site of origin from parental forms. It would appear to be less valid during the postspeciation, phyletic-specialization phase of radiation.

It is presumed that the natural regulations of endemism and species abundance for insular avifaunas are stochastic in process. By this hypothesis, chance elements associated with isolation are of major importance early in the adaptive radiation of monophyletic bird groups, and less important later in this radiation when deterministic and chance elements associated with ecology (area, habitat, niche) predominate.

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