Rarity in Neotropical Forest Mammals and Its Ecological Correlates

HÉCTOR T. ARITA

Department of Wildlife and Range Sciences
School of Forest Resources and Conservation
University of Florida
Gainesville, FL 32611, U.S.A.

JOHN G. ROBINSON

Department of Wildlife and Range Sciences
School of Forest Resources and Conservation
University of Florida
Gainesville, FL 32611, U.S.A.

KENT H. REDFORD

Center for Latin American Studies
University of Florida
Gainesville, FL 32611, U.S.A.

Abstract: *Local density and size of distributional range have been used to characterize rarity, but conclusions are weakened by their possible lack of independence. The usefulness and validity of using these two variables were tested with data on distribution, local density, body size, and feeding habits for a set of 100 Neotropical forest mammals.*

In a bivariate plot of distributional range against local density, species clustered according to their trophic or taxonomic groups. This indicates that diet and phylogenetic history have an influence on rarity. A negative correlation was found between distribution and abundance. However, this correlation was weaker within trophic or taxonomic groups, and vanished when body size was held constant. These results show that both distribution and abundance are valid and independent estimators of rarity when comparing species with similar sizes and ecological traits. Regression analysis showed that larger animals tend to have lower densities and wider distributional ranges. Rarity is clearly associated with body size.

A dichotomous classification of rarity based on area of distribution and local density is suitable for Neotropical forest mammals. Species in each of four categories created by such a scheme require different conservation and management policies that are determined by the ecological charac-

Resumen: *La densidad a nivel local y el tamaño del área de distribución son dos parámetros que pueden ser usados para medir la rareza de una especie. Sin embargo, la utilidad de estas variables se ve limitada por una posible correlación entre ellas. En este trabajo se analiza la validez de la distribución y la abundancia como estimadores de rareza entre los mamíferos de los bosques neotropicales utilizando datos sobre densidad local, distribución, tamaño corporal y hábitos de alimentación de una muestra de 100 mamíferos neotropicales.*

En una gráfica de distribución contra densidad local, las especies se agruparon de acuerdo con sus hábitos de alimentación y categorías taxonómicas. Este resultado demuestra la influencia que la dieta y la historia filogenética ejercen sobre la rareza. Se encontró una correlación negativa entre la distribución y la abundancia. Sin embargo, la correlación fue menor cuando se compararon especies dentro de un determinado grupo taxonómico o de alimentación y la correlación parcial, manteniendo constante el tamaño corporal, fue cercana a cero. Esto significa que la distribución y la abundancia son estimadores independientes de la rareza si la comparación se restringe a especies con tamaños y rasgos ecológicos similares. Se demostró mediante regresión multiple que los animales de mayor talla tienden a poseer densidades más bajas y áreas de distribución más amplias. La rareza está claramente asociada con el tamaño del animal.

Es posible clasificar los mamíferos de los bosques neotro-

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teristics of the species. Final conservation strategies must also be shaped by political and economic constraints.

picales en cuatro categorías de rareza mediante un sistema dicotómico basado en el área de distribución y la densidad local. Las características ecológicas de las especies en cada una de estas categorías determinan diferentes requerimientos en cuanto a su conservación. Sin embargo, los pasos encaminados al uso y conservación de estas especies se verán también afectados por factores políticos y económicos.

Introduction

Ecology has been defined as the study of the distribution and abundance of animal and plant species (Andrewartha & Birch 1954; Krebs 1985). Distribution can be quantified by the number of sites in which a species is present (Hanski 1982; Gotelli & Simberloff 1987), or on the biogeographic scale by the area of the distributional range (Rapoport 1975, 1982). Abundance refers to local population density, the number of individuals that are found in a given site (Brown 1984). For a conservation biologist, the study of the distribution and abundance of organisms acquires a special meaning. He or she is particularly interested in the rare species, those whose scarity or restricted range makes them more prone to extinction (Terborgh 1974; Terborgh & Winter 1980). The study of rarity is a central concern in modern conservation biology.

The intuitive feeling that a rarer species is more prone to extinction has been supported both by theoretical studies and by empirical data. Several demographic models (MacArthur 1972; Richter-Dyn & Goel 1972; Goodman 1987; Lande 1988; Pimm et al. 1988) show that the probability of extinction of a local population declines as its size increases, and field studies have supported these models (Diamond 1984; Pimm et al. 1988). From the population genetics viewpoint, low densities mean higher probabilities of depleting genetic variation and lower chances of long-term survival (Soulé & Wilcox 1980; Frankel & Soulé 1981; Schonewald-Cox et al. 1983; Lande & Barrowclough 1987). On a regional scale, a species present in many sites should have better chances of survival than a species with restricted distribution. In the same way, a habitat specialist should be more sensitive to perturbations than a species that occurs in a variety of habitats.

However, rarity is not the only factor promoting extinction. Karr (1982), for example, found little support for the hypothesis that initial rarity was the cause of the majority of bird extinctions in Barro Colorado Island. Terborgh (1974) listed six traits that are correlated with proneness to extinction; restricted distributional range is on the list, but low local density is excluded. Lande (1987, 1988) has discussed how life history characteristics, such as territorial behavior, colonization ability, and intraspecific interactions, can determine the probability of extinction of a given species. Pimm et al. (1988) demonstrated that migratory birds are at a greater risk of extinction than resident species. Finally, Burke & Humphrey (1987) found that rarity is only one of a series of variables determining the endangerment of some vertebrates of Florida. These studies do not prove false the notion that rarity and probability of extinction are related, but they do show that a host of other factors can have an important effect as well.

Although the importance of studying rare species has been recognized, few papers have dealt with rarity and its ecological correlates. Exceptions include Karr (1977) on Neotropical birds, Thomas & Mallorie (1985) on Moroccan butterflies, Rabinowitz et al. (1986) on British plants, and Hubbell & Foster (1986) on tropical woody plants.

In this paper, we examine how well distribution and abundance characterize rarity, and we analyze the ecological correlates of these variables and their importance to conservation. We use the data set assembled by Robinson & Redford (1986) for Neotropical forest mammals, adding new information on distribution.

Relationship Between Rarity, Abundance, and Distribution

Rare animals have been described as those species with a low local density, a reduced geographic range, a restricted selection of habitats, or a combination of these conditions. A classification of species according to their rarity based on these criteria was proposed by Rabinowitz (1981). The possibility that these three ways of being rare were correlated was rejected by Rabinowitz et al. (1986) for British plants. However, a number of papers have reported a statistical relation between at least two of the ways of being rare, namely low local density and restricted distributional range (MacNaughton & Wolf 1970; Brown 1984). The implications of such correlation for conservation are analyzed in the following paragraphs.

Two models of the dynamics of regional distribution provide contrasting predictions regarding the correlation between distribution and abundance (Gotelli & Simberloff 1987). Levins's (1969) model predicts no correlation, whereas Hanski's (1982) core-and-satellite model generates a bimodal distribution of species according to the number of sites that they occupy and predicts a positive correlation between local abundance and regional distribution. For a broader scale, Brown & Maurer (1987) have presented an analysis of the ecological and energetic constraints that could be determining the observed relationship between local densities and distributional ranges of North American birds.

Several studies have provided empirical tests for these theories. A positive correlation between local density and number of sites occupied was found by Hanski (1982) for a variety of organisms, and similar results have been shown by MacNaughton & Wolf (1970), Bock & Ricklefs (1983), Bock (1984, 1987), Brown (1984), Gotelli & Simberloff (1987), and Brown & Maurer (1987). Negative correlations have been reported by Willson (1974), Adams & Anderson (1982), and Schoener (1987).

For the study of rarity in conservation biology, knowing the magnitude of the correlation between distribution and abundance is of central importance. In a dichotomous classification of rarity using these two variables, the number of species in each of the four possible categories is determined by the association between the variables. Figure 1 illustrates the effect of correlation between distribution and abundance on the frequency of the categories of rarity. In the extreme case where the correlation is perfect, it would be possible to predict the value of one of the variables by knowing the other, making redundant the use of both variables to assess the rarity of a species. Conversely, if the correlation is close to zero, the variables would be independent estimators of rarity.

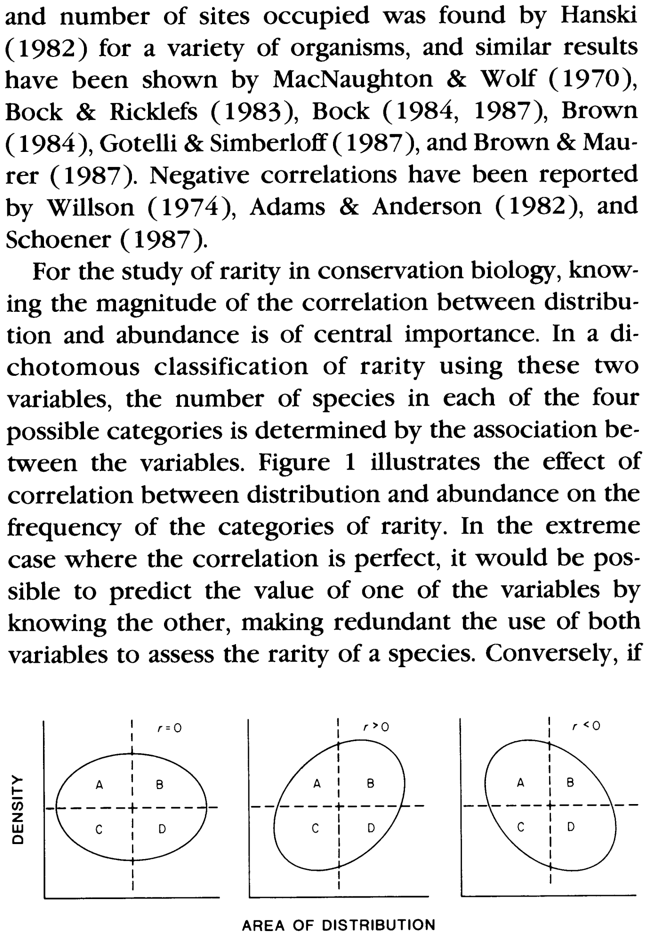


Figure 1. Relative frequency of the types of rarity determined by local density and area of distribution. When no correlation exists between distribution and abundance (left), there is an equal number of species in each category: 25 percent. If the correlation is positive (center), categories B (widespread and abundant) and C (restricted and rare) have more species than A or D. A negative correlation (right) produces more species of categories A (restricted but abundant) and D (widespread but locally rare). Ellipses represent the frequency distribution of two normally distributed variables.

Rarity in Neotropical Mammals

To test these ideas, we analyzed available data on distribution and abundance for a group of Neotropical mammals. Data on body mass, diet, and density were extracted from Robinson & Redford (1986); details on the sources and methods used to obtain these data can be found in that paper. It is important to emphasize that both Robinson & Redford (1986) and the present study focused on forest species, and the results and conclusions should not be interpreted as representative of the whole Neotropical mammal fauna. We deleted some species because no reliable information on distribution was available. Additionally, due to the nature of this study, we avoided the use of data for genera with no specified species, restricting the analysis to the comparison among species. The final data set included one hundred species (Table 1).

We gathered information on distribution (see references in Table 1) and plotted the ranges on a standard map of tropical America that included a grid of nonaligned dots separated by a distance of 2.5 degrees. We tallied the number of dots included in the range of each species, and calculated the areas of the distributional ranges (in thousands of km^2) by a regression formula fitted using the area of the countries of South and Central America as known areas.

Relationship Between the Variables

Preliminary analyses showed the convenience of using log-transformed instead of raw variables. The distribution of the logarithms of body mass did not differ significantly from a normal distribution ($P > 0.5$, Shapiro-Wilk test), and while logged values of area and density differed from a normal distribution ($P < 0.01$ and $P < 0.05$, respectively), the fit was much better than using raw data. We relied on the robustness of the statistical methods that follow to include slightly nonnormal distributions.

We first correlated area of distributional range and local density. Pearson's product-moment correlation coefficients were first calculated for the entire data set, and then for subsets defined by taxonomic and trophic characteristics. We found a negative correlation between distribution and abundance when all species were combined ($r = -0.23$, $P < 0.05$). In contrast, coefficients within taxonomic and trophic groups varied from positive to negative but, with the exception of carnivorous species, none differed significantly from zero (Table 2). Furthermore, tests of homogeneity (Sokal & Rohlf 1981) revealed no significant differences

Table 1. Diet classification, body mass, density, and area of distribution of Neotropical forest mammals.

	Food	*Mass (g)*	*Density (ind/km^2)*	*Area (thousands of km^2)*
Marsupialia				
Caluromys derbianus	FO	1,300	13.4	217.9 (1)
Caluromys philander	FO	300	59.8	2,016.3 (1)
Caluromysiops irrupta	FO	250	10.0	79.6 (1)
Didelphis marsupialis	FO	1,041	55.3	10,731.8 (1)
Marmosa cinerea	IO	127	25.0	3,953.1 (1)
Marmosa fuscata	IO	60	113.0	494.6 (1)
Marmosa murina	IO	45	43.0	8,103.3 (1)
Marmosa noctivaga	IO	60	15.0	4,506.5 (1)
Marmosa robinsoni	IO	49	123.5	1,047.9 (1)
Monodelphis brevicaudata	IO	80	63.0	7,688.3 (1)
Metachirus nudicaudata	IO	400	8.3	10,593.4 (1)
Philander opossum	IO	400	62.9	9,486.7 (1)
Primates				
Cebuella pygmea	IO	122	389.6	1,463.0 (2)
Callithrix argentata	IO	380	8.5	1,463.0 (2)
Callithrix humeralifer	IO	380	116.7	218.0 (2)
Callithrix jacchus	IO	259	33.0	2,431.4 (2)
Saguinus nigricollis	IO	360	17.4	217.9 (2)
Saguinus fuscicollis	IO	364	26.9	2,016.3 (2)
Saguinus mystax	IO	517	24.2	771.3 (2)
Saguinus labiatus	IO	520	15.9	356.2 (2)
Saguinus imperator	IO	520	42.3	632.9 (2)
Saguinus midas	IO	500	9.8	1,601.3 (2)
Saguinus oedipus	IO	435	51.4	79.6 (2)
Saguinus leucopus	IO	440	1.7	10.4 (2)
Leontopithecus rosalia	IO	745	4.6	79.6 (2)
Aotus azarae	FO	873	3.6	1,463.0 (3)
Aotus lemurinus	FO	873	63.0	909.6 (3)
Aotus nigriceps	FO	873	34.1	1,186.3 (3)
Callicebus moloch	FO	1,166	15.4	5,198.2 (2)
Callicebus torquatus	FO	1,000	16.5	1,878.0 (2)
Pithecia hirsuta	FO	1,800	37.5	1,878.0 (4)
Pithecia monachus	FO	1,800	5.1	2,016.3 (4)
Pithecia pithecia	FO	1,809	5.1	1,463.0 (4)
Chiropotes albinasus	FO	2,847	6.5	494.6 (2)
Chiropotes satanas	FO	2,896	9.3	1,878.0 (2)
Saimiri sciureus	FO	688	62.3	6,166.6 (2)
Cebus albifrons	FO	2,005	9.5	3,261.4 (2)
Cebus apella	FO	3,445	12.4	1,146.8 (2)
Cebus capucinus	FO	3,250	12.1	356.2 (2)
Cebus olivaceus	FO	2,900	15.2	1,878.0 (2)
Alouatta caraya	FH	6,500	42.2	2,293.0 (2)
Alouatta palliata	FH	6,679	47.6	771.3 (2)
Alouatta pigra	FH	6,500	12.0	217.9 (2)
Alouatta seniculus	FH	6,185	29.3	5,198.2 (2)
Ateles belzebuth	FH	7,500	9.1	2,016.33 (2)
Ateles geoffroyi	FH	7,500	18.0	1,186.3 (2)
Ateles paniscus	FH	7,775	11.3	2,984.7 (2)
Lagothrix flavicaudata	FH	10,000	7.3	10.4 (2)
Lagothrix lagothrica	FH	10,000	10.3	3,399.8 (2)
Edentata				
Bradypus tridactylus	HB	2,400	170.9	1,186.3 (5)
Bradypus variegata	HB	3,725	438.3	1,108.5 (5)
Choloepus didactylus	HB	4,150	57.5	4,368.1 (5)
Choloepus hoffmanni	HB	9,000	133.7	1,601.3 (5)
Cyclopes didactylus	MY	400	15.4	6,166.6 (5)
Tamandua mexicana	MY	4,210	5.2	909.6 (5)
Tamandua tetradactyla	MY	4,560	6.6	12,391.9 (5)
Myrmecophaga tridactyla	MY	27,000	0.1	12,530.2 (5)
Cabassous unicinctus	MY	4,800	0.7	3,123.1 (5)

Table 1. Continued.

	Food	Mass (g)	Density (ind/km^2)	Area (thousands of km^2)
Tolypeutes matacus	MY	1,066	13.3	4,368.1 (5)
Dasypus novemcinctus	IO	3,544	21.1	12,668.5 (5)
Euphractus sexcinctus	IO	4,350	3.0	7,124.9 (5)
Priodontes maximus	MY	39,400	0.4	8,795.0 (5)
Lagomorpha				
Sylvilagus brasiliensis	HZ	1,017	4.0	7,688.3 (6)
Sylvilagus floridanus	HZ	1,025	35.0	2,016.3 (7)
Rodentia				
Sciurus granatensis	FG	250	98.9	1,601.3 (8)
Liomys adspersus	FG	45	720.0	24.6 (8)
Heteromys anomalus	FG	75	438.7	632.9 (8)
Akodon urichi	FG	40	200.0	1,186.3 (8)
Calomys callosus	FG	15	400.0	3,814.8 (8)
Neacomys tenuipes	FG	20	400.0	1,878.0 (8)
Rhipodomys mastacalis	FG	90	172.0	1,186.3 (8)
Zygodontomys brevicauda	FG	50	58.0	2,846.4 (8)
Echimys semivillosus	FG	200	73.5	356.2 (8)
Proechimys semispinosus	FG	300	334.5	3,814.8 (8)
Sphiggurus insidiosus	FG	1,000	29.7	494.6 (9)
Coendou bicolor	FG	5,000	6.3	1,324.6 (9)
Coendou prehensilis	FG	3,360	43.5	7,965.0 (9)
Myoprocta acouchy	FG	552	8.6	2,431.4 (9)
Dasyprocta punctata	FG	3,600	19.7	4,783.1 (9)
Agouti paca	FG	8,227	27.5	11,561.8 (9)
Hydrochaeris hydrochaeris	HB	31,500	17.8	13,221.9 (9)
Carnivora				
Nasua nasua	FO	3,880	15.1	13,498.6 (10)
Potos flavus	FO	2,490	24.4	18,478.8 (10)
Procyon cancrivorus	FO	10,100	3.8	9,071.7 (10)
Procyon lotor	FO	8,850	10.0	2,154.7 (10)
Conepatus semistriatus	FO	1,700	13.8	11,008.5 (10)
Eira barbara	FO	3,980	1.0	14,328.6 (10)
Galictis vittata	CA	2,910	2.4	13,083.6 (10)
Felis yagouarundi	CA	5,000	0.5	15,712.0 (10)
Felis pardalis	CA	10,460	0.8	15,158.7 (10)
Felis concolor	CA	37,000	0.1	19,862.2 (10)
Panthera onca	CA	68,750	0.1	16,265.4 (10)
Perissodactyla				
Tapirus bairdii	FH	300,000	0.5	1,186.3 (10)
Tapirus terrestris	FH	148,950	1.6	11,838.5 (10)
Artiodactyla				
Tayassu tajacu	FH	17,520	11.9	13,360.2 (10)
Tayassu pecari	FH	28,550	4.9	11,838.5 (10)
Mazama americana	FH	26,100	10.5	14,190.3 (10)
Mazama gouazoubira	FH	17,350	10.4	2,431.3 (10)
Odocoileus virginianus	HB	40,000	2.8	7,411.6 (10)

Note: *Dietary classification as follows: FO, frugivore-omnivore; IO, insectivore-omnivore; FG, frugivore-granivore; FH, frugivore-herbivore; HB, herbivore-browser; MY, myrmecophage; HZ, herbivore-grazer; CA, carnivore. Data on feeding habits and density from Robinson & Redford (1986). Data on distribution from the references in the last column, as follows: (1), Streilein (1982); (2), Wolfheim (1983); (3), Hershkovitz (1983); (4), Hershkovitz (1979); (5), Wetzel (1982); (6), Hershkovitz (1950); (7), Chapman et al. (1980); (8), J. F. Eisenberg, personal communication; (9), Mares & Ojeda (1982); (10), R. M. Wetzel, unpublished maps made available by J. F. Eisenberg.*

in correlation coefficients between taxonomic groups ($P > 0.1$) or feeding categories ($P > 0.1$). The inferences on correlations within groups should be interpreted with caution, because of the small sample sizes.

These results show that a negative association between distribution and abundance of Neotropical forest mammals is apparent only when comparing species of different taxonomic or trophic categories. If taxonomic affiliation and diet are controlled, no correlation can be shown between distribution and abundance. The implications of these results are analyzed in the following sections.

Table 2. Product-moment correlation coefficients between distribution and abundance for taxonomic and trophic groups of Neotropical forest mammals.

	n	*r*
Order		
Marsupialia	12	0.19
Primates	38	0.26
Lagomorpha	2	-.-
Edentata	13	−0.29
Rodentia	17	−0.38
Carnivora	11	−0.41
Perissodactyla	2	-.-
Artiodactyla	5	-.-
Trophic group		
Frugivore-omnivore	25	−0.03
Insectivore-omnivore	23	0.20
Frugivore-granivore	16	−0.31
Frugivore-herbivore	16	−0.03
Herbivore-browser	6	−0.36
Herbivore-grazer	2	-.-
Myrmecophage	7	−0.33
Carnivore	5	−0.88*
Total	100	−0.23*

* $P < 0.05$.

Types of Rarity

Species were classified according to their rarity by arbitrarily setting the limits of categories at the medians of area of distribution and density. By doing this, we assigned half of the species to the category of locally rare, and the other half to locally abundant; half of the species were defined as widespread and half as having a restricted distribution. While subjective, this method recognizes that scarcity and commonness are comparative terms and that rare and abundant species are only the extremes on a continuum of possible states.

The slight negative correlation between the distribution and abundance produced an apparently higher frequency of species in type A (restricted and locally abundant) and D (widespread and locally rare) than in types B and C (29 in A and D, 21 in B and C, Table 3). However, the departure from the null distribution (25 species in each category) is not statistically significant ($X^2 = 2.56, P = 0.11$).

A plot of the variables produced clearly defined but overlapping clusters of species grouped taxonomically (Fig. 2). Marsupials and rodents cluster in the upper half of the graph, showing the tendency of these animals to be locally abundant. Perissodactyls, represented by the two species of tapirs, lie in the lower half. Edentates and lagomorphs are clustered in the right side (broad distribution), whereas many primates are concentrated in the left side (restricted distribution). Both carnivores and artiodactyls are clearly clustered in the lower right quadrant (broad distribution but low local density).

To test the significance of these patterns, we compared the observed frequencies within each group with the frequency distribution obtained for the whole sample (29 species in A and D, 21 species in B and C); any deviation from this null distribution would imply an effect of taxonomic affiliation. For the smaller groups (with <25 species) we computed the exact probabilities of a deviation equal or greater than the one ob-

Table 3. Neotropical forest mammals classified according to their rarity.

Category A:
restricted distribution
and high density

Caluromys philander
Marmosa fuscata
Marmosa robinsoni
Cebuella pygmea
Callithrix humeralifer
Saguinus nigricollis
Saguinus fuscicollis
Saguinus mystax
Saguinus labiatus
Saguinus imperator
Saguinus oedipus
Aotus lemurinus
Aotus nigriceps
Callicebus torquatus
Pithecia hirsuta
Alouatta caraya
Alouatta palliata
Ateles geoffroyi
Bradypus tridactylus
Choloepus hoffmanni
Sylvilagus floridanus
Sciurus granatensis
Liomys adspersus
Heteromys anomalus
Akodon urichi
Neacomys tenuipes
Rhipodomys mastacalis
Echimys semivillosus
Sphiggurus insidiosus

Category B:
wide distribution
and high density

Didelphis marsupialis
Marmosa cinerea
Marmosa murina
Monodelphis brevicaudata
Philander opossum
Callithrix jacchus
Callicebus moloch
Saimiri sciureus
Alouatta seniculus
Bradypus variegata
Choloepus didactylus
Cyclopes didactylus
Dasypus novemcinctus
Calomys callosus
Zygodontomys brevicauda
Proechimys semispinosus
Coendou prehensilis
Dasyprocta punctata
Agouti paca
Hydrochaeris hydrochaeris
Potos flavus

Category C:
restricted distribution
and low density

Caluromys derbianus
Caluromysiops irrupta
Callithrix argentata
Saguinus midas
Saguinus leucopus
Leonthopithecus rosalia
Aotus azarae
Pithecia monachus
Pithecia pithecia
Chiropotes albinasus
Chiropotes satanas
Cebus capucinus
Cebus olivaceus
Alouatta pigra
Ateles belzebuth
Lagothrix flavicauda
Brachyteles arachnoides
Tamandua mexicana
Coendou bicolor
Procyon lotor
Tapirus bairdii

Category D:
wide distribution
and low density

Marmosa noctivaga
Metachirus nudicaudatus
Cebus albifrons
Cebus apella
Ateles paniscus
Lagothrix lagothrica
Tamandua tetradactyla
Myrmecophaga tridactyla
Cabassous unicinctus
Tolypeutes matacus
Euphractus sexcinctus
Priodontes maximus
Sylvilagus brasiliensis
Myoprocta acouchy
Nasua nasua
Procyon cancrivorus
Conepatus semistriatus
Eira barbara
Galictis vittata
Felis yagoaurundi
Felis pardalis
Felis concolor
Panthera onca
Tapirus terrestris
Tayassu tajacu
Tayassu pecari
Mazama americana
Mazama gouazoubira
Odocoileus virginianus

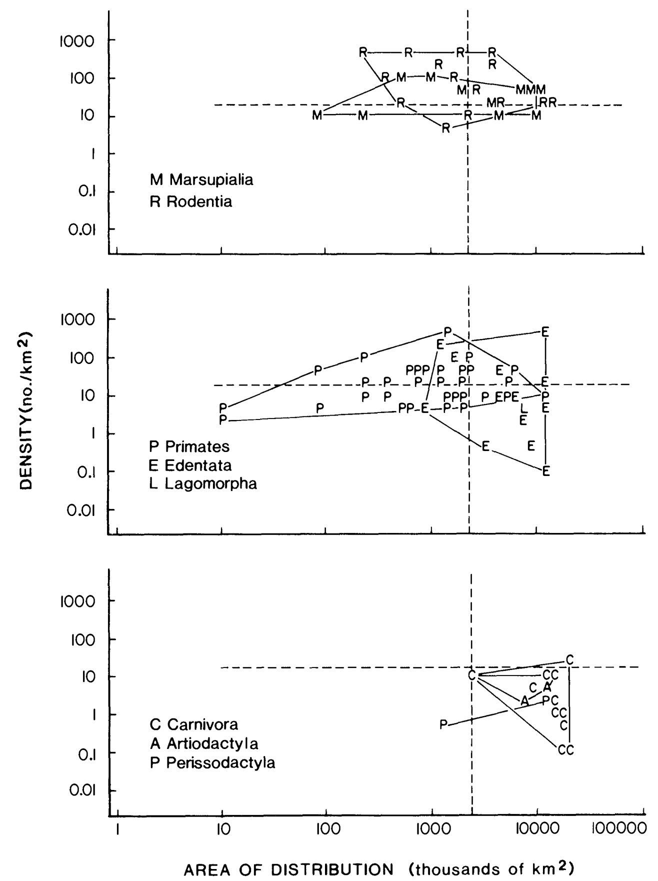


Figure 2. Classification of Neotropical mammals according to their local density and area of distribution by taxonomic groups. Broken lines are drawn at the medians of the two variables for the whole data set, and determine the categories of rarity discussed in the text.

Table 4. Number of species in each category of rarity for Neotropical forest mammals classified according to taxonomic and trophic groups. Probabilities are for deviations $\geq$ the one observed from a four-group multinomial distribution with probabilities 0.29, 0.21, 0.29, and 0.21. Probabilities for all groups except primates ($n \leq 25$) are exact probabilities computed using the multinomial distribution. For primates, the probability was approximated using a chi-square test.

	Categories				
	A	*B*	*C*	*D*	P
All Species	29	21	21	29	
Order					
Marsupialia	3	5	2	2	0.40
Primates	15	4	15	4	<0.01**
Edentata	2	4	1	6	0.32
Lagomorpha	1	0	0	1	1.00
Rodentia	8	7	1	1	0.02*
Carnivora	0	1	1	9	0.001**
Perissodactyla	0	0	1	1	1.00
Artiodactyla	0	0	0	5	0.005**
Trophic Group					
Frugivore-omnivore	5	4	10	6	0.13
Insectivore-omnivore	10	6	4	3	0.26
Frugivore-granivore	8	6	1	1	0.03*
Frugivore-herbivore	3	1	5	7	0.24
Herbivore-browser	2	3	0	1	0.32
Herbivore-grazer	1	0	0	1	1.00
Myrmecophage	0	1	1	5	0.07
Carnivore	0	0	0	5	0.005**

*P < *0.05,* **P < *0.01.*

served using the multinomial probability distribution. For primates, we calculated an approximate probability using the chi-square test, which provides accurate values for multinomial distributions with large sample sizes (Mendenhall et al. 1986). Primates, rodents, carnivores, and artiodactyls showed significant deviations from the null distribution (in all cases $P < 0.05$, Table 4), suggesting an effect of taxonomic affiliation on rarity.

The analysis when species were categorized on the basis of trophic characteristics yielded the results shown in Figure 3. Frugivore-herbivores, insectivore-omnivores, and frugivore-omnivores show no apparent pattern, having approximately the same number of species in each quadrant. Frugivore-granivores tend to concentrate in the upper part of the graph, showing their relatively high densities. Browsers and grazers concentrate in the right part of the plot, the region of the widespread species. Myrmecophages and carnivores seem to concentrate in the lower right quadrant (broad distribution and low density). Only the patterns of the frugivore-granivores and the carnivores are statistically significant ($P < 0.05$, Table 4). Our data suggest an effect of diet on rarity, but results are not conclusive.

As in other comparative studies, it is not easy to separate the effects of ecological parameters from the effect of phylogenetic history, because these two features are not independent. In this case, for example, all the rodent species except one are frugivore-granivores, a category that is not represented in any other taxonomic group. The patterns associated with feeding habits and taxonomic grouping may represent two manifestations of a single phenomenon.

The Effect of Body Size

A negative correlation between body mass and average local density has been demonstrated for Neotropical mammals (Eisenberg 1980; Robinson & Redford 1986) and for some other animal groups (Damuth 1981; Peters 1983; Peters & Wassenberg 1983; Peters & Raelson 1984), although Morse et al. (1988) found weak or nonsignificant relationships between density and body length in tropical beetles. A positive correlation between body size and area of distribution has been proposed by Brown (1981) and by Brown & Maurer (1987). As both distribution and abundance are related to body size, we expected a strong effect of body mass on the classification of species on the basis of their rarity.

As a first approach to this idea, we investigated the

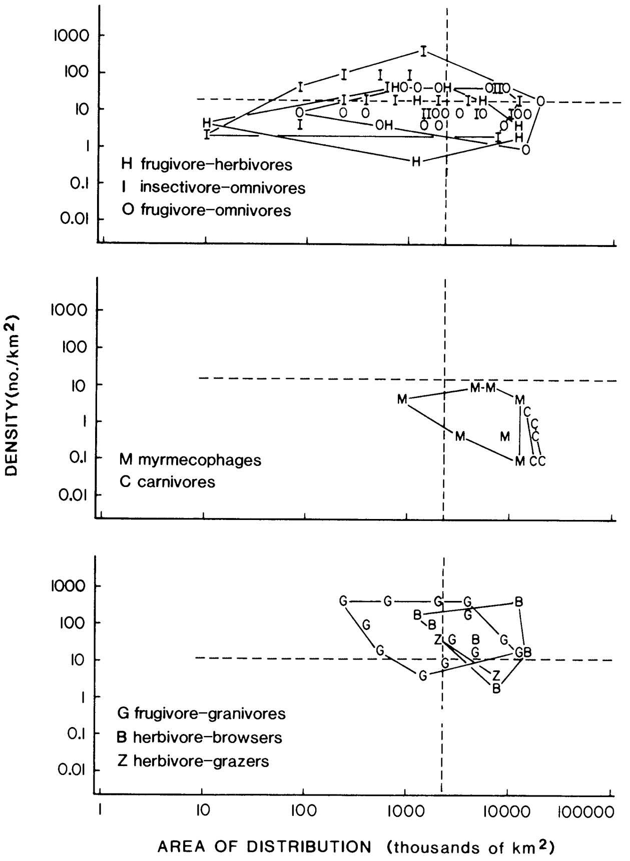


Figure 3. Classification of Neotropical mammals according to their distribution and abundance by trophic categories.

correlations between the three variables. In accord with Robinson & Redford (1986), the correlation between body mass and density was negative ($r_{md} = -0.67, P < 0.001$), whereas body mass and area of distribution were positively related ($r_{ma} = 0.32, P < 0.01$). As discussed earlier, a slight correlation between area and density was demonstrated ($r_{ad} = -0.23, P < 0.05$). For Neotropical forest mammals, bigger animals tend to have wider distributional ranges but lower local densities.

The negative correlation between distributional range and density contradicts the results of many published studies on other groups, mainly birds (Bock & Ricklefs 1983; Bock 1984, 1987). This pattern suggests differences in distribution and abundance patterns between birds and mammals, but this could only be tested by having data on birds and mammals from different parts of the world. One possible explanation for the differences among taxonomic groups is the relative influence of body size on the correlation between local density and area of distribution. None of the previous studies have controlled for body size, and the reported correlations could be strongly determined by the dependence of both rarity variables on body size. To test this idea, we calculated the partial correlations for pairwise combinations of variables. Partial correlation coefficients measure the association between two variables when the rest are held constant (Sokal & Rohlf 1981).

The correlations between area and body mass and between density and body mass changed very little ($r_{ma.d} = 0.22, r_{md.a} = -0.65$), whereas the correlation between area and density was drastically reduced ($r_{ad.m} = -0.03$). This result indicates that the association between area of distribution and local density is highly dependent on the common variation produced by body size, and that for a set containing only species of comparable size we would expect no correlation between those variables. The ultimate explanation for this pattern has to be related with the many ecological parameters that are associated with body size, such as diet, home range and territory size, individual and population growth rate, and carrying capacity (Eisenberg 1981; Calder 1983; Peters 1983). The effect of body size on rarity that we have demonstrated is probably only a combination of the effects of all these life history traits.

This result explains why the observed association between distribution and abundance for the whole Neotropical mammal data set vanishes when the analysis is performed by taxonomic or trophic groups; the variation in body size within each subgroup is much less than the variation for the whole set. This conclusion accords with an analysis reported by Brown & Maurer (1987). They used a discriminant analysis of three variables (body mass, area of distribution, and local abundance) for a set of North American birds grouped in trophic categories. Their first discriminant variable, which explained 87 percent of the variance, was highly correlated with the logarithm of body mass (canonical correlation = 0.98), and had much lower correlations with the other two variables, logarithm of area (canonical correlation = 0.03) and local density (canonical correlation = −0.21). This indicates that in this particular set, body size is the single best variable to discriminate the trophic groups, showing that variation in body size is greater among trophic groups than within these groups.

From the observed correlations, it could be predicted that for a given set of species, larger animals would tend to fall in the lower right corner of the graph of density versus area of distribution, in the zone of widespread species with low local density. Smaller animals would tend to be locally abundant with restricted distributions and to fall in the upper left corner of the graph. Finally, the quadrants in the upper right and lower left corners would tend to have animals of intermediate sizes, the exact position of each species depending on other factors besides size.

To analyze this idea, we performed a multiple regression using the logarithm of body mass as dependent variable and the logarithms of area and density as independent variables. The equation obtained by least-squares fit was:

$$\ln \text{MASS} = 0.22 \ln \text{AREA} - 0.71 \ln \text{DENSITY} + 7.68,$$

which is equivalent to the expression:

$$\text{MASS} = 2158.78\ \text{AREA}^{0.22}\ \text{DENSITY}^{-0.71}$$

These results demonstrated that as the body mass of a species increases, area of distribution tends to increase and local density tends to decrease (Fig. 4). As a consequence, species in category D (widespread but locally rare) are the largest, followed by those in categories C, B, and A in that order (Fig. 5).

The analysis shows that body mass has a strong effect on rarity among Neotropical forest mammals. It is also clear that both taxonomic position and diet have some influence on body mass. The ultimate causes of rarity are very difficult to discern because of the multiplicity of variables that are correlated with body mass. As we have already discussed, many life history parameters that are related to local density and area of distribution are not independent of body size. In our data set, knowing the size of a species can help to predict its relative position in our bidimensional rarity space (Fig. 4), and this has great pragmatic value. However, we are far from knowing the ultimate ecological causes of rarity.

Implications for Conservation

A dichotomous classification of rarity based on distribution and local abundance is suitable for this set of Neotropical forest mammals. The correlation between area of distribution and local density is very slight and allows the allocation of species to one of the four categories of rarity (Table 3). The fact that this correlation vanishes when body size is controlled indicates that a better classification of rarity would be obtained by comparing only species of similar sizes. This procedure would yield classifications with equal numbers of species in each of the four categories of rarity (Fig. 1). Therefore, a dichotomous classification is most powerful when applied only to groups of species of similar size. However, as Rabinowitz et al. (1986) have pointed out, the dichotomous classification can be used even if the correlation between the variables is different from zero, because only a perfect correlation would produce a lack of species in two of the categories in Figure 1.

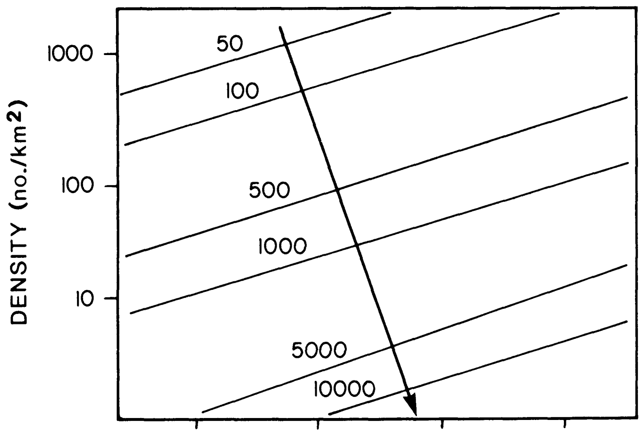
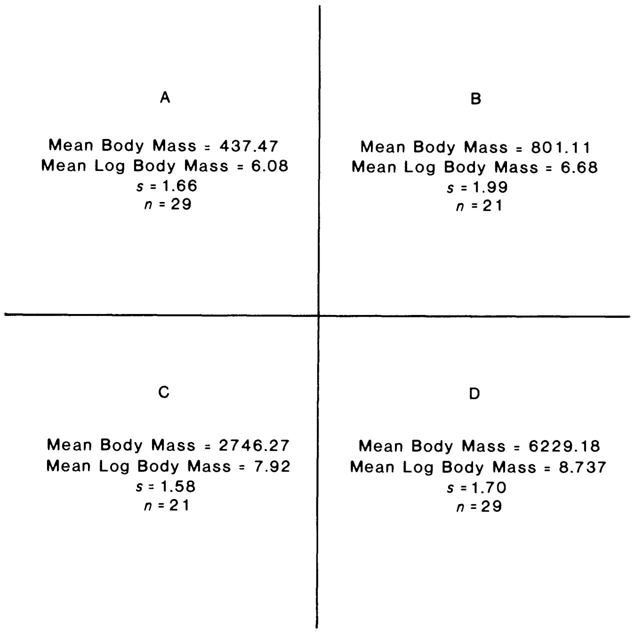


Figure 4. Nomogram showing the relationship between body size, local density, and area of distribution. Body mass is expressed as isopleths and is given in grams. Note the log scale in the density and area axes. The arrow points to the direction of increasing body size.



A
Mean Body Mass = 437.47
Mean Log Body Mass = 6.08
$s = 1.66$
$n = 29$

B
Mean Body Mass = 801.11
Mean Log Body Mass = 6.68
$s = 1.99$
$n = 21$

C
Mean Body Mass = 2746.27
Mean Log Body Mass = 7.92
$s = 1.58$
$n = 21$

D
Mean Body Mass = 6229.18
Mean Log Body Mass = 8.737
$s = 1.70$
$n = 29$

Figure 5. Body mass statistics for each rarity category. Each quadrant shows the mean body mass, the mean and the standard deviation of the natural logarithm of mass, and the sample size. Categories are as in Figure 1. Means of these categories are significantly different (one-way ANOVA, $P < 0.001$). The means of categories A and B and those of C and D are not significantly different (Duncan's multiple comparison test, $P > 0.05$).

There is a further complication to the classification of species based on their rarity. When we restricted the analysis to the Neotropics we imposed an artificial ceiling on the ranges of certain species and neglected the fact that some species extend their distribution into North America. The raccoon (*Procyon lotor*), for example, is a species with restricted distributional range and low density in Central and South America, but its status in North America is exactly the opposite. The decision of whether or not the raccoon deserves protection in Central and South America depends on whether we are interested in protecting the species as a whole or individual populations in different countries. This is not only a biological question, but it involves nationalistic feelings that cannot be included in a classification of rarity.

Different conservation and management policies are required for each category of species. Species in category C (restricted and locally rare) should be the target of conservation efforts. The combination of high risk of extinction for demographic or genetic causes and an absence of secondary sources to "rescue" vanishing populations makes them especially sensitive. Species that are widespread and locally abundant (type B) probably do not require special care, with the possible exception of those species that require high densities to successfully breed.

Species with restricted distributions but high local densities (type A) deserve some concern. However, some factors may contribute to decrease their probability of extinction. The ranges of many of these species coincide with those of species of category C, so the creation of reserves aimed at the conservation of species in category C may contribute to the preservation of species in category A. Some other species in this category are rodents and other animals that readily adapt to disturbed zones, and probably represent no special concern from the point of view of conservation.

Finally, widespread species with low local densities constitute a complex situation. These species, being the largest, require large preserves to assure their survival in a given site. A conservation strategy that would take advantage of the broad distributional ranges of these species would require international cooperation, and experience shows that this is often difficult.

A classification of species based on their rarity is a convenient and useful indicator of possible vulnerability, but it is no substitute for detailed population and community studies that should be conducted to establish the best management strategies. The study of rarity and of the different ways in which an organism can be rare is in its infancy. The tremendous importance of knowing the factors that produce rarity should encourage much more research in this branch of conservation biology.

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Literature Cited

Adams, D. E., and R. C. Anderson. 1982. An inverse relationship between dominance and habitat breadth in Illinois forests. American Midland Naturalist **107**:192–195.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois.

Bock, C. E. 1984. Geographical correlates of abundance vs. rarity in some North American winter landbirds. Auk **101**: 266–273.

Bock, C. E. 1987. Distribution-abundance relationships of some Arizona landbirds: a matter of scale? Ecology **68**:124–129.

Bock, C. E., and R. E. Ricklefs. 1983. Range size and local abundance of some North American songbirds: a positive correlation. American Naturalist **122**:295–299.

Brown, J. H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. American Zoologist **21**:877–888.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist **124**:255–279.

Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. American Naturalist **130**:1–17.

Burke, R. L., and S. R. Humphrey. 1987. Rarity as a criterion for endangerment in Florida's fauna. Oryx **21**:97–102.

Calder, W. A., III. 1983. Ecological scaling: mammals and birds. Annual Review of Ecology and Systematics **14**:213–230.

Chapman, J. A., J. G. Hockman, and M. M. Ojeda. 1980. *Sylvilagus floridanus.* Mammalian Species (American Society of Mammalogists) **136**:1–8.

Damuth, J. 1981. Population density and body size in mammals. Nature (London) **290**:699–700.

Diamond, J. M. 1984. "Normal" extinctions of isolated populations. Pages 191–246 in M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago, Illinois.

Eisenberg, J. F. 1980. The density and biomass of tropical mammals. Pages 35–55 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology, an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Eisenberg, J. F. 1981. The mammalian radiations. University of Chicago Press, Chicago, Illinois.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and evolution. Cambridge University Press, Cambridge, England.

Goodman, D. 1987. The demography of chance extinction. Pages 191–246 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Gotelli, N. J., and D. E. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. American Naturalist **130**:18–35.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos **38**:210–221.

Hershkovitz, P. 1950. Mammals of northern Columbia. Preliminary report no. 6: rabbits (Leporidae). Distribution of the South American forms. Proceedings U.S. National Museum. **100**:327–373.

Hershkovitz, P. 1979. The species of sakis, genus *Pithecia* (Cebidae, Primates), with notes on sexual dimorphism. Folia Primatologica **31**:1–22.

Hershkovitz, P. 1983. Two new species of night monkeys, genus *Aotus* (Cebidae, Platyrrhini). A preliminary report on *Aotus* taxonomy. American Journal of Primatology **4**:209–243.

Hubbell, S. P., and R. B. Foster. 1986. Commonness and rarity in a Neotropical forest: implications for tropical tree conservation. Pages 205–231 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Karr, J. R. 1977. Ecological correlates of rarity in a tropical forest bird community. Auk **94**:240–247.

Karr, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. Ecology **63**:1975–1978.

Krebs, C. J. 1985. Ecology: the experimental analysis of distribution and abundance. 3rd ed. Harper and Row, New York.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist **130**:624–635.

Lande, R. 1988. Genetics and demography in biological conservation. Science **241**:1,455–1,460.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87–123 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237–240.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York.

MacNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science **167**:131–139.

Mares, M. A., and R. A. Ojeda. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pages 393–432 in M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania. 539 pp.

Mendenhall, W., R. L. Schaeffer, and D. D. Wackerly. 1986. Mathematical statistics with applications. 3rd ed. Duxbury Press, Boston, Massachusetts.

Morse, D. R., N. E. Stork, and J. H. Lawton. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. Ecological Entomology **13**:25–37.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, England.

Peters, R. H., and J. V. Raelson. 1984. Relations between individual size and mammalian population density. American Naturalist **124**:498–517.

Peters, R. H., and K. Wassenberg. 1983. The effect of body size on animal abundance. Oecologia (Berlin) **60**:89–96.

Pimm, S. L., L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist **132**:757–785.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 in H. Synge, editor. The biological aspects of rare plant conservation. Wiley, Chichester, England.

Rabinowitz, D., S. Cairns, and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pages 182–204 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Rapoport, E. H. 1975. Areografía: estrategias geográficas de las especies. Fondo de Cultura Económica, México.

Rapoport, E. H. 1982. Areography: geographical strategies of species. Pergamon, Oxford, England.

Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. Theoretical Population Biology **3**:406–433.

Robinson, J. G., and K. H. Redford. 1986. Body size, diet, and population density of Neotropical forest mammals. American Naturalist **128**:665–680.

Schoener, T. W. 1987. The geographical distribution of rarity. Oecologia **74**:161–173.

Schonewald-Cox, C. M., S. M. Chambers, B. McBryde, and W. L. Thomas. 1983. Genetics and conservation: a reference for managing wild animal and plant populations. Benjamin Cummings, Menlo Park, California.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. Freeman, San Francisco, California.

Soulé, M. E., and B. A. Wilcox. 1980. Conservation biology, an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Streilein, K. E. 1982. Behavior, ecology, and distribution of South American marsupials. Pages 231–250 in M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania. 539 pp.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. Bioscience **24**:715–722.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–133 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology, an evolutionary-ecological perspective. Sinauer, Sunderland, Massachusetts.

Thomas, C. D., and H. C. Mallorie. 1985. Rarity, species richness, and conservation: butterflies of the Atlas mountains of Morocco. Biological Conservation **33**:95–117.

Wetzel, R. M. 1982. Systematics, distribution, ecology, and conservation of South American edentates. Pages 345–375 in M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania. 539 pp.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology **55**:1,017–1,029.

Wolfheim, J. H. 1983. Primates of the world: Distribution, abundance, and conservation. University of Washington, Seattle, Washington.