RANDOMNESS, AREA, AND SPECIES RICHNESS[1]

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Abstract. Thorough censuses have been made of breeding birds on islands in Pymatuning Lake, a reservoir at the Pennsylvania-Ohio border. Analysis of the censuses yields the conclusion that for these islands the variation of the number of resident avian species with island size is that which one would expect if the birds were distributed randomly, with the probability of a breeding pair residing on an island proportional to the area of the island and independent of the presence of other pairs. This type of random placement of individuals can yield species-area relations which differ from those commonly employed for analysis of biogeographic data.

Key words: avian ecology; island biogeography; random placement; species-area relations.

Introduction

The way in which the number of species residing on an island or other discrete patch of habitat varies with the size of the patch has long been an important question in ecology. (For some early references, see de Candolle 1855, Jaccard 1908, Arrhenius 1921, 1923*a, b*, Gleason 1922, 1925, Cain 1938, Williams 1943.) It is of concern to fieldworkers seeking to estimate the species richness of areas larger than those accessible to study. The question is also of theoretical interest; relations between species richness and area can reflect such basic matters as the spatial distribution of habitats, the dynamics of population growth and extinction, and the statistics of dispersal and habitat selection. (For surveys, see Mac Arthur and Wilson 1967, Simberloff 1974, Diamond and May 1976, Connor and McCoy 1979.) In recent years attempts have been made to extract principles for the design of nature preserves from species-area data (e.g., Terborgh 1974, Diamond 1975, 1976, Sullivan and Shaffer 1975, Wilson and Willis 1975, Helliwell 1976, MacMahon and Wieboldt 1978, Faaborg 1979, Usher 1979; a pertinent critique is that of Simberloff and Abele 1976). In this article we discuss existing theories of species-area relations and show that a recently published theory (Coleman 1981) that emphasizes the role of randomness in such relations is in nearly perfect agreement with censuses we have taken of the breeding birds of islands in a freshwater lake.

It has been common practice to assume that when all other conditions are constant, such as geographic location and proximity to sources of immigration, the number s of species within a chosen group (e.g., vascular plants, birds, mammals, arthropods) is related to the area a of the sampled region by either a power function (Arrhenius 1921, 1923*a, b*),

$$s = ca^z, \tag{1}$$

with c and z positive constants, or by an exponential (i.e., semilogarithmic) relation (Gleason 1922, 1925),

$$s = G + \kappa \log a, \tag{2}$$

with G and κ positive constants. In early work the latter relation was preferred, particularly by plant ecologists, but in recent years attention has been focused on the power function. Since its derivation by Preston (1960, 1962*a, b*; see also Mac Arthur and Wilson 1967, May 1975), the power function has been almost universally employed in research in island biogeography: field observations are summarized by reports of the parameters c and z (often only z is reported) determined by linear regression analysis based on the logarithmic form of Eq. 1,

$$\log s = \log c + z \log a; \qquad (3)$$

the task of interpreting data is generally taken to be one of determining how z varies with taxonomic group or degree of isolation. (An exception is Gould's recent discussion [1979] of reasons for the variation of c.)

Current research on species-area relations has centered on the verification and application of the equilibrium theory of island biogeography, which was proposed by Preston (1962a, b) and Mac Arthur and Wilson (1963), and which was extensively developed by the latter two authors (Mac Arthur and Wilson 1967) and many subsequent investigators (e.g., Hamilton et al. 1963, Hamilton and Armstrong 1965, Hamilton 1967, Mayr 1965, Diamond 1969, 1970a, b, 1971, 1972, 1973, Simberloff 1969, 1970, 1971, 1972, 1974, 1976, Simberloff and Wilson 1969, 1970, Wilson and Simberloff 1969, Terborgh 1971, 1973, Mac Arthur et al. 1972, Power 1972, Diamond et al. 1976, Diamond and Mayr 1976, Mayr and Diamond 1976, Weissman and Rentz 1976, Diamond and May 1977, Terborgh et al. 1978). The theory rests on the assumption that the number of species residing in a habitat patch is the result of a balance between immigration and extinction. A goal of the theory is the explanation of the dependence of species richness upon such factors as area and the proximity and magnitude of sources of immigrants. Attainment of the goal requires knowledge of or assumptions about the influence of these factors upon rates of immigration and extinction. The theory has been applied to explain patterns of species richness observed not only for real islands, such as oceanic (e.g., Hamilton et al. 1963, Hamilton and Armstrong 1965, Terborgh 1971, 1973, Diamond et al. 1976, Diamond and Mayr 1976, Mayr and Diamond 1976, Terborgh et al. 1978) or land bridge islands (Mac Arthur et al. 1972, Power 1972, Weissman and Rentz 1976, Diamond and May 1977), but also for such patches of habitat as isolated forests (Galli et al. 1976), mountain tops (Cook 1974, Johnson 1975, Behle 1978), caves (Culver 1970, Culver et al. 1973, Veuilleumier 1973), ponds (Hubbard 1973, Keddy 1976), weed lots (Crowe 1979), mangrove clumps (Simberloff 1969, 1971, 1972, 1974, 1976, Simberloff and Wilson 1969, 1970, Wilson and Simberloff 1969), moored floats, i.e., small "artificial islands" (Schoener 1974a, b, Schoener et al. 1978), inflorescences as habitats for insects (Seifert 1975, Brown and Kodric-Brown 1977), rodents as hosts for ectoparasites (Dritschilo et al. 1975), and even troops of monkeys whose intestinal tracts are habitats for protozoa (Freeland 1979). The data required to test or apply the theory are often difficult to obtain. Current debates about the magnitudes of relaxation times for establishment of equilibrium reflect the difficulty of measuring rates of immigration and extinction (e.g., Lynch and Johnson 1974, Simberloff 1976, Wilcox 1978). Moreover, experimenters have found that one cannot always be certain of the com-

position or even the location of sources of immigration (Slud 1976: Discussion). Quantitative determination of the influence of area on the rate of extinction has been particularly difficult to achieve, and recommendations made to designers of nature preserves, when based solely on the theory of island biogeography, should be treated with caution (Simberloff and Abele 1976).

As the number s of species (of the chosen group) residing in a patch is often small, it is significant that s changes only by jumping from one integral value to another, and one may question the precise meaning of such concepts as the rate of change of s (ds/dt), the rate I at which species immigrate into the patch, and the rate E at which species already present become extinct. Nevertheless, it is clear that any reasonable interpretation of the meaning of ds/dt, I, and E (as, say, derivatives of average values of stochastic variables) will lead to a balance law of the form:

$$ds/dt = I - E. \qquad (4)$$

In the equilibrium theory of island biogeography, emphasis is laid on cases in which $ds/dt = 0$, but the theory can be, and often is, extended to nonequilibrium situations in which E does not equal I (e.g., Brown 1971, Abbot and Grant 1976, Heller 1976). If one were able to express accurately I and E as functions of the area a of the patch and the number s of species present, then the equilibrium equation $I = E$ or, more generally, integration of Eq. 4 with appropriate initial conditions, would give a relation between s and a. Unfortunately, theory does not give an accurate characterization of I and E as functions of s and a (even if, for I, the location and magnitude of sources of immigration are known). If there are functions $\hat{E}$ such that $E = \hat{E}(s, a)$, the theory of population dynamics is not sufficiently advanced to give us their form. This does not mean that there is no validity to arguments that rest upon assumptions about qualitative properties of the dependence of I and E on area, species number, and the proximity and size of sources of immigration. Indeed, arguments of the type given by Mac Arthur and Wilson (1967:19–32) appear to be correct in their qualitative conclusions and have stimulated much research in biogeography. It does mean, however, that the general balance law expressed in Eq. 4 does not, as yet, determine the precise form of species-area relations.

In our work we have been concerned with groups of islands, or habitat patches, among which there is interaction in the sense that the patches, although discrete and easily identifiable, are not completely isolated for the species under consideration. Of course, for such islands the definition of "residency" requires consideration of the natural history of the taxa in question. (The residence of an aquatic insect [e.g., a mayfly] is usually taken to be the place where it spends the greater part of its life. For birds, on the other hand,

the place of nesting is usually considered the residence, even though a member of a migratory species may spend the bulk of its life elsewhere, and may even change its residence annually.) While confining attention to cases in which the residence of each individual can be defined unambiguously, we have sought to allow for the possibility that an individual residing in one patch may communicate with another patch either by repeated visits (as might be performed by a bird which forages in regions remote from that in which it breeds) or by the dispersal of offspring to the second patch (as by a plant with wind-borne seeds or an aquatic insect able to lay its eggs in a pond other than that in which it spent its immature stages). As we shall see below, the concept of "species extinction," which is basic to the equilibrium theory of island biogeography, can appear artificial for strongly interactive patches, and in certain cases it may be impossible to give a precise meaning (whether artificial or not) to the rates of extinction and immigration.

Preston's derivation (1962*a, b*) of Eq. 1 rested not on the balance law shown in Eq. 4, but rather on two basic assumptions: (1) that for each island in the group under consideration, the abundances of the species present are given by his "canonical lognormal distribution" (this assumption implied a fixed, albeit complicated, relation between the numbers of species present and the total number of individuals present), and (2) that the total number of individuals residing on an island is proportional to its area a (which in view of (1), implies a relation between s and a). Preston employed numerical arguments to show that the relation between s and a derived in this manner is, for large s, approximated by Eq. 2 with $z \approx 0.26$. May (1975) later showed that for the canonical lognormal distribution, the correct value of z in Preston's derivation of Eq. 1 (for large s) is one-fourth. May observed that Preston's argument yields Eq. 1 in the limit of large s if the canonical lognormal distribution is replaced by more general lognormal distributions, provided the parameter which Preston called "γ" is assumed constant among the islands under consideration. (For the canonical distribution, $\gamma = 1$.) May showed that the values of z which can be obtained by Preston's argument, using plausible choices of γ, fall in the range 0.15–0.39.

The correctness of the assumption (1) may be questioned. If the species abundance relation for each island in some group of islands is lognormal with a prescribed value of the parameter γ, then the species abundance relations for a combination of any two or more islands of the group of islands will not also be lognormal. The lognormal distribution, like many (but not all) abundance relations, lacks the "stability under combination" appropriate for islands among which there is strong interaction. In general, it would appear that any theory employing an a priori assumption about the form of the species abundance relation for each island in a group rests on tenuous ground. A preferable alternative would be a theory employing information about only the overall abundances of the species in the union of the group of islands, and permitting one to deduce, from a clearly stated statistical assumption about the way individuals are distributed in space, the probability that a particular species is represented on a given island. Such a theory was recently constructed by Coleman (1981). The statistical assumption explored in that research is that the probability that an individual known to reside somewhere in a group of islands actually resides on a particular island is proportional to the area of the island and is independent of the presence on that island of other individuals. In addition to presupposing statistical homogeneity for the spatial distribution of environmental influences (environmental influences are here the things, other than the members of the group of species under study, that affect an individual's arrival at, or survival on, a particular island), this assumption, called the *hypothesis of random placement*, presupposes a lack of correlation in the locations of individuals. It may be considered a "zeroth-order hypothesis" whose consequences can be derived and tested with rigor and which should be considered before one postulates the presence of communities resulting from nonrandom associations of species. In cases in which its consequences are not in good quantitative accord with field observations, the zeroth-order hypothesis must be rejected, and one may consider hypotheses that do not assign zero value to the correlations in the locations of individuals. When rendered mathematically precise, such hypotheses, whether they describe an "attraction" resulting from, for example, the tendency of individuals with the same requisites to reside in the same habitat, or a "repulsion" resulting from agonistic behavior and/ or competitive exclusion, will yield theories of much greater complexity than that based on the hypothesis of random placement.

In the following section we shall review some experimentally verifiable consequences of the hypothesis of random placement. We shall then present a summary of extensive census data for breeding birds on islands in Pymatuning Lake, and we shall show that the data are in accord with the hypothesis.

For the birds that inhabit them, the islands in Pymatuning Lake are poorly isolated, or strongly interactive. Although a breeding bird has a definite and identifiable island of residency, the bird may visit or forage for food on several islands or on the mainland each year, or even each day, and is capable of changing residency from one breeding season to the next. For such strongly interactive islands the concepts of immigration and extinction appear inappropriate. It is particularly artificial to apply the word *extinct* to a

group of birds, many of which are still living, but have changed residency, and may even someday return to their original island of residence. Moreover, because breeding sites are selected each year during a brief period that depends on the species under consideration and are generally abandoned within a few months, *rates I* and *E*, of immigration and extinction do not appear to have any meaning at all here. On the other hand, the language and mathematical concepts of the theory of random placement have meaning for both the well-isolated islands for which the equilibrium theory of island biogeography was originally intended and for the strongly interactive islands considered here; for the latter, a "placement" may be thought of as a "choice" made by an individual early in the breeding season. Of course, concepts that have meaning are not necessarily applicable or correct, and the fact that consequences of the hypothesis of random placement are well confirmed by a thorough study of a group of strongly interactive islands does not settle the question of whether the hypothesis will yield correct species-area relations for weakly interactive islands, where the constraints on immigration and emigration can imply an intraspecific correlation in placement resulting from a sharing of ancestors. As far as we know, the complete censuses of individuals required for verification of the hypothesis of random placement are not yet available for large-scale systems of weakly interactive islands.

THEORY OF RANDOM PLACEMENT

Consider a collection $\mathbf{C}$ of N individuals from S species, with n_i the number of individuals in $\mathbf{C}$ belonging to the ith species, and suppose that each member of $\mathbf{C}$ resides in one of K nonoverlapping regions, or islands, which have areas $a_1, a_2, \ldots, a_K$. In the absence of further information, a reasonable preliminary assumption about the locations of the members of $\mathbf{C}$ would be that these N individuals are distributed in accord with the hypothesis of random placement mentioned above. In our present notation, this hypothesis may be stated as follows: for each k, $k = 1$, $2, \ldots, K$, the probability Q_k that a particular individual of $\mathbf{C}$ resides in the kth region is independent of the locations of other individuals and is given by

$$Q_k = \beta a_k \tag{5}$$

with β a constant. Because each member of $\mathbf{C}$ is in one of the K regions under consideration, there holds

$$\sum_{k=1}^{K} Q_k = 1, \tag{6}$$

and Eq. 5 reduces to

$$Q_k = \alpha_k, \tag{7}$$

where α_k is the relative area of the kth region, i.e.,

$$\alpha_k = \alpha_k \bigg/ \sum_{l=1}^{K} a_l. \tag{8}$$

Random placement implies that the probability that no member of the ith species resides in the kth region is simply $(1 - Q_k)^{n_i}$, which is the same as $(1 - \alpha_k)^{n_i}$, and hence the probability $p_i(k)$ that at least one member of the ith species does reside in the kth region is here given by the formula,

$$p_i(k) = 1 - (1 - \alpha_k)^{n_i}. \tag{9}$$

Under the hypothesis of random placement, the number s of species to be found residing in a given region is a random variable whose magnitude depends on the area a of the region. Eq. 9 implies that the mean value $\bar{s}$ and the variance σ^2 of s are determined as follows from knowledge of the region's relative area, $\alpha = a/\Sigma_k a_k$, and the overall abundances $n_1, n_2, \ldots, n_S$ of the S species represented in $\mathbf{C}$ (cf. Coleman 1981):

$$\bar{s}(\alpha) = S - \sum_{i=1}^{S} (1 - \alpha)^{n_i}, \tag{10}$$

$$\sigma^2(\alpha) = \sum_{i=1}^{S} (1 - \alpha)^{n_i} - \sum_{i=1}^{S} (1 - \alpha)^{2n_i}. \tag{11}$$

The curve obtained by plotting $\bar{s}$ against α is called the *expected species-area* curve. It should be emphasized that here the overall abundance n_i of each of the S species represented in $\mathbf{C}$ is treated as a known quantity, not as a random variable. If only a probability distribution were specified for the list $\mathbf{n} = (n_1, n_2, \ldots, n_S)$, the present results would be "conditional upon $\mathbf{n}$", and replacement of each n_i in Eqs. 10 and 11 by its mean value $\bar{n}_i$ would not, in general, yield correct formulae for $\bar{s}$ and σ^2.

In the experiments described below, the K nonoverlapping regions are islands in a lake, and $\mathbf{C}$ is the set of all male birds which breed during a particular year on the islands. The number a_k is the area of the kth island, and α_k is the fraction of the total area of the K islands which belongs to that island. For each i, n_i is the total number of breeding males (or breeding pairs) in $\mathbf{C}$ which belong to the ith species, and this number was determined by careful and repeated censuses. The censuses also yield s_k, the number of species that have breeding pairs on the kth island. A test of the appropriateness of the hypothesis of random placement can, therefore, be obtained by plotting the observed values of s_k against α_k and seeing how the experimental points (α_k, s_k) lie relative to the expected species-area curve obtained by inserting the known values of n_i into Eq. 10. If the hypothesis of random placement holds, the experimental points (α_k, s_k) should be randomly distributed about the graph of $\bar{s}(\alpha)$ obtained from Eq. 10, and roughly two-thirds of the points (α_k, s_k) should fall within the band bounded by the graphs of $\bar{s}(\alpha) + \sigma(\alpha)$ and $\bar{s}(\alpha) - \sigma(\alpha)$ obtained from Eqs. 10 and 11. Systematic or excessively large departures of the experimental points (α_k, s_k) from the expected species-area curve determined by Eq. 10
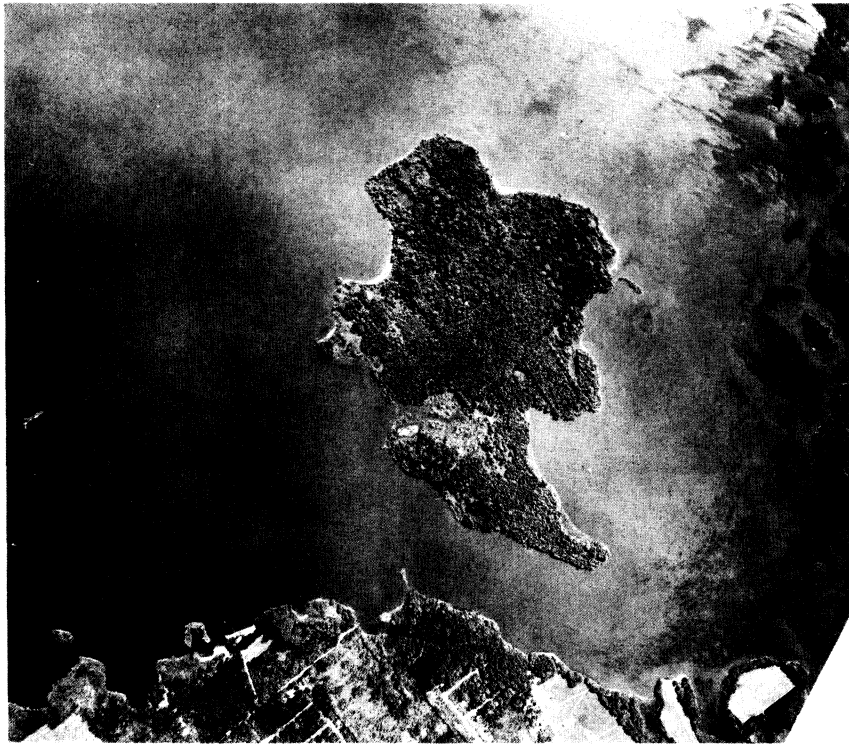
Fig. 1. Aerial photograph of Clark Island, the largest island studied. The vegetation forming a regular pattern with a rectilinear texture is planted pine; it is nearly surrounded by deciduous forest. A large swamp is visible at the left-center of the island; a smaller swamp may be seen at the upper left. Smaller islands appear at the right and lower left of the field of view.

would indicate that the breeding birds comprising **C** do not obey the hypothesis of random placement.

Before describing the experimental methods and results, we will point out some consequences of Eqs. 10 and 11.

The *species abundance distribution function* (for **C**) is the function h such that, for each positive integer n, $Sh(n)$ is the number of species represented in **C** by precisely n individuals. It is easily shown that Eq. 10 implies that as α increases from 0 to 1, $d\bar{s}(\alpha)/d\alpha$ decreases from N to $Sh(1)$. Moreover, if we put, for each value of α,

$$z(\alpha) = \frac{d \log \bar{s}(\alpha)}{d \log \alpha}, \qquad (12)$$

then Eq. 10 yields:

$$z(\alpha) = \frac{\alpha \sum_{i=1}^{S} n_i (1 - \alpha)^{n_i - 1}}{1 - \sum_{i=1}^{S} (1 - \alpha)^{n_i}}$$

$$= \frac{\alpha \sum_{n=1}^{\infty} h(n) n (1 - \alpha)^{n-1}}{1 - \sum_{n=1}^{\infty} h(n)(1 - \alpha)^{n}}, \qquad (13)$$

for $0 < \alpha < 1$, and

$$z(0) = 1, \qquad z(1) = h(1). \qquad (14)$$

Thus, the hypothesis of random placement implies that, as the relative area α varies from 0 to 1, the slope of a plot of the logarithm of the expected number of species vs. the logarithm of the area should decrease from 1 to $h(1)$. (For a discussion of this point see Coleman [1981: Section 3]). Because $h(1)$ is the fraction of the total number of species in **C** that are represented by only one individual, $h(1)$ can be expected to be small compared to unity, which, by Eq. 14, here implies that $z(1)$ is significantly less than $z(0)$.

There are many published reports of cases in which z decreases with increasing α (e.g., Wilson and Taylor 1967, Whitehead and Jones 1969, Heatwole 1975). Of particular relevance are the recently published observations of K. A. Rusterholz and R. W. Howe (1979), who studied the distribution of birds among islands in a Minnesota lake. Although most of their data are based on single rather than repeated censuses, and they do not make a sharp distinction between the sighting of an individual on an island and the determination of whether it was breeding on the island, their data do show a definite and pronounced tendency for z to decrease as α increases and, in broad features, are in accord with our observations for the birds on the islands in Pymatuning Lake. Of course, an exper-
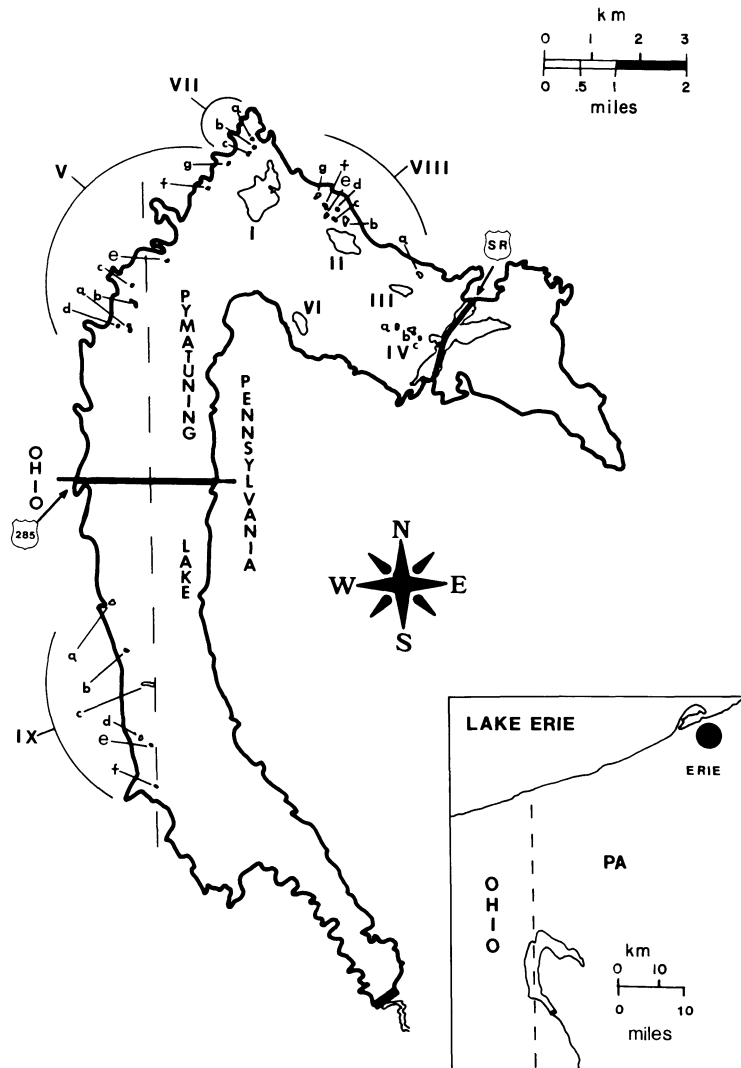
FIG. 2.   Map of Pymatuning Lake showing the islands studied and their code numbers. The names and areas of the four largest of these islands are: I, Clark, 69.4 ha; II, Harris, 22.8 ha; III, Whaley, 9.4 ha; and VI, Tuttle, 9.1 ha. The next largest islands are IVb (2.7 ha) and Ve (1.4 ha). The smallest island shown is IXe (0.09 ha). United States Highway 285 forms a causeway over the lake. The symbol SR indicates a Pennsylvania state route that traverses a dam which on its southeast side impounds the upper region of the lake.

imental observation that z decreases with α does not, by itself, confirm the hypothesis of random placement. Preston's (1962a, b) original derivation of Eq. 2 yields the power function, with z constant, only in the limit of large s (i.e., large a) and suggests that z should be larger at small a than in the limit of large a. (See the discussion of May [1975] and the data shown by Hamilton [1967]). Schoener (1976) has recently given reasons for expecting that z should, in general, decrease with increasing a when the tenets of the equilibrium theory of island biogeography hold and there is competition for an area-dependent resource.

METHODS

Pymatuning Lake was formed in 1932 by the flooding of gently rolling terrain along the Shenango River.

A description of the region and its avifauna was given by Grimm (1952). The crests of the hills of the original terrain are the islands seen today in the lake; they have been left undisturbed, and in several cases contain stands of trees that were present in 1932 (Fig. 1). Fieldwork was conducted on 41 of these islands (Fig. 2) in the years 1975–1979. Thorough censuses of breeding birds were taken on 17 islands in 1978 and on 30 islands in 1979. Each of the islands studied in 1978 was reexamined in 1979.

The vegetation on the islands was investigated in detail. Plant densities, and the diversities of plant species, foliage heights, and habitat types were studied by M. A. Mares, M. R. Willig, T. E. Lacher, Jr., and K. E. Streilein. In general, the vegetation is typical of lowland Eastern Deciduous Forest. Most islands of

TABLE 1. Area a_k, relative area α_k, and number s_k of resident species for each island of Pymatuning Lake surveyed throughout the breeding season. The island code names are those of Fig. 2. For 1978 the index k runs from 1 to 17, for 1979 from 1 to 30.

		1978		1979	
Code	a_k (hectares)	α_k	s_k	α_k	s_k
I	69.44	0.5739	34	0.5488	35
II	22.83	0.1887	28	0.1804	26
III	9.40	0.0777	17	0.0743	24
IVa	0.72	0.0060	6	0.0057	6
IVb	2.68	0.0222	10	0.0212	9
IVc	0.33	0.0027	2	0.0026	1
Va	0.49	0.0041	3	0.0039	2
Vb	0.63	0.0052	2	0.0050	7
Vc	0.91	0.0075	5	0.0072	3
Vd	0.78	0.0064	3	0.0062	3
Ve	1.44	0.0119	5	0.0114	6
Vf	0.55	0.0045	5	0.0043	5
Vg	0.94	0.0078	4	0.0074	4
VI	9.14	0.0755	24	0.0722	28
VIIa	0.27	0.0022	1	0.0021	4
VIIb	0.26	0.0021	0	0.0021	0
VIIc	0.18	0.0015	0	0.0014	0
VIIIa	0.72	. . .	. . .	0.0057	3
VIIIb	0.98	. . .	. . .	0.0077	8
VIIIc	0.55	. . .	. . .	0.0043	2
VIIId	0.26	. . .	. . .	0.0021	2
VIIIe	0.10	. . .	. . .	0.0008	0
VIIIf	0.25	. . .	. . .	0.0020	3
VIIIg	0.26	. . .	. . .	0.0021	4
IXa	0.28	. . .	. . .	0.0022	3
IXb	0.39	. . .	. . .	0.0031	2
IXc	0.69	. . .	. . .	0.0055	5
IXd	0.85	. . .	. . .	0.0067	4
IXe	0.09	. . .	. . .	0.0007	1
IXf	0.13	. . .	. . .	0.0010	3

area larger than 0.6 ha contain deciduous stands with closed canopies at a height of ≈ 25 m; the dominant trees are usually maple (*Acer*), cherry (*Prunus*), and oak (*Quercus*). Often, various vines (e.g., *Vitus, Parthenocissus*, and *Rhus*) form a complex network extending through the subcanopy. Islands I, II, and III (Clark, Harris, and Whaley) contain planted stands of regularly spaced Norway Spruce (*Picea abies*) and Red Pine (*Pinus resinosa*), with little or no understory. There are marshes on several islands; in them, willows (*Salix*) are the dominant trees, and grasses and sedges predominate in open areas. On some smaller islands the principal woody plants are sumacs (*Rhus*) and poplars (*Populus*). The peripheries of most islands contain sandy beaches as well as areas of dense shrubs, e.g., dogwood (*Cornus*), arrowwood (*Viburnum*), and willow (*Salix*). Clark Island, the largest, contains a small marsh in which emergent plants such as cattails (*Typha*) and water lilies (*Nuphar*) interdigitate with willows and grasses.

In 1978 and 1979, the avifauna of the islands was studied throughout the breeding season (May to July). Nocturnal species were excluded from this study. In order to confine our observations to birds that nest
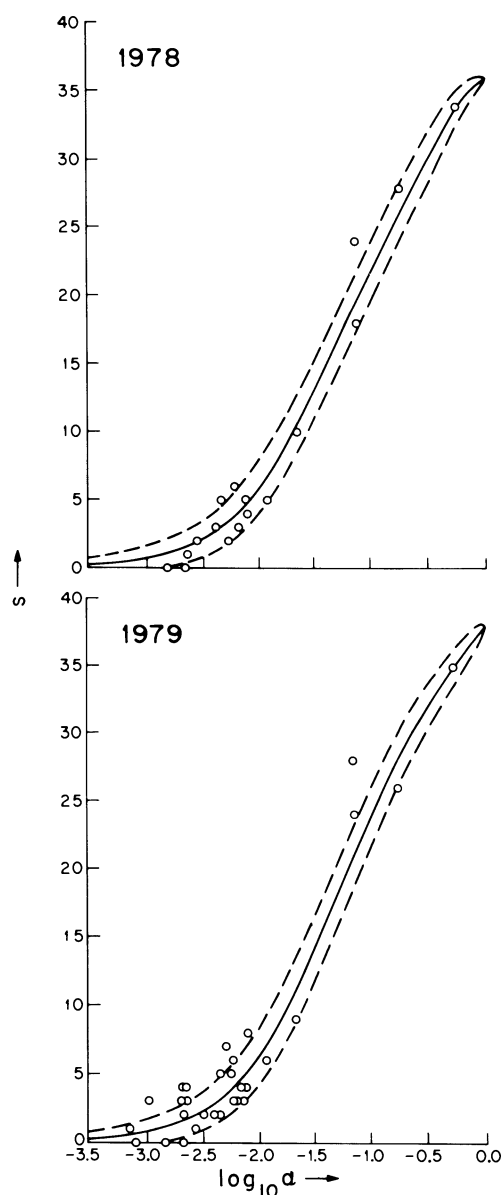

FIG. 3. Comparison of field data with consequences of the hypothesis of random placement: the number s of species vs. the logarithm of the relative area α. The solid curve is $\bar{s}$, and the dashed curves are $\bar{s} + \sigma$ and $\bar{s} - \sigma$; $\bar{s}$ and σ are calculated from Eqs. 10 and 11 using the overall species abundances n_i listed in Table 2. The observed values of s_k listed in Table 1 are shown as circles.

and forage on the islands, we also excluded, a priori, waterfowl, swallows, swifts, and raptors. However, no swifts or hawks were actually found nesting on the islands. Slud (1976) discusses reasons for omitting various avian species from island surveys. Teams of up to 16 investigators performed repeated transect sweeps of island interiors and boat surveys of edge habitats to determine the numbers and locations of resident pairs of birds. When territorial males were

TABLE 2. Overall census data for birds on islands in Pymatuning Lake, 1978 and 1979: n_i is the number of breeding pairs of the ith species residing in the union of all the islands, ν_i is the number of islands on which the species occurred, and i is the species rank according to abundance. For example, in 1978 there was a total of four pairs of Ruffed Grouse breeding on 3 of the 17 islands studied, and the species ranked 25th in abundance.

	n_i		ν_i		i	
Bird species	1978	1979	1978	1979	1978	1979
Galliformes						
Tetraonidae						
Ruffed Grouse	4	2	3	2	25	33
Cuculiformes						
Cuculidae						
Yellow-billed Cuckoo	1	5	1	4	36	28
Apodiformes						
Trochilidae						
Ruby-throated Hummingbird	2	3	2	3	34	29
Coraciiformes						
Alcedinidae						
Belted Kingfisher		1	0	1		36
Piciformes						
Picidae						
Common Flicker	6	8	2	3	19	24
Hairy Woodpecker	5	3	3	2	23	30
Downy Woodpecker	6	9	3	5	20	23
Passeriformes						
Tyrannidae						
Eastern Kingbird	6	12	4	9	22	18
Great Crested Flycatcher	2	9	2	4	32	22
Eastern Phoebe		1	0	1		37
Eastern Wood Pewee	20	24	4	4	14	11
Corvidae						
Blue Jay	16	18	3	3	16	14
Common Crow	19	15	5	6	15	15
Paridae						
Black-capped Chickadee	53	53	6	6	5	5
Sittidae						
White-breasted Nuthatch	3	6	2	3	29	26
Troglodytidae						
House Wren	42	46	5	5	8	7
Short-billed Marsh Wren		2	0	1		31
Mimidae						
Catbird	74	66	11	15	3	3
Turdidae						
Robin	22	19	4	5	13	12
Wood Thrush	28	14	4	3	10	17
Veery	22	24	4	3	12	10
Bombycillidae						
Cedar Waxwing	30	19	4	8	9	13
Sturnidae						
Starling	2		2	0	33	
Vireonidae						
Warbling Vireo	8	1	2	1	17	34
Red-eyed Vireo	60	50	5	6	4	6
Parulidae						
Yellow Warbler	85	119	13	21	1	1
Yellowthroat	6	12	3	3	21	19
Prothonotary Warbler		1	0	2		35
American Redstart	3	15	1	3	27	16

Table 2. Continued.

Bird species	n_i		ν_i		i	
	1978	1979	1978	1979	1978	1979
Icteridae						
Red-winged Blackbird	45	44	10	11	6	8
Common Grackle	25	64	5	13	11	4
Brown-headed Cowbird	7	6	4	4	18	27
Northern Oriole	4	10	3	4	26	21
Thraupidae						
Scarlet Tanager	2	7	2	3	30	25
Fringillidae						
Cardinal	43	35	6	5	7	9
Rose-breasted Grosbeak	4	10	3	5	24	20
American Goldfinch	3		1	0	28	
Rufous-sided Towhee	2	1	2	1	31	38
Swamp Sparrow		2	0	1		32
Chipping Sparrow	1		1	0	35	
Song Sparrow	79	78	14	24	2	2

sighted, their locations were mapped, and observations of nests, females, and young were recorded. Each island was visited from 2 to 10 times in the breeding season; the larger islands were visited more frequently and by larger teams of investigators. Censuses began at dawn and ended at noon. Several days of such fieldwork on an island usually sufficed for the construction of a map of the location of the resident males. The procedures were repeated several times during the breeding season, and subsequent comparison of the maps obtained showed good agreement between censuses. The assumption was made that territorial males are successfully paired with females and hence can be identified as breeding pairs; this assumption was confirmed sufficiently often by sightings of females, nests, and/or young to give us confidence in its validity. More detailed information about the methods will be published elsewhere, along with island-by-island species abundance data, but we wish to emphasize here that the methods and the criteria for identification of breeding pairs were followed rigorously. The values of s_k shown in Table 1 and of n_i shown in Table 2 are the result of 2200 man-hours of observation.

The total number, S, of species with breeding pairs on the islands studied was 36 in 1978 and 38 in 1979. The total number of breeding pairs, summed over species and islands, was 740 in 1978 and 814 in 1979. Tables 1 and 2 contain all data required to verify the calculations we report and discuss below.

RESULTS AND DISCUSSION

Employing Eqs. 10 and 11 and the values of n_i shown in Table 2, we have calculated the values that the hypothesis of random placement yields for $\bar{s}(\alpha)$ and $\sigma(\alpha)$. The results of these calculations are shown in Fig. 3, where we have also plotted the experimental results shown in Table 1. The way the data points (α_k, s_k) fall relative to the expected species-area curve is clearly in accord with the hypothesis of random placement. These points are rather evenly distributed about the graph of $\bar{s}(\alpha)$, without inordinately large departures of s_k from $\bar{s}(\alpha_k)$. Of the 17 values of s_k obtained in 1978, 12 (70.6%) lie within the interval from $\bar{s}(\alpha_k) - \sigma(\alpha_k)$ to $\bar{s}(\alpha_k) + \sigma(\alpha_k)$; of the 30 values of s_k obtained in 1979, 15 (50%) lie within such an interval. As $\bar{s}(\alpha_k)$ and $\sigma(\alpha_k)$ are *theoretical* values of the mean and standard deviation in s_k, and the average of 0.706 and 0.500 is 0.60, not only the central tendency but also the spread in the experimental data is in accord with the theory of random placement.

Because the set of islands studied in 1979 was larger than the set studied in 1978, a given island studied in both years had a larger value of α in 1978 than in 1979. However, as the total area $\Sigma_k a_k$ is known for both years, one may convert the function $\bar{s}$ shown in Eq. 10 into a relation between the expected number $\bar{s}$ of resident species and the island area a. Graphs of $\bar{s}/S$ as a function of a (actually log a) are shown in Fig. 4 along with the corresponding data points (a_k, s_k/S). The solid and dashed curves are calculated from the theoretical relation Eq. 10 using the values of n_i for 1978 and 1979; the agreement between these two curves is a consequence of the fact that the normalized overall species abundance relations for the two years were of similar form. In this figure we again see experimental points evenly distributed about expected values derived using the theory of random placement.

One may ask whether the power function of Eq. 1 or the exponential relation of Eq. 2, with the constants c and z or G and κ, suitably adjusted, can give a better fit to the data of Table 1 than the theoretical species-area relation $\bar{s}$ of Eq. 10 does. To examine this possibility, we employed the species-area data for 1978 and
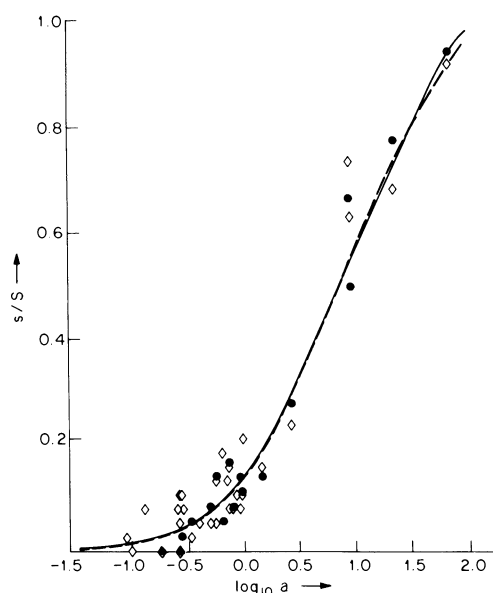
FIG. 4. Species-area data for two years. The observed values of s_k/S are plotted against $\log a_k$: ●, 1978; ◇, 1979. The two nearly coincident curves show $\bar{s}/S$ calculated from Eq. 10 using the values of n_i for each year: $- - -$, 1978; ———, 1979.

1979 separately to determine the parameter pairs (c, z) and (G, κ) by least-squares linear regression analyses based on Eq. 3 (the logarithmic form of Eq. 1) and Eq. 2 (with $\log = \log_{10}$). The results are given in Table 3 and Fig. 5. As $\log s$ (appearing in Eq. 3) is not finite at $s = 0$, for these calculations we set aside the data points with $s_k = 0$ and took the total number of islands to be $K' = 15$ in 1978 and $K' = 27$ in 1979, instead of the actual values ($K = 17$ for 1978 and $K = 30$ for 1979). In Table 3 we list the values that these constants give to the root mean-square deviations $\Delta_{(P)}$, $\Delta_{(E)}$, and $\Delta_{(R)}$, associated with Eqs. 1, 2, and 10:

TABLE 3. Values of the parameters in Eqs. 2 and 3 derived from the data in Table 1 by linear regression analysis.

Parameters	Year	
	1978	1979
K'	15	27
Power function		
c	4.298	4.993
z	0.600	0.543
$\Delta_{(P)}$	5.8	4.1
Exponential function		
G	6.549	8.333
κ	14.453	12.743
$\Delta_{(E)}$	3.9	3.4
Random placement		
$\Delta_{(R)}$	1.7	2.2
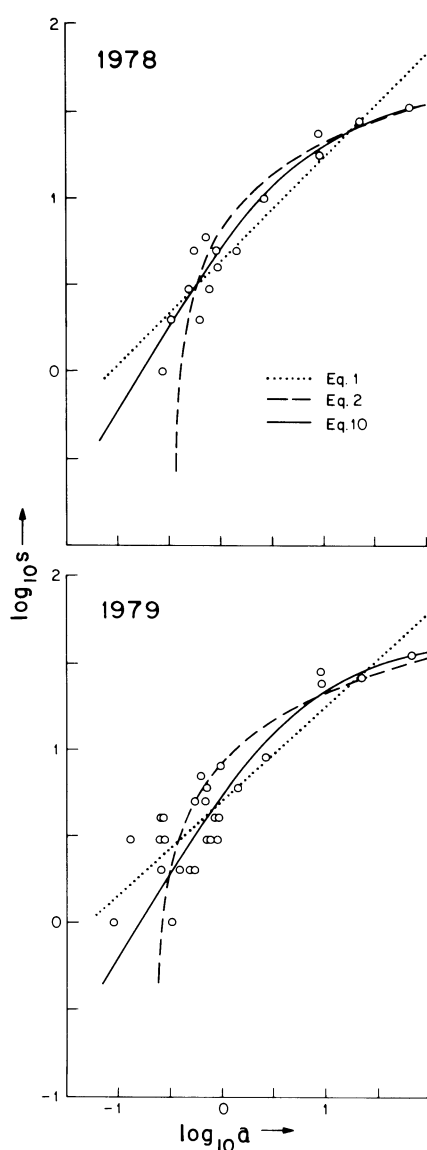
FIG. 5. Comparison of observed values of s with those calculated from the power function of Eq. 1, the exponential relation of Eq. 2, and the expected species-area function $\bar{s}$ derived from the hypothesis of random placement (Eq. 10). The parameter pairs (c, z) and (G, κ) are as in Table 3.

$$\Delta^2_{(P)} = \frac{1}{K'} \sum_{k=1}^{K'} [s_k - ca_k^z]^2, \tag{15}$$

$$\Delta^2_{(E)} = \frac{1}{K'} \sum_{k=1}^{K'} [s_k - G - \kappa \log a_k]^2, \tag{16}$$

$$\Delta^2_{(R)} = \frac{1}{K'} \sum_{k=1}^{K'} [s_k - \bar{s}(\alpha_k)]^2. \tag{17}$$

It is interesting that the standardized measures of deviation $\Delta_{(P)}$, $\Delta_{(E)}$, and $\Delta_{(R)}$, while differing greatly among themselves, are approximately reproducible from year to year. Our calculations show clearly that:

(1) the power function of Eq. 1 gives a rather poor fit to the species-area data of Table 1, with $\Delta_{(P)}$ in the range 4.1–5.8 (species per island); (2) the exponential relation of Eq. 2 gives a somewhat better fit, with $\Delta_{(E)}$ in the range 3.4–3.9; and (3) the best fit of all is given by the expected species-area relation $\bar{s}$ based on the theory of random placement, for which $\Delta_{(R)}$ is ≈ 2. This last conclusion is strengthened by the observation that the function $\bar{s}$ is determined from overall species abundance data, rather than by regression analysis of species-area data, and hence does not contain free parameters which may be adjusted to lessen the mean-square deviation.

When the experimental points with $s_k = 0$ are included, and the actual values of K are employed in Eqs. 16 and 17, our analysis yields the following results for the parameters G and κ of Eq. 2 and the mean-square deviations $\Delta_{(E)}$ and $\Delta_{(R)}$: $G = 6.986$, $\kappa = 13.871$, $\Delta_{(E)} = 3.8$, and $\Delta_{(R)} = 1.7$ for 1978; $G = 8.446$, $\kappa = 12.425$, $\Delta_{(E)} = 3.35$, and $\Delta_{(R)} = 2.1$ for 1979. Thus, the conclusions (1), (2), and (3), stated above, are not affected by the omission of the data points with $s_k = 0$. Of course, such points could not be shown in Fig. 4 where the ordinate is log s, but these points do appear in Figs. 2 and 3.

As we have seen, the hypothesis of random placement does not imply that $z(\alpha)$, the logarithmic derivative of the expected (i.e., averaged) species-area function $\bar{s}$, should be a constant. Because the random variable s_k has a large variance, it would be difficult to compute the dependence of z on α (or on a) directly from experimental data points (a_k, s_k) of the type given in Table 1. However, under the hypothesis of random placement, we may compute $z(\alpha)$ from Eq. 13, using the numbers n_i in Table 2. The result of such a calculation (Fig. 6) gives the dependence on island area of the slopes of the solid curves shown in Fig. 5. The calculated values of z shown in Fig. 6 are very sensitive to the relative area, and Preston's (1962a, b) "canonical value" of 0.26 (or 0.25 [May 1975]) appears to be without particular significance. For 1979 the theoretical value of $z(\alpha)$ at the smallest island studied (IXe, which contained 1 species) is $z_{min} = 0.154$, and the value of $z(\alpha)$ at the largest island (I, with 35 resident species) is $z_{max} = 0.982$; for 1978, $z_{min} = 0.159$ and $z_{max} = 0.966$.

We have shown that the hypothesis of random placement accounts for the distribution of bird species among the islands of Pymatuning Lake better than the commonly employed empirical relations. The hypothesis allows one to predict not only the mean number of species on an island, but also the variation in species richness. Although a lack of statistical correlation in location of individuals is subsumed in the hypothesis, the fact that our study confirms its consequences does not contradict the presence of intra-specific or interspecific competition. Our field data are compatible with the assumption that the birds act in
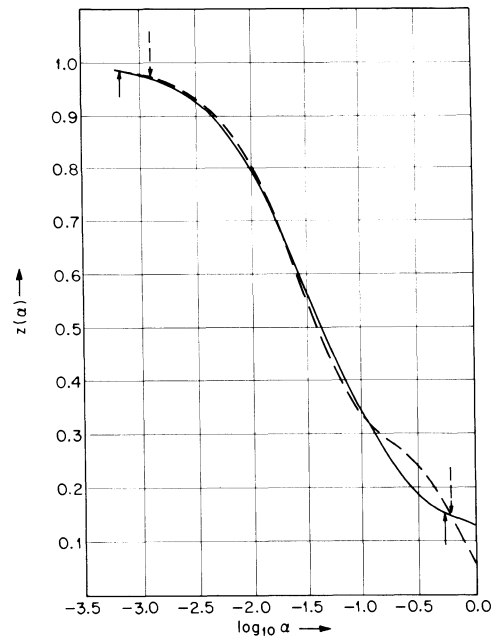

FIG. 6. Dependence of z on island size according to Eq. 13: ...., 1978; ———, 1979. The largest and smallest islands surveyed each year are indicated with arrows.

an approximately independent manner when they select breeding sites; this does not imply that the birds do not compete for food or other requisites, either during the breeding season or in other seasons during which they are away from the breeding area.

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