APPLICATION OF ISLAND BIOGEOGRAPHIC THEORY TO WILDLIFE PRESERVES

By

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Recent studies of isolated faunal communities suggest that the island biogeographical model might serve as a predictor of the species changes likely to occur in wildlife preserves and sanctuaries. The biogeographical model and empirical evidence both imply that preserve faunal communities experience species depletion as a result of increasing isolation. Factors affecting species specific vulnerability to extirpation from isolated preserves are discussed. Differences between continental preserve and previously studied insular animal communities are emphasized. No relation between preserve size and the number of extant large mammal species could be established for 13 comparable East African preserves. However, in the Everglades National Park analysis revealed a substantive species-area relation. The model is believed to be appropriate for predicting the equilibrium number of species as preserves develop toward total isolation. A comparison of model predictions with available data from two preserves supports the hypothesis that extirpation towards a stable equilibrium may be associated with the wildlife preserve phenomenon.

Chairman

INTRODUCTION

Active management is now accepted as a necessary measure for maintaining ecosystems at a steady state. This approach seems particularly applicable to small areas preserved as vignettes of larger natural systems but surrounded by developed areas. Resource management strategies are generally referenced to past conditions and do not sufficiently consider changes which may occur in the future. The development of these strategies has been based mostly on an inductive approach consisting of the long-term recording of empirical data, the observation of correlated structural changes in the system and finally reactive management. This scheme has generally not resulted in tested hypotheses or advancement of theory. The opposite approach may prove more effective in providing insight into the nature of biological systems. This is the deductive logic format based on the formulation of falsifiable hypotheses and their subsequent acceptance or rejection.

Recent advances in ecological theory have mainly concerned the dynamics of ecosystem processes. This contrasts markedly from the more classical descriptions of structural components. This study applies the deductive format to the dynamic processes controlling the plant and animal communities of nature preserves.

The theory of island biogeography (MacArthur and Wilson, 1963, 1967) constitutes a deductive explanation of the characteristics of island biotic communities. The theory suggests that these communities result from a dynamic equilibrium between species immigration and extinction rates. These two rates are in turn controlled by factors such as island size and distance from the nearest gene pool. Considerable empirical evidence in support of the theory has since been accumulated (Diamond, 1969; Simberloff, 1969; Simberloff and Wilson, 1969; Terborgh and Faaborg, 1973).

Recent interpretations have also suggested that the same model might explain the equilibrium number of species on continental areas separated from surrounding gene pools (Diamond, 1973, 1975a; Hooper, 1971; Kolata, 1974; May, 1975; Slater, 1975; Sullivan and Shaffer, 1975; Terborgh, 1974, 1975; Wilson and Willis, 1975). This proposition appears tentatively verified by three independent lines of evidence from faunal communities in naturally occurring continental isolates and recently isolated continental areas. First, the faunal species equilibrium in naturally occurring isolated areas such as mountaintops (Brown, J.H., 1971), caves (Culver, 1970), alpine grasslands (Vuilleumier, 1970) and in ponds and lakes (Hubbard, 1973) is predictable from this model. Secondly, the extirpation of species toward an equilibrium on recently isolated areas such as land bridge islands is understandable using a perspective derived from the model (Diamond, 1973, 1975a). Finally, observable extinction rates on a recently isolated man-made island (viz. Barro Colorado in the Panama Canal Zone) were predicted by use of this approach (Terborgh, 1975; Willis, 1974).

Changes in isolated wildlife communities should also be predictable from island biogeographic theory. However, specific application of the theory to areas such as national parks and wildlife preserves, fast becoming isolates because of encroaching civilization, has not yet been attempted. Therefore the applicability of the theory to these areas needs to be demonstrated. The purpose of this study is to determine the feasibility of applying island biogeographic theory to wildlife preserves. This is achieved by application of the island model to specific preserve communities.

The fundamental hypothesis of this study is that the island biogeographic model is applicable to preserve communities. Two comparisons of model predictions with available preserve data will be used to test the hypothesis. Additional objectives are:

1. to refine and develop the equations necessary to predict quantitative changes in isolated wildlife communities.
2. to predict changes in two specific preserves and compare the predictions with empirical results.
3. to elucidate some characteristics contributing to species' vulnerability to extinction in isolated communities.
4. to make recommendations for further research necessary to fully understand species changes in isolated preserves.

THE DERIVATION OF THE SPECIES-AREA RELATION

The pioneering work of Preston (1962) produced the mathematical model upon which the theory of island biogeography (MacArthur and Wilson, 1967) is based. Preston's model describes numerical distribution patterns of species and individuals within defined areas. A relation between the number of species versus the number of individuals within discrete areas was first observed in plant communities by Arrhenius (1921) and Gleason (1922) and in animal communities by Willis (1922). The use of a logarithmic function to describe the species-individuals relation was first introduced by Fisher et al. (1943). Finally Preston (1948) fitted species abundance data into a graph which produced a lognormal species abundance distribution.

A number of hypotheses have been proposed to explain the observed lognormal distribution of species abundances. One suggestion is that if beneficial genes are fixed at a rate proportional to population size, the relative abundance of species in a large community will be lognormally distributed (Fisher, 1958). Another explanation proposes that a degree of organization exists in which interactions between species are somehow regulated (Odum et al., 1960). Possibly a hierarchical relation among the species of communities relate rarer species to a more abundant species by constant proportions. In this case the relationships of species to individuals might be logarithmic by definition.

A statistical explanation of the lognormal distribution of species has also been proposed (May, 1975). In equilibrium communities, the distribution of relative abundances is governed by many, more or less independent factors. These factors, compounded multiplicatively, govern the distribution of species abundances in a community. When the Central Limit Theorem is applied to such a product of factors the lognormal distribution is obtained.

The latter two hypotheses are supported by empirical distributions of certain unrelated parameters of human societies. Wealth in the United States and in the world is lognormally distributed (Preston, 1948; May, 1975). Alternatively, the distribution of human populations among nations of the world and the distribution of the gross national products of nations is also lognormal (May, 1975). Similarly, the lognormal species distribution can be described statistically and probably reflects some relations between species within equilibrium communities.

Based on the assumption that the relative abundances of species contained in discrete communities (i.e. the species community of a continent or island) conform to a lognormal distribution, Preston (1962) proposed his "canonical hypothesis". When the number of species containing various numbers of individuals is plotted as a function of the number of individuals (Fig. 1), the curve is referred to as the species curve. The distribution of the total number of individuals in each abundance class is referred to as the individuals curve (Fig. 2). The canonical distribution in a lognormal distribution of species abundances characterized by an individual's curve that terminated at its crest (Fig. 3). This corresponds to the last observed point on the species curve. In other

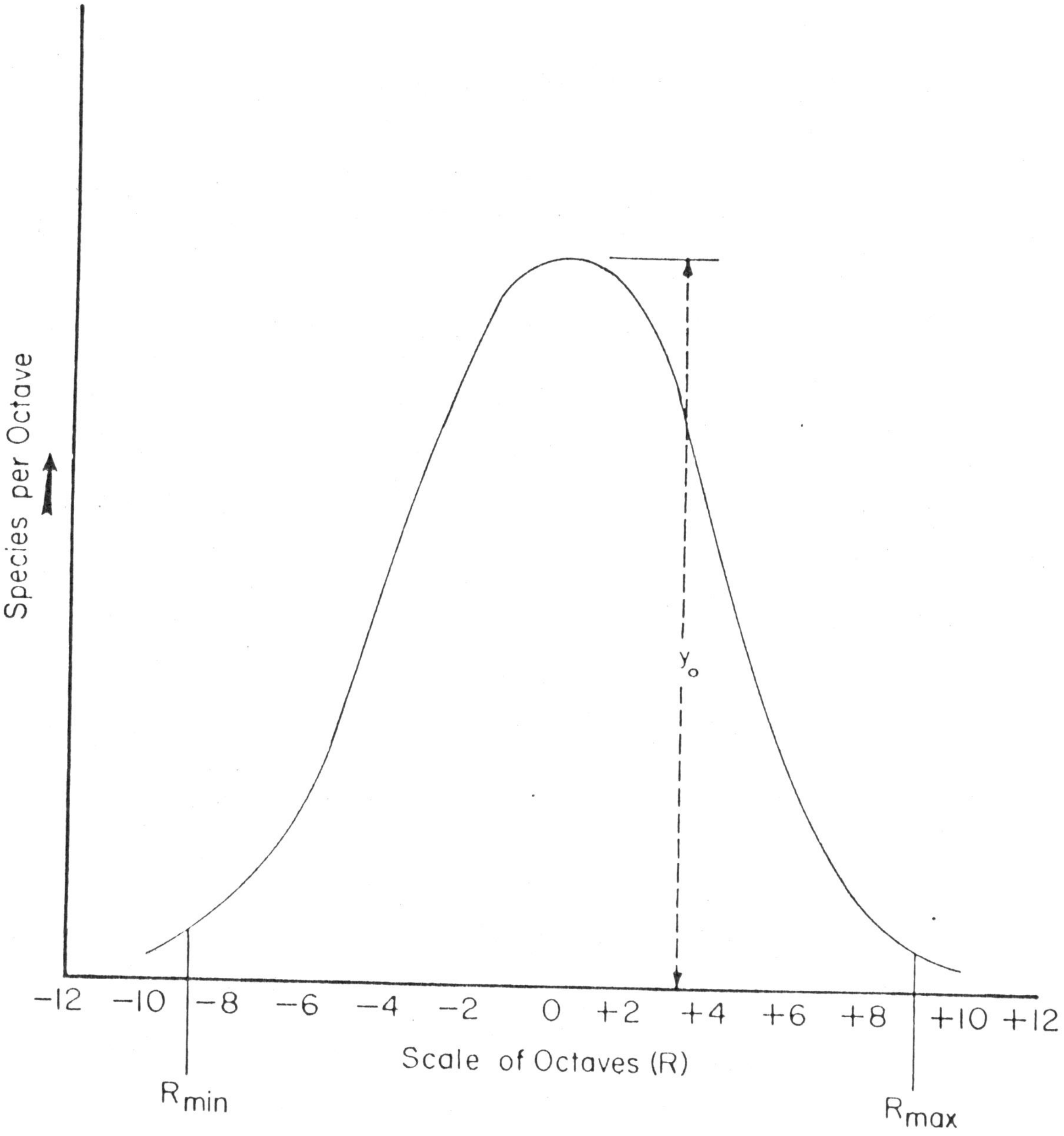

Species per Octave
y_o
−12
−10
−8
−6
−4
−2
0
+2
+4
+6
+8
+10
+12
Scale of Octaves (R)
R_{min}
R_{max}

Fig. 1. The species curve. For any given biological community at equilibrium there will be found to exist a few species that are very abundant and many species that are very rare. The abundance class (e.g. from say 95 to 105 individuals) represented by the most abundant species is called the modal octave, R_O. Each successive octave to the right of the modal represents a doubling of the preceeding abundance class (e.g. 200, 400, 800, etc.) while each octave to the left of the modal octave represents a halving of the previous class (e.g. 50, 25, 12.5, etc.). The number of species containing individuals of the various abundances are then graphed (on the oridnate) as a function of the octaval abundance classes to derive the species curve. Because the abscissa is a logarithmic scale a log normally distributed species abundance relation would plot as a normal curve.

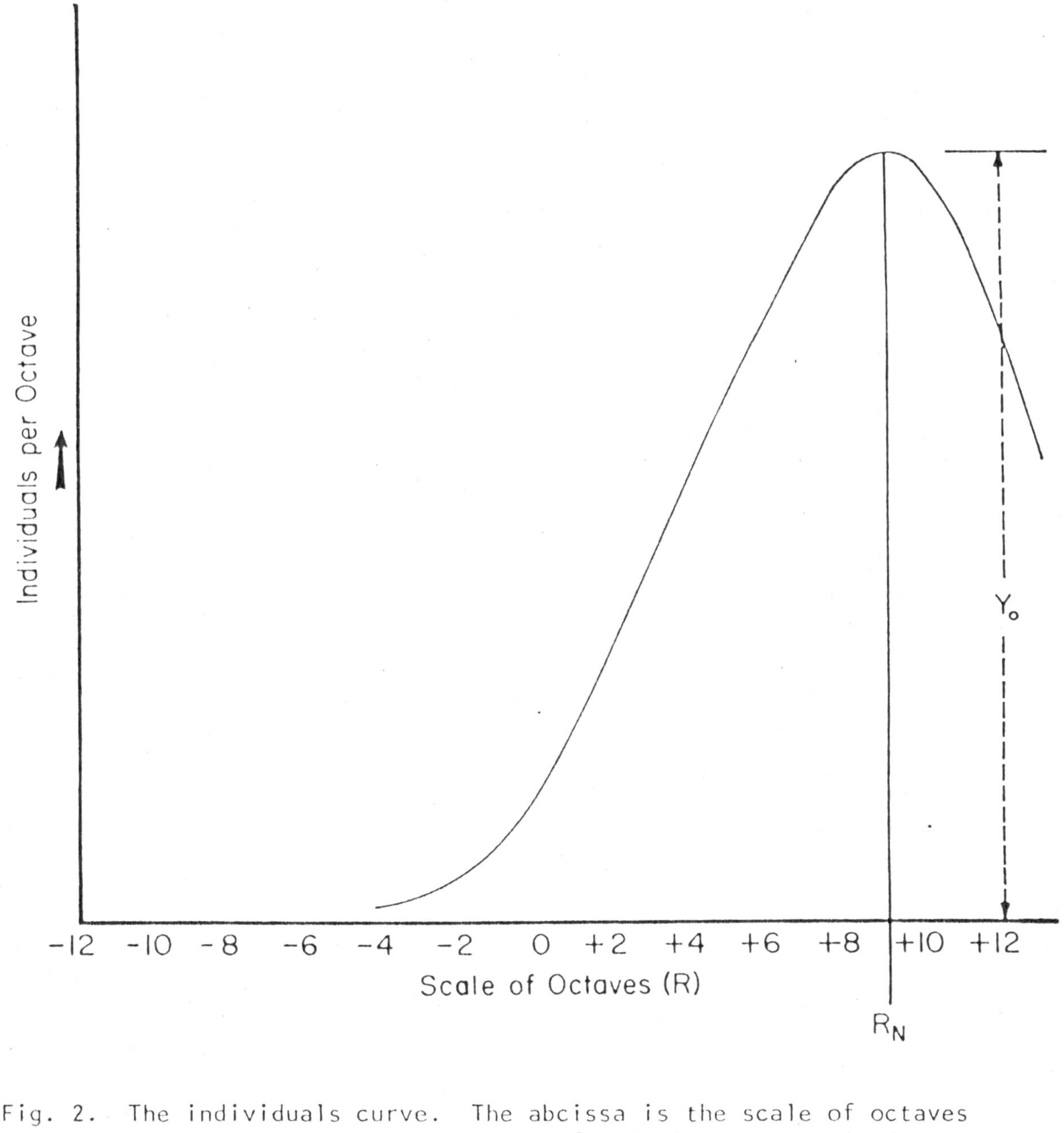


Fig. 2. The individuals curve. The abcissa is the scale of octaves while the ordinate is the total number of individuals contained in each abundance class along the abcissa. Y_o is the number of individuals contained in octave R_N. The above curve is produced when the number of species found in each abundance class in Fig. 1 is multiplied by the number of individuals represented by that class. After Preston (1962).

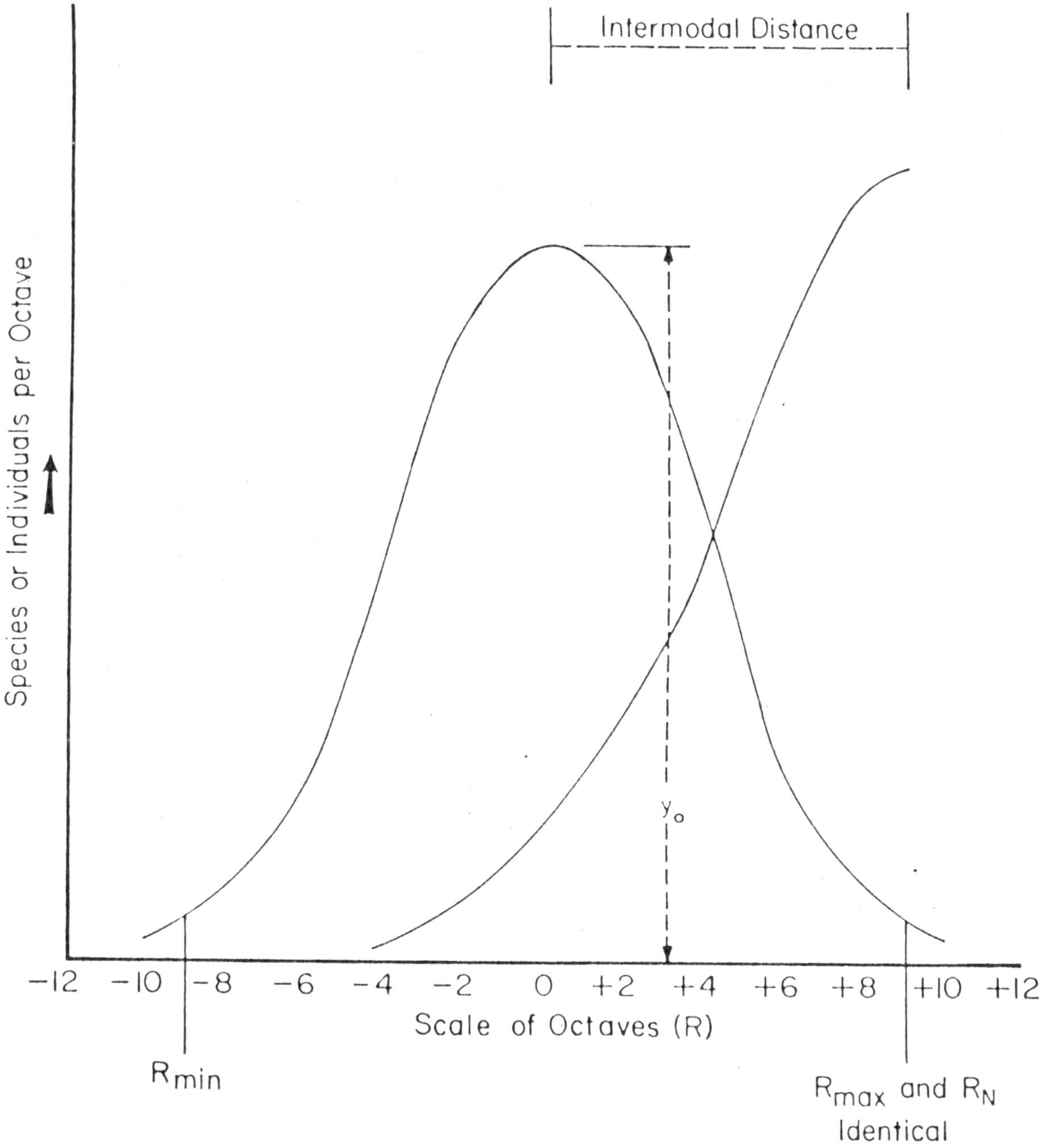


Fig. 3. The canonical distribution. The distribution resulting when the individuals curve (above right) associated with a specific species curve (above left) terminates at its crest ($R_{max} = R_N$). According to Preston's canonical hypothesis (1962) this curve is characteristic of discrete communities.

words, the abundance class containing the greatest number of individuals corresponds to the most abundant species in the community. This unique formulation of the species curve leads to an independent derivation of the species area relation.

The species curve is described by:

$$Y = Y_o \exp - (aR)^2 \tag{1}$$

where

R = scale of abundance classes or octaves

Y = the number of species in the Rth octave to the right or left of the mode

Y_o = the number of species found in the modal octave (i.e. the octave containing the maximum number of species)

a = an arbitrary constant related to the logarithmic standard deviation (σ)

The individuals curve is described by the equation:

$$Y = n_o Y_o \exp (-a^2R^2 + R \ln 2)$$

where

n_o= the number of individuals in the modal octave

The distance between the crests of the above two curves, i.e. the intermodal distance, is $\ln 2/2a^2$ or $\sigma^2 \ln 2$ (Preston, 1948). Preston's canonical hypothesis fixes the values of α and σ and thus the distance between the crests of these two curves. As a result, the family of canonical lognormal distributions is dependent on only one parameter, S, the total number of species in the ensemble. This is in contrast to general lognormal species abundance distributions, which are dependent on two parameters for unique specification.

A number of equations, defining unique features of a species ensemble, result from the above formulation. Parameter values for an array of canonical distributions were calculated (Preston, 1962). Relations between the various parameters are investigated and quantified by the use of various graphical comparisons of the computed values (Preston, 1962). One such comparison involves $\log_{10}$ I/M versus $\log_{10}$ S where:

I = the total number of individuals in the ensemble

m = the number of individuals in the least abundant species

S = the total number of species (Fig. 4).

The following results from a least squares analysis of the computed values for $\log_{10}$ I/M versus $\log_{10}$ S:

$$\log I/M = 3.821 \log S - 1.21 \tag{3}$$

Preston (1962) determines a range of m values and finds that $m \simeq 1$ (Appendix 1). The species-area relation can be derived from equation (3) by invoking the relation between I and density of individuals or pairs per unit area (p):

$$I = pA \tag{4}$$

where

A = area.

Substituting this value of I into equation (3) and solving for S yields:

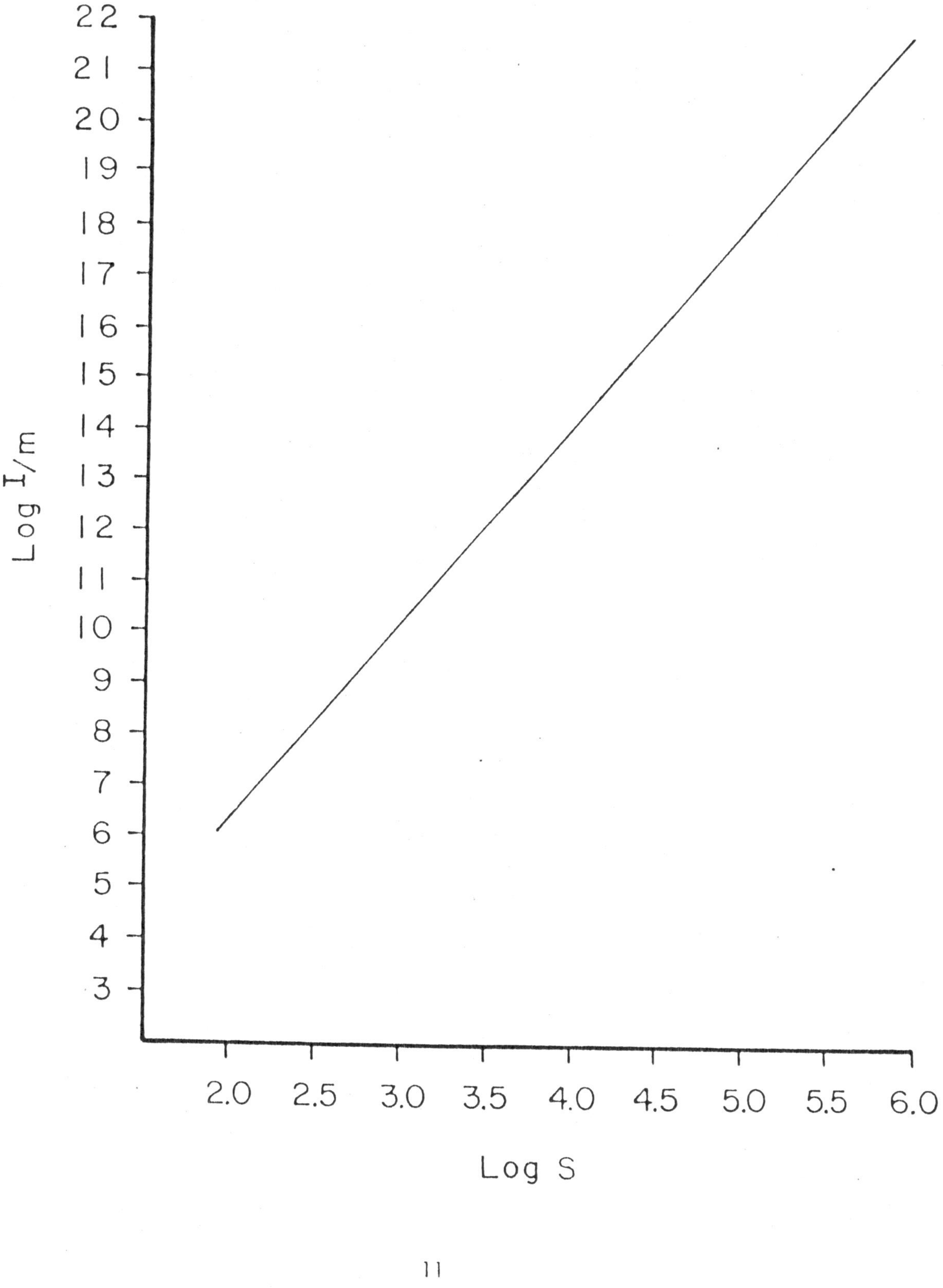
$$\log S = 0.262 \log (pA/m) + 0.316 \tag{5}$$

or more precisely

$$S = 2.07 (p/m)^{0.262} A^{0.262}. \tag{6}$$

Equation (6) is the species-area equation for a complete lognormal ensemble for which the density (p) does not substantially change over a range of areas. When this equation is fitted to ensembles containing from 100 to 1000 species it becomes:

$$S = 1.83 (p/m)^{0.27} A^{0.27}. \tag{7}$$



Log I/m
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
Log S

Fig. 4. The relation of I/m to S where:

S = total number of species in the ensemble
I = the total number of individuals in the ensemble
m = the number of individuals in the rarest species

The species-area relation is derivable from an equation of the above line derived from the least squares analysis of the computed parameter values.

It is important to note that the values in the above equation apply only to areas containing complete ensembles. Values of the parameters change for sample areas. In MacArthur and Wilson (1967) and in other recent biogeographic literature the equation takes the general form:

$$S = CA^z \tag{8}$$

where

S = total number of species

C = a coefficient dependent on the species diversity within the taxon, the zoogeographic region and the degree of isolation

A = area of the island

z = the slope of the line obtained from a log-log regression of island species versus island area

MacArthur and Wilson (1967) incorrectly defined the coefficient C by

$$C = 1.83\ p/m \tag{9}$$

The correct form of the equation is:

$$C = 1.83\ (p/m)^z \tag{10}$$

Since Preston's canonical distribution applies specifically to complete ensembles, to the extent that island communities represent intergrious ensembles, MacArthur and Wilson's application of the generalized form of the species area relation is appropriate.

QUANTIFYING THE PREDICTED CHANGES

MacArthur and Wilson's theory of island biogeography (1967) asserts that the size and characteristics of island biotic communities are determined by a dynamic equilibrium of immigration and extinction rates (Fig.5). The key factors regulating the magnitude of these processes are the distance of the island from the nearest species pool and the island size. It seems intuitive that these same elements are also of importance in determining the size of species communities in isolated continental areas.

Mathematical models will provide insight into the changes leading to the attainment of the species equilibrium predicted to occur withing isolated wildlife preserves. Valuable information can also be developed about the equilibration process occurring between the initial isolation and the final stable equilibrium. A number of models have recently been developed to predict species changes within isolated preserves.

Predicting the Equilibrium Number of Species

Long standing observations established a relation between island size and the corresponding number of resident plant and animal species (Fisher, 1943; Darlington, 1957). Darlington (1957) observed that the number of reptile species found on islands in the West Indies increased by 50 percent for every 10-fold increase in island size. This same relation was independently derived from Preston's (1962) model of finite species communities.

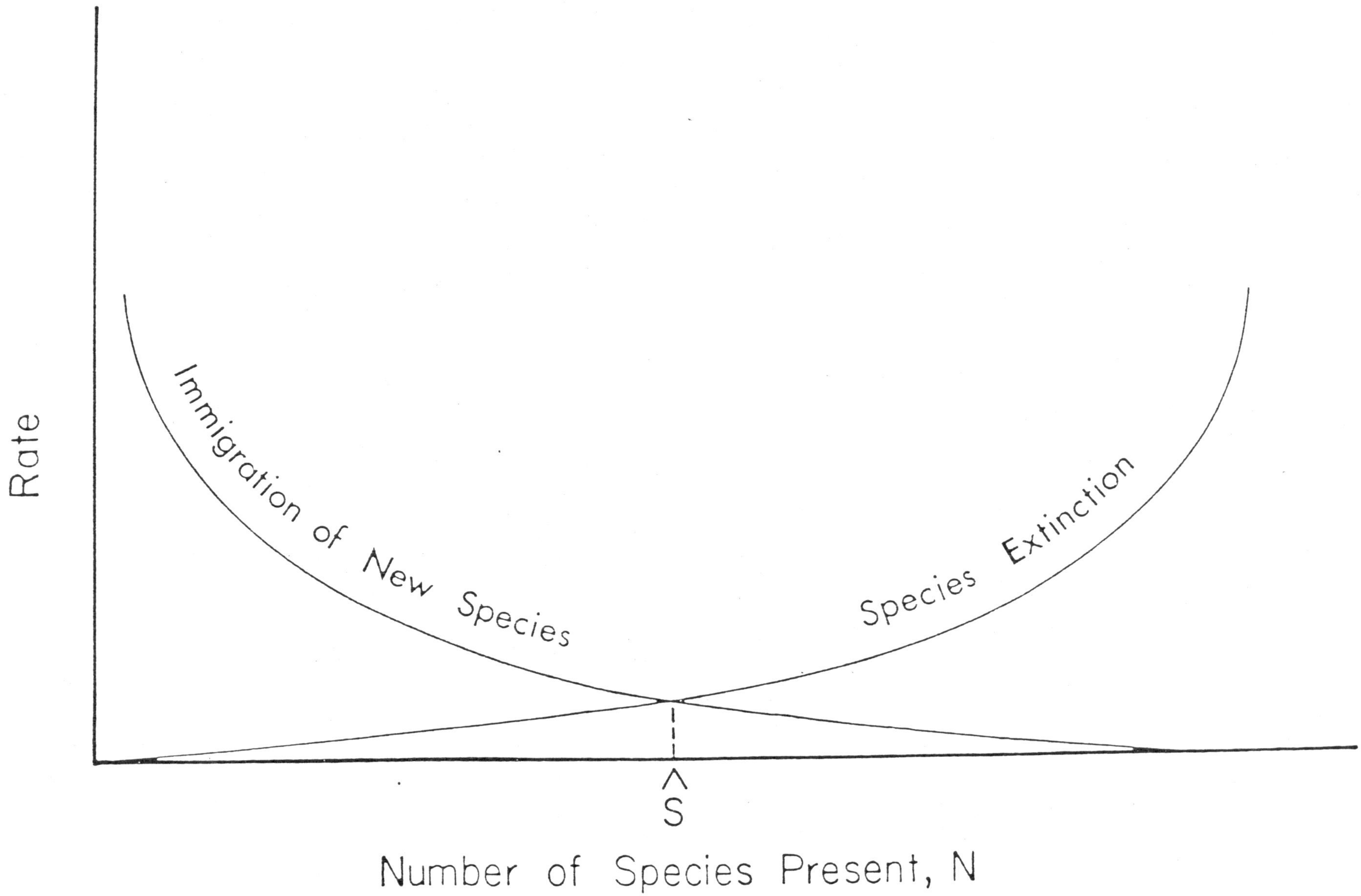

Rate
Immigration of New Species
Species Extinction
$\hat{S}$
Number of Species Present, N

Fig. 5. Equilibrium model for the biota of a single island (MacArthur and Wilson, 1967). The equilibrium number of species, S, is determined by a dynamic relation between immigration and extinction rates.

Any discretely bounded area that has achieved a relatively stable, dynamic, equilibrium will contain a characteristic number of resident species dependent upon its size. This is referred to as the species equilibrium number and is designated $\hat{S}$. Given the size of any discretely bounded and isolated area, equation (8) serves as a predictor of $\hat{S}$ for the biotic communities of the area. The predictive accuracy of equation (8) is dependent upon empirical values for the coefficient C and the exponent z.

Initially a preserve will contain a species complement characteristic of the larger biotope of which it is a part. But as the preserve becomes progressively more isolated from the surrounding natural habitat the species ensemble will slowly be reduced and eventually achieve a lower number of species appropriate to the smaller area and newly equilibrated community. Thus equation (8) would seem appropriate for predicting the number of species that will inhabit isolated preserves if and when equilibrium is reached.

However, two major difficulties were encountered when attempting to use equation (8) as a predictor of $\hat{S}$ for preserve communities. First is the derivation of a value for z. Changes in z values are most pronounced between isolated and non-isolated areas. Yet differences exist even among different groups of completely isolated oceanic islands (Table 1). To date, all z values have derived from equilibrated insular community data subjected to a log-log species-area regression analysis. Since groups of equilibrated preserves do not presently exise, appropriate empirical z values are unavailable, and therefore the island community values must be utilized.

Table 1. Empirically derived z values for a number of insular areas. These values represent the slope of the line obtained from a log-log regression of island species versus island area. The range of z values for insular areas is generally 0.20 - 0.35.

Taxa	Locality	z Value	Source
Land plants	Galapagos Islands	0.325	Kroeber, 1916
Land plants	Various areas	0.220	Williams, 1943
Land vertebrates	Islands of Lake Michigan	0.239	Preston, 1962
Birds	Madagascar and Comoros	0.280	Preston, 1962
Amphibians and reptiles	West Indies	0.301	Preston, 1962
Carabid beetles	West Indies	0.340	Darlington, 1943
Ponerine ants	Melanisia	0.300	Wilson, 1967
Birds	West Indies	0.237	Hamilton et al., 1964
Birds	East Indies	0.280	Hamilton et al., 1964
Birds	East Central Pacific	0.303	Hamilton et al., 1964
Birds	Islands of Gulf of Guinea	0.489	Hamilton and Armstrong, 1965
Birds	New Guinea Satellite Islands	0.220	Diamond, 1972
Birds	South American Parano Islands	0.286	Vuilleumier, 1970

The second difficulty involves the derivation of a value for the coefficient C. Values of C are dependent upon both the population density and the species diversity of the taxon under consideration. These values will vary within the same taxon in different regions of the world and between taxa in the same region (MacArthur and Wilson, 1967). Lower C values will be associated with areas where the quality of the environment is less suitable for a specific taxon. Finally, C will decrease as a function of increased isolation. Well-developed explanations of the magnitude of the coefficient C do not exist, and thus precise predictions of C values are not possible. Only in situations where C is empirically derivable can it be used in conjuction with equation (8) to predict the present species numbers of an area.

Predicting the Extinction Rate and the Equilibration Time

The rate of species extirpations predicted to occur in preserve communities should be understandable from the equilibrium concept. Two models have recently been developed to quantify extinction rates in isolated communities. The predictive value of both models in tentatively verified by comparison to documented changes in the numbers of resident bird species on the land bridge islands off the coast of New Guinea (Diamond, 1972, 1973, 1975a; Terborgh, 1975).

Diamond (1972) refers to the process of species depletion, which occurs from the time an area becomes isolated until it achieves a dynamic equilibrium, as relaxation. He has developed a model to describe this process based on constant coefficients of immigration and extinction (Appendix B). The concept of relaxation time is introduced here to estimate the time period between the initial isolating process and the eventual stable equilibrium. Based on this formulation, the reduction of a species community to equilibrium should be 90 percent complete after 2.3 relaxation time intervals. Relaxation time is quantified by:

$$\exp.\ (-t/t_r) = S_t - \hat{S}/S_o - \hat{S} \qquad (11)$$

where

t = time since isolation

t_r = relaxation time

S_t = number of species present at some time t

S_o = initial species number i.e. number present at onset of isolation

$\hat{S}$ = equilibrium number of species

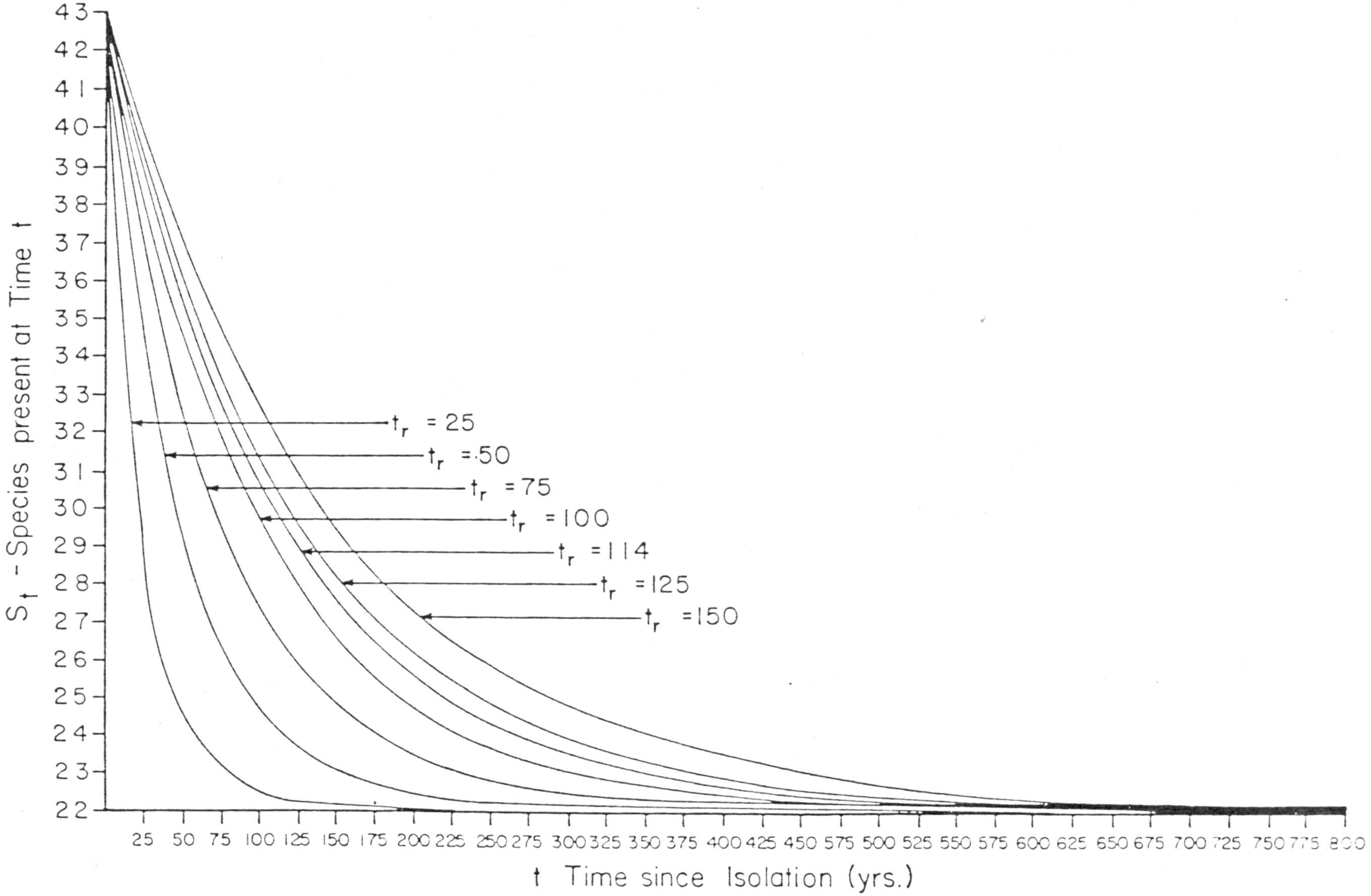
Relaxation time is the length of time required for a further reduction in species from the present level to e^{-1} (36.8 percent) of the present departure from the original species complement.

From this, relaxation time serves as a measure of the extinction rate constant (Table 2) and clearly represents a negative exponential (Fig. 6). If this model is a true reflection of the process, a number of conclusions are immediately implied. Before considering these implications an alternative model is considered.

The second model is derived from the kinetics of species loss on the New Guinea satellite islands (Terborgh, 1974, 1975). This model assumes that immigration has a negligible effect in retarding the rate of species loss from islands with communities in excess of $\hat{S}$. Thus only extinction needs to be considered in the relaxation process. This model is comprised of the following three equations:

Table 2. Response values for the number of species (S_t) present at various times since isolation (t) from the equation ($S_t - \hat{S}$) = exp ($-t/t_r$) where t_r = relaxation time; S_o = initial species number and $\hat{S}$ = species equilibrium number. These values of S_t are produced when S_o = 43 and $\hat{S}$ = 22 associated with the large mammal community of the Mkomozi Game Reserve. These values provide insight into the rate of species change occurring in isolated areas.

Time Since Isolation (t) in Years	Values of t_r						
	25	50	75	100	114	125	150
25	29.73	34.74	37.10	38.35	38.86	39.19	39.78
50	24.84	29.73	32.85	34.74	35.54	36.08	37.10
75	23.05	26.69	29.73	31.92	32.88	33.53	34.74
100	22.38	24.84	27.55	29.73	30.73	31.44	32.85
125	22.14	23.72	25.99	28.02	29.01	29.73	31.13
150	22.05	23.05	24.84	26.69	27.63	28.33	29.73
175	22.02	22.63	24.04	25.65	26.52	27.18	28.54
200	22.01	22.38	23.47	24.84	25.63	26.24	27.55
225	~22.00	22.23	23.05	24.21	24.92	25.47	26.69
250		22.14	22.75	23.72	24.34	24.84	25.99
275		22.09	22.54	23.34	23.88	24.33	25.36
300		22.05	22.38	23.05	23.51	23.91	24.84
325		22.03	22.28	22.81	23.21	23.56	24.41
350		22.02	22.20	22.63	22.97	23.28	24.04
375		220.1	22.14	22.49	22.78	23.05	23.72
400		22.01	22.10	22.38	22.63	22.86	23.47
600		~22.00	22.01	22.05	22.11	22.17	22.38
800			~22.00	22.01	22.02	22.03	22.10


43
42
41
40
39
38
37
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35
34
33
32
31
30
29
28
27
26
25
24
23
22
S_t - Species present at Time t
t_r = 25
t_r = 50
t_r = 75
t_r = 100
t_r = 114
t_r = 125
t_r = 150
25 50 75 100 125 150 175 200 225 250 275 300 325 350 375 400 425 450 575 500 525 550 575 600 625 650 675 700 725 750 775 800
t Time since Isolation (yrs.)

Fig. 6. Extinction curves implicit in the equation exp $(-t/t_r) = (S_t - \hat{S}) / (S_o - \hat{S})$ where t = time since isolation, t_r = relaxation time, S_t = number of species present at time t, S_o = initial species number and $\hat{S}$ = species equilibrium number. The above family of curves is produced when $S_o = 43$ and $\hat{S} = 22$ (S_o is the number of large mammal species in the Mkomazi Game Reserve and $\hat{S}$ is an equlibrium estimate for this community) and t_r is varied as shown. Based on this formulation, more extinctions will occur in earlier years than in later years.

$$-\frac{dS}{dt} = K_3 S^2 \tag{12}$$

where

$\frac{dS}{dt}$ = the instantaneous rate of change in the number of species per unit time

S = the number of species at time t

K_3 = the extinction rate coefficient which is in turn defined as:

$$K_3 = \frac{\frac{1}{S_o} - \frac{1}{S_P}}{T} \tag{13}$$

where

S_o = the initial number of species

S_P = the present number of species

T = the time since isolation

$$S_t = \frac{S_o}{1 + K_3\ S_o\ T} \tag{14}$$

where S_t = the number of species present after some period of elapsed time t.

Terborgh (1975) introduces a technique for applying this model to the extinction process in isolated natural preserves. This is based on a method of empirically deriving the extinction coefficient, K_3, for any isolated preserve of known size. Values of the extinction coefficient are estimated from a log (K_3) versus log (area) plot (Fig. 7). This line is obtained from equation (13) in conjunction with avifaunal data from five islands off the coast of New Guinea. A larger number of values would be necessary to establish a significant linear relation. Terborgh suggests that these values of K_3 should also apply to wildlife preserves and that by using them in conjuction with equation (14) a prediction of extirpations can be obtained.

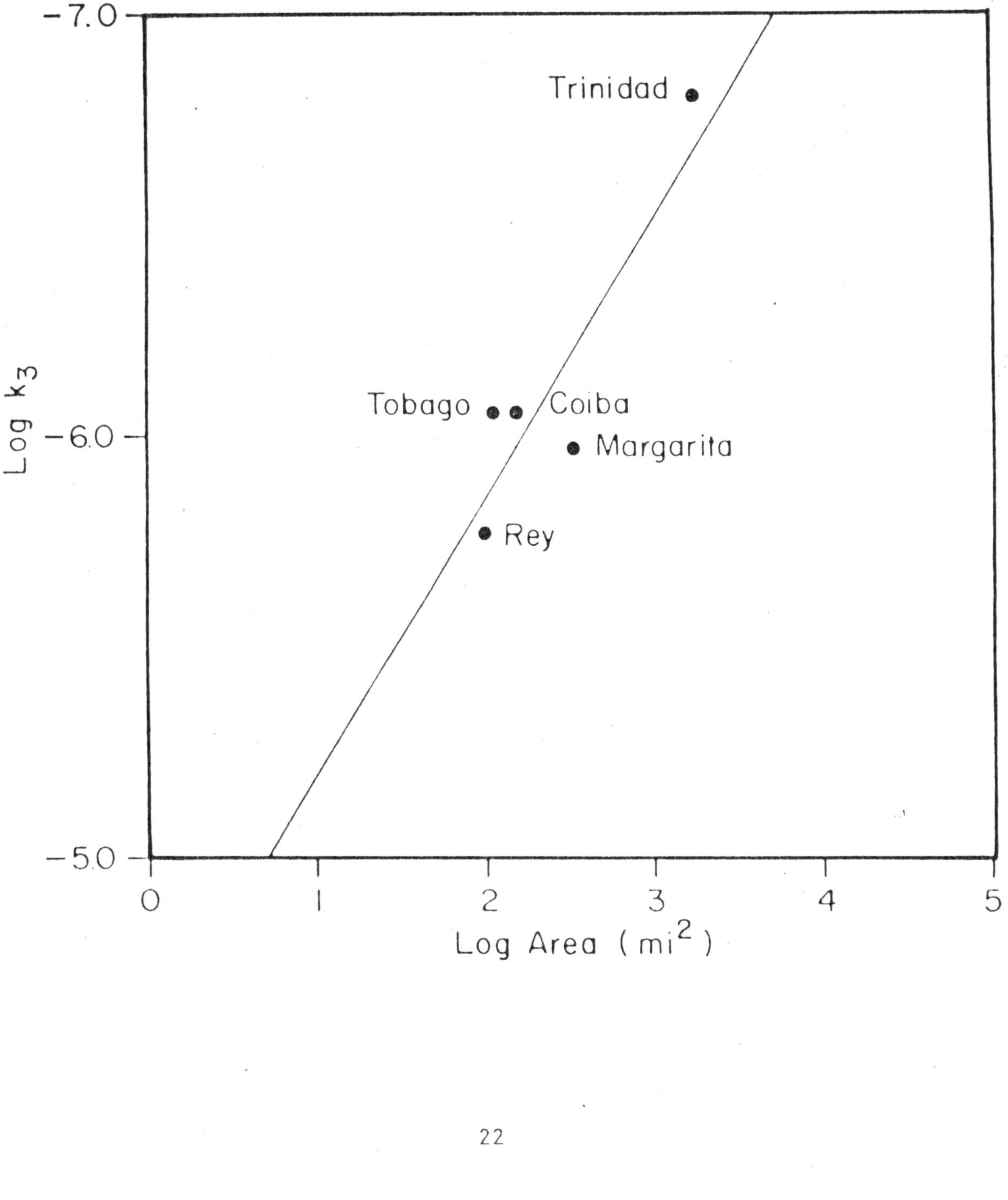
Fig. 7. Double log regression of extinction coefficient K_3 (ordinate) and island area (abcissa). Values of K_3 for each of these five islands were computed from :

$$K_3 = \frac{\frac{1}{S_o} - \frac{1}{S_p}}{T}$$

where

S_o = the initial species number
S_p = the present species number
T = the time since isolation

Values of K_3 can be drawn from this line and used to predict changes likely to occur in wildlife preserves (from Terbough, 1975).


-7.0
-6.0
-5.0
Log k3
0
1
2
3
4
5
Log Area (mi2)
Trinidad
Tobago
Coiba
Margarita
Rey

Unlike the negative exponential extinction rate used in the Diamond model (equation [11]), this model is characterized by a nearly linear extinction rate (Fig. 8). The assumption of linearity is not supported by the theoretical model (Fig. 5) or by the empirical evidence presented here. The underlying assumptions that immigration will not selectively affect the extinction rate on different islands is possibly too simplistic. Distance from the mainland is a major factor influencing the species equilibrium number and cannot be ignored from either extinction or immigration considerations. A regression line derived from equilibrating species communities in areas comparable to wildlife preserves will be necessary to provide a model of the relaxation process in preserves.

It appears that the Diamond model presents a more realistic picture of the relaxation process for two reasons. First, the higher number of initial extirpations implied by a negative exponential seems intuitive and is somewhat corroborated by data from recently isolated areas (Willis 1974). Secondly, in contrast to the Terborgh model, this model is based on immigration and extinction curves similar to those predicted by biogeographic theory (Fig. 5). The validity of the rates implied by these curves has been both experimentally (Hubbard, 1973; Simberloff and Wilson, 1969) and theoretically (Gilroy, 1975) substantiated. Based on available data, this form seems to provide the most realistic picture of the equilibration process.

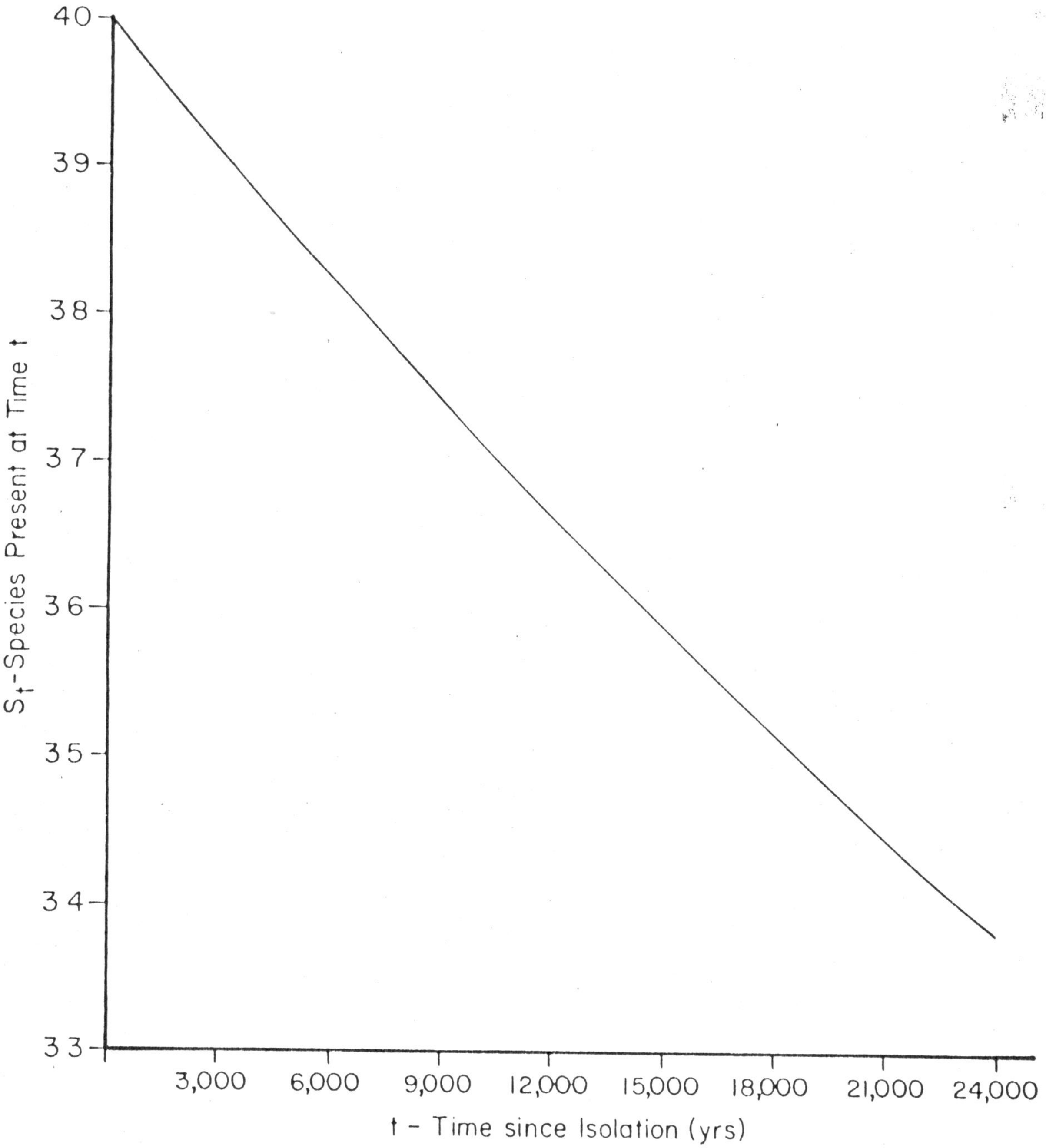
Fig. 8. The extinction rate underlying the Terborgh equilibrium model (Terborgh, 1975). The curve is produced from

$$S_t = \frac{S_o}{1 + K S_o T}$$

where

S_t = number of species present at time t
S_o = initial number of species
K_3 = an extinction coefficient
T = time since isolation

This specific curve is produced from the following values associated with the Everglades mammal community: $S_o = 40$, $S_t = 39$, $T = 20$, $K_3 = 1.9 \times 10^{-7}$ and an area of 2200 mi^2.


40
39
38
37
36
35
34
33
S_t-Species Present at Time t
3,000
6,000
9,000
12,000
15,000
18,000
21,000
24,000
t - Time since Isolation (yrs)

KEY FACTORS REGULATING THE SIZE AND COMPOSITION OF ISOLATED PRESERVE COMMUNITIES

Both theoretical and empirical evidence suggest that isolated faunas decrease in the number of species as a function of degree of isolation and time since isolation. Yet few studies have identified or described the variables underlying these changes. Evidence suggests that a number of parameters exert a strong influence on the evolution and maintenance of equilibrium communities. Understanding these parameters will improve conservationists' ability to maintain the integrity of the processes regulating wildlife communities in isolated preserves. Furthermore, this knowledge can lead to a maximization of the number of species being naturally maintained in preserves. This chapter concerns the parameters that regulate the species equilibrium in isolated species communities.

Factors Influencing the Species Equilibrium Number

Large preserves will generally maintain a higher percentage of their original species complement than smaller preserves. The validity of this contention is supported by the response curve of the species-area equation (Fig. 9). This also indicates that the incremental increase in the number of species declines for larger areas. In other words, a larger area involves a smaller species accrual than a similar increase in a smaller area. Darlington (1957) first recorded this phenomenon in his observations of West Indian herpetofauna. He observed that an approximately ten-fold increase

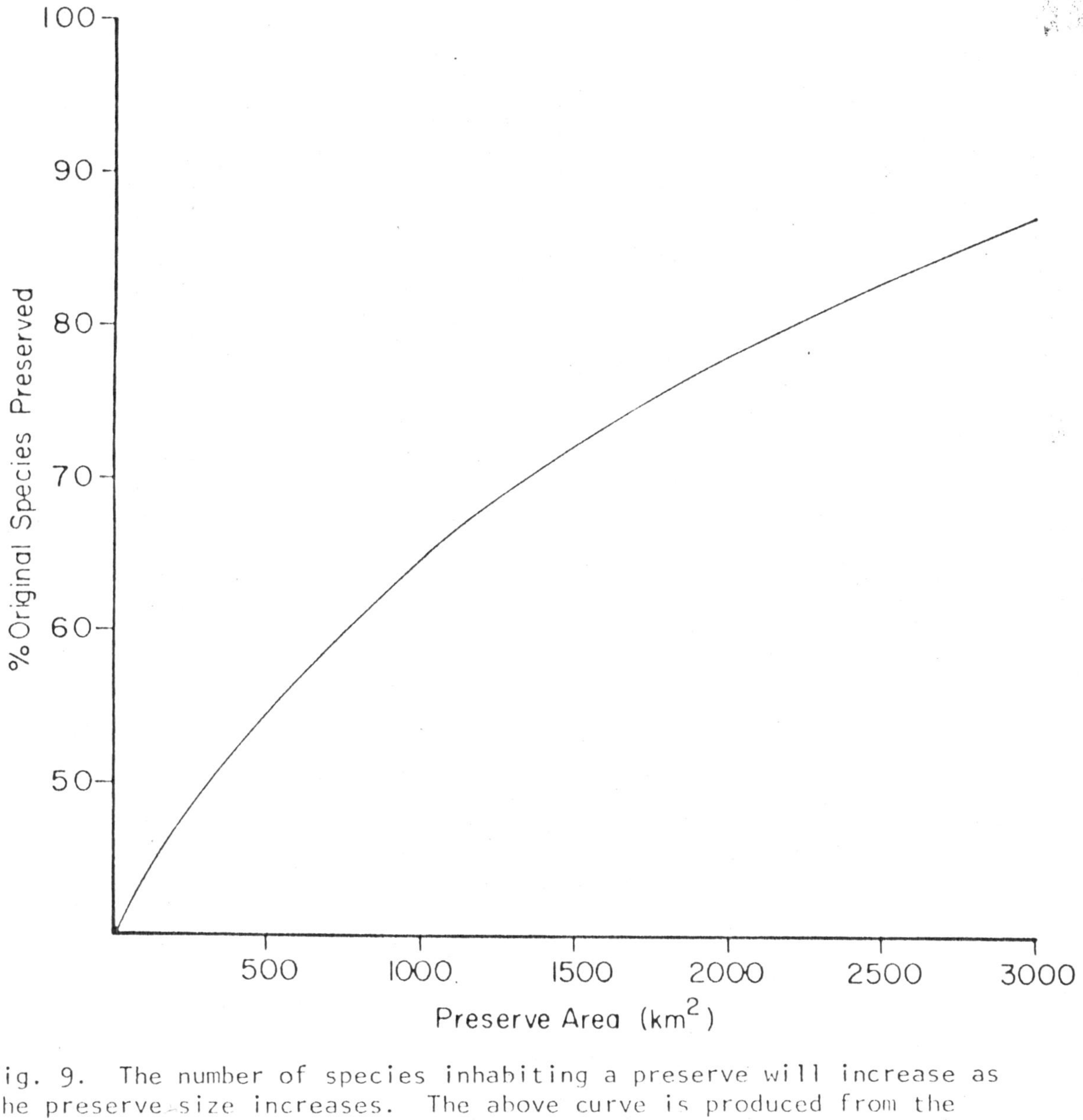


Fig. 9. The number of species inhabiting a preserve will increase as the preserve size increases. The above curve is produced from the species-area equation, $S = CA^z$ when $C = 10$ (an arbitrary constant) and $z = 0.27$ (exponent value for isolates).

in island size leads to a doubling of the number of reptile species on an island. Later analyses of this relation (Preston, 1962; MacArthur and Wilson, 1967) reveal that in general, each ten-fold increase in area corresponds with an 80 percent increase in species number (Fig. 10). Thus, for every order of magnitude increase in island size there should be a 1.86 fold increase in species numbers (Fig. 10). This relation is verified by avifaunal data from the New Guinea satellite islands (Fig.11).

The degree of isolation in an area will significantly affect the number of species found there. When z in equation (8) is derived for different species communities its magnitude changes in relation to the degree of isolation in the area. Isolated areas exhibit z-values between 0.20 - 0.35 while areas representing only samples of larger communities exhibit z-values ranging from 0.11 - 0.17 (Table 1). This implies that as an area becomes more isolate, size plays an increasingly important role as a predictor of the species number. Further, the predictive value of the species area relation is most apparent when applied to isolated communities characterized by an internal equilibrium. Conversely, in continental sample areas, the predictive power of equation (8) becomes more dependent on the value of C. This is because of the low values of the exponent z associated with sample areas. This implies a reduced importance of the area variable (A) as a predictor of the species equilibrium number ($\hat{S}$) in these areas.

Wildlife preserves are presently more similar to the sample area formulation. Thus equation (8) may be a poor predictor of the number of species presently found in preserves. However, this equation should still

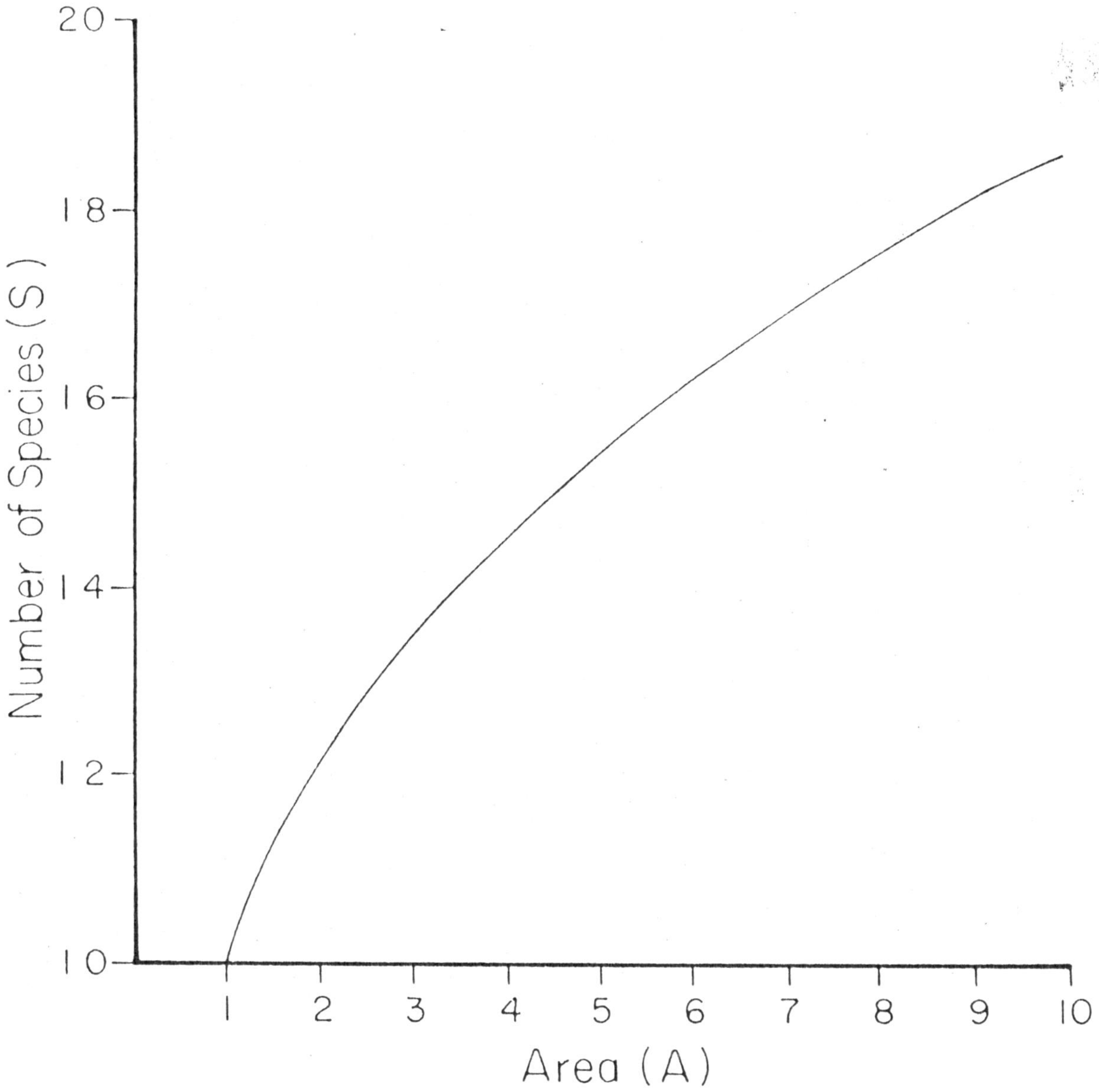


Fig. 10. A demonstration of the numerical relation between area and the number of species inhabiting isolated communities implicit in the species-area equation $S = CA^z$. The above curve results when $z = 0.27$ (exponent value for insular areas) and $C = 10$ (an arbitrary value). The curve demonstrates that a 10-fold increase in island area leads to a 1.86 fold increase in species number.

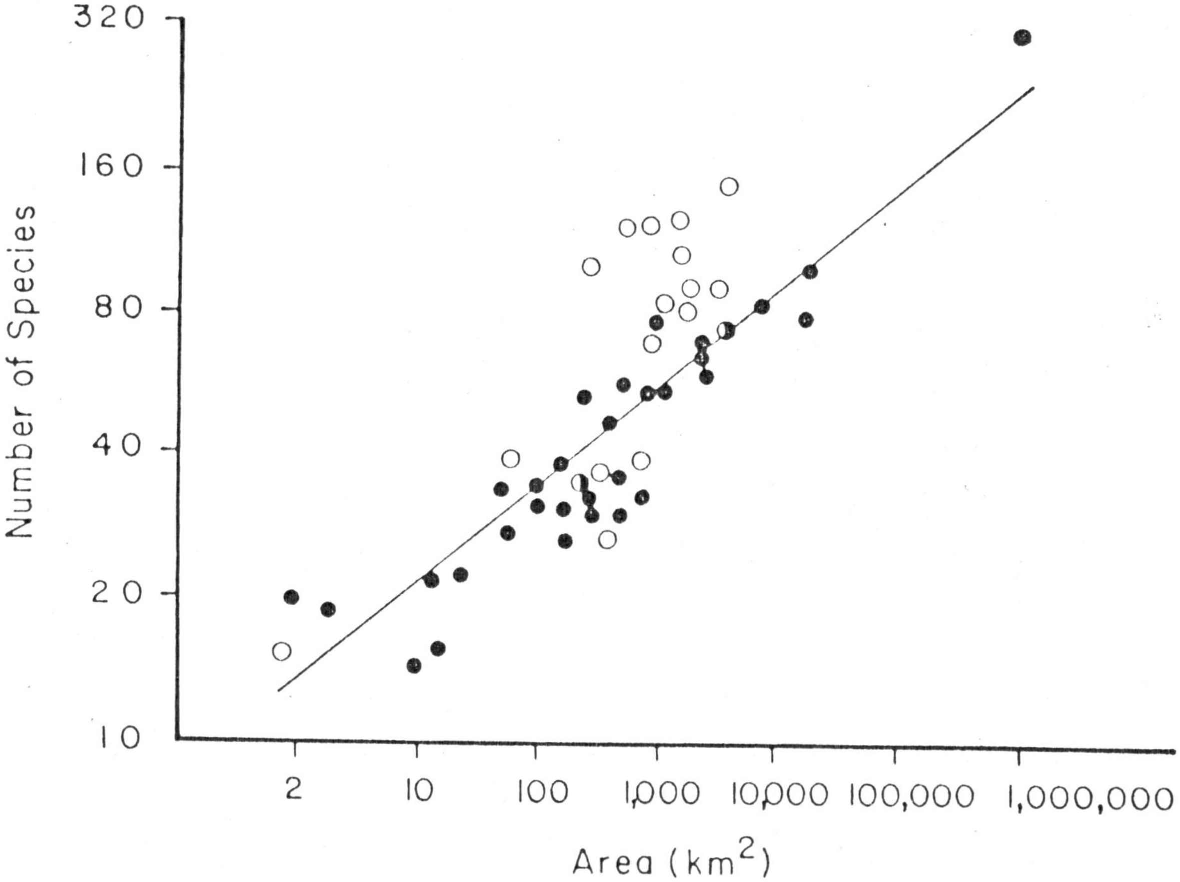


Fig. 11. A comparison of the present species-area relation between equilibrated and non-equilibrated islands. The ordinate represents the number of resident, non-marine, lowland species on New Guinea satellite islands plotted on a $\log_2$ scale. The abcissa represents the area of these islands (km^2) plotted on a $\log_{10}$ scale. Closed dots represent islands presumed to be at equlibrium. Open dots represent land bridge islands located on a shallow shelf or volcanic islands which have not yet achieved an equilibrium condition (from Diamond, 1972, 1975).

effectively predict the species equilibrium number attained at the onset of an internal equilibrium. This underlies the important distinction between present preserve communities and the equilibrium communities towards which they are evolving.

Predictions of the species equilibrium in wildlife preserves will be dependent on the vegetational and habitat diversities of preserves. Vegetational diversity exerts a strong influence on the number of faunal species in most communities. It has been shown that bird species diversity is linearly related to foliage height diversity (MacArthur et al, 1966) and sigmoidally related to percent vegetation cover (Karr and Roth, 1971). A relation has also been observed between habitat diversity and mammalian species diversity (Harris, 1972). Both of these observations indicate that faunal diversity is differentially related to environmental diversity, which is regulated by a number of climatic, edaphic and biological factors.

Successional or man-induced changes in vegetational diversity will significantly affect the number of species inhabiting an area. Evidence supporting this statement comes from Barro Colorado, a recently created island in the Panama Canal zone. This area contained both forest and secondary growth communities at the time of its formation in 1917. By 1969 the entire island had become forested. Willis (1974) attributes the extirpation of 32 bird species during this period to the loss of second growth and forest edge. This particular example of species loss resulted from changes in environmental diversity that probably resulted from isolation.

Another important parameter regulating the species equilibrium number is the distance of a preserve from surrounding species pools. A tenet of island biogeographic theory is that more species will be found on islands near the mainland. It follows from island biogeographic theory and empirical island data that the species equilibrium number characteristic of isolated equilibrated preserves will also be related to the distance to surrounding species pools. With expanding civilization, source of immigrant species will become increasingly limited to other preserves and thus the feasibility of species exchange between isolated preserves will become increasingly important in affecting preserve species numbers.

Recent studies of turnover rates in insular bird communities support the dynamic equilibrium hypothesized by the island biogeographic model. In one such study Diamond (1969) analyzed avifaunal turnover rates on nine Channel Islands off the coast of California. He compared an early survey of breeding bird species on these islands with recent data and even though the accuracy of these data has been questioned (Lynch and Johnson, 1974), I remain convinced that Diamond's conclusions are valid (Appendix C).

Diamond calculates percentage turnover for each island as:

$$T = E + I/S_{1917} + S_{1968} - S_{Int} \tag{15}$$

where

E = the number of breeding bird species present in 1917 but absent in 1968

I = the number of breeding bird species present in 1968 but absent in 1917

S_{1917} = the total number of breeding bird species present in 1917

S_{1968} = the total number of breeding bird species present in 1968

S_{Int} = the number of bird species introduced by man between 1917 and 1968

No correlation was found between species turnover rates and either distance from the mainland or island size. A possible explanation of this derives from the fact that the immigration rate is inversely proportional to the distance from the mainland while the extinction rate is directly proportional to distance. Since turnover rate is defind as a function of both immigration and extinction and because these two processes are oppositely related to distance, there can be no simple relation between turnover rate and distance.

An inverse relation between an island's number of species (birds) and turnover rate was observed in the Channel Island study. This observation results from the relation between island habitat complexity and area. Other authors have observed that the number of bird species in different habitats is correlated with the vegetational complexity of the habitats (MacArthur et al., 1966). A small island with rich vegetation is comparable to a large island with poor vegetation in terms of the number of species it can support. However, the relation between island size and turnover is mostly due to the relative effect species changes will have on different size communities. In other words, on an island with three species, one extinction represents a 33 percent turnover rate while a community with 30 species, one extinction represents a 3 percent turnover rate.

However, the relation between species numbers and vegetational complexity on islands is not completely applicable to wildlife communities in preserves. Preserve boundaries are usually created and defended so that a maximum number of species are protected. Therefore the number of species inhabiting preserves is not necessarily a simple function of overall vegetational diversity or visa versa. Consequently, comparisons between the vegetational diversity and the number of species may not yield any more insight than area considered as a single factor. On the other hand, these parameters taken together should yield a significant degree of predictive power. Even large preserves, if initially supersaturated, will exhibit high extinction rates. Positive design and mitigative management schemes are necessary to counter these effects.

Species Specific Vulnerability to Extirpation

Few studies have identified the underlying biological variables regulating the changes likely to occur in preserves as a result of isolation, and thus the nature of species specific extirpation is not well understood. A number of theoretical explanations and hypotheses are presented here to stimulate scientific debate and management awareness.

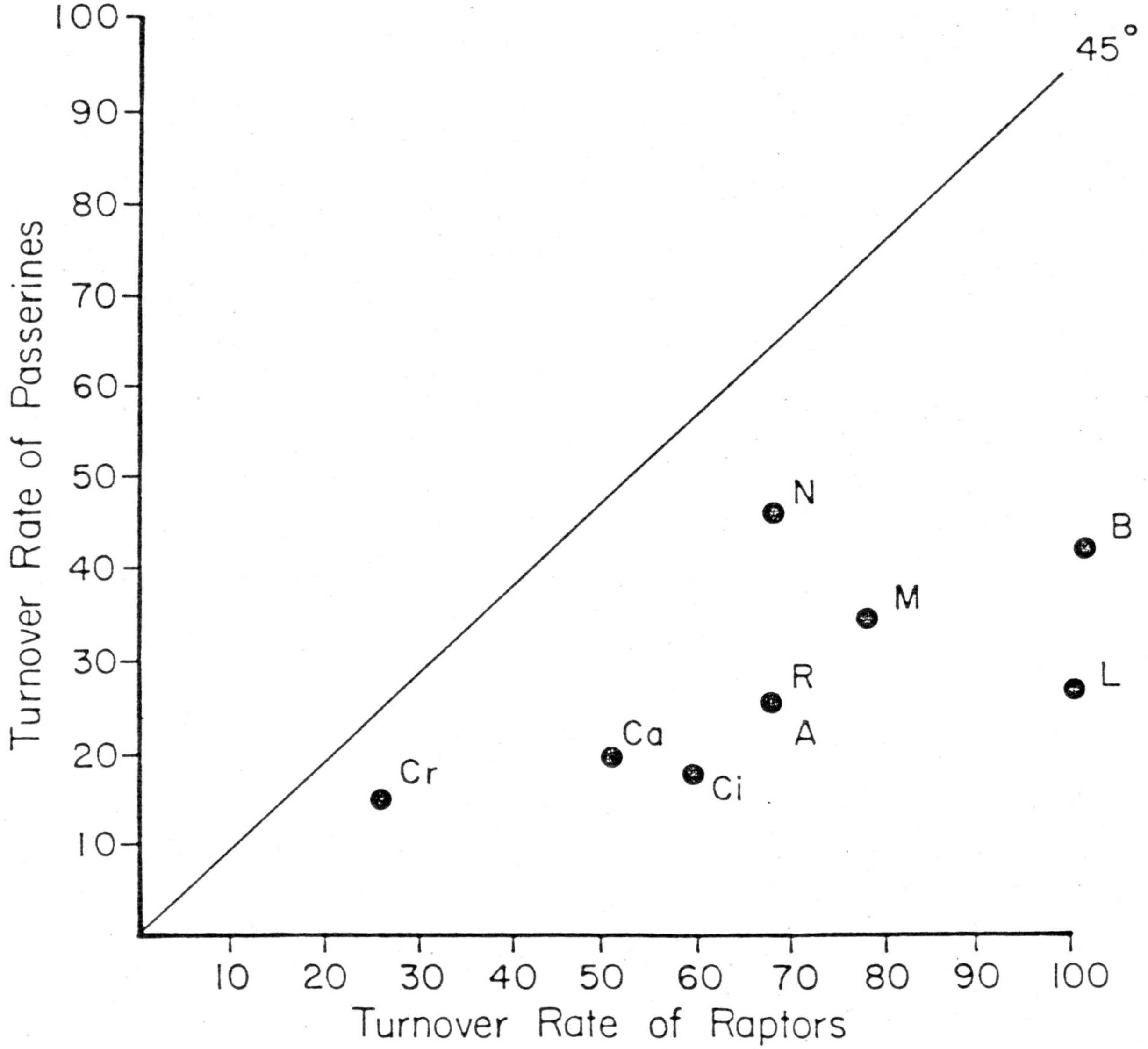
The species most vulnerable to extirpation will be those represented by small populations. Small populations restricted spatially or temporally because of resource requirements will be vulnerable to catastrophic changes that may destroy critical resources or the organisms themselves. For example, extreme climatic events may destroy vegetational resources within a localized area. A small population of specialized animals obligatorily dependent on these resources would be extirpated from the area.

Reproductive characteristics may also strongly influence vulnerability to extirpation at low population levels (Southwood et al., 1974). Certain species with low reproductive rates must maintain populations above a minimum critical density in order to remain viable (Mertz, 1971; Southwood et al., 1974). If such a population is reduced significantly below the critical minumum it may be impossible to regain the equilibrium condition, and the remaining population will become inviable. For example, some species exhibit colonial nesting habits and will reproduce only in specialized areas or in large groups. Whenever preserve size is inadequate to fulfill the minimum population requirements of a species, extirpation of the species will occur.

Species that represent the largest members of certain guilds (as opposed to the largest species per se) or are high in the trophic pyramid generally exhibit large home ranges, low densities and low reproductive rates. Many of these species are dependent upon a highly dispersed food supply and possess a high metabolic demand. These attributes all contribute to the likelihood that the species will be extirpated from small preserves where the various requirements are not fulfilled.

Other factors further indicate that species at the top trophic levels may be the most vulnerable to extirpation from isolated preserves. One recent study suggests that species at higher trophic levels exhibit greater population size changes due to immigration or extinction than species on lower levels of the trophic pyramid (Hunt and Hunt, 1974). This is supported by the Channel Island data. In the Channel Islands percent turnover is consistently higher for predatory birds than for passerines (Fig. 12). Whereas a significant negative correlation exists between island area and predator turnover rate, no correlation exists between island size and passerine turnover rate. A reasonable explanation of this phenomenon is that predatory birds utilize entire islands rather than patches of habitat because of their dispersed resource requirements.

Fig. 12. Comparative turnover rates of birds of prey versus passerines for the Channel Islands (Hunt and Hunt, 1974). The individual data points derive from the following islands: L - Los Coronodos, N - San Nicolas, Cl - San Clemente, Ca - Santa Catalina, B - Santa Barbara, M - San Miguel, R - Santa Rosa, Cr - Santa Cruz, A - Anacapa. If the turnover rate of the two groups were equal, the data points would be dispersed around the 45° line. The degree to which the points fall to the right of the 45° line indicates the disparity between equal turnover rates. In all cases the turnover rate of raptors exceeded that of passerines.


100
90
80
70
60
50
40
30
20
10
Turnover Rate of Passerines
45°
N
B
M
R
L
A
Ca
Cr
Ci
10
20
30
40
50
60
70
80
90
100
Turnover Rate of Raptors

Thus predators will only be found on islands above a minimum size. An additional study found a highly significant ($P < 0.001$) correlation between species numbers and habitat island size (Galli et al., 1976). In this case, predators were observed in only the largest forest islands. In addition to supporting the minimum area hypothesis for predators, this evidence strongly supports the continental island hypothesis because it is taken directly from forest islands in a continental area.

As previously noted, a number of avifaunal extirpations have been observed on Barro Colorado Island during the past 50 years. Only 32 of the recorded 45 extirpations are attributable to changes in vegetation structure (Willis, 1974). Of the 13 remaining extirpations, a majority of the species are characterized by specialized, carnivorous feeding habits. The area probably became too small to support these species, with their larger living space requirements. Generally, species on upper trophic levels will probably experience a high extinction pressure in isolated preserves.

The distance effect influences island communities through changes in the immigration rate. Immigration can exert a selective effect on the composition of faunal communities on both oceanic and continental islands. These areas will experience a rather continuous "bombardment" of colonizing species with high turnover and dispersal rates (Diamond, 1975b). This constant replenishment of r-selected species will tend to maintain a greater percentage of species with certain population characteristics. Thus immigration will express itself through a selection process via the relative colonizing ability of the various available species. This is supported by the distribution of bird species on the New Guinea satellite islands (Diamond, 1973). More sedentary species are found only in the immediate vicinity of the New Guinea mainland while colonizing species inhabit the most distant islands. Other factors being equal in clusters of preserves, those species with colonizing ability will be selected for because of their ability to exchange individuals between noncontiguous populations. Taxa unable to exchange individuals with neighboring populations will be selected against.

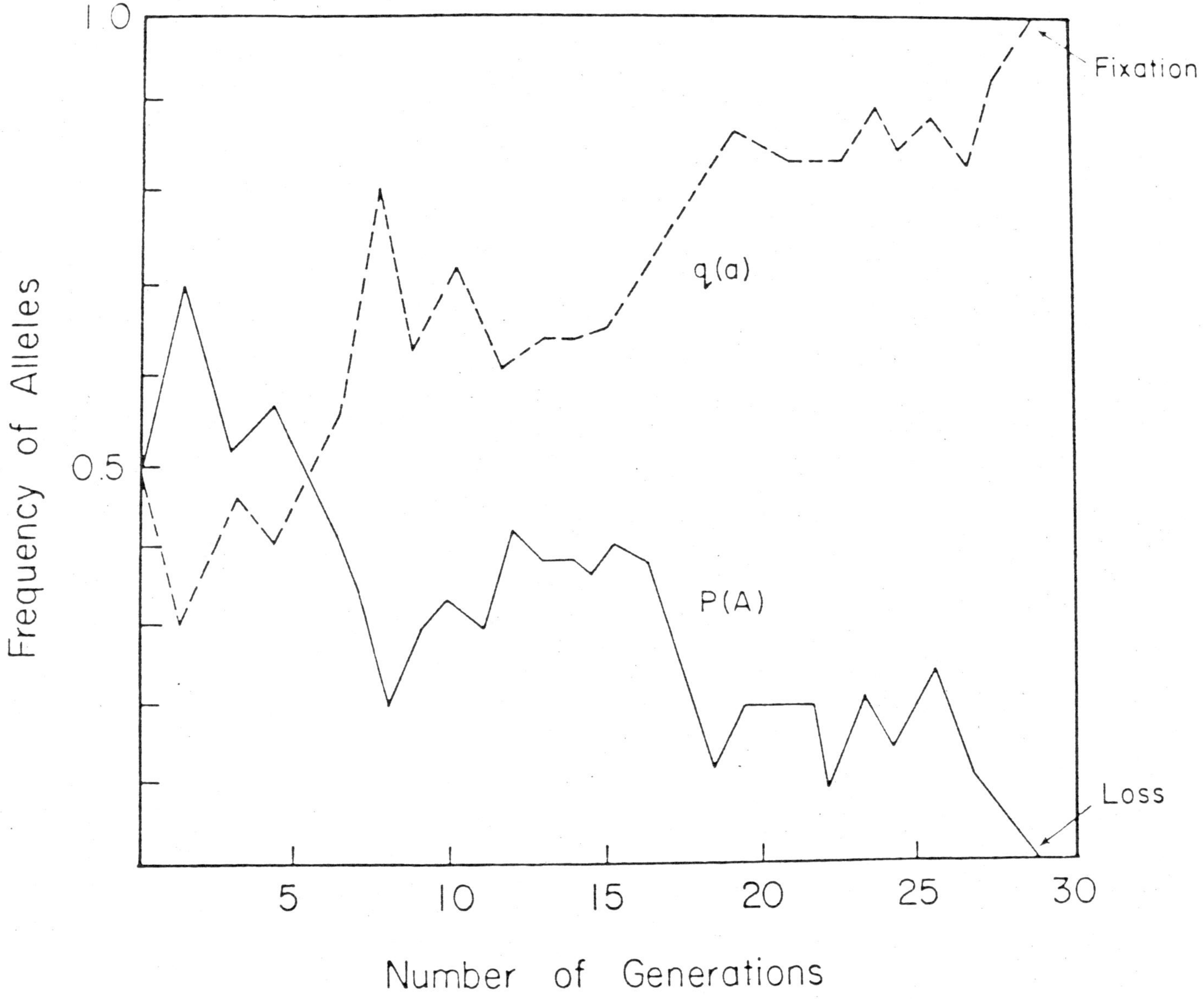
Genetic factors are thought to be among the most important mechanisms regulating the variability and stability of small populations. Some recent theoretical studies (Crow, 1969; Wright, 1970) emphasize the importance of genetic changes in small populations, yet very little empirical evidence has appeared to lend credence to these predicted changes. These genetic changes are expressed by the spread and fixation of homozygotic, recessive allele pairs in small populations (Crow, 1969; Frankel, 1974; Wright, 1970). The mechanisms causing these changes are genetic drift and inbreeding.

Inbreeding results from the natural increase in the frequency of sib-mating in small populations. Increased sib-mating results in an increase in homozygous recessive genotypes. These genotypes will generally decrease the viability or fertility of population members, and inbreeding will therefore tend to decrease the population size. In addition, at the population level, inbreeding may result in differentiation between populations and increased genetic uniformity within populations. Differentiation of populations in the same or in different preserves will not necessarily lead to the loss of genetic diversity and may result in better adapted populations. However, increasing genetic uniformity within populations may lead to greater fluctuations in population numbers and consequently to an increase in the probability of a random extinction.

Genetic drift is the alteration of gene frequencies in small populations due to the random sampling of the gene pool that occurs in each generation. This may lead to the loss of genetic heterogeneity in small populations. Certain alleles may be permanently lost due to the effects of random sampling. In populations of less than 100 individuals alleles can be lost at rates from about 0.01 to 0.1 per locus per generation (Wilson and Bossert, 1971). This phenomenon has been demonstrated by simulation of a population of 12 individuals (Fig. 13). A reduction in genetic heterozygosity can dramatically increase the chances of random extinctions in small populations by increasing the presence of deleterious characteristics in the population and reducing the population's ability to adapt to changing conditions.

Recent evidence suggests that small island populations may be differentiated by their degrees of genetic flexability (Soulé, 1972). In a study of phenotypic variation in insular lizard populations, Soulé found that if a population is relatively variable for character A, it will also be relatively variable for characters B, C, etc. He concludes that some pervasive quality of a gene pool or the gene pool environment interaction determines the level of variation. This quality is identified as the average genetic heterozygosity of the population. If the average genetic heterozygosity can be estimated from the general level of phenotypic variation then this parameter might also be used to measure the average genetic flexibility of a species. In this way the relative vulnerability of small species populations to processes such

Fig. 13. A computer simulation of the effects of genetic drift in a population of 12 individuals. Allele a with a frequency of q becomes fixed while allele A, with a frequency of p is lost. Smaller real world populations may achieve these end points in shorter time intervals (from Wilson and Bossert, 1971, p. 86).


1.0
0.5
Frequency of Alleles
q(a)
P(A)
Fixation
Loss
5
10
15
20
25
30
Number of Generations

as genetic drift and inbreeding may be measurable. This appears to be the most promising method for measuring genetic vulnerability of small populations.

The selective forces governing species composition in preserves are presently not well understood. Recent design criteria proposed for wildlife preserves and derived from island biogeographic theory pertain exclusively to maximizing the size of species communities within preserves rather than maintaining their structural integrity. Only a few of the mechanisms proposed in this chapter to explain selective species extirpations in wildlife preserves are supported by extensive empirical observations. Additional field research is essential for the development of management guidelines to insure preservation of present species diversity in isolated wildlife communities.

ESTIMATION OF THE PARAMETERS IN THE SPECIES-AREA EQUATION

Most of the recent research involving the application of island biogeographic theory to wildlife preserves is based primarily on data concerned with the dynamics of island communities. Researchers and others have extrapolated results from island situations and implied that these might also successfully be used to describe the changes likely to take place in nature preserves. To understand the changes predicted for wildlife preserves the distinction between island and preserve communities is essential. In addition, to successfully predict future changes in present preserve communities, modifications in the island biogeographic approach to isolated communities are necessary.

The species contained within the demarcated boundaries of continental areas represent a sample from a larger community. These species ensembles will be influenced by their interactions with surrounding species, and thus they do not necessarily represent communities. On the other hand, species ensembles of insular areas represent insular communities characterized by an independence from contiguous environments. This contrast results because present preserve boundary areas are frequently indistinguishable from areas within preserves, while islands are surrounded by totally inhospitable environments.

Stable insular communities have presumably developed an internal, dynamic equilibrium whereas continental sample areas are more strongly influenced by interaction with contiguous species communities. Therefore, parameter values empirically derived from insular areas may or may not apply directly to continental areas.

Preston (1962) empirically established that values for his exponent z ranged between 0.11 - 0.17 for sample areas and between 0.20 - 0.35 for insular areas. The latter values have since been verified by others (Table 1). In biological terms, this means that there is much less of a relation between the number of species and the size of the area for continental samples than for insular areas. An empirical evaluation of the correspondence between large mammal species and preserve area will demonstrate the point.

Species-area date for 13 East African savanna preserves (Table 3) were analyzed in the following manner. The logarithm of the number of species was regressed against the logarithm of the area of the preserve. Least squares analysis yielded the predictive equation:

$$\log S = 1.55 + 0.02 \log A \qquad (16)$$

But the logarithmic form of equation (8) is:

$$\log S = \log C + z \log A \qquad (17)$$

and therefore the antilog of 1.55 represents the coefficient C while 0.02 represents the exponent z. The allometric derivation of the regression equation is:

$$S = 35,48A^{0.02} \qquad (18)$$

The statistical relevance of this relation is insignificant ($R = 0.02$), and thus there exists essentially no relation between the number of large mammal species and size of area for the preserve data utilized. It seems that in East African savanna preserves area is not the factor presently regulating species numbers. Yet, as these same preserves be-

Table 3. The number of large mammal species presently occurring in 13 East African savanna parks (Williams, 1968), the area and the species number predicted from a regression of present species against recorded area.

Preserve	Area sq Km^2	# of Large Mammal Species Presently Indigenous to the Area	# of Large Mammal Species Predicted By Equation (8)
Mikumi National Park, Tanzania	1,266	29	41.3
Ngorongoro Crater Tanzania	6,475	33	42.3
Ruaha National Park Tanzania	12,950	41	42.9
Serengeti National Park, Tanzania	14,504	55	43.0
Mkomazi Game Reserve, Tanzania	3,276	39	41.7
Amboseli Masai Game Reserve, Kenya	2,361	45	41.5
Mara Masai Game Reserve, Kenya	1,813	52	41.3
Nairobi National Park, Kenya	114	44	39.0
Samburu-Isiolo Game Reserve, Kenya	298	44	39.8
Tsavo National Park Kenya	21,358	48	43.3
Kidepo Valley National Park, Kenya	1,005	36	40.8
Murchinson Falls National Park, Uganda	4,003	31	41.9
Queen Elizabeth National Park, Uganda	1,987	35	41.3

come increasingly isolated and mimic islands surrounded by seas of civilization, the insular parameters may apply quite well.

The degree of the present species area relation among wildlife preserves within any zoogeographic region is derivable from the above analysis technique. However, in many areas, including the South Florida region, a lack of species-area data makes it impossible to invoke this analysis. Nevertheless, if some species data were available, a rough estimate of the degree of the present species-area relation within individual preserves could be obtained from equation (8).

Everglades National Park covers 567,018 hectares (Ross-MacDonald, 1971), of which 283,401 ha are terrestrial. There are presently 25 terrestrial mammal species inhabiting the park (Table 4). The species-area relation of the mammal community of the Everglades could be derived if appropriate parameter values for the coefficient C and the exponent z were available.

The coefficient C, defined by equation (10), is dependent on the overall density of individuals (p) in the area. This analysis concerns the entire mammal community and thus p represents the combined density of mammal species of the Everglades. Mammalogists and ecologists have not generally measured total community density, and therefore it is necessary to approximate the density by using many sources of varying accuracy and credibility (Table 5). The individual estimates represent the number most likely to occur when averaged over different years, habitat types, ets. Even though the overall density figure is but a rough estimate, it seems most likely that it lies between 11 and 17 animals per

Table 4. Terrestrial mammal species and subspecies found in the Everglades National Park (from Layne, 1974 and Robertson, 1966).

Common Name	Species
Opossum	Didelphis, Virginiana Kerr
Short-tailed shrew	Blarina brevicauda, Say
Least shrew	Cryptotis parva, Say
Eastern mole	Scalopus aquaticus, Lennaeus
Marsh rabbit	Sylvilagus palustris, Bachman
Eastern cottontail	Sylvilagus floridanus, J. A. Allen
Grey squirrel	Sciurus carolinensis, Gmelin
Fox squirrel	Sciurus niger, Linnaeus
Fox squirrel	
Southern flying squirrel	Glaucomys volans, Linnaeus
Rice rat	Oryzomys palustris, Harlan
Cotton mouse	Peromyscus gossypinus, LeConte
Hispid cotton rat	Sigmodon hispidus, Say and Ord
Round tailed muskrat	Meofiber alleni, True
Gray fox	Urocyon cinereoargenteus, Schreber
Black bear	Ursus americanus, Dallas
Racoon	Procyon lotor, Linnaeus
Long-tailed weasel	Mustela frenata, Lichtenstein
Mink	Mustela vison, Schreber

hectare with a mean of 14 (14.14 was the computed mean). Based on this estimate, the value of C resulting from equation (10) varies between 2.45 and 2.87 when z is varied over the entire range for sample areas (0.11 - 0.17).

When sample area values for the coefficient C, the exponent z and the area of the Everglades are used in equation (8) a range of predicted values for the present number of mammal species is obtained (Figure 15). The equation that most closely predicts the present number of terrestrial mammal species in the park (25 species) is:

$$S = 2.87A^{0.17} \tag{19}$$

Since this exponent value, 0.17, is close to the range of exponent values associated with isolated areas (0.20 - 0.35), this may imply that the terrestrial mammal community of the Everglades may already by experiencing some effects of isolation.

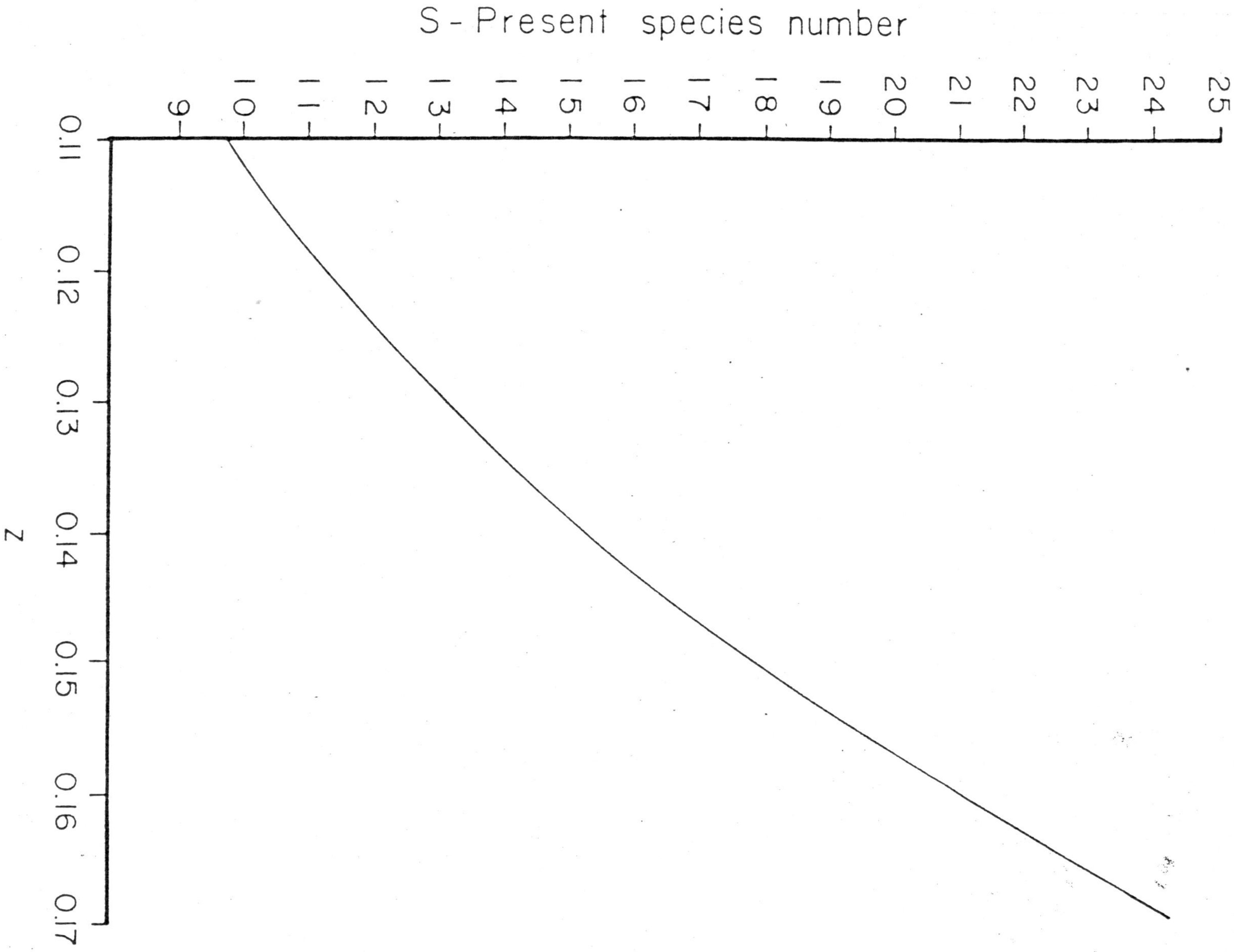
Table 5. Estimated abundance of the terrestrial mammal fauna of the Everglades National Park. Many of these estimates are approximations because of inadequate species data in the literature.

Species Common Name	Scientific Name	Animals/hectare	Source
Opossum	*Didelphis virginiana*	0.02	Mohr, 1943
Short-tailed shrew	*Blarina brevicauda*	<<2.47≃1.0	Mohr, 1943, Layne 1974
Least shrew	*Cryptotis parva*	<<2.47≃1.0	Layne, 1974
Eastern mole	*Scalopus aquaticus*	?	
Hispid cotton rat	*Sigmodon hispidus*	3.7	Provo, 1957
Round-tailed muskrat	*Neofiber alleni*	1.24	Birkenholz, 1962, Layne, 1974
Gray fox	*Urocyon cinereoargenteus*	0.002	Bowman, pers. comm.
Black bear	*Ursus americanus*	0.000025	Schemnitz, 1972
Racoon	*Procyon lotor*	0.025	Dorney, 1954
Long-tailed weasel	*Mustela frenata*	0.002	Mohr, 1943
Mink	*Mustela vison*	0.0012	Mohr, 1943
Marsh rabbit	*Sylvilagus palustris*	0.74	Layne, 1974
Eastern cottontail	*Sylvilagus floridanus*	<<0.25≃0.10	Mohr, 1943, Layne, 1974
Gray squirrel	*Sciurus carolinensis*	1.24	Mohr, 1943
Fox squirrel	*Sciurus niger*	~0	Layne, 1974

Table 5 - continued

Species		Animals/hectare	Source
Common Name	Scinetific Name		
Southern flying squirrel	*Glaucomys volans*	~0	Layne, 1974
Rice rat	*Orysomys palustris*	~2.47	Negus et al., 1961
Cotton mouse	*Peromyscus gossypinus*	2.47	McCarley, 1954
Eastern spotted skunk	*Spilogale putorius*	<<0.0124≈0.005	Layne, 1974
Striped skunk	*Mephistis mephistis*	<0.0124	Mohr, 1973
River otter	*Lutra canadensis*	0.0124	Layne, 1974
Panther	*Felis concolor*	0.000015	Schemnitz, 1972
Bobcat	*Lynx rufus*	0.0074	Layne, 1974
White-tailed deer	*Odocoileus virginianus*	0.0099	Layne, 1974
Nine-banded armadillo	*Dasypus novemcinctus*	<<0.25≈0.1	Layne, 1974
	Total density	14.14/ha/	

Fig. 14. The number of mammal species predicted to be present in the Everglades National Park (ordinate) over Preston's range of exponent values for sample areas (abcissa). The curve is produced from the equation $S = 1.83\ (p/m)^{z}\ A^{z}$ when $p = 14.14$ animals/hectare and $a = 283{,}401$ ha, which are the values associated with the Everglades.


S-Present species number
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
Z
0.11
0.12
0.13
0.14
0.15
0.16
0.17

EQUILIBRIUM PREDICTIONS

A specific application of the island biogeographic model and various equations can be demonstrated on the two ecologically distinct wildlife preserves already referred to. Both areas are functionally isolated in certain respects, but neither has achieved total isolation. In each case the analysis is conducted as if both of the preserves will some day become islands. Equation (8) is used to predict the equilibrium number of species that would occur if these areas were to become islands and in one case the equilibration time is predicted from equation (11). The model predictions are then tested against reality.

As wildlife preserves transform from sample areas to islands, one would expect the animal communities to equilibrate accordingly. Since sample continental areas generally contain more species per unit area than equilibrated islands, newly demarcated preserves might be considered to be "supersaturated" with species. This makes the equilibration process tantamount to species extirpation. This implication is tested in each of the following applications.

The Mkomazi Game Reserve, Tanzania

The Mkomazi Game Reserve covers 3276 km^2 along the Kenya-Tanzania border contiguous with the Tsavo National Park of Kenya. Although legally gazetted as a game reserve in 1952, the area became functionally isolated from surrounding habitat (Masailand) in the early 1940's. Surrounding mountains, rising as high as 1800 m above the plain, effectively close over 50 percent of the steppeland periphery while long standing villages preclude immigration through the few existing passes on the Tanzania side. Free movement to and from Tsavo National Park still exists for some species and indeed highly mobile species such as elephant (Loxodonta africana Blumbach) migrate across the border seasonally. But relative to the entire large mammal ensemble, the effects of Tsavo and other Kenya free land seems minimal. For the purposes of this analysis, the large mammal category includes the orders Primata, Carnivora (Canidae, Felidae and Hyaenidea only), Orycteropodidae, Proboscidea, Perissodactyla and Artiodactyla.

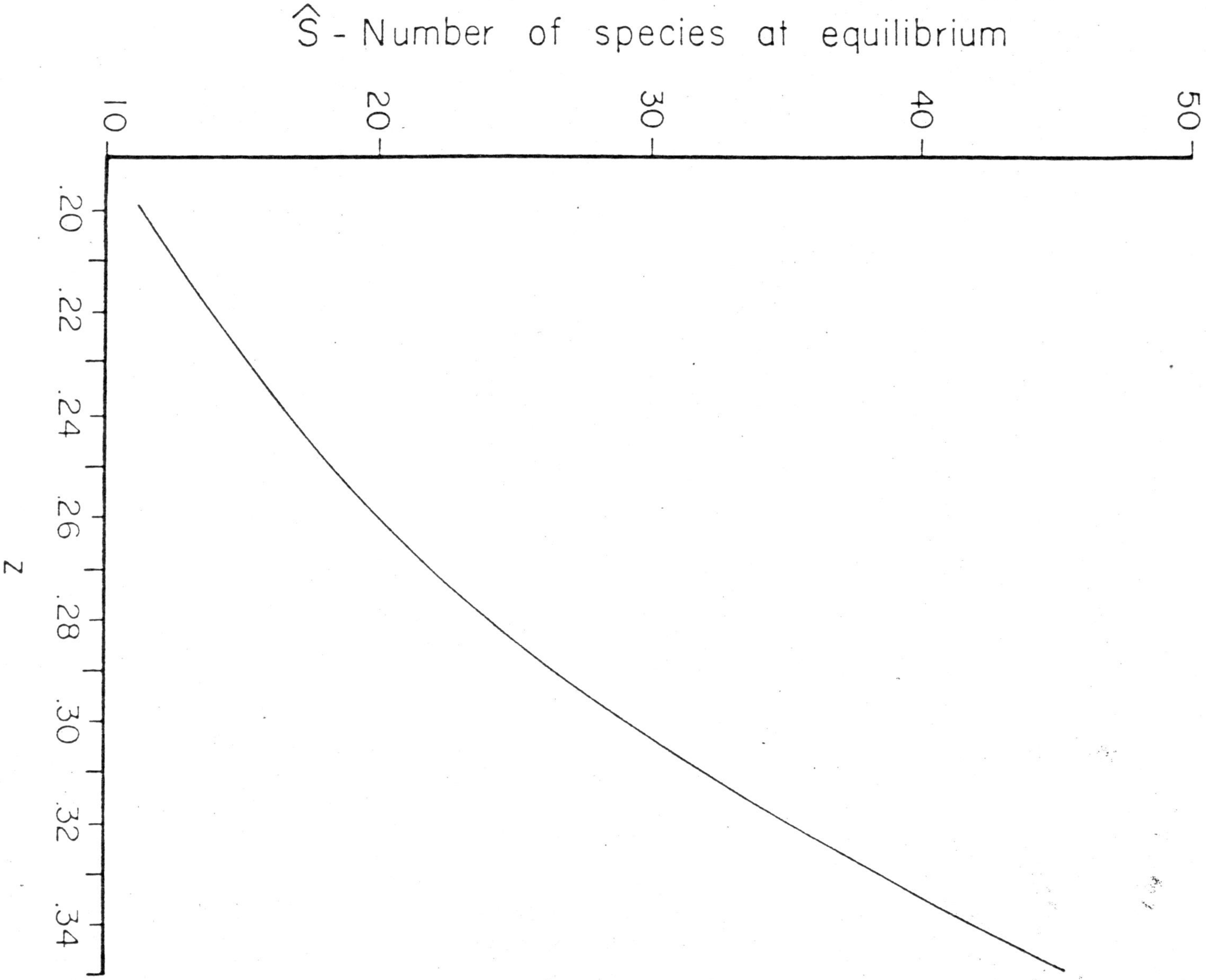
To calculate the equilibrium number of species, values of C and z and the use of equation (8) are necessary. The value of C can be obtained by use of equation (10) and a density estimate. The overall density has been estimated to be 3.0 animals/km^2 (L. D. Harris, pers. comm.). This method of estimating C should lead to an overestimate of $\hat{S}$ (the equilibrium number of species) since it is based on present conditions rather than equilibrated ones. Even though C should decrease as the area equilibrates the theory is presently inadequate to predict C for the totally isolated community. Values for the exponent z for equilibrated wildlife preserves do not exist either and therefore the entire range of z values for isolated areas are used in predicting the equilibrium number (Fig. 15). The median value of 0.27 from the observed range 0.20 - 0.35 yields the equation:

$$\hat{S} = 1.35A^{0.27} \qquad (20)$$

The corresponding $\hat{S}$ value for the large mammal community of the Mkomazi preserve is 21.97 (≃22) species. Recall that the present number of species is 39 and therefore some 17 species are predicted to be extirpated from the reserve before equilibrium is achieved.

Equation (11) can now be used to solve for the amount of time required for the Mkomazi to reach this natural equilibrium value (in the

Fig. 15. The relation between the predicted equilibrium number of large mammal species in the Mkomazi Game Reserve and values of the exponent z is associated with isolated areas (0.20 - 0.35). The above curve is produced from the equation $\hat{S} = (1.35)\ (3276)^z$ where 1.35 is derived from large mammal densities in the Mkomazi and 3276 km^2 is the area of the reserve.


Ŝ - Number of species at equilibrium
10
20
30
40
50
Z
.20
.22
.24
.26
.28
.30
.32
.34

absence of management forces). The original number of species present, S_o, was 43; the present number of extant species, S_t, is 39 and the time (t) from isolation (1942) until the research ended in 1967 is 25 years (Harris, 1972). The corresponding relaxation time, t_r, is 119.05 years. In other words, 274 (2.303 x 119.05) years from 1967, 90 percent of the digression towards natural equilibrium should have occurred. Since this process is projected to occur at a negative exponential rate (Fig. 6), the actual number of species going extinct in early years should greatly exceed that of later years.

Historical records (Harris, 1972) suggest that at least four and maybe five large mammal species have been extirpated from this area in recent decades. These include the Eastern white-bearded wildebeest (Connochaetes taurinus Burchell); greater kudu (Tragelaphus strepsiceros Pallas); sable antelope (Hippotragus niger Harris); colobus monkey (Colobus angolensis Sclater); and possibly the oribi (Ourebi ourebi Zimmerman). Only four of these extirpations are certain because of doubt concerning the status of the oribi (wildebeest were succsssfully reintroduced into the area by Harris in 1965). These data fit the expected pattern, and one can not help but speculate whether or not the predicted 15 extirpations (90 percent of 17) will occur during the next 265 years. The evidence supports the thesis that extirpations are at least sometimes associated with the game preserve movement. It would be presumptuous to assert that the extirpations to date resulted solely from the preserve phenomenon per se. To the contrary, several other factors such as cattle grazing and elicit hunting have been the proximal causes. Yet one cannot deny that extirpations have occured in spite of positive conservation and

and management activities within the reserve and the proximal factors should not be confused with the ultimate phenomenon.

The Everglades National Park

The Everglades National Park lies at the southern tip of the Florida peninsula. The park includes a wide variety of ecosystem types, including a portion of Florida Bay and associated islands, coastal prairie, mangrove forests, cypress swamps and the everglades--an extensive freshwater marsh covered by many ponds and hammocks. The everglades was originally a continuous "river of grass" spanning the 161 km between Lake Okeechobee and Florida Bay. It has since become partitioned by highways, canals and other changes associated with development.

The southern everglades area was legally incorporated as a national park in 1947. Areas surrounding the park have been drained, bisected by major highways, diked and otherwise impacted. Most of the surrounding area is contained by the water conservation areas and is thus subject to dramatic water level fluctuations. In addition, one third of the land area surrounding the park is affected by some form of private ownership (Anon., 1976) and is under constant developmental pressure. Development in surrounding areas significantly enhances the isolation of the Everglades faunal community (Oxley, et al 1974). Furthermore, changes in surrounding areas affect resource availability within the park ecosystem and consequently influence species abundance and community interactions (McCluney, 1971; Thomas, 1974). The park is thus at least somewhat functionally isolated.

To predict the equilibrium number of species for the terrestrial mammal community within Everglades National Park the same procedure is followed as in the Mkomazi example. A value of C can be estimated for the overall mammal density in the Everglades (Table 5). Again, this should lead to an overestimate of $\hat{S}$. Equilibrium species number estimates are calculated for the entire range of exponent values for isolates (Fig. 16). The resultant equation for the equilibrium number of terrestrial mammal species in the Everglades National Park is:

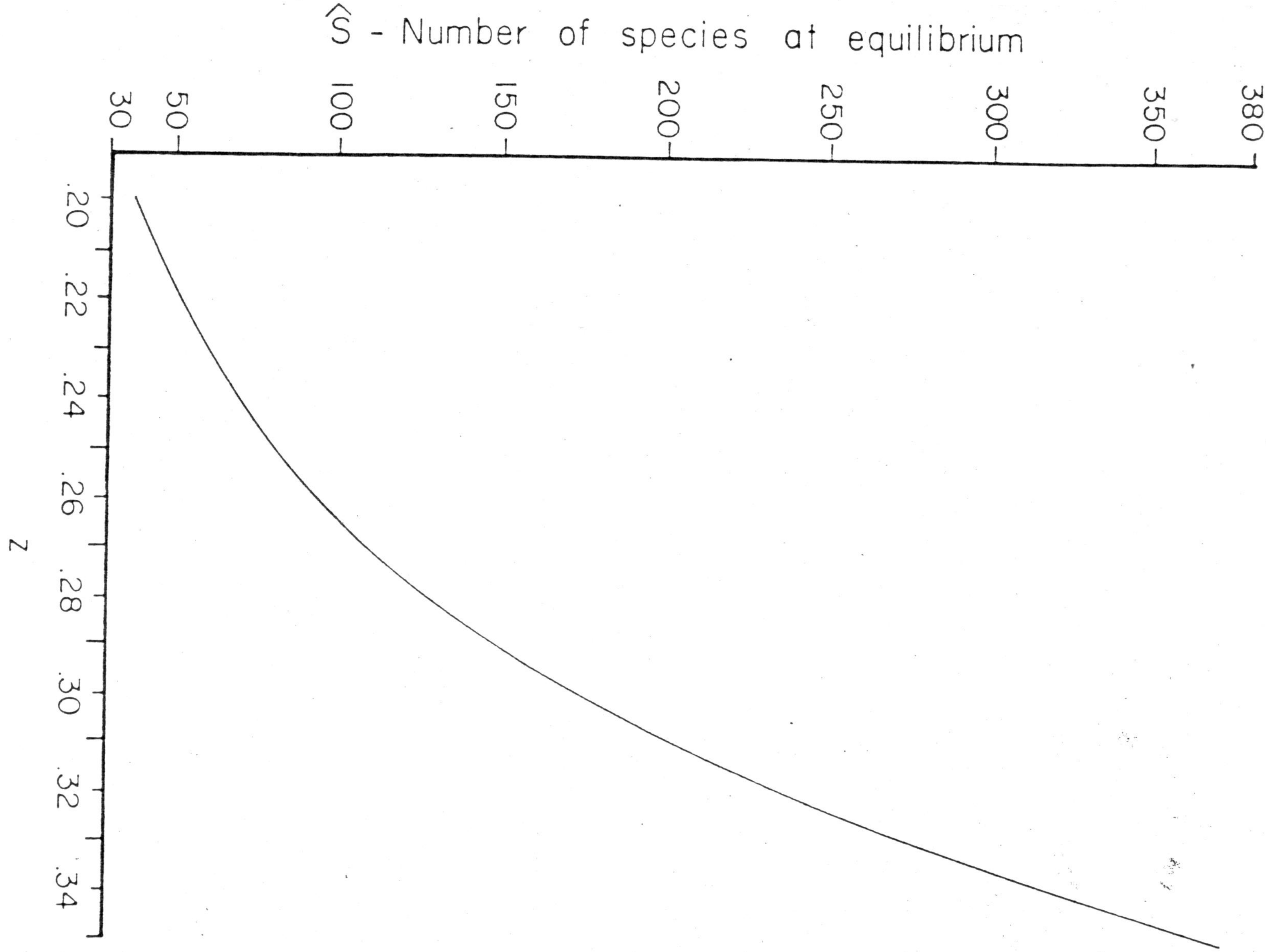
$$\hat{S} = 3.74\,A^{0.27} \tag{21}$$

The species prediction for the equilibrated Everglades National Park terrestrial mammal community is 110.92 ≃ 111 species.

Parameter values and the extant number of mammal species for the Everglades National Park were derivable from species data and the species-area equation. However, from the above analysis and resultant large estimate of the Everglades mammal fauna it is clear that reasonable estimates of the species equilibrium number, equilibration time, and extinction rate are not currently derivable. Identification and further quantification of the factors influencing the parameters of the species-area equation is necessary before an accurate estimate of the equilibrated Everglades mammal community is obtainable.

At least one mammal species has become extirpated from Everglades National Park in recent decades. The Florida red wolf (Canis rufus floridanus), which disappeared from most of the state in the early 1900's (Layne, 1974), but probably persisted longer in southern Florida than elsewhere (Bailey, 1930). This single extirpation is certainly not attributable to the isolation of the Everglades National Park. However, a number of mammal populations are rare or declining in the park and presently included on the endangered species list (Anon., 1973).

Fig. 16. The relation between the predicted equilibrium number of mammal species in the Everglades National Park and values of the exponent z associated with isolated areas (0.20 - 0.35). The above curve is produced from the equation $S = (3.74)\ (283{,}401)^z$ where 3.74 is derived from the terrestrial mammal density in the Everglades (Table 5) and 283,401 hectares is the area of the park.


Ŝ - Number of species at equilibrium
30
50
100
150
200
250
300
350
380
.20
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.32
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Z

These include the Florida panther (Felis concolor coryi), black bear (Ursus americanus floridanus), Everglades fox squirrel (Sciurus niger shermani), Everglades mink (Mustela vison evergladensis) and the round-tailed muskrat (Neofiber alleni nigrescens). The continued decline of these and other species in spite of conservation and management activity supports the hypothesis that a certain degree of decline and extirpation towards a more stable equilibrium may be inevitable in isolated wildlife sanctuaries.

TOWARD THE PRESERVATION OF BIOGEOGRAPHICALLY INTEGRATED WILDLIFE COMMUNITIES

For nearly a decade ecologists have studied the dynamics of insular animal communities with allusions to applying the theory and results to preserve design and management. However, to date there has been no explicit application into the resource management discipline. This study provides the first application of predictive equations and biological concepts to specific preserve communities. Predictions of species depletion within increasingly isolated preserves are supported by mammal species data in the two examples researched.

The distinction between areas at equilibrium and newly created and artificially bounded preserves is critical for understanding the nature of species changes in present preserve communities. Whereas area is a poor predictor of the present number of large mammal species in East African savanna preserves (equation [18]), it seems to be a much better predictor for the Everglades National Park (Fig. 14). As these areas develop some degree of equilibrium one might suppose that a species-area relation would emerge. Equations introduced here to calculate the species equilibrium number and equilibration time serve only as predictors of what might happen if the natural equilibration process is allowed to proceed undaunted. As predictive tools, they function as yardsticks for conservationists to measure our ability to mitigate the extinction process within preserves.

Analysis of the factors regulating the coefficient C and the exponent z in the species-area equation identifies the important factors influencing species numbers in wildlife preserves. The coefficient

C is influenced by vegetational diversity, environmental heterogeneity, species diversity within the taxon, and the degree of isolation. The exponent z is primarily influenced by the degree of isolation of the area. Both C and z are interrelated because of their mutual dependence on isolation. Since increasing isolation of wildlife preserves is a seemingly inescapable result of expanding human civilization, modification of factors such as environmental heterogeneity would seem to provide a feasible means of countering the isolation process.

The hypothesis that species at the top of the trophic pyramid are highly vulnerable to extirpation pressure seems to be supported by the Everglades data. A large percentage of the rare and endangered species of the Everglades terrestrial mammal community are top carnivores. These include the Florida panther (Felis concolor coryi) of which there are probably less than 50 surviving in the wild (Anon., 1976); the black bear (Ursus americanus floridanus) of which there are far fewer than 100 surviving in the Everglades National Park (Schemnitz, 1972); the Everglades mink (Mustela vison evergladensis) with a population in the low hundreds (Goodwin, 1976) and the Florida weasel (Mustela frenata peninsulae), which is generally considered very rare (Brown, L. N., 1971).

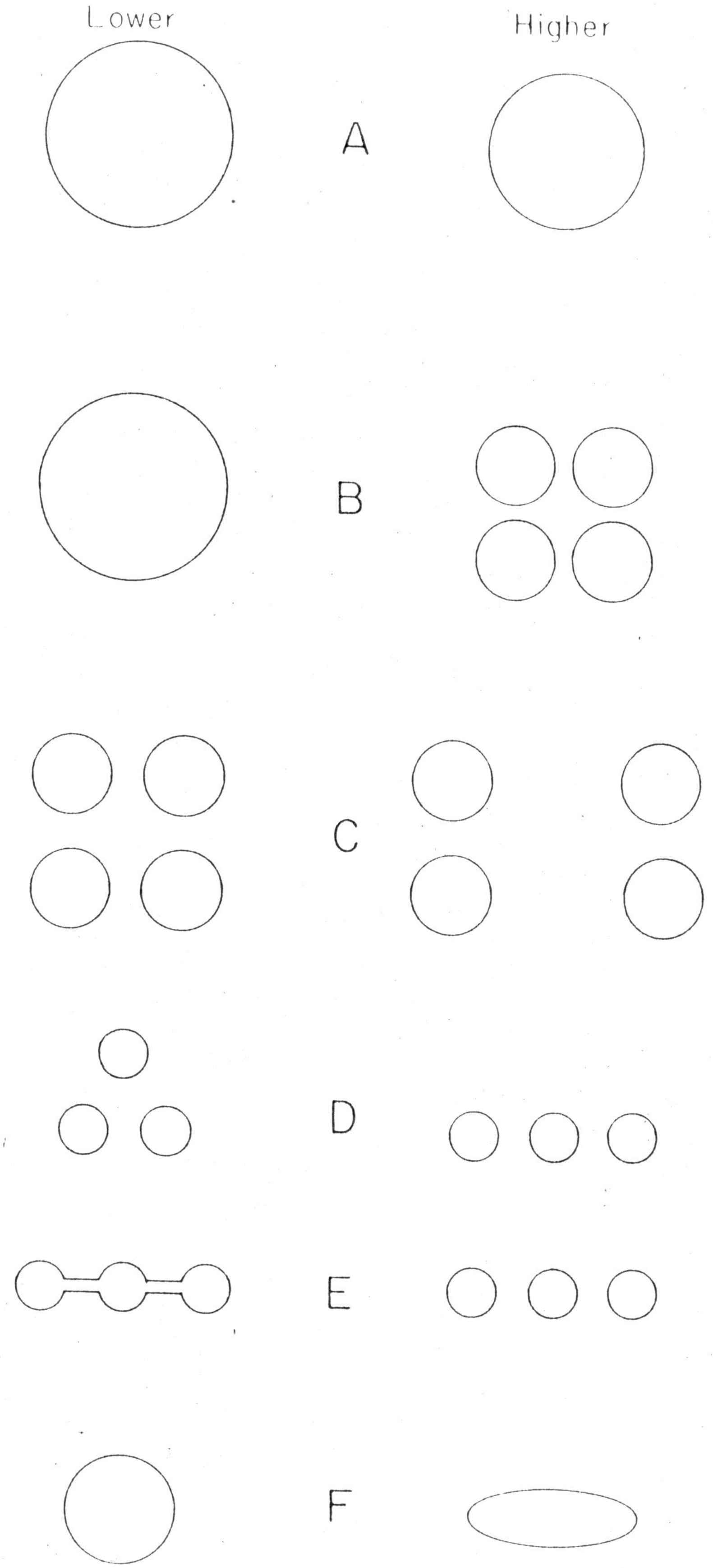
The number of mammal species presently inhabiting the Everglades area is significantly less than many other areas of equivalent size. Simpson (1964) showed that species densities are lower on well defined peninsulas than on nonpeninsular areas of similar topographic relief and latitude. This hypothesis is confirmed by a comparison of the total number of mammal species in peninsular Florida with a similar, nonpeninsular area of equal size at an equal latitude (Simpson, 1964). Furthermore, Simpson has also observed that in the United States topographic gradients explain many of the major differences in species density. Greater topographical diversity increases the variety of ecological conditions and thus the variety of ecological niches in a region. A topographically flat area situated on the distal end of a peninsula such as the Everglades National Park will contain a paucity of mammal species compared to a topographically heterogeneous, truly continental area of similar size and latitude. The species-area equation is insensitive to geographic or topographic differences between areas. This may partially explain the large estimate of the species equilibrium number for Everglades National Park predicted by the species-area equation.

A number of geometric principles are suggested by biogeographic theory have recently been developed (Diamond, 1975a; Wilson and Willis, 1975), and might serve as criteria governing the design of natural preserves (Fig. 17). These principles suggest methods to minimize extinction rates and maximize species numbers by modifying the shape, size and orientation of the preserves. Each principle is derived from generalizations suggested by the previously discussed observations. These include the following principles for the strategy and design of wildlife preserves:

Principle A. A large preserve is more advantageous than a small preserve because it will hold more species at equilibrium (Fig. 9) and it will most likely have a lower turnover rate and thus a lower extinction rate.

Principle B. A completely contermanous preserve is better than a fragmented one because smaller species populations would be more vulnerable to extinction than larger populations asso-

Fig. 17. Some preserve design principles derived from island biogeographic theory. In each case, the design on the left results in a lower instantaneous extinction rate than on the right (from Diamond, 1975a).


Lower
Higher
A
B
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ciated with a larger unified area.

Principle C. A clumped group of preserves is preferable to preserves spaced widely apart because of the distance effect.

Principle D. If the preserves must be disjunct then a clumped arrangement is preferable to a more linear arrangement because the chances of recolonization are increased with a clumped arrangement.

Principle E. Disjunctive preserves connected by corridors of protected habitat are better than unconnected preserves. Corridors between preserves increase intermixing between isolated species populations and thus increase their chance for survival.

Principle F. A preserve should be nearly circular in shape to minimize the peninsula effect. A preserve in the shape of a peninsula or with peninsula like appendages will maintain fewer species because of increased chances of random extinction and an increased edge to area ratio.

Principle G. When a large increment of regional diversity can be obtained by fractionating a large area into smaller but largely separated refugia, such a strategy should be employed. On the other hand, if a large increment of regional diversity cannot be attained by disassociation and separation, more species will probably be preserved by leaving the large area intact.

Further research into design alternatives is necessary. Simberloff

(1976) has demonstrated that the combined species of two smaller preserves may exceed the number of species contained in one large preserve of equal area (Appendix 4). Moreover, this contention is supported by experimental evidence involving arthropod communities on red mangrove (Rhizophora mangle) islands (Simberloff, 1976). The combined number of arthropod species recorded on an artificially created archipelago was greater than the number of species inhabiting the undivided island. This runs counter to the claim that a single large refuge maight be expected to contain more species than a number of small refugia. Additional data (Simberloff, 1976) suggest that there is a limit beyond which subdivision produces population sizes so small that extinction rates are greatly increased. This supports the hypothesis that small populations within a community will be highly vulnerable to extirpation pressure.

CONCLUSIONS AND RECOMMENDATIONS

The predictive relation between the number of resident species and the size of an area can be used to estimate the size of species communities in wildlife preserves. Comparison of these estimates with the size of extant preserve communities provides information about the degree to which the species-area relation dominates community size. Knowledge of the factors underlying the species-area equation can provide insight into the parameters regulating species numbers in preserves.

Knowledge of the extinction rate constant (Fig. 6) computed from a valid mathematical model serves as a valuable guide to the temporal pattern of the extinction process. A comparison of predicted extinctions with reality will provide a means of measuring the effectiveness of attempts to reduce extinction pressure. This will provide a valuable measure of the success or failure of conservation and preserve management techniques.

Further field research is necessary to provide the data for testing hypotheses derived from biogeographic theory concerning the design and management of isolated communities. Simberloff's (1976) study of island archipelagos is a first step in this direction. Further evidence is needed before park designers and managers can confidently rely on biogeographic theory.

The complexity of factors governing the equilibration process has not been clearly articulated. Each taxon and biogeographic region must be considered separately to establish a valid species-area relation. The degree of present isolation is also important since completely isolated areas reflect a much stronger relation than partially differentiated areas. Perhaps of greatest importance is the underlying environmental heterogeneity. Therefore, the next major step in advancing the equilibrium species number predictions will involve the inclusion of measures of environmental heterogeneity. In addition, the effects of the isolation factor on continental islands will be further refined so that it can be directly applicable to preserve communities.

APPENDIX A
ESTIMATING THE VALUE OF M

The parameter m, the number of individuals or pairs in the rarest species, is significant in defining the boundaries of the species curve associated with the canonical distribution. It also plays a major role in the species-area relation. The value of m defines the position of the species curve along the abcissa and thus it affects the number of individuals grouped in each octave. For this reason, the relation between I, the total number of individuals, and S, the total number of species, is really between I/m and S and not between I and S directly.

A number of empirically derived values of m exhibit a tendency to approximate unity (Preston, 1962), and thus the number of individuals of a canonical ensemble is fixed, given the total number of species. As m is increased above 1, the species curve is moved to the right along the abcissa and the number of individuals per species will be increased. Another possibility is that the total number of species in the ensemble be increased to compensate for the increased number of individuals. This same process will occur in reverse when m falls significantly below 1.

A biological explanation of this phenomenon is that in the equilibrium situation the environment is most efficiently exploited by a maximum number of species. This contention is supported by recent ecological theory (MacArthur, 1969; Odum, 1969). As the environment becomes maximally exploited, a limit will be reached when the number of species is the maximum consistent with the total number of individuals. The value of S, the total number of species in the ensemble, for a community approaching this limit corresponds with $m \simeq 1$.

APPENDIX B
A MODEL OF SPECIES RELAXATION
(Diamond, 1972)

This model is based on avifaunal data from the New Guinea land bridge islands. It is proposed that these islands have experienced a reduction in species numbers since they became isolated 10,000 years ago. This occured as a result of an extinction rate (E) which consistently exceeded the immigration rate (I). These rates are defined by the model through the use of constant coefficients for immigration and extinction. These coefficients are K_i and K_e respectively. The formula defining these rates are:

$$E = K_e\, S(t) \tag{2.1}$$

$$I = K_i\, (S^* - S[t]) \tag{2.2}$$

where

E = extinction rate

$S(t)$ = the instantaneous species number i.e. the number of species in the area at any time t (in years)

I = immigration rate

S^* = the number of species in the mainland species pool

$S^* - S(t)$ = the number of species available as potential immigrants,

The species equilibrium number, $\hat{S}$, is defined in this model as:

$$\hat{S} = K_i\, S^* / (K_i + K_e) \tag{2.3}$$

If an area initially supports a species complement S_o, the rate at which $S(t)$ declines from S_o towards $\hat{S}$ is obtained by integrating the following differential equation:

$$\frac{dS}{dt} = I - E = [K_i + K_e]\left[\frac{K_i S^*}{K_i + K_e} - S(t)\right] \qquad (2.4)$$

Given the condition that $S(t) = S(o)$ at $t = 0$, this integration yields

$$[S(t) - \hat{S}]/[S(o) - \hat{S}] = \exp(-t/t_r) \qquad (2.5)$$

where

t_r = the relaxation time i.e. the length of time required for a further reduction in species from the present level to 1/e (36.8 percent) of the present departure from the original species complement.

Equation (2.5) defines the time period over which equilibrium is achieved (equilibration time) and the slope of the extinction curve during this period. Based on this concept, the reduction of a species community to equilibrium would be 90 percent complete after 2.3 relaxation time intervals. Based on the equations of this model estimates of the equilibration time are derivable for preserve communities.

APPENDIX C
SOME THOUGHTS ON RECENT CRITICISMS OF AVIFAUNAL TURNOVER RATE STUDIES

Lynch and Johnson (1974) have strongly criticized methods used by recent authors (Diamond, 1969, 1971; Terborgh and Faaborg, 1973) to obtain estimates of avifaunal turnover rates on islands. Their principal objection to these studies is that many of the documented immigrations and extinctions are examples of "Pseudoturnoever" based on improper evaluation of faulty or imcomplete faunal data. They identify the problem as one of determining the breeding status of rare bird species in island communities. Lynch and Johnson underline the need for "detailed faunal data, carefully taken and critically interpreted". They support their claims by citing examples from Diamond (1969) of species classified as immigrations or extirpations that Lynch and Johnson classify as migratory or transient species.

I have carefully studied these objections to Diamond's data (1969) and have concluded that some criticism is justified. Diamond (1969) himself points out that much of his data may be faulty due to inadequate sampling procedure and small sample size. He then ignores his own warning and bases some of his conclusions on unsubstantiated data. He also makes generalizations about isalnd bird communities without sufficient empirical evidence.

However, I did not find that the most important conclusions of Diamond's (1969) study were invalidated by the above observations. The magnitude of the turnover rates is obviously overestimated in the Channel

Island study. However, comparison of these rates to each other is not necessarily impugned by the overestimation of individual turnover rates. More importantly, Diamond does not attempt to derive a relation between species numbers and either island area or distance of an island from the mainland. Large disparities in ecological diversity between islands make a consideration of size and distance effects inappropriate (Diamond, 1969). The most important conclusion of the Channel Island study is that an inverse correlation exists between percentage turnover rate and the species number of each island. Selected shifts in classification between transient and resident species will not alter the significance of this conclusion. The Channel Island study also provides statistically significant data supporting the existence of a dynamic equilibrium on island communities (MacArthur and Wilson, 1963, 1967).

APPENDIX D

A COMPARATIVE MODEL OF THE SPECIES COMPOSITION OF A LARGE PRESERVE VERSUS TWO PRESERVES OF EQUAL SIZE

A model is available that compares the species equilibrium number ($\hat{S}$) of two ecologically identical islands receiving immigrants from an identical source area (MacArthur and Wilson, 1967). Each island is assumed to exhibit identical immigration and extinction rates. In each case the immigration rate is a negative linear function of distance.

Consider the species number on each of the smaller islands. Each island will contain $\hat{S}$ species, which is a random sample of the P species comprising the species pool associated with the source area. There is a probability of $\hat{S}/P$ that a species on one of these islands will also be found on the second island. A proportion of the species on the second island defined by $1 - \hat{S}/P$ will be different from the species found on the first island. Thus the second island contains $\hat{S}(1 - \hat{S}/P)$ species not found on the first island. The two islands combined will contain the following number of unique species:

$$\hat{S} + \hat{S}(\quad - \hat{S}/P) = \hat{S}(2 - \hat{S}/P) \qquad (4.1)$$

Based on this sample model Simberloff (1976) presents an interesting comparison between the equilibrium species number expected for one large preserve of Area A_1 and two small preserves each of area $A_2 = A_1/_2$. For each preserve $\hat{S}$ is defined by $S = CA^2$ (see equation [8] in the text).

If each of the smaller preserves contains S_2 species then the two smaller preserves combined will contain the following number of unique species:

$$S_2 + S_2(1 - S_2/_P) = 2S_2 - S_2{}^2/_P \quad (4.2)$$

where

P = the number of species in the species pool of the source area

In contrast, the larger preserve contains S_1 species defined by

$$S_1 = CA_1{}^z = C(2A_2)^2 \quad (4.3)$$

In completely isolated areas the value of z has been empirically observed to approach 0.27. Thus at equilibrium

$$S_1 = 1.2\ CA_2{}^{0.27} \quad (4.4)$$

and

$$S_1 = CA_2{}^{0.27} \quad (4.5)$$

therefore

$$S_1 = 1.2S_2 \quad (4.6)$$

Based on this relation, when will the number of unique species in both smaller preserves exceed the number of unique species in the larger preserve? The situation in question will occur when

$$1.2S_2 < 2S_2 - S_2{}^2/P \quad (4.7)$$

This equation simplifies to

$$0.80 > S_2/_P \quad (4.8)$$

and since $S_1 = 1.2S_2$ then

$$0.96 > S_1/_P \quad (4.9)$$

Thus whenever the larger preserve contains less than 96 percent of the species in the source region, equation (4.7) will be valid. Since few large preserves will ever maintain 98 percent of the species in a region, the combined species of two smaller preserves will usually exceed the number of species contained in one larger preserve of equal area.

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BIOGRAPHICAL SKETCH

Ronald I. Miller was born on September 30, 1949, in Brockton, Massachusetts. Between September of 1967 and June of 1973, he attended Brandeis University in Waltham, Mass. Also during this time he completed coursework in the natural sciences at Harvard University. In June of 1973, he received a Bachelor of Arts degree in Environmental Sciences from Brandeis.

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