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INTRA-ARCHIPELAGO VERTEBRATE DISTRIBUTIONS: THE SLOPE OF THE SPECIES-AREA RELATION

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The number of species on an island increases with increasing island area. Several hypotheses have been advanced to account for this phenomenon, but the equilibrium theory of island biogeography is now ascendant (Simberloff 1974). The equilibrium theory postulates that an island's biota is determined by a dynamic balance between the immigration of species new to the island and the local extinction of species already present (Preston 1962; MacArthur and Wilson 1963, 1967). Island area affects species number as follows. The probability that all individuals in a population will die simultaneously, i.e., the probability that a population will become extinct, increases as population size decreases. Of course, populations are larger on larger islands. Therefore, the probability that a population will become extinct is a decreasing function of island area, and small islands record more frequent extinctions and support fewer species than large islands.

Two theoretical approaches have been used to derive the mathematical form of the species-area relation. The first approach does not involve a mechanistic explanation such as equilibrium theory. Rather, all that is necessary is (1) to designate a particular species-abundance distribution and (2) to assume that the number of individuals on an island is proportional to island area. Thus, the log-series species-abundance distribution generates an exponential species-area relation (Fisher et al. 1943) and the lognormal and broken-stick species-abundance distributions generate power functions (Preston 1962; May 1975). With notable exceptions, e.g., disturbed communities (Stenseth 1979), lognormal species-abundance distributions predominate (Preston 1962; Stenseth 1979) and it is reasonable to use a power function to describe the species-area relation (May 1975; Connor and McCoy 1979; Stenseth 1979; Sugihara 1981).

Coincidentally, equilibrium theory allows predictions about the exponent (z) of the power function relating species number to island area (MacArthur and Wilson 1967; Diamond et al. 1976; Schoener 1974). All that is necessary is to: (1) specify functions relating immigration and extinction rates to island species number, S ; (2) assume that the change in S with time, dS/dt , equals the number of immigrations minus the number of extinctions; (3) solve for S ; and (4) solve for z which equals

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$d\log S/d\log A$, where A is island area. The predicted relationship between immigration rates and z -values has been verified for birds by examining a series of archipelagos which differ in their degree of isolation (Schoener 1974). I will examine the affect of simultaneous variation in immigration and extinction rates on z -values. To accomplish this, I will incorporate the relative immigration and extinction rates of amphibians, reptiles, nonvolant mammals, bats, and birds into an equilibrium model. Predicted z -values will be compared with observed z -values for 10 archipelagos. In addition, the history of colonization of an archipelago is known to affect its z -value (Brown 1971, 1978; Barbour and Brown 1974). I will use the equilibrium model to explore the relationship between z -values and an archipelago's history. First I will comment on statistical procedures used to calculate the parameters of the power function from species-area data.

CALCULATION OF THE POWER FUNCTION

The following power function relates species number to island area:

$$S = kA^z, \quad (1)$$

where k and z are fitted parameters. With one exception (Sepkoski and Rex 1974), species-area data have been fit to the power function using least-squares linear regression after taking the logarithm of equation (1):

$$\log S = \log k + z \log A. \quad (2)$$

While equations (1) and (2) are mathematically equivalent, they are not statistically equivalent for least-squares regression (Zar 1968; Glass 1969). The objective of least-squares regression is to find parameter values which minimize the residual sum of squares. In the case of equation (1), the quantity minimized is

$$\Sigma(S_i - \hat{S}_i)^2, \quad (3)$$

where S_i is the observed and \hat{S}_i the predicted number of species for a particular A_i . In the case of equation (2), the quantity minimized is

$$\Sigma(\log S_i - \log \hat{S}_i)^2. \quad (4)$$

Obviously, expressions (3) and (4) are not equal and different parameter values, k and z , will result (Glass 1969).

To determine whether expression (3) or expression (4) should be minimized, it is necessary to understand how random error, ϵ_i , affects the dependent variable. If the error term is multiplicative, i.e.,

$$S_i = kA_i^z \epsilon_i, \quad (5)$$

the logarithmic transformation is correct because the error in S_i becomes homoscedastic. However, if the error term is additive, i.e.,

$$S_i = kA_i^z + \epsilon_i, \quad (6)$$

the logarithmic transformation is incorrect and expression (3) should be minimized. This can be accomplished by fitting species-area data to the power function with nonlinear least-squares regression.

With species-area data, it is rarely possible to examine the error term directly because each A_i corresponds to a single S_i . Two criteria remain by which the appropriate regression model (eq. [5] or [6]) may be chosen. First, residuals from the predicted regression line may be examined for trends. Barring trends in the residuals, biological insight may indicate how the error term enters the regression equation. In equation (5), the error in S_i increases with increasing A_i . For closely studied archipelagos, the error in S_i is probably independent of A_i . For example, for the taxa considered here, there is no reason to expect the error in S_i to be greater for Great Britain than for other islands in the British Isles. As another example, in the Gulf of California, the distributions of diurnal lizards are well known, but the distributions of nocturnal lizards are poorly known. The resulting error in S_i is probably one or two species per island and is independent of A_i (R. W. Murphy, personal communication). Moreover, factors which operate independently of island area, e.g., isolation, affect S . Thus, error in S_i is largely independent of A_i and the regression model represented by equation (6) is appropriate.

Thirty-six species area data sets (Appendixes A through H) were fit to the power function using both iterative, nonlinear regression and the logarithmic transformation and linear regression. To determine which method gave the better fit to the power function, the proportion of unexplained variance after regression was examined. That is the residual sum of squares (expression [3] or [4]) was examined as a proportion of the total variance in S for nonlinear regression and as a proportion of the total variance in $\log S$ for linear regression (for linear regression that is equivalent to examining the quantity $1 - r^2$, where r is the correlation coefficient). For 30 data sets, the proportion of unexplained variance was minimized by nonlinear regression (table 1) and no trends were present in the residuals. Note the different parameter values, k and z , generated by the two regression models. Henceforth, z -values generated by the iterative, nonlinear fit to the power function will be considered.

Stenseth (1979) analyzed 46 species-area data sets to determine whether the better fit was obtained with a power function (19 data sets) or an exponential function (27 data sets),

$$S = \ln\alpha + k \ln A.$$

Stenseth's best fit function minimized expression (3). However, to fit the power function, Stenseth used linear regression and log transformed data. Clearly, the proportion of unexplained variance in the dependent variable is minimized if nonlinear regression is used to fit untransformed species-area data to the power function (table 1). If Stenseth had used this procedure, the power function may have given the best fit to a larger number of his data sets. This potential is illustrated in table 1. I also fit my 36 species-area data sets to an exponential function. When the exponential function and the power function fit by linear regression are compared, the exponential function minimizes the proportion of unexplained variance for 18 data sets (table 1). However, when the power function is fit by nonlinear regression, the exponential function minimizes the proportion of

unexplained variance for only eight data sets (table 1). Connor and McCoy (1979) did a similar analysis. The fit 100 species-area data sets to four functions one of which was the power function, and they used linear regression to fit the power function. Nevertheless, in 43 instances, the power function was determined to be the best fit function. Again this number would probably be increased if nonlinear regression had been used to fit the power function.

The first statements about z -values concerned their consistent magnitude. Preston (1962) noted that most z -values fall between 0.17 and 0.33 and provided a theoretical reason. May (1975) extended Preston's theory. Given the range of ecologically reasonable lognormal species-abundance distributions and the assumption that population size is proportional to island area, May concluded that z -values should fall between 0.15 and 0.39. If the logarithmic transformation and linear regression are used to fit species-area data to the power function, statistical artifact will cause most z -values to fall in this range (Connor and McCoy 1979). With one exception (Sepkoski and Rex 1974), z -values have been calculated using the logarithmic transformation and linear regression. Therefore the consistent magnitudes of z -values cannot be construed as support for Preston's and May's theory (Connor and McCoy 1979; but see Sugihara 1981). However, if nonlinear regression is used to fit the power function, z -values are calculated directly and statistical artifact is not a problem. Using iterative, nonlinear regression, 27 of 36 z -values fall between 0.15 and 0.39 while nine do not (table 1).

THE EQUILIBRIUM MODEL

To model the processes which affect an insular biota, MacArthur and Wilson (1967) assumed: (1) immigration and extinction rates are linear functions of S and (2) for a given S , extinction rates are monotonically decreasing functions of island area. Following Wilson (1969), at equilibrium

$$\lambda(P - \hat{S}) = \mu\hat{S}, \quad (7)$$

where λ and μ are per-species immigration and extinction rates, respectively, P is the number of species in the source fauna, and \hat{S} is the number of species on an island at equilibrium. Note that an island's extinction rate is a product of two numbers, the number of species on the island and the per-species extinction rate. The assumption that extinction rates are monotonically decreasing functions of island area ensures that $d\mu/dA$ is always negative.

Schoener (1974) improved upon this model by examining the relation between μ and A . Schoener modeled this relation by allowing μ to equal μ_N/\bar{N} , where \bar{N} is the average population size and μ_N is a proportionality factor which increases with increasing likelihood of an individual dying. Schoener allowed \bar{N} to take one of two extreme forms. In his case 1, limiting resources are not shared between species, species abundances are independent, and $\bar{N} = \rho'A$, where ρ' is the density of individuals in the average population. To incorporate the different population densities maintained by different vertebrate taxa, I will weight ρ' by a

TABLE 1
SPECIES-AREA DATA FIT TO THE POWER FUNCTION USING LINEAR AND NONLINEAR REGRESSION AND TO THE EXPONENTIAL FUNCTION

ARCHIPELAGO	NONLINEAR FIT TO POWER FUNCTION‡				LINEAR FIT TO POWER FUNCTION			EXPONENTIAL FUNCTION	
	N	z	σz §	k	$\frac{\Sigma(S_i - \hat{S}_i)^2}{\Sigma(S_i - \bar{S}_i)^2}$	z	k	$\frac{\Sigma(\log S_i - \sqrt{\log \hat{S}_i})^2}{\Sigma(\log S_i - \log \bar{S}_i)^2}$	$\frac{\Sigma(S_i - \hat{S}_i)^2}{\Sigma(S_i - \bar{S}_i)^2}$
Bass Strait									
Amphibians	4	.207	.076	1.42	.11*	.301	.79	.07*	.03*
Reptiles	9	.195	.087	2.59	.50*	.187	2.45	.60	.53*
Nonvolant mammals	14	.329	.044	1.53	.12†	.382	1.14	.26†	.16†
Birds	13	.274	.055	3.69	.21†	.339	2.42	.28†	.17†
British Channel Islands									
Amphibians	4	.403	.280	.36	.42	.251	.60	.51	.51
Reptiles	4	.472	.214	.38	.16	.287	.75	.21	.32
Nonvolant mammals	5	.416	.099	1.12	.09*	.329	1.51	.11*	.21*
Birds	4	.202	.039	17.87	.05*	.191	18.53	.06*	.09*
British Isles									
Amphibians	10	.093	.057	1.55	.79	.110	.92	.84	.80
Reptiles	10	.049	.081	1.98	.97	-.003	2.49	.99	.97
Nonvolant mammals	7	.473	.110	.08	.08†	.323	.18	.28*	.21†
Bats	8	.273	.044	.38	.11†	.234	.31	.26†	.20†
Birds	6	.175	.045	17.54	.17*	.154	14.62	.28*	.24*
California Channel Islands									
Amphibians	5	.337	.165	.43	.26	.243	.65	.29	.35
Reptiles	8	.423	.320	.48	.62	.234	1.02	.58	.69
Nonvolant mammals	8	.351	.136	.55	.30†	.283	.73	.17†	.37*
Birds	8	.322	.108	5.28	.29†	.213	8.40	.36*	.40*

proportionality factor c . For simplicity's sake, I will incorporate c and μ_N into a single proportionality factor θ (see below). Substituting into equations (7) and (2),

$$\lambda(P - \hat{S}) = (\theta/\rho'A)\hat{S}, \quad (8)$$

$$\hat{z} = \frac{d \log \hat{S}}{d \log A} = \frac{1}{1 + \rho'A\lambda/\theta}. \quad (9)$$

In Schoener's case 2, resources are limiting, species abundances are complementary, and $\bar{N} = \rho A/S$, where ρ is the density of individuals of all species combined. Substituting into equations (7) and (2),

$$\lambda(P - \hat{S}) = (\theta/\rho A)\hat{S}^2, \quad (10)$$

$$\hat{z} = 1 - \frac{1}{2 - (\hat{S}/P)}. \quad (11)$$

Schoener's two cases are points on a continuum. To demonstrate this, I will examine the relation between the density of individuals in the average population, the density of individuals of all species combined (ρ), and S . If limiting resources are not shared between species (case 1), realized and fundamental niches coincide, the density of individuals in the average population (defined to be ρ' for case 1) is independent of S , and $\rho = \rho'S$. As Schoener (1974) notes, this is unrealistic. As S increases, competitors will be added, the realized niche of each species will be restricted to some portion of its fundamental niche, and the relation between ρ and S will become more complex because the density of individuals in the average population will no longer be independent of S . At the other extreme (case 2), all species might compete for a single resource. In this case, species abundances are complementary and ρ is independent of S . Moreover, if a single consumer is present ($S = 1$), cases 1 and 2 are equivalent, and $\rho = \rho'$. Hence, for larger values of S , the density of individuals in the average population equals ρ'/S . This too is unrealistic. As species are added to a community, their collective fundamental niches will include a greater portion of the resource spectrum, and competition will restrict realized niches to those portions of the resource spectrum where species are efficient consumers. Thus, as S increases, consumer efficiency will increase, a greater portion of the available resources will be harvested, and ρ will increase (Wright 1980). In addition, as S increases a progressively larger proportion of resources will be harvested by the most efficient consumers present in the source fauna. Therefore the increment in ρ attained by adding a single species to a community will decline as S increases. This may be modeled by letting the density of individuals in the average population equal ρ'/S^x , where $0 \leq x \leq 1$. Now,

$$\bar{N} = \rho'A/S^x. \quad (12)$$

When x is large interspecific competition depresses \bar{N} . When x is small interspecific competition has little effect on \bar{N} . Substituting into equation (7),

$$\lambda(P - \hat{S}) = (\theta/\rho'A)\hat{S}^{(1+x)}. \quad (13)$$

Schoener (1974) solved equation (13) for $x = 0$ (case 1) and $x = 1$ (case 2). For intermediate values of x , I obtained iterative solutions for \hat{S} after assigning values

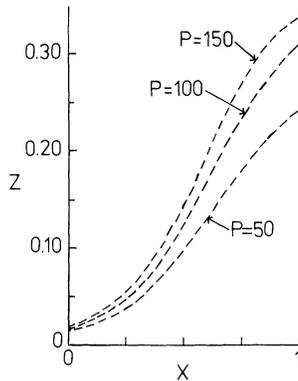


FIG. 1.—The effect of competition on the slope of a log-log species-area curve, z , as represented by three simulations of equation (13). The abscissa may be thought of as an index of the intensity of competition. Large values of x and large values of z correspond to intense competition. Differences in the size of the source fauna, P , have an ever greater effect on z as x increases. See text for further explication. In each simulation, $\lambda = 0.45$, $\rho' = 1$, and $\theta = 0.15$. To calculate z , A assumed two values, 10 and 50.

to all other parameters. These iterative solutions were used to examine the relation between z and x . As x increases, the importance of interspecific competition increases and z -values increase (fig. 1). This is true because competition causes a disproportionate increase in extinction rates on small islands. To see this, examine the relation between \bar{N} and S . From equation (12), $d\bar{N}/dS$ is always negative and $d^2\bar{N}/dS^2$ is always positive. In other words, increases in S always lead to decreases in \bar{N} (when $x \neq 0$) and the effect is greatest when S is small, i.e., on small islands. Thus, with competition, the addition of a new species causes a disproportionate increase in extinction rates on small islands and large z -values result.

RELATIVE IMMIGRATION AND EXTINCTION RATES

Different taxa have different dispersal abilities. Among vertebrates, birds and bats are the champion overwater colonists (Carlquist 1965; Baker and Genoways 1978). The ability to fly ensures that birds and bats have greater dispersal abilities than nonvolant vertebrates. For example, I have observed 140 terrestrial birds from 26 species in flight between islands in Gatun Lake, Panama. (These figures exclude species which regularly commute over the lake, e.g., vultures.) Bats also fly freely between islands and to the mainland (Charles Handley, personal communication) but, terrestrial, nonvolant vertebrates rarely cross the lake, only three individuals from three species having been observed. In addition, birds and bats can actively fly toward a landfall while nonvolant vertebrates must be passively rafted across water gaps.

Among nonvolant vertebrates, immigration rates should increase as the ability to survive rafting increases. Because their skin is water permeable, amphibians are less likely to cross ocean barriers than any other vertebrate group except

obligately freshwater fishes (Myers 1953; Carlquist 1965). Nonvolant mammals are less likely to cross water barriers than reptiles (Carlquist 1965), primarily because mammals succumb more quickly to starvation.

Within each vertebrate group, different species have different dispersal abilities. For example, for psychological reasons, some birds are reluctant to cross even the narrowest openings in their forest habitats, and these species rarely, if ever, immigrate to oceanic islands (e.g., Diamond et al. 1976). On the average, birds have much higher immigration rates than nonvolant vertebrates. If representative species from each taxon are considered, the per-species immigration rates of terrestrial vertebrates can be ranked from high to low as follows: (1) birds and bats, (2) reptiles, (3) nonvolant mammals, and (4) amphibians. Between-taxa differences in immigration rates will be incorporated into the equilibrium model by assigning the following relative values to λ : $0 < \lambda_A < \lambda_{NVM} < \lambda_R < \lambda_{BB} < 1$, where $\lambda = \lambda_A$ for amphibians, $\lambda = \lambda_{NVM}$ for nonvolant mammals, $\lambda = \lambda_R$ for reptiles, and $\lambda = \lambda_{BB}$ for birds and bats.

Extinction rates decline as population sizes increase. Physiological constraints suggest that poikilotherms should maintain higher population densities than ecologically similar homeotherms. The basal metabolic rates of poikilotherms are an order of magnitude lower than the basal metabolic rates of homeotherms, and the disparity between the metabolic rates of free-ranging homeotherms and poikilotherms is even greater than the disparity between their basal metabolic rates. For example, free-ranging insectivorous birds require 35 times more energy per day than do free-ranging iguanid lizards of equal body weight (Bennett and Nagy 1977). Therefore lizards should require much smaller territories than birds and mammals of equal body weight (Schoener 1968; Turner et al. 1969; Harestad and Bunnell 1979), and within the confines of an island, lizards should be able to maintain much larger populations than birds or mammals.

A causal relationship between metabolic rates, population densities, and per-species extinction rates has been noted previously. Nonpasserine birds have lower metabolic rates and concomitantly lower island extinction rates than passerine birds (Faaborg 1977). Lizards experience lower extinction rates than birds and mammals on islands in the Gulf of California (Case 1975; Lawlor, in press). Poikilothermic vertebrates experience lower extinction rates than birds on Mona Island in the Caribbean (Terborgh and Faaborg 1973). In the West Indies, *Anolis* lizards are nearly immune to extinction while avian extinctions are a regular phenomenon (Williams 1969; Ricklefs and Cox 1972; Wright 1981). Finally, on Barro Colorado Island, Panama, poikilotherms and homeotherms have experienced very different extinction rates (table 2; Wright 1979). Barro Colorado Island was isolated from the mainland in 1914 when the Chagres River was dammed to flood Gatun Lake and complete the Panama Canal. Early workers, F. M. Chapman for birds, E. R. Dunn for amphibians and reptiles, and R. K. Enders for mammals, produced faunal lists for the island in the 1920s and 1930s. In the intervening years, poikilotherms have experienced significantly lower per-species extinction rates than homeotherms ($\chi^2_c = 4.74$, $p < .05$). Thus, the relative extinction rates suggested by physiological constraints on population size are verified; poikilotherms experience lower per-species extinction rates than homeotherms.

TABLE 2
EXTINCTIONS OF VERTEBRATES WHICH INHABIT MATURE FOREST ON BARRO
COLORADO ISLAND, PANAMA

No. of Species	Amphibians*	Reptiles*	Nonvolant Mammals†	Birds‡
Extirpated	3	3	9	16
Originally present	34	61	45	105

* Species current status on Barro Colorado determined from Myers and Rand (1969) and Mittermeier (1972).

† Species current status determined by Charles Handley, Jr. (personal communication).

‡ Species current status determined from Willis and Eisenmann (1979).

To incorporate between-taxa differences in population densities into the equilibrium model, the constant ρ' will be weighted by the proportionality factor c , where $0 < c_H < c_P$ and $c = c_H$ for homeotherms and $c = c_P$ for poikilotherms. Although μ_N may vary between taxa, c and μ_N will be combined into a single parameter θ , where $0 < \theta_P < \theta_H$. The available data indicate that taxonomic differences in population densities parallel taxonomic differences in extinction rates. With respect to their affects on extinction rates, differences in μ_N must either reinforce differences in population densities or be relatively unimportant. Therefore combining μ_N and c into a single parameter is justified.

The magnitudes of immigration and extinction rates are rarely known. However, hypothetical differences in λ and μ can be substantiated by examining the ratio of μ to λ . The following predictions can be deduced from the hypothetical relative values of μ and λ : (1) $\mu_{BB}/\lambda_{BB} < \mu_{NVM}/\lambda_{NVM}$, (2) $\mu_R/\lambda_R < \mu_{NVM}/\lambda_{NVM}$, and (3) $\mu_R/\lambda_R < \mu_A/\lambda_A$. To test these predictions, observed values of μ/λ were generated from equation (7): $\mu/\lambda = P/\hat{S} - 1$. \hat{S} will vary with the size of the largest island in an archipelago, and different archipelagos have different source faunas, P . Therefore only intra-archipelago comparisons of μ/λ will be attempted.

For nine of the 10 archipelagos analyzed (West Indies excepted), it was possible to identify a source fauna. For each source fauna, the number of species in each vertebrate taxon was determined from field guides or, if reliable field guides were not available, from references cited in the Appendices. A species was not included in the source pool which might colonize an archipelago unless its range included coastal areas adjacent to the archipelago and appropriate habitats were available on the archipelago. For seven of the nine archipelagos, \hat{S} was taken to be the number of species on the most species-rich island in the archipelago. The islands of the Gulf of California extend over six degrees of latitude, and the ranges of many potential colonists have their northern or southern limit on the adjacent mainland within these six degrees of latitude. Therefore, for oceanic and landbridge islands in the Gulf of California, \hat{S} was taken to be the total number of species in the archipelago. Because of their different Pleistocene histories, oceanic and landbridge islands in the Gulf of California were treated as separate archipelagos (see below).

Out of 26 instances in which μ/λ for one taxon is predicted to be greater than μ/λ for a second taxon, the prediction is realized 26 times (table 3, $p < .001$, sign

TABLE 3
OBSERVED VALUES OF $P/\hat{S} - 1$

Archipelago	Amphibians	Reptiles	Nonvolant Mammals	Bats	Birds
Bass Strait67	.25	.6432
British Channel Islands	4.26	1.00	3.17	...	1.13
British Isles	1.86	.33	.59	.25	.20
California Channel Islands	2.70	2.23	4.26	...	1.50
Great Basin	1.4467
Gulf of California (landbridge)	1.50	.43	1.13	...	1.00
Gulf of California (oceanic)	4.00	.82	2.70	...	1.50
Lake Michigan79	1.44	4.0033
Tres Marias	9.00	2.23	10.11	...	2.85

test). Note that islands in Lake Michigan are separated from the mainland by fresh water. Therefore the water-permeable skin of amphibians should not be a particular disadvantage and λ and μ/λ should be equal for reptiles and amphibians. In the two instances in which μ/λ was predicted to be equal for two taxa, the following results were obtained: (1) $\mu/\lambda = 0.205$ for birds and $\mu/\lambda = 0.200$ for bats in the British Isles and (2) $\mu/\lambda = 0.786$ for amphibians and $\mu/\lambda = 1.439$ for reptiles on islands in Lake Michigan.

In summary, observed and predicted values of μ/λ are in close agreement. This supports the concept that island distributions are determined by a balance between immigration and extinction rates and lends further credence to the relative immigration and extinction rates hypothesized for the vertebrate taxa.

Z-VALUES

If interspecific competition does not depress \bar{N} , relative z -values can be predicted from equation (9). Only intra-archipelago comparisons of predicted and observed z -values will be attempted because z -values are known to vary between archipelagos (MacArthur and Wilson 1967; Diamond et al. 1976; Harner and Harper 1976; Schoener 1974). In equation (9), ρ' is a constant; between-taxa differences in population densities were incorporated into θ . In addition, for each archipelago the same range of island areas was used to compute z for each taxon. In equation (9), A now also becomes a constant, and relative z -values can be predicted from relative values of λ and θ . The following predictions result: (1) z -values for birds and bats should be equal; (2) z -values for birds and bats should be less than z -values for nonvolant mammals; (3) z -values for reptiles should be less than z -values for nonvolant mammals; (4) z -values for reptiles should be less than z -values for amphibians.

The z -statistic will be used to test the null hypothesis that two z -values are equal (table 4). In 24 comparisons one z -value is predicted to be greater than another. In 15 of these 24 comparisons, the null hypothesis cannot be rejected but, for nine comparisons, the null hypothesis can be rejected and, in each instance, the

TABLE 4

z-STATISTIC USED TO TEST THE NULL HYPOTHESIS THAT TWO z-VALUES ARE EQUAL

Archipelago	$z_{\text{Bird}} < z_{\text{NVM}}$	$z_{\text{Bat}} < z_{\text{NVM}}$	$z_{\text{R}} < z_{\text{NVM}}$	$z_{\text{R}} < z_{\text{A}}$
Bass Strait78	...	1.38	.11
British Channel Islands	2.02	...	-.23	-.19
British Isles	2.50	1.68	3.10	.45
California Channel Islands17	...	-.21	-.24
Great Basin	1.76
Gulf of California (landbridge)	2.38	...	2.57	...
Gulf of California (oceanic)	-.32	...	-.74	...
Lake Michigan	-.0898	...
West Indies	9.36	7.86	2.79†	6.87†

NOTE.—The z -statistic equals the difference between two z -values divided by the square root of their summed variances. Positive values indicate that observed z -values are in accord with predictions. If the absolute value of the z -statistic is greater than 1.96, the null hypothesis that two z -values are equal can be rejected. z -values and their asymptotic standard deviations were obtained using nonlinear regression.

† To avoid the effect of in situ speciation, z -values were calculated without the Greater Antilles.

prediction is confirmed. However, the asymptotic standard deviations reported for z -values (table 1) are estimates of actual standard deviations. If sample sizes are small, the estimate is invariably too small and the significance level of the z -statistic comes into doubt. Therefore nonparametric statistics were also used to test the null hypothesis that observed z -values do not conform to the above predictions. In seven of 24 comparisons, observed and predicted relative z -values do not agree (table 4). The probability that seven or fewer comparisons should disagree by chance is .032 (sign test), and the null hypothesis is rejected. If the magnitudes of the differences between pairs of z -values are also considered, the null hypothesis is again rejected ($T = 50.5$, $p < .05$, Wilcoxon signed-ranks test) and predicted and observed z -values are seen to be in close agreement.

If linear regression and the logarithmic transformation of the power function are used to determine z -values, similar results are obtained. Again, there are 24 comparisons in which one z -value is predicted to be greater than another. The prediction is realized in 21 instances (table 1), which would occur by chance with a probability of less than .001 (sign test).

If interspecific competition depresses \bar{N} , the size of the source fauna, P , also affects z -values (eqq. [11], [13]). As the importance of interspecific competition increases, the affect of P on z increases (fig. 1) and confidence in the predictions tested above must decline. In fact, if species abundances are completely complementary, the absolute magnitudes of z -values can be predicted from equation (11) if \hat{S}/P is known. However, if species abundances are entirely complementary, species must be ecologically equivalent. This violates the competitive exclusion principle whence the postulated role of competition must be too great and predicted z -values too large (fig. 1). The z -values predicted using equation (11) and observed z -values are compared in figure 2. As expected predicted z -values are consistently greater than observed z -values.

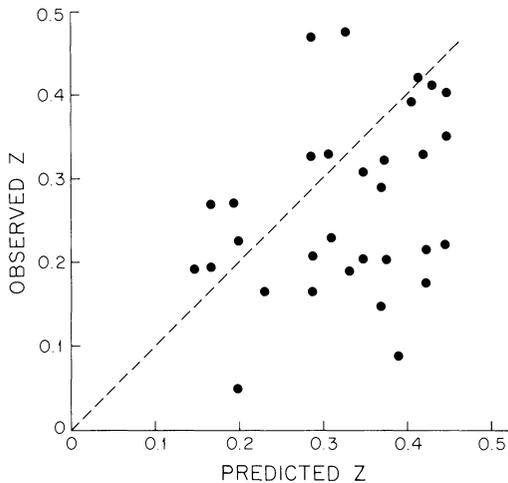


FIG. 2.—The z -values predicted by equation (11) are contrasted with observed z -values. If predicted and observed z -values were equal, points would fall on the dashed line. The null hypothesis that the data points are distributed evenly above and below the dashed line is rejected ($\chi^2 = 3.90$, $p < .05$), a disproportionate number of points fall below the line.

NONEQUILIBRIAL ARCHIPELAGOS

Islands differ in their history of colonization. Truly oceanic islands were never connected with continental land masses and were colonized solely by overwater dispersal. On the other hand, many islands which lie on continental shelves have repeatedly been separated from and connected with the adjacent continent as sea levels oscillated. Sea level and climatic changes associated with the Wisconsin glaciation (14,000 BP) are of particular importance zoologically. Islands which lie on continental shelves within the 110 m contour of ocean depths were connected with the adjacent mainland during the Wisconsin glaciation (e.g., Diamond 1972), and simultaneously many present-day "habitat islands" were part of a continuous expanse of similar habitat (e.g., Brown 1971). While connected to their source faunas, these islands-to-be experienced very high immigration rates and supported nearly a complete complement of the species in the source fauna. After the landbridge between island and source fauna was broken, immigration rates dropped precipitously. Many species which could not disperse overwater or through hostile habitats were represented, however, by relict populations on the island. Relict insular populations attributable to immigration during the Wisconsin glaciation have been found in the avifaunas of large landbridge islands in the neotropics (MacArthur et al. 1972; Terborgh 1975) and the southwest Pacific (Diamond 1972), in the saurofauna of landbridge islands in the Gulf of California (Case 1975; Wilcox 1978), and in the mammalian fauna of habitat islands in the Great Basin (Brown 1971, 1978).

These relict populations have been hypothesized to have a systematic effect on z -values. It has been noted that different sample areas within a continent characteristically generate low z -values ($z < 0.20$); archipelagos whose immigration and

extinction rates would be expected to be in equilibrium characteristically have intermediate z -values ($0.20 < z < 0.35$); and archipelagos with relict populations where extinction rates would be expected to exceed immigration rates characteristically have high z -values ($z > 0.35$; Brown 1978). Clearly, the z -values reported here, even those calculated after taking the logarithmic transformation of the power function (table 1), do not support this pattern. For example, in the Tres Marias Islands, where immigration and extinction rates would be expected to be in equilibrium, reptiles have a z -value of 0.391. As another example, landbridge islands in the Gulf of California were created by eustatic increases in sea level between 6,000 and 12,000 yr BP. These landbridge islands support large numbers of relict lizard populations (Case 1975; Wilcox 1978). Nevertheless, the z -value for the saurofauna is only 0.165. With the exceptions of Raza and Tortuga, the so-called oceanic islands in the Gulf of California were separated from mainland Mexico between one and five million yr BP by continental drift (Murphy, in press). Genetic divergence data indicate that several relict lizard populations still survive on these islands (Murphy, in press). Surprisingly, the z -value for the saurofauna of the older islands ($z = 0.231$) is greater than the z -value for the younger, landbridge islands.

Reference to the equilibrium model may elucidate the effect of relict, supraequilibrium faunas on z -values. Let $S(t)$ equal the number of species present on an island at time t . Equation (8) applies when extinction and immigration rates are in equilibrium or when $dS(t)/dt = 0$. Under nonequilibrium conditions, $dS(t)/dt \neq 0$, and from equation (8)

$$dS(t)/dt = \lambda(P - S) - (\theta/\rho'A)S. \quad (14)$$

The general solution of equation (14) is

$$S(t) = \lambda P/y + Ce^{-yt}, \quad (15)$$

where $y = \lambda + \theta/\rho'A$ and C is a constant whose value will be determined by the initial values of t and S . If t is the time since an archipelago became isolated from its source fauna, at $t = 0$, $\hat{S} < S(t) < P$. From equation (8), the first term on the right side of equation (15) equals \hat{S} . Therefore, $0 < C < (\theta/\rho'A)P/y$. Now

$$z(t) = \frac{(\lambda P/y^2 + tCe^{-yt})(\theta/\rho'A)}{\lambda P/y + Ce^{-yt}}. \quad (16)$$

The relationship between z and t is plotted in figure 3 for three simulations involving different values of λ and $\theta/\rho'A$, but with P and C held constant. First, note that an archipelago which supports relict populations initially has a z -value lower than its equilibrium z -value. With time, the supraequilibrium z -value increases to a maximum value which exceeds \hat{z} and then gradually declines to \hat{z} . The reason for this pattern is straightforward. Before being isolated from its source fauna, each island-to-be will contain the number of species typical of similar areas in the source fauna. Therefore, at the instant that an archipelago is isolated from its source fauna, the archipelago and sample areas from the source fauna should generate equal, low z -values. Extinction rates are higher on small islands than on large islands, and, with time, relict species will become extinct more quickly on

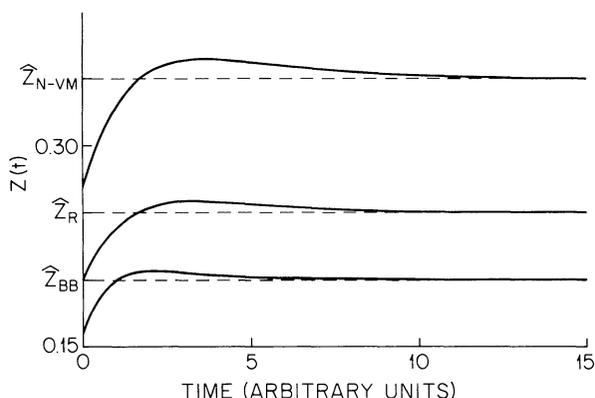


FIG. 3.—Three simulations of equation (16) are plotted. In each simulation, the slope of a log-log species-area curve, z , is plotted as a function of time, t , for an archipelago which initially supported a supraequilibrium fauna. In each simulation, the parameters P and C from equation (16) were set equal to 100 and 19, respectively. Values for λ and $\theta/\rho'A$ were chosen to generate representative values of \hat{z} for three vertebrate taxa. For reptiles, $\hat{z}_R = 0.25$, $\lambda = 0.45$ and $\theta/\rho'A = 0.15$. For nonvolant mammals, $\hat{z}_{NVM} = 0.35$, $\lambda = 0.37$, and $\theta/\rho'A = 0.20$. For birds and bats, $\hat{z}_{BB} = 0.20$, $\lambda = 0.80$, and $\theta/\rho'A = 0.20$.

small islands than on large islands. Therefore, species number will decline most quickly on small islands, and z -values will increase to their maximum as small islands equilibrate. Eventually, relict populations will also become extinct on large islands, and the archipelago will approach a lower equilibrium z -value.

For a given archipelago, different taxa will approach their equilibrium z -values at different rates (fig. 3). If immigration and extinction rates are high (birds and bats) the approach to \hat{z} should be rapid. If immigration and extinction rates are relatively low (amphibians and reptiles), the approach to \hat{z} should be slow. This may explain the z -values observed for lizards on oceanic and landbridge islands in the Gulf of California. The z -values for lizards on landbridge islands may still be increasing toward its maximum, and the z -value for lizards on the older "oceanic" islands may be near its maximum. Finally, intertaxa comparisons of z -values could generate spurious inferences about the history of colonization of an archipelago because different taxa have different equilibrium z -values and different taxa approach their equilibrium z -values at different rates (fig. 3).

With the exception of the West Indies, the archipelagos examined here were once contiguous with the adjacent mainland. If relict populations and nonequilibrium z -values persist on these archipelagos, the fit between observed z -values and predicted values of \hat{z} (table 4) may be suspect. Relict nonvolant mammal populations are known to occur on Great Basin mountaintops (Brown 1971, 1978) and relict lizard populations are known to occur on both landbridge and older "oceanic" islands in the Gulf of California (Case 1975; Wilcox 1978; Murphy, in press). Thus, three comparisons of z -values, two conforming with predictions and one not, are suspect. These same archipelagos do not support relict populations of other vertebrate taxa (Brown 1971, 1978; Case 1975; Lawlor, in press). Moreover,

there is no evidence to suggest that relict vertebrate populations are found on the remaining six archipelagos. Rather, there is evidence to the contrary. Extinction rates are lowest on large islands, and large islands should support relict populations and a supraequilibrium number of species longer than small islands. Therefore, if relict populations are present, large islands should fall above the species-area regression for an archipelago. In fact, large islands consistently fell below the species-area regression for each of the remaining six archipelagos. This suggests that these large islands do not support supraequilibrium numbers of species, the z -values reported in table 4 are equilibrium values, and the comparison of observed z -values with predicted values of \hat{z} is vindicated.

If an archipelago was initially devoid of life, immigration rates would initially exceed extinction rates. To model this case initial values of $t = 0$ and $S = 0$ apply to equation (15). Hence, $C = -\lambda P/y$,

$$S(t) = \frac{\lambda P}{y} (1 - e^{-\mu t}), \quad (17)$$

$$z(t) = \frac{1}{\lambda \rho' A / \theta + 1} + \frac{\theta t / \rho' A}{1 - e^{-\mu t}}. \quad (18)$$

The first term on the right side of equation (18) equals \hat{z} and the second term is always negative. Therefore as an archipelago which was initially devoid of life is colonized, its z -value will approach \hat{z} monotonically as extinction and immigration rates approach an equilibrium.

SUMMARY

This paper investigates the exponent, z , of the power function relating island species number to island area. Two methods used to fit the power function to species-area data are contrasted. In the past, the logarithm of the power function has been fit to species-area data by linear regression. However, the underlying regression model may be inappropriate, and, in any event, the residual sum of squares is minimized and predictive accuracy increases when the power function is fit directly by nonlinear regression.

Theory predicts that z -values should fall in a narrow range and observed z -value are in close agreement. When the power function is fit by linear regression, the consistent magnitude of z -values may be due to statistical artifact (Connor and McCoy 1979). If the power function is fit by iterative, nonlinear regression, statistical artifact does not affect z -values and most observed z -values still fall within the predicted range.

The equilibrium theory of island biogeography allows predictions about z -values. Equilibrium theory postulates that insular biota are determined by a dynamic balance between the immigration of species new to an island and the extinction of species which are already present. The effect of different immigration and extinction rates on z -values is examined after incorporating the relative immigration and extinction rates of terrestrial vertebrate taxa into an equilibrium model. Predicted and observed relative z -values are in close agreement.

Data indicate that z -values are also affected by an archipelago's history of

colonization. I use the equilibrium model to predict changes in z -values with time for archipelagos which were colonized solely by overwater dispersal and for archipelagos which were initially contiguous with their source fauna and were colonized overland.

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APPENDIX

Island area, island species number, and species number in the source fauna summarized for eight archipelagos. Introduced species are not included. The same data for mountaintops in the Great Basin can be found in Brown (1978, table 1). The same data for islands in Lake Michigan can be found in Hatt et al. (1948, tables 12, 14). For each archipelago, the smallest island used in the analyses was determined by the vertebrate taxon which had the most restricted distribution or for which the least distributional information is known (see text). For example, the only vertebrates found on Shoe and Pismire Islands in Lake Michigan are birds, and Shoe and Pismire are only one-sixth as large as the next smallest island studied by Hatt et al. (1948). Therefore Shoe and Pismire were not included in the present analysis.

TABLE A1

BASS STRAIT

	Area (km ²)	Amphibians ^A	Reptiles ^B	Nonvolant Mammals ^C	Birds ^D
Source (Tasmania)		10	15	31	29
Flinders	1,330	6	12	19	22
King	1,100	6	9	13	24
Cape Barren	445	...	11	11	17
Bruny	368	...	5	...	28
Maria	142	5	10	...	22
Clarke	115	...	2	5	...
Three Hummock	80	7	...
Deal	20	...	6	8	7
Badger	10.1	2
Prime Seal	8.9	3	3
West Sister	6.1	4	6
Babel	4.4	2
East Sister	4	1	...
Erith	4	4	5
Waterhouse	3.7	...	5	1	...
Great Dog	3.3	1
Dover	3	1	6
Swan	3	...	2
Preservation	3	3	6
Long	3	1	...

SOURCE.—^ALittlejohn and Martin (1974), anurans only; ^BRawlinson (1974); ^CHope (1973); ^DAbbott (1973), passerine birds only.

TABLE A2
BRITISH CHANNEL ISLANDS

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Birds ^C
Source fauna		16	8	38	105
Jersey	116.3	3	4	9	49
Guernsey	63.5	1	2	5	38
Alderney	7.9	1	1	3	26
Sark	5.2	1	0	2	27
Herm	1.3	0	1	2	—

SOURCE.—^AFrazer (1949); ^BSouthern (1964); ^CDobson (1952) all land bird species, does not include marine or freshwater bird species.

TABLE A3
BRITISH ISLES

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Bats ^B	Birds ^C
Source fauna		17	8	46	15	205
Britain	229,850	6	6	29	12	171
Ireland	85,114	3	1	13	7	102
Lewis	2,137	0	1	2	2	67
Skye	1,738	4	3
Shetland	984	2	2	35
Mull	910	2	2
Anglesey	708	4	4
Islay	603	2	3	5	2	...
Mann	575	1	1	4	3	72
Orkney	490	1	0	4	2	67
Arran	427	4	3
Wight	380	5	5	...	4	...

SOURCE.—^ASmith (1951); ^BSouthern (1964); includes recent extinctions; ^CLack (1942, 1969); all land and freshwater bird species.

TABLE A4
CALIFORNIA CHANNEL ISLANDS

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Birds ^C
Source fauna		11	28	26	93
Santa Cruz	249.	3	6	4	37
Santa Rosa	218.	2	2	3	25
Santa Catalina	194.	3	8	5	34
San Clemente	145.	0	2	2	24
San Nicholas	57.	0	2	2	11
San Miguel	36.	1	2	2	15
Anacapa	2.8	1	2	1	14
Santa Barbara	2.6	0	1	1	10

SOURCE.—^ASavage (1967); ^Bvon Bloeker (1967); ^CDiamond (1969), all land and freshwater bird species.

TABLE A5
GULF OF CALIFORNIA (landbridge islands)

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Birds
Source fauna		5	33	45 ^C	70
Tiburon	1212	1	12	11	32 ^D
Cedros	348	1	7	4	...
Magdalena	290	0	7	8	...
Santa Margarita	205	0	8	7	...
San Jose	194	0	11	7	...
Espiritu Santo	99	2	13	6	...
Espiritu Santo	74				22 ^E
Partida Sur	25				16 ^E
San Marcos	31.5	0	11	2	...
Coronados	8.5	0	10	3	...
Natividad	7.2	0	2	1	...
Encantada Grande	7	0	2	—	...
Danzante	4.9	0	7	2	9 ^E
Smith	4.5	0	3	2	...
Turner	4	3	...
Mejia	3.5	0	3	2	...
San Ildefonso	2.6	0	3
San Francisco	2.6	0	8	2	...
San Martin	2.3	2	...
San Diego	1.3	0	3	1	...
Todos Santos	1.2	2	...
El Muerto9	0	2	1	...
San Roque8	1	...
Las Animas5	0	2
Ballena5	0	4
Santa Ines5	0	2
San Geronimo4	1	...

SOURCE.—^AMurphy and Ottley (in press); ^BLawlor (in press); ^CHuey (1964); ^DRossem (1932); ^EM. Cody (personal communication).

TABLE A6
GULF OF CALIFORNIA (oceanic islands)

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Birds ^C
Source fauna		5	33	45 ^D	70
Angel de la Guarda ...	632	0	10	3	20
Cerralvo	163	1	6	2	22
Carmen	151	0	10	4	15
San Lorenzo Sur	44.5	0	4	2	13
San Esteban	43	0	5	1	20
Santa Catalina	43	0	6	1	...
Montserrat	19.4	0	6	2	...
Santa Cruz	11.6	0	3	1	...
San Lorenzo Norte ...	8.5	0	4	2	10
Tortuga	6.3	0	2	1	...
San Pedro Nolasco ...	3.2	0	5	2	...
Partida Norte	2.1	0	3	...	8
San Pedro Martir	1.8	0	2	...	7
Salsipuedes	1.8	0	3	1	5
Raza	1.1	0	2	...	1
Granito4	1	—

SOURCE.—^AMurphy and Ottley (in press); ^BLawlor (in press); ^CM. Cody (personal communication); ^DHuey (1964).

TABLE A7
TRES MARIAS ISLANDS

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals	Birds ^B
Source fauna		20 ^C	55 ^D	56 ^E	140
Maria Madre	145 ^A	2	17	5*	36
Maria Magdalena	84.2	1	12	...	35
Maria Cleofas	22.5	0	9	...	32
San Juanito	8.8	0	5	...	15

SOURCE.—^AMcDiarmid et al. (1976); Zweifel (1960); ^BGrant and Cowan (1964); ^CJalisco, anurans only, from Zweifel (1960); ^DJalisco, from Zweifel (1960); ^EBaker (1967).

TABLE A8
WEST INDIES

	Area (km ²)	Amphibians ^A	Reptiles ^A	Nonvolant Mammals ^B	Bats ^C	Birds ^D
Cuba	111,463.2	38	87	23	27	68
Hispaniola	73,146.8	51	104	18	17	73
Jamaica	11,525.5	20	33	7	21	66
Puerto Rico	8,860.4	21	32	7	13	55
Guadeloupe	1,510	5	14	1	10	34
Martinique	1,106	3	10	3	9	38
Dominica	790	2	12	1	12	39
St. Lucia	603.5	4	13	2	8	42
Barbados	430	2	8	1	6	16
St. Vincent	344.5	4	12	2	9	35
Grenada	311	4	16	3	12	35
Antigua	281.8	3	11	0	7	20
St. Croix	212.4	5	11	20
Grand Cayman	183.9	2	10	28
St. Kitts	176.1	3	9	0	4	21
Barbuda	162.2	1	7	...	6	20
Marie Galante	150.2	0	5	...	1	14
Montserrat	101	3	10	0	7	22
Nevis	93.3	2	9	19
Anguilla	90.7	0	9	1	5	11
St. Martin	90.7	1	9	...	5	13
Mona	54.4	1	9	1	...	12
Desirade	27.2	1	3	19
St. Bartholomew	24.6	0	8	13
St. Eustatius	19.9	1	9	...	5	18
Saba	13	1	6	...	3	12

SOURCE.—^AMacLean et al. (1977); ^BVarona (1974); includes recent extinctions; ^CBaker and Genoways (1978); Nevis and St. Bartholomew omitted because their faunas are "poorly known"; ^DLack (1976); Columbiformes to Passeriformes.

LITERATURE CITED

- Abbott, I. 1973. Birds of Bass Strait. *Proc. R. Soc. Victoria* 85:197–223.
- Baker, R. H. 1967. Distribution of recent mammals along the Pacific coastal lowlands of the Western Hemisphere. *Syst. Zool.* 16:28–37.
- Baker, R. J., and H. H. Genoways. 1978. Zoogeography of Antillean bats. Pages 53–98 in F. B. Gill, ed. *Zoogeography in the Caribbean*. Phila. Acad. Nat. Sci. Spec. Publ. no. 13.
- Barbour, C. D., and J. H. Brown. 1974. Fish species diversity in lakes. *Am. Nat.* 108:473–489.
- Bennett, A. F., and K. A. Nagy. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697–700.
- Bloeker, J. C. von, Jr. 1967. Land mammals of the Southern California islands. R. N. Philbrick, ed. *Proc. Symp. Biology California Channel Islands*. Santa Barbara Botanic Garden. Santa Barbara, Calif.
- Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.* 105:467–478.
- . 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Nat. Mem.* 2:209–227.
- Carlquist, S. 1965. *Island life*. Natural History, New York.
- Case, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* 56:3–18.
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *Am. Nat.* 113:791–833.

- Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc. Natl. Acad. Sci. USA* 64:57-63.
- . 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* 69:3199-3203.
- Diamond, J. M., M. E. Gilpin, and E. Mayr. 1976. Species-distance relation for birds of the Solomon Archipelago, and the paradox of the great speciators. *Proc. Nat. Acad. Sci. USA* 73:2160-2164.
- Dobson, R. 1952. *The birds of the Channel Islands*. Staples, London.
- Faaborg, J. 1977. Metabolic rates, resources and the occurrence of non-passerines in terrestrial avian communities. *Am. Nat.* 111:903-916.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12:42-58.
- Frazer, J. F. D. 1949. The reptiles and amphibia of the Channel Isles and their distribution. *Br. J. Herpetol.* 1:51-53.
- Glass, N. R. 1969. Discussion of calculation of power function with special reference to respiratory metabolism in fish. *J. Fish. Res. Board Can.* 26:2643-2650.
- Grant, P. R., and I. M. Cowan. 1964. A review of the avifauna of the Tres Marias Islands, Nayarit, Mexico. *Condor* 66:221-228.
- Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight—a reevaluation. *Ecology* 60:389-402.
- Harner, R. F., and K. T. Harper. 1976. The role of area, heterogeneity and favorability in plant species diversity of pinyon-juniper ecosystems. *Ecology* 57:1254-1263.
- Hatt, R. T., J. Van Tyne, L. C. Stuart, and C. H. Pope. 1948. Island life in Lake Michigan. *Cranbrook Inst. Sci. Bull.* 27:1-175.
- Hope, J. H. 1973. Mammals of the Bass Strait Islands. *Proc. R. Soc. Victoria* 85:163-195.
- Huey, L. M. 1964. The mammals of Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.* 13:85-168.
- Lack, D. 1942. Ecological features of the bird faunas of the British small islands. *J. Anim. Ecol.* 11:9-36.
- . 1969. The numbers of bird species on islands. *Bird Study* 16:193-209.
- . 1976. *Island biology. Studies in ecology. Vol. 3.* University of California Press, Berkeley.
- Lawlor, T. E. In press. Biogeography of mammals on islands in the Gulf of California, Mexico. *In* T. J. Case and M. L. Cody, eds. *Biogeography of the islands in the Sea of Cortez*. University of California Press, Berkeley.
- Littlejohn, M. J., and A. A. Martin. 1974. The amphibia of Tasmania. Pages 251-289 *in* W. D. Williams, ed. *Junk, The Hague*.
- MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* 53:330-342.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- . 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- McDiarmid, R. W., J. F. Copp, and D. E. Breedlove. 1976. Notes on the herpetofauna of western Mexico: new records from Sinaloa and the Tres Marias Islands. *Nat. Hist. Mus. L. A. County Contrib. Sci. no.* 275.
- MacLean, W. P., R. Kellner, and H. Dennis. 1977. Island lists of West Indian amphibians and reptiles. *Smithsonian Herpetol. Info. Serv. No.* 40.
- May, R. M. 1975. Patterns of species abundance and diversity. Pages 81-120 *in* M. L. Cody and J. M. Diamond, eds. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Mass.
- Mittermeier, R. A. 1972. Turtles recorded from Barro Colorado Island, Canal Zone. *J. Herpetol.* 6:240-241.
- Murphy, R. W. In press. Origin and evolution of the herpetofauna on the islands in the Sea of Cortez. *In* T. J. Case and M. L. Cody, eds. *Biogeography of the islands in the Sea of Cortez*. University of California Press, Berkeley.
- Murphy, R. W., and J. R. Ottley. In press. A checklist of the amphibians and reptiles on the islands in

- the Sea of Cortez. In T. J. Case and M. L. Cody, eds. *Biogeography of the islands in the Sea of Cortez*. University of California Press, Berkeley.
- Myers, C. W., and A. S. Rand. 1969. Checklist of the amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. *Smithson. Contrib. Zool.* 10:1-11.
- Myers, G. S. 1953. Ability of amphibians to cross sea barriers, with special reference to Pacific zoogeography. *Proc. 6th Pacific Sci. Congr.* 4:19-27.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43:185-215; Part II. 43:410-432.
- Rawlinson, P. A. 1974. Biogeography and ecology of the reptiles of Tasmania and the Bass Strait area. Pages 291-339 in W. D. Williams, ed. *Biogeography and ecology in Tasmania*. Junk, The Hague.
- Ricklefs, R. E., and G. W. Cox. 1972. Taxon cycles in the West Indian avifauna. *Am. Nat.* 106:195-219.
- Rossem, A. J. van. 1932. The avifauna of Tiburon Island, Sonora, Mexico, with descriptions of four new races. *Trans. San Diego Soc. Nat. Hist.* 7:119-150.
- Savage, J. M. 1967. Evolution of the insular herpetofaunas. R. N. Philbrick, ed. *Proc. Symp. Biology Calif. Channel Islands*. Santa Barbara Botanic Gardens, Santa Barbara, Calif.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-141.
- . 1974. The species-area relation within archipelagos: models and evidence from island land birds. Pages 629-642 in *Proc. 16th Int. Ornithol. Congr.*, Canberra, August, 1974.
- Sepkoski, J. J., and M. A. Rex. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. *Syst. Zool.* 23:165-188.
- Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. *Annu. Rev. Ecol. Syst.* 5:161-182.
- Smith, M. 1951. *The British amphibians and reptiles*. Collins, London.
- Southern, H. N. 1964. *The handbook of British mammals*. Blackwell Scientific, Oxford.
- Stenseth, N. C. 1979. Where have all the species gone? On the nature of extinction and the Red Queen hypothesis. *Oikos* 33:196-227.
- Sugihara, G. 1981. $S = CA^z$, $z \approx 1/4$: a reply to Connor and McCoy. *Am. Nat.* 117:790-793.
- Terborgh, J. 1975. Faunal equilibria and the design of wildlife preserves. Pages 369-380 in F. Golley and E. Medina, eds. *Tropical ecological systems: trends in terrestrial and aquatic research*. Springer-Verlag, New York.
- Terborgh, J., and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* 90:759-779.
- Turner, F. B., R. I. Jennrich, and J. D. Weintraub. 1969. Home range and body size of lizards. *Ecology* 50:1076-1081.
- Varona, L. S. 1974. *Catálogo de los mamíferos vivos y extinguidos de las Antillas*. Academia de Ciencias de Cuba, Habana.
- Wilcox, B. A. 1978. Supersaturated island faunas: a species-age relationship for lizards on post-Pleistocene land-bridge islands. *Science* 199:996-998.
- Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* 44:345-389.
- Willis, E. O., and E. Eisenmann. 1979. A revised list of birds of Barro Colorado Island, Panama. *Smithson. Contrib. Zool.* 291:1-31.
- Wilson, E. O. 1969. The species equilibrium. *Brookhaven Symp. Biol.* 22:38-47.
- Wright, S. J. 1979. Competition between insectivorous lizards and birds in central Panama. *Am. Zool.* 19:1145-1156.
- . 1980. Density compensation in island avifaunas. *Oecologia* 45:385-389.
- . 1981. Extinction-mediated competition: the *Anolis* lizards and insectivorous birds of the West Indies. *Am. Nat.* 117:181-192.
- Zar, J. H. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. *BioScience* 18:1118-1120.
- Zweifel, R. G. 1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico. 9. Herpetology of the Tres Marias Islands. *Bull. Am. Mus. Nat. Hist.* 119(2):77-128.