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*THE ENVIRONMENTAL CONTROL OF INSULAR VARIATION IN BIRD SPECIES ABUNDANCE**

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Theory.—It can be assumed that the number of species found breeding on a given island is a resultant of (*a*) the chances of reaching the island by dispersal, and (*b*) the chances, once there, of becoming reproductively established by the finding of vacant or available ecological niches or spheres.[1] Isolation in this instance may have two roles: either a direct one which influences the probability of dispersing individuals reaching islands, or an indirect one influencing the success of any particular colonization attempt by effects on the previous filtering of species of plants and animals upon which new colonizers may be dependent for ecological support.[2] Information on the relative importance of the two facets of the colonization problem (viz., isolation and ecologic diversity) may be gained by the quantifying and testing of the influence on species numbers of various factors of the insular environment by multiple regression and variance analysis. Thus it is possible to determine the ability of an environmental variable to predict species numbers independently of variation in other parameters. It is the interaction of these variables in the natural regulation of species numbers which we seek to unravel for different phyletic groups in various geographical regions.[3–6]

Objectives of the Present Study.—That numbers of plant and animal species increase with area has long been known.[7–9] It is equally well known that isolated islands tend to have fewer species than their less isolated counterparts. For bird species in the widely separated islands of the East-Central Pacific, this phenomenon (the distance effect) has been documented by Mayr,[10,11] Zimmerman,[12] and others.[13] The positive species-area relation and the negative species-isolation relation are in opposition to one another (cf. data of Table 1 with Fig. 1). Since within archipelagos small islands tend to be more isolated than larger ones, the question arises as to whether the distance effect reflects the operation of isolation *per se* or the influence of reduced area (= reduced ecologic diversity) or both. This is our point of departure for testing the theories of Preston[14, 15] who has built a comprehensive hypothesis[15] around the possibility that insular species-area relations for plants and animals are described by a log-normal equation whose first approximation is

TABLE 1

UNIFACTORIAL ANALYSES OF INSULAR VARIATION IN BIRD SPECIES NUMBERS*

	Model I		Model II	
Archipelago	r	b	r	g
Species-area relation (YX_1)				
East Indies:	0.85	0.0015	0.94	0.38
East-Central Pacific:	0.94	0.0016	0.85	0.55
West Indies:	0.78	0.0016	0.96	0.24
Species-elevation relation (YX_2)				
East Indies:	0.82	0.0219	0.85	0.82
East-Central Pacific:	0.69	0.0160	0.72	0.06
West Indies:	0.49	0.0058	0.10	0.06
Species-isolation relation (YX_3) (distance from source)				
East Indies:	−0.31	−0.1576	−0.53	−0.23
East-Central Pacific:	−0.45	−0.2910	−0.75	−0.51
West Indies:	−0.003	−0.0007	0.04	0.03
Species-isolation relation (YX_4) (distance to nearest island)				
East Indies:	−0.33	−0.8203	−0.56	−0.51
East-Central Pacific:	−0.01	−0.0116	−0.79	−0.85
West Indies:	0.26	0.4624	0.28	0.38
Species isolation relation (YX_5) (area adjacent island)				
East Indies:	−0.51	−0.0002	−0.31	−0.16
East-Central Pacific:	−0.01	−0.0001	0.59	0.25
West Indies:	0.59	0.0010	0.69	0.16

* Model I = $y = bx$, where $x = x^z$ with $z = 1$; Model II = $y = bx^z$, with $z \neq 1$.
r = Correlation coefficient (for Model II, of logarithms of X and Y values); b = regression coefficient for Y on X; z = exponential coefficient (Model II).

$$\hat{Y} = 10\,X^{0.27}, \qquad (1)$$

or

$$\log \hat{Y} = 1.0 + 0.27 \log X, \qquad (2)$$

in which Y = species numbers (dependent variable) and X = area (independent variable).

Preston considers insular biotas as "isolates" in comparison to continental "samples" of equivalent area, but of greater species/individuals ratios. He derives equation (1) from theoretical considerations of the relation of total individuals to

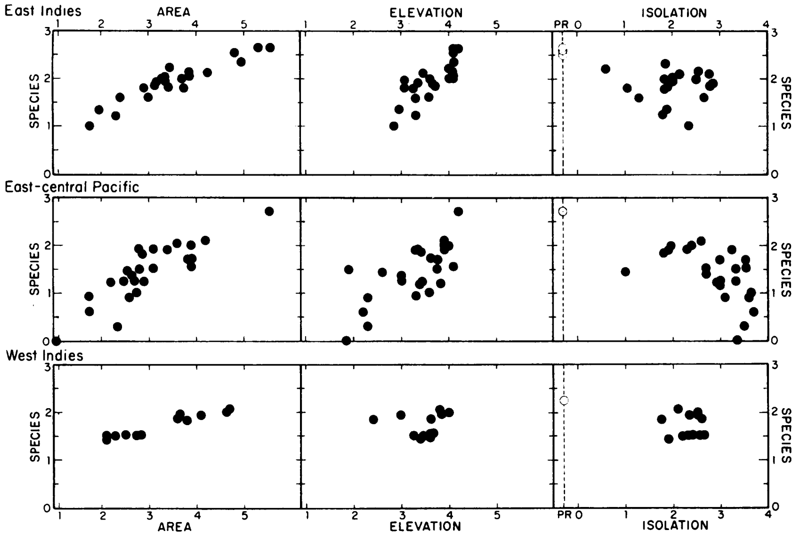

FIG. 1.—Scatter diagrams for log–log plottings of insular numbers of breeding bird species and three environmental variants for three oceanic archipelagos. Logarithms of species numbers (Y) are plotted against logarithms of area (X_1), elevation (X_2), or isolation (distance from major avifaunal source, X_3). For East Indies, source region (point of reference = PR) is Sunda Shelf; for East-Central Pacific, New Guinea; for West Indies, nearest American mainland point.

total species in the "universe." In tests of species-area relations for seven vertebrate and plant groups of insular distribution, he finds[15] an array of species-area coefficient values (z) by equation (4) (see below) of 0.239 to 0.333 with a mean of 0.285. He considers the observed mean to be in satisfactory agreement with his theory [eq. (1)].

As Preston's theory raises the remarkable possibility of a constant relation between insular area and species numbers for all plant and animal groups, there is a definite need for the testing of the validity of his equation for various groups of organisms. Below, we summarize the results of a multifactorial study of the environmental control of the bird species abundance on the islands of three separate archipelagos. The archipelagos whose avifaunas (i.e., land and fresh water bird species)[16] are considered are: the East Indies (22 islands), the East-Central Pacific (25 islands), and the West Indies (12 islands).[15]

Methods and Statistical Techniques.—The following results are derived by a computer study in which multiple regression and variance analysis were carried out by the "SLURP" method ("statistical laboratory utility regression package") of the Harvard Computing Center. Variance (= coefficient of multiple determination = R^2)[17] for Y for each estimating equation is derived by least squares estimates and is analyzed by calculations of the contribution to R^2 of each independent variable (X), independent of other X's included in the analysis.

In the present paper, we consider only predictions by arithmetic-to-arithmetic and logarithmic-to-logarithmic models. In single regression form, the models (to be hereafter designated I and II) are:

$$\hat{Y} = a + bX \qquad \text{[linear regression]} \quad (3)$$

and

$$\log \hat{Y} = \log b + z \log X \qquad \text{[nonlinear regression]} \quad (4)$$

The models are easily modified for multiple regression by inclusion of additional independent variables.[18, 19] In this manner (where a, b, and z, representing intercept, regression, and exponential coefficients, are constants set by solution of simultaneous equations) we test, for the archipelagos cited, the ability of X_1, X_2, X_3, X_4, and X_5 to predict Y. The first two X's (area, elevation) are considered positive indices of ecological diversity and habitable space on islands, X_3 and X_4 (distance from zoögeographic source region and from nearest neighboring island, respectively) are used as alternate, positive measures of isolation, and X_5 is used as a "catchall," additional variable which, it is thought *a priori*, might negatively index isolation insofar as production of endemics is concerned.[3, 6] Thus by both multiple linear and multiple nonlinear regression, the variance of bird species numbers for the islands of each archipelago is partitioned according to the per cent of variation ($= R^2 \times 100$) accounted for by variation in each environmental factor.

Results.—(a) *Insular variation of bird species numbers in the East Indies:* Multiple linear regression analysis accounts for 89 per cent of the insular variation ($R^2 = 0.8919$) in bird species numbers (Y) and reveals that 72 per cent can be accounted for by variation in insular area independent of other environmental factors (Table 2). The remaining important, independent contributor to the variance of Y is elevation (15%). Each of the measures of isolation (X_3, X_4, X_5) contribute insignificant, fractional percentages and may be disregarded as "movers" of the dependent variable (Y) in this archipelago.

TABLE 2

PARTIAL REGRESSION AND EXPONENTIAL COEFFICIENTS AND ANALYSES OF VARIANCE FOR DATA IN FIGURES 2–4

Controlled regression (Y on X independent of other X's)	Model I b	Model II z	Analysis of variance by contributions* to the coefficient of multiple determination	
Species numbers on area (X_1)			East Indies:	Model I: $R^2 = 0.8919$; $X_1 = 0.7219$; $X_2 = 0.1483$; $X_3 = 0.0076$, $X_4 = 0.00620$, $X_5 = 0.0079$. Model II: $R^2 = 0.9227$; $X_1 = 0.8748$, $X_2 = 0.0409$; $X_3 = 0.0016$, $X_4 = 0.0026$, $X_5 = 0.0028$.
East Indies:	0.0010	0.2799		
East-Central Pacific:	0.0013	0.3028		
West Indies:	0.0014	0.2372		
Species numbers on elevation (X_2)				
East Indies:	0.0101	0.2304		
East-Central Pacific:	0.0041	0.2297	East-Central Pacific:	Model I: $R^2 = 0.9658$; $X_1 = 0.8839$, $X_2 = 0.0204$, $X_3 = 0.0602$, $X_4 = 0.0005$, $X_5 = 0.0008$. Model II: $R^2 = 0.9055$; $X_1 = 0.0126$, $X_2 = 0.0238$, $X_3 = 0.1027$, $X_4 = 0.0158$, $X_5 = 0.0365$.
West Indies:	−0.0011	0.0290		
Species numbers on isolation (X_3)				
East Indies:	−0.0722	−0.0280		
East-Central Pacific:	−0.1419	0.0666		
West Indies:	0.0239	−0.0170		
Species numbers on isolation (X_4)			West Indies:	Model I: $R^2 = 0.7542$; $X_1 = 0.6126$, $X_2 = 0.0028$, $X_3 = 0.0042$, $X_4 = 0.0080$, $X_5 = 0.1265$. Model II: $R^2 = 0.9363$; $X_1 = 0.9271$, $X_2 = 0.0011$, $X_3 = 0.0004$, $X_4 = 0.0076$, $X_5 = 0.0001$.
East Indies:	−0.2507	−0.0392		
East-Central Pacific:	0.0233	−0.3551		
West Indies:	0.2293	0.1154		
Species numbers on isolation (X_5)				
East Indies:	−0.0001	−0.0360		
East-Central Pacific:	0.0000	0.1307		
West Indies:	0.0005	0.0021		

* Following coefficient of multiple determination (R^2), contributions to such are given for each X.

Multiple nonlinear regression accounts for 92 per cent of the variation in log Y. Of this, log area accounts for 87 per cent, and log elevation accounts for 4 per cent. The three measures of isolation (log X_3, log X_4, log X_5) each account for less than 1 per cent of the variation in log Y. Figure 2 compares Model I and Model II for multiple regression analyses of the species data for 22 islands of the East Indies and shows (by insert for average absolute prediction errors) the greater predictive power of multiple nonlinear analysis (Model II). Here, the corrected species-area slope (z) is 0.280 (Table 2).

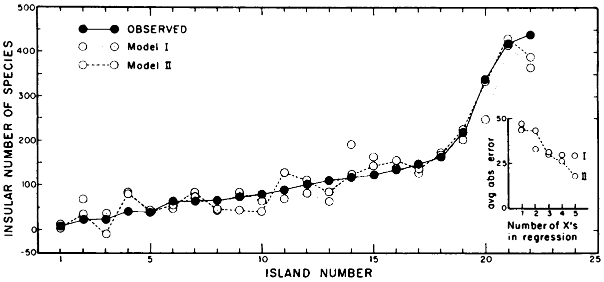

FIG. 2.—Variation in species numbers throughout the islands of the East Indies. Note the predicted values determined by multiple linear (Model I) and nonlinear (Model II) regression. Insert shows average absolute prediction errors for the two models with varying ("best single," "best two," "best three," etc.) numbers of X's being used. Note the better predictions obtained by Model II. Islands and their numbers: 1, Christmas; 2, Bawean; 3, Engano; 4, Lingga; 5, Savu; 6, Simalur; 7, Bangka; 8, Mentawei; 9, Alor; 10, Wetar; 11, Billiton; 12, Sumba; 13, Nias; 14, Lombok; 15, Sumbawa; 16, Timor; 17, Flores; 18, Bali; 19, Celebes; 20, Java; 21, Borneo; 22, Sumatra.

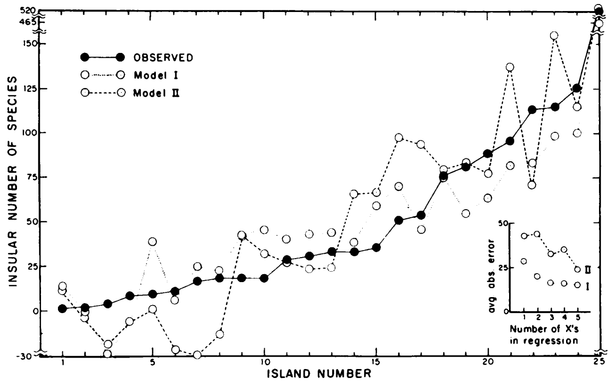

FIG. 3.—Variation in bird species numbers throughout 25 islands of the East-Central Pacific. Note the greater prediction accuracy obtained by Model I, as compared with Model II in multiple regression analysis (see caption for Fig. 2). Islands and their numbers: 1, Wake; 2, Line; 3, Henderson; 4, Tuamotu; 5, Kusaie; 6, Marquesas; 7, Society; 8, Ponape; 9, Marianas; 10, Tonga; 11, Santa Cruz; 12, Palau; 13, Samoa; 14, Rennell; 15, Hawaii; 16, New Hebrides; 17, Fiji; 18, Louisiade; 19, Tanimbar; 20, Kei; 21, D'Entrecasteaux; 22, Solomons; 23, Buru; 24, Ceram; 25, New Guinea.

(b) *Insular variation of bird species numbers in the islands of the East-Central Pacific:* From both the size of R^2 (0.9658) and small size of the average absolute prediction error (Table 2), it appears that Model I is a somewhat better predictor than Model II for bird species numbers in this archipelago (Fig. 3). Area alone accounts for 88 per cent of the variation in Y. Elevation accounts only for 2 per cent, but isolation (X_3), measured as distance from New Guinea, accounts for 6 per cent. The remaining two X's are negligible contributors to the Y variance. By Model II, 92 per cent of the variation in log Y is attributable to the log X's. Of this, 72 per cent is explained by variation in area, and 10 per cent by X_3. The other X's are of negligible influence. Since the majority of the islands of the East-Central Pacific (with the exception of New Guinea) are smaller and more isolated than the islands of the East Indies, the reduced influence on Y of elevation and the apparent increased influence of isolation are not unexpected. The species-area slope (z), when corrected by removal of influences of environmental factors other than area, is 0.303 (Table 2).

(c) *Insular variation of bird species numbers in the West Indies:* For this archipelago, Model II is the better predictor (94% compared to 75% by Model I) of the insular variation in bird species abundance (Fig. 4). Area (X_1) is the only major "mover" of Y, accounting for 93 per cent of the variation in Y. The slope (z) for area and species numbers, independent of variation in other X's, is 0.237 (Table 2).

Discussion.—Of numerous possible interpretations of these findings, emphasis

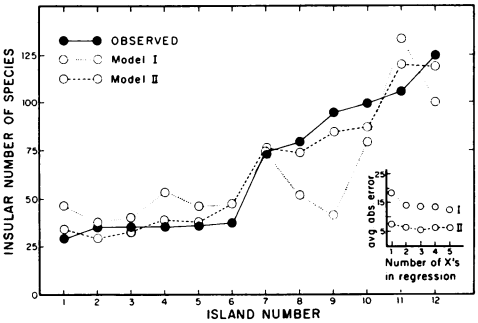

FIG. 4.—Variation in bird species numbers for 12 islands of the West Indies. Note the greater prediction accuracy obtained by Model II, as compared with Model I, in multiple regression analysis (see caption for Fig. 2). Islands and their numbers: 1, Grenada; 2, St. Vincent; 3, St. Lucia; 4, Virgin; 5, Dominica; 6, Guadalupe; 7, Bahamas; 8, Puerto Rico; 9, Isle of Pines; 10, Jamaica; 11, Hispaniola; 12, Cuba.

will be placed on the following three topics which relate the present report to the previous studies of Preston,[14,15] MacArthur and Wilson,[13] and Hamilton *et al.*[3–6]

(a) *Preston's equation for insular variation in bird species numbers:* As noted above, Preston[15] has attempted to adduce evidence for the hypothesis that the biotas of oceanic islands are not merely samples of adjacent mainland biotas—but rather are truly coadapted biotas with numbers of insular species being related to area by the exponential 0.27 [see eq. (1)]. The examples presented by Preston, however, deviate from his theoretical value for the species-area constant. The range of z values is wide, varying from 0.239 to 0.333 with a mean of 0.285.

By Preston's unifactorial species-area analysis method,[15] the z values for the avifaunas of the three archipelagos discussed in this communication are 0.38, 0.55, and 0.24 (Table 1). However, following corrections (i.e., the removal of the influences on the Y's of the other X's) the z values became 0.2799, 0.3028, and 0.2372, with a mean of 0.273 (cf. Tables 1 and 2). For insular variation in bird species numbers, the results of this study thus offer support for the general validity of Preston's thesis that area is the major determinant of insular species abundance, and that such is characterized by a species-area relation with $z = 0.27$.

The application of multiple linear regression (Model I) to the species data for the three archipelagos is of interest since it gives partial regression coefficients for area ($b_{yx_1 \cdot x_2 - x_5}$) which are very close to one another (viz., 0.0010, 0.0013, and 0.0014; see Table 2). A standard statistical interpretation of these values is that both in the Pacific and Caribbean regions the number of bird species increases by about 1.2 species for each 1,000 square miles increase in area. The ecological significance of this and the preceding empirical observation remains to be elucidated (see (c) below).[20]

(b) *The distance effect in relation to isolation and reduced habitat or ecologic diversity:* For the bird fauna of the isolated islands of the East-Central Pacific we expected that isolation and area would contribute jointly to species abundance. Indeed, Mayr[10,11] has quantified the decrease in insular number of land bird species in the East-Central Pacific associated with increased distance from New Guinea. More recently, MacArthur and Wilson[13] have utilized Mayr's finding in another way. They assume that the hypothetical species-area curve for large and small islands in the New Guinea region would predict the avifaunal size for the other islands of the East-Central Pacific were it not for the direct operation of the distance effect. From this species-area curve, they predict the hypothetical species number for each island. The hypothetical "per cent saturation value" can then be derived for each island by the difference between this value and the observed number of species. This value, plotted against distance, indicates decreased saturation values away from New Guinea[13] (see also Fig. 5).

MacArthur and Wilson[13] use this as an example of distance influencing the chances of dispersors or "propagules" reaching an isolated target island. If these per cent saturation values truly represent the operation in the East-Central Pacific of such a distance effect on the dispersal chances of birds, then their variation should be relatively independent of insular area. However, as can be seen in Figure 5, there is positive relationship between insular area and per cent saturation. This is here interpreted as a reminder that small, isolated islands may have reduced bird species communities for at least two reasons: (*i*) a result of isolation influencing the dispersal of birds themselves, and (*ii*) a result of isolation influencing the dispersal to the islands of units of avian ecological support.[2] Which is more important in this case is uncertain, and the possibility exists that these small islands isolated in the East-Central Pacific are in fact avifaunally saturated for their particular insular ecologies; that is to say, these islands may be ecologically as well as avifaunally depauperate.

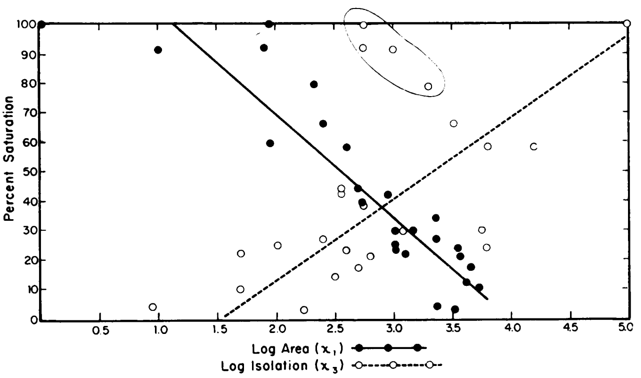

FIG. 5.—Values for avifaunal saturation percentages in the islands of the East-Central Pacific plotted against logarithms of distance from New Guinea (following MacArthur and Wilson[13]) and logarithms of area of the islands. To show that while a negative relation exists between insular avifaunal saturation and distance from New Guinea, a positive relation also exists between the saturation values and the area of the islands. Thus decrease in saturation of isolated insular avifaunas is not independent of area (see text). The four islands (20–23; see Fig. 3) encircled are adjacent to New Guinea; as such they are part of the so-called source region and should not be included in the analysis.

(c) *Monophyletic and polyphyletic aspects of insular species abundance:* The findings here reported deal with polyphyletic species assemblages (resulting from repeated colonizations) and emphasize an important role for area in the regulation of insular variation in the numbers of breeding bird species. In these cases, isolation is not as important as we have previously shown for the Darwin Finches, a monophyletic assemblage of bird species resulting from speciation following a single invasion,[3] and elevation is not as important as we found it to be for the land plants of the Galapagos Archipelago.[6] It is perhaps expected that isolation should be more important than area in the origin of species than in the primarily postspeciation spread of species throughout an archipelago. It is not unexpected for plant species numbers to vary more closely with a factor that indexes ecological diversity (altitude) than with insular area *per se*.

In this latter instance, our studies[6] do not support Preston's hypothesis of a species-area curve constant for insular faunas and floras. Whether other studies of insular variation in floral richness will support Preston's thesis[15] or our finding[6] remains to be seen. But for the present, we consider it possible that Preston's formula [eq. (1)] may be valid primarily for animal species—in particular for those species that are predominantly density-dependent in the regulation of their numbers of individuals, and thus are space-demanding in the sense that they spread themselves out in nonrandom ways.[20]

Summary.—(1) From multiple regression analyses of environmental correlates (area, elevation, isolation) of insular bird species abundance in the East Indies, West Indies, and East-Central Pacific, evidence is presented for the following: (*a*) that for each archipelago, area is the major predictor of insular variation in species numbers; (*b*) that the species-area curve is nonlinear or curvilinear in the first two archipelagos, but linear in the third one; (*c*) that when effects of environmental variables other than area are removed, the species-area slopes (z) by Model II (nonlinear variation) are, respectively, 0.280, 0.237, and 0.303; and (*d*) that by Model I (linear variation) corrected species-area relations are such that partial regression coefficients are, respectively, 0.0010, 0.0014, and 0.0013.

(2) The uniformity of the z values (average = 0.273) approaches closely Preston's theoretical exponential of 0.270 for species-area curves for isolates, and our findings support his theory insofar as bird species are concerned. Previous studies of plant species abundance in the Galapagos Islands reveal elevation, not area, as the major determinant, and the possibility exists that Preston's formula for isolates (species number = 10 $\text{area}^{0.27}$) is not applicable to all groups of plant and animal species. The suggestion is made that it will predict most accurately insular species-area relations for space-demanding animals whose individual numbers are primarily regulated by density-dependent means.

We are indebted to Ernst Mayr, W. F. Blair, R. H. MacArthur, R. K. Selander, and E. O. Wilson for interest and assistance. Mrs. Beverly Lee programmed the data and made possible the study at the Harvard Computing Center. The study was financed by an NSF grant.

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* Species abundance as used in this communication refers simply to the number of species, and not to the relative abundance of species according to their numbers of individuals.

[1] Miller, A. H., in *Ornithologie als Biologische Wissenschaft* (Heidelberg: Carl Winter, 1949), p. 84.

[2] For colonization of islands by bird species, the indirect role of isolation (i.e., its influence on the dispersal of plant, insect, and other animal species on which birds of specialized foraging and feeding ecologies depend) is expected to be most important. Realization of this possibility permits the postulation that bird species dependent upon plant material (grains, seeds, etc.) should colonize isolated islands more rapidly than bird species which feed on insects, and the latter, in turn, should colonize remote islands more rapidly than predator bird species. Here it is assumed that the more isolated islands will "pick up" dispersing plants, insects, birds, and mammals listed in decreasing order of facility for crossing water gaps.

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[15] *Ibid.*, **43**, 185, 410 (1962).

[16] We are indebted to E. O. Wilson and R. H. MacArthur for generously making available to us their data for insular number of bird species in the East Indies and East-Central Pacific. References for the data are to be found in their paper.[13] In the near future we hope to publish a longer, more extensive survey of species-area phenomena in birds, and at that time we plan to cite the species data as well as environmental data used in the present study.

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[18] Croxton, R. E., and Cowden, D. G., *Applied General Statistics* (New York: Prentice-Hall, Inc., 1939).

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[20] Our chief concern here has been to document empirical observations for nonlinear and linear relations between bird species numbers and insular area. The ecological significance of this is a problem for the future [cf. Crowell, K. L., *Am. Naturalist*, **97**, 194 (1962)]. Here are three approaches to its resolution: (1) the equilibrium concepts of Preston,[15] and MacArthur and Wilson;[13] (2) inquiries into the relation between insular area and habitat or niche diversity;[6] and (3) consideration of the sizes of area or habitable space necessary for new colonizers to become truly established as self-maintaining species populations [cf. Serventy, D. L., *West Australian Nat.*, **3**, 59 (1951)].

THE IN VITRO FORMATION OF A DNA-RIBOSOME COMPLEX

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The general process of information transfer from gene to protein has been resolved into two stages—transcription and translation. In the first stage, the information for the order of amino acids in the primary structure of the protein is transcribed from the deoxyribonucleotide sequence of the gene into the corresponding ribonucleotide code of complementary RNA, cRNA. During the translation step, the genetic message is finally decoded. cRNA molecules become bound to ribosomes and then dictate the assembly of specific polypeptide sequences.[1]

Although transcription and translation are obviously linked biochemically, it is not known whether they are physically connected as well. In considering this point three possibilities present themselves: (1) the two stages are *uncoupled*—cRNA is released from its DNA template and moves to another site within the cell before protein synthesis is initiated; (2) they are *completely coupled*—protein synthesis occurs only when cRNA is attached to the gene; (3) they are *transiently coupled*—the translation of the cRNA message begins when the cRNA molecule is still bound to DNA and continues after its release from the DNA template.

The available data concerning the physical aspects of transfer of RNA to ribosomes in biological systems is meager. In phylogenetically advanced organisms, possessing well-defined nuclei, intranuclear RNA and protein synthesis may be separated by a membrane from cytoplasmic protein synthesis. Beermann and Clever[2] have suggested that cRNA, accumulating on the "puff" fibrils of giant dipteran