

BODY SIZE, DIET, AND POPULATION DENSITY
OF NEOTROPICAL FOREST MAMMALS

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This paper is dedicated to the memory of Jairo Ramírez, who encouraged our interest in these questions. He was a casualty of the Volcan del Ruiz eruption on November 13, 1985. We miss him.

Accounting for the variation in the population density among different animal species is a central goal of animal ecology (Andrewartha and Birch 1954). Among mammals, density is closely related to the average adult body mass of the species and to the trophic level occupied by the species (Mohr 1940; Clutton-Brock and Harvey 1977; Eisenberg 1980; Damuth 1981*a*; Peters 1983; Peters and Raelson 1984). In addition, after the body mass and trophic position of species have been taken into account, population densities appear to vary with habitat (Eisenberg 1980) and biogeographical area (Peters and Raelson 1984). Peters and Raelson have been impressed by the predictive power of these relations: "Because these relations appear so powerful . . . they should be examined as fully as possible before they come into widespread use" (1984, p. 499).

Four requirements must be fulfilled before the variation in population densities can be accounted for successfully. (1) More extensive data must be collected. Analyses have usually relied on only a few, often unreliable, density estimates for each species. (2) Closer attention must be paid to the methods used in different studies to estimate population density. Some analyses have lumped "ecological" estimates (densities achieved by species in appropriate habitats) and "crude" estimates (densities achieved in the geographical region). (3) Trophic categories must be more carefully distinguished. Analyses have been restricted to such coarse-grained categories as "carnivore-omnivore" and "herbivore." (4) The analysis must be restricted to species living in well-defined habitats. Analyses have, by necessity, lumped population densities collected in different environments and different geographical regions.

These requirements are met by a data set derived from mammals living in Neotropical forests. In this data set, there are several estimates for the densities of some species, and the densities of others are reliable because they are based on

long-term studies. All of the studies provide the information necessary to calculate ecological densities. In addition, the diets of species are described, allowing the definition of narrow trophic categories. Finally, because so many estimates from a single habitat are available, the influence of habitat and geographical area on population density is slight.

We consider the factors accounting for the variation in population densities in this Neotropical mammal sample. The population density of a species in a given area is limited to the number of animals the area can support. This limit is, by definition, equivalent to the amount of energy available to the population divided by the average energetic requirements of individual animals (Damuth 1981*a*). Which factors determine the energetic requirements of animals, and which factors determine the amount of energy available to the total population?

It is probable that the energetic requirements of individuals depend largely on their body masses. Although the specific relationship between energetic requirements and body mass has not been elucidated, basal metabolic requirements do scale positively to body mass (Zeuthen 1953). Energetic requirements are generally proportional to basal metabolic requirements; thus, they should also scale positively to body mass (McNab 1980).

The amount of potentially available energy depends on the availability of appropriate resources. Which resources are appropriate depends on the diet of the animals. In general, a species whose diet is restricted to a narrow range of food types (e.g., seeds) has less energy available to it in a given area than a species taking food items from a wider range of food types (e.g., seeds, fruits, and insects). Similarly, a species relying on resources at high trophic levels has less energy available to it in a given area than a species feeding on resources at low trophic levels (Lindeman 1942; Eisenberg and Thorington 1973). An important assumption of this argument is that the effects on population densities of interspecific competition for resources are independent of the effects of body mass and diet.

If the energy used by a population depends on the diet, and if energy requirements depend on body mass, then diet and body mass should account for the interspecific variation in population density. We tested this general hypothesis in Neotropical forest mammals by deriving four specific predictions.

1. Population densities of species decline with increasing body mass. This relationship has been described from a number of other mammalian samples. Larger-bodied species have lower population densities than smaller-bodied species.

2. Population densities of species depend on their diets. Table 1 presents the dietary classification system that we adapted from Eisenberg (1981). These dietary categories recognize that diets of most species are not restricted to single food types (e.g., fruits) but usually combine different types (e.g., fruits and animal material). The categories are ranked in the table such that species placed in categories high on the list have a catholic diet and/or feed on resources at low trophic levels and species in categories low on the list have narrow diets and/or feed on resources at high trophic levels. We therefore predicted that, at a given body size, densities of grazers or browsers would be higher than densities of

TABLE 1
DIETARY CATEGORIES IN THIS STUDY
(ADAPTED FROM EISENBERG 1981)

Herbivore-grazer	>50% grasses
Herbivore-browser	>50% leaves and twigs
Frugivore-herbivore	>50% fruits, remainder mostly plant material
Frugivore-granivore	Mostly fruits and seeds
Frugivore-omnivore	>50% fruits, remainder mostly invertebrates and vertebrates
Insectivore-omnivore	>50% invertebrates
Myrmecophage	>75% ants and termites
Carnivore	>50% vertebrates

NOTE.—The relative proportion of different food items in the diet varies with the sampling method used. Generally, methods that estimate the time animals spend eating different foods, the frequency at which different items are taken, and the volume of different items in the stomach all give comparable results. Estimating the time that animals spend foraging for different food items overestimates the importance of animal material in the diet, relative to the other methods. Accordingly, such estimates were corrected when assigning species to dietary categories.

frugivore-herbivores, which should be higher than densities of frugivore-granivores, and so on.

To rank the dietary categories on the basis of energy or resource availability per unit area, we used the following arguments. More food should be available to browsers or grazers than to frugivore-herbivores, which specialize on the fruiting structures of the plant. The diet of frugivore-granivores is specialized for seeds, which are only part of the fruiting structure; therefore, resource availability per unit area to such species should be even less. Frugivore-omnivores also take only a part of the fruit, usually the pericarp, and in addition usually rely on invertebrates, which are at a higher trophic level. Moreover, all frugivorous species must deal with a spatially heterogeneous and temporally pulsed resource. Insectivore-omnivores are largely secondary consumers, myrmecophages are exclusively so, and carnivores are often tertiary consumers.

3. Within each dietary category, the population densities of species decline with increasing body mass. This prediction does not repeat prediction 1; rather, it demonstrates the effect of body mass on population density because diet and body mass co-vary (Clutton-Brock and Harvey 1977, 1983). Larger frugivore-omnivores, for instance, should occur at lower densities than smaller ones.

4. The magnitude of the effect of body mass on population density varies with diet (Peters 1983; Peters and Raelson 1984) because the size range of available and accessible food varies with both body mass and diet (Schoener 1968; Harestad and Bunnell 1979; Peters 1983). An increase in body mass usually increases the availability of large food items and decreases the availability of small food items. However, the magnitude of this effect varies with diet. (a) As body mass increases, carnivore and herbivore-browser densities decline more rapidly than

frugivore densities, because body mass does not affect frugivore access to small-sized food items (Waser and Case 1981; Terborgh 1983), but does affect access by herbivore-browsers and carnivores (Jarman 1974; Harestad and Bunnell 1979; but see Damuth 1981*b*). (*b*) Carnivore densities decline more rapidly than myrmecophage densities because larger and smaller myrmecophages have access to the same small food items. As noted above, however, these arguments assume that interspecific interactions affect population densities independently of the effects of body mass and diet. For example, if interspecific competition has a greater effect on the densities of small carnivores than on those of large carnivores, or if interspecific competition has a lesser effect on the densities of myrmecophages than on the densities of frugivore-omnivores, then variation in the effect of body mass on population densities may be less a consequence of food availability than of interspecific interactions (Damuth, pers. comm.).

METHODS

We examined the relationships among diet, body mass, and population density by least-squares regression analyses. The analyses were restricted to mammalian species occurring in Neotropical forests, including evergreen, deciduous, and riparian gallery forests. Of the 103 species in the data set, there were 12 marsupials, 39 primates, 13 edentates, 2 lagomorphs, 19 rodents, 11 carnivores, 2 perisodactyls, and 5 artiodactyls (see the Appendix). For each species, values for adult body mass (M in grams) and population density (D , the number per square kilometer) were taken from both the published literature and unpublished manuscripts. There were 258 body-mass estimates for these 103 species and 480 density estimates.

Adult body mass, the independent variable, was calculated for each species by averaging adult male and female body-mass measurements. Average masses for each sex were weighted means if sample sizes were available and simple means if sample sizes were not available. Measures that did not distinguish the sex of the animals were discarded unless they were the only estimate available. Regression analysis assumes that the error in measuring the independent variable is negligible (see Harvey and Mace 1982). This source of error is not important, however, if the analysis is over a broad range of body masses (see Peters 1983). Any error was minimized by averaging a number of body-mass measurements.

Most of the intraspecific variation in population density probably results from habitat-related geographical variation in density. Since density is the dependent variable, minimizing this variation is not required. However, because the number of density estimates varied among species, we also averaged all estimates for each species to avoid the bias resulting from the unequal contributions of certain species to the data set. Most of the densities were estimated by different authors at different locations, but we also used estimates by different authors at the same location; we averaged different estimates by the same author at the same location to produce a single estimate; and we took the midpoint if authors provided a range of densities. We used ecological rather than crude densities (see Eisenberg et al. 1979). When crude densities were reported, we converted them to ecological

densities if habitat information and extent were available. If they were not available, we did not use the estimate.

Within each dietary category we estimated the relationship between the population densities and the body masses of species with the simple regression model: $\log D = \log a + b \log W$. Logarithmic transformation of both axes are required to fit the linear model. This is equivalent to the power function $D = a W^b$.

To determine whether population densities of species varied with diet, we examined the extent to which membership of a species in one dietary category affected its population density. Pairwise comparisons were made among all categories using a stepwise multiple regression. A dummy variable C was created, and all members in one dietary category were assigned a score of 1 and all members in the other a score of 0. This dietary variable was introduced into the regression after the contribution of body mass had been determined. If the contribution of diet accounted for a significant ($P < 0.05$) portion of the variance in population density, then it was included in the multiple-regression model: $\log D = \log a' + b' \log W + cC$. For each pair of dietary categories, this procedure indicates whether diet significantly affects population density.

To determine whether the extent of the decline in population density with increasing body mass varied with diet, we compared the regression slopes of the different dietary categories using covariance analysis (Snedecor and Cochran 1974).

RESULTS

The results are numbered to facilitate comparison with the corresponding prediction.

1. If dietary differences are not considered, population densities of Neotropical mammalian species decline significantly with body mass (fig. 1). Body mass alone accounts for 45% of the variation in the population densities (table 2). There is considerable scatter around the regression line, but most of it falls within one order of magnitude of the line.

2. Population densities vary with diet. The effect of diet on population density is as predicted, and is consistent across the whole range of body masses. Comparisons of the elevation of the regression lines between each pair of dietary categories are presented in table 3 (the differences in the elevation of the regressions equal the differences in the average population densities of species in the sample across the range of body-mass estimates). Including diet accounted for a significant (at least $P < 0.05$) portion of the variance in population density in all but four pairwise comparisons. All four were immediately adjacent categories in table 1. Species whose diet allows them to have access to an abundance of resources have high average population densities for their body masses. As predicted, at a given body mass, population densities of herbivore-browsers are greatest. The ranking of other dietary categories in descending order is frugivore-herbivores, frugivore-granivores, frugivore-omnivores, insectivore-omnivores, myrmecophages, and carnivores.

3. For all categories except herbivore-browsers, population densities decline

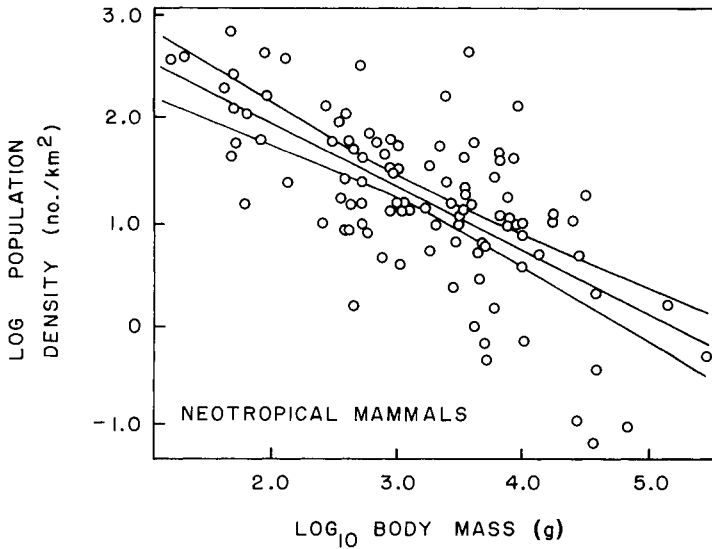


FIG. 1.—Effect of body mass (g) on mean population density (no. per km²) for a sample of 103 Neotropical mammal species. The regression line and 95% confidence estimates are plotted.

TABLE 2
EFFECT OF BODY MASS ON POPULATION DENSITY

Dietary Category	<i>b</i>	<i>S_b</i>	<i>a</i>	<i>S_{xy}</i>	<i>r</i> ²	<i>P</i>	\bar{X}	\bar{Y}	<i>n</i>
Herbivore-browser	-1.33	.39	6.99	.45	.74	.05	3.94	1.74	6
Frugivore-herbivore	-.88	.12	4.64	.23	.79	.001	4.19	.96	16
Frugivore-granivore	.59	.11	3.37	.42	.62	.001	2.58	1.86	20
Frugivore-omnivore	-.61	.20	3.15	.37	.31	.005	3.21	1.19	24
Insectivore-omnivore	-.67	.18	3.07	.50	.38	.005	2.53	1.38	23
Myrmecophage	-1.02	.24	4.08	.42	.78	.01	3.66	.34	7
Carnivore	-.99	.25	3.64	.29	.84	.05	4.12	-.43	5
All groups	-.61	.07	3.12	.59	.45	.001	3.20	1.22	103

NOTE.—Body mass (*M*) is in grams; density (*D*) is the number per square kilometer. *b* is the slope; *S_b*, the standard error of the slope; *a*, the intercept; *S_{xy}*, the standard error of the estimate; *r*², the coefficient of determination; *P*, the probability that the null hypothesis (slope = 0) was falsely rejected; \bar{X} , log₁₀ geometric mean of body mass (g); \bar{Y} , log₁₀ geometric mean of population density; *n*, the sample size of the species' means.

significantly ($P < 0.05$) with body mass within a dietary category (table 2). Regression analysis was not performed on herbivore-grazers because this category included only two mean values. Compared to the regression that does not consider dietary differences, body mass accounts for a greater proportion of the variation in population density (compare *r*² values) within five of the seven dietary categories (table 2). Figures 2 and 3 illustrate the regression lines and the 95% confidence intervals for the seven dietary categories. Confidence intervals are especially broad for herbivore-browsers and myrmecophages, in part because of

TABLE 3

EFFECT OF DIET ON POPULATION DENSITY: SIGNIFICANCE OF PAIRWISE COMPARISONS OF ELEVATION AMONG DIETARY CATEGORIES

Dietary Category	HB	FH	FG	FO	IO	MY	CA
Herbivore-browser	—	0.05	0.025	0.001	0.001	0.005	0.001
Frugivore-herbivore		—	NS	0.01	0.001	0.001	0.001
Frugivore-granivore			—	0.025	0.001	0.001	0.001
Frugivore-omnivore				—	NS	0.025	0.001
Insectivore-omnivore					—	NS	0.05
Myrmecophage						—	NS
Carnivore							—

NOTE.—HB is herbivore-browser; FH, frugivore-herbivore; FG, frugivore-granivore; FO, frugivore-omnivore; IO, insectivore-omnivore; MY, myrmecophage; CA, carnivore. NS is not significant.

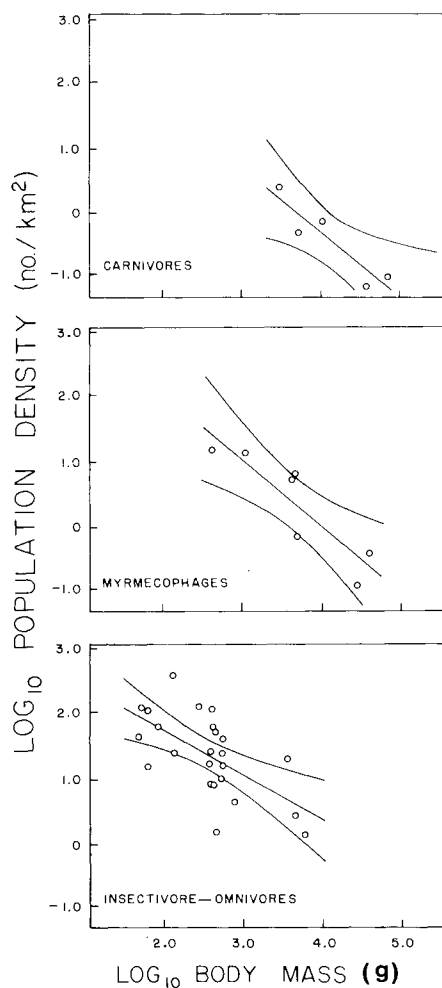


FIG. 2.—Effect of body mass (g) on mean population density (no. per km²) for Neotropical mammal carnivores, myrmecophages, and insectivore-omnivores. The regression line and 95% confidence estimates are plotted.

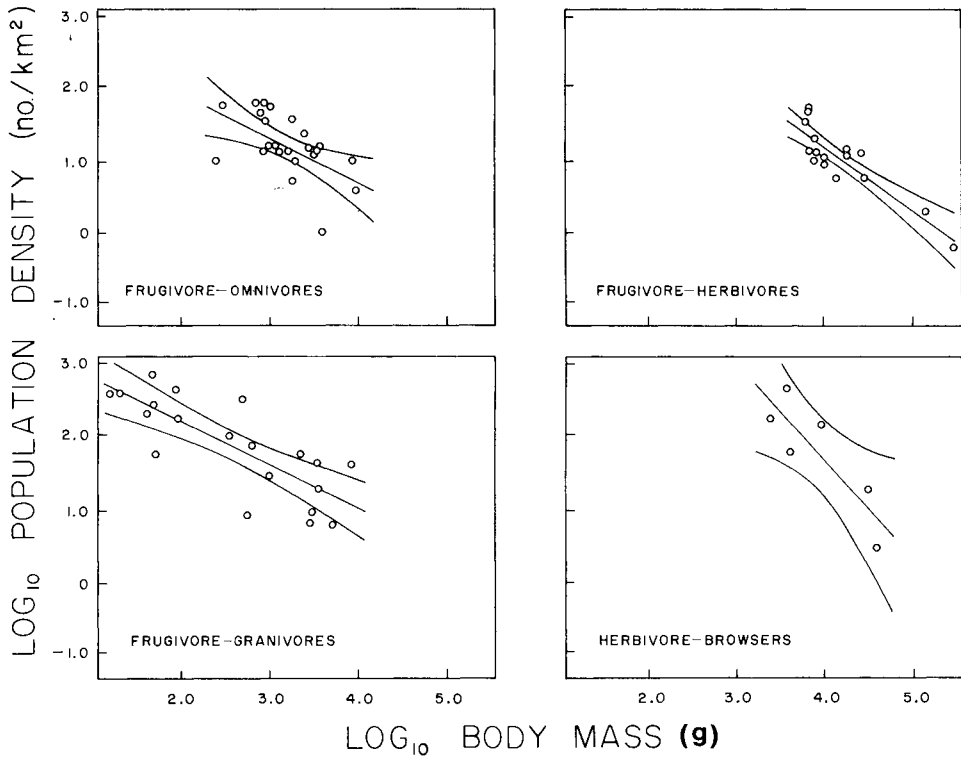


FIG. 3.—Effect of body mass (g) on mean population density (no. per km²) for Neotropical mammal frugivore-omnivores, frugivore-granivores, frugivore-herbivores, and herbivore-browsers. The regression line and 95% confidence estimates are plotted.

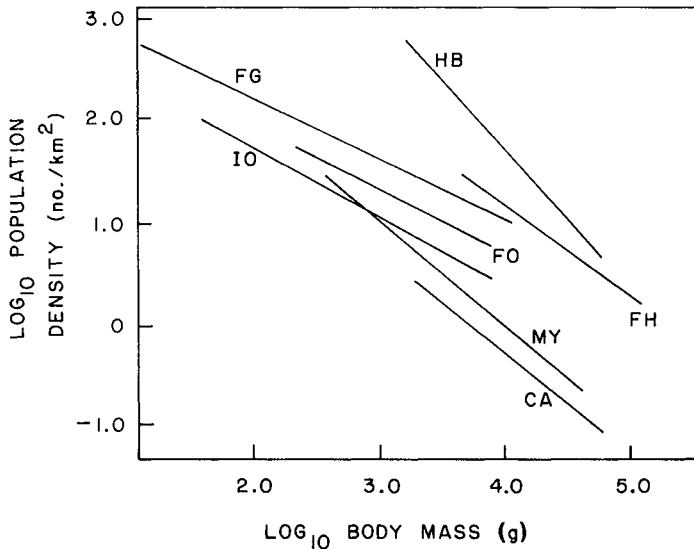


FIG. 4.—Effect of body mass (g) on mean population density (no. per km²) for herbivore-browsers (HB), frugivore-herbivores (FH), frugivore-granivores (FG), frugivore-omnivores (FO), insectivore-omnivores (IO), myrmecophages (MY), and carnivores (CA). The regression line for each dietary class is illustrated.

TABLE 4
MAGNITUDE OF THE EFFECT OF BODY MASS ON POPULATION DENSITY:
REGRESSIONS FROM TROPICAL AREAS

HABITAT AND DIETARY CATEGORY	REGRESSION VALUE					SOURCE
	<i>b</i>	<i>S_b</i>	<i>a</i>	<i>r</i> ²	<i>n</i>	
Tropical herbivore	-0.56	0.039	2.80	0.45	75	Peters & Raelson 1984
Malaysian forest herbivore	-0.60	0.089	2.61	0.81	13	Damuth 1981a
Neotropical forest herbivore	-0.55	0.069	4.37	0.61	44	this study
Tropical carnivore and omnivore	-1.02	0.072	4.03	0.70	50	Peters & Raelson 1984
Neotropical forest carni- vore and omnivore	-0.85	0.090	3.89	0.61	59	this study

NOTE.—*b* is the regression slope; *S_b*, the standard error of the slope; *a*, the intercept (\log_{10} body mass (g) = 0); *r*², the coefficient of determination; *n*, the number of species in the sample.

the small sample sizes in these dietary categories. Figure 4 illustrates the different regression lines of the seven dietary categories.

4. As expected, the magnitude of the effect of body mass on population density was more pronounced for herbivore-browsers and carnivores than for the frugivores. The decline for herbivore-browsers was significantly greater than the decline for frugivore-herbivores ($0.05 < P < 0.10$), for frugivore-granivores ($P < 0.05$), and for frugivore-omnivores ($0.05 < P < 0.10$). Contrary to expectation, however, the slopes of the regression lines of myrmecophages and carnivores were very similar and did not differ significantly from one another, and the slopes of the carnivore and myrmecophage regressions did not differ significantly from those of the frugivorous dietary categories. The lack of significance might be, in part, the consequence of small numbers of species in three of the seven dietary categories.

Since Mohr's (1940) study, it has been recognized that smaller species usually occur at higher densities than larger species. Subsequent analyses of the relationship between body mass and population density either have divided species into broadly defined trophic levels (traditionally, herbivores and carnivores) and analyzed these categories separately (Damuth 1981a; Peters 1983; Peters and Wasenberg 1983; Peters and Raelson 1984) or have focused on narrowly defined taxonomic and dietary groups (Clutton-Brock and Harvey 1977; Robinson and Ramírez 1982; Robinson and Janson 1986; Robinson et al. 1986). The present study extends both sets of conclusions: narrowly defined diets, rather than broadly defined trophic categories, account for much of the variation in population density in a taxonomically broad sample of Neotropical forest mammals.

It has also been recognized that the magnitude of the effect of body mass on population density varies with trophic position (Peters 1983; Peters and Raelson 1984). To compare the regression slopes with previously published results based on tropical data, we lumped together four categories (herbivore-grazer, herbivore-browser, frugivore-herbivore, and frugivore-granivore) to form a new "herbivore" category; the other four then formed a new "carnivore and omnivore" category (table 4). Regression results are shown and compared with published

slopes. All three studies indicate that the regression slopes of herbivorous species are shallower than those of carnivorous species. In this study, the slopes differ significantly ($F = 6.5$, $df = 1, 100$, $P < 0.025$). When herbivores and carnivores are broadly defined, herbivore densities generally decline more slowly than carnivore densities as body mass increases.

DISCUSSION

Since the pioneering work of Andrewartha and Birch (1954), efforts to account for variation in animal abundance have focused on describing either capacity rules or allocation rules (Brown 1981). *Capacity rules* specify which resource limits animal abundance in a given environment, and the availability of usable energy in that environment is frequently the resource specified. A resource is considered limiting when its availability varies with the density of the population irrespective of the actual proximate mechanism that affects the population (Watson and Moss 1970). *Allocation rules* specify the way that limiting resources are allocated among species.

If animal abundance is determined solely by capacity rules, then population densities can be predicted by dividing the energy available to each species by the total energetic requirements of the animals of that species. We have argued that the energy available to animals of a particular species depends on their diet and that their energy requirements depend on their body masses. Because diet and body mass account for much of the variation in population density, capacity rules would seem to be important for structuring mammal communities in Neotropical forests.

This statement must be qualified because there is considerable scatter in the mean population densities around the regression lines. These deviations from the expected values may partly result from methodological difficulties. Density estimates are notoriously inaccurate (e.g., see discussions in Glanz 1982; Emmons 1984; Deffer and Pintor 1985). In addition, dietary categories are approximations: not all species within a category eat the same things and forage in the same ways. However, the deviations may also reflect ecologically important interactions. Population densities might be influenced by interspecific interactions and the allocation of limiting resources among species. Eisenberg (1980) and Waser (1986) found preliminary evidence of density compensation in a number of Neotropical primate communities. In addition, population densities of species are not necessarily correlated and may vary independently of locality, even within a specified habitat type such as Neotropical forest. For instance, densities of titi monkeys *Callicebus* are highest around forest openings and in early successional forest, but uakari monkeys are almost restricted to undisturbed flooded lowland forest (Robinson et al. 1986).

The ability of diet and body mass to accurately predict population density still does not demonstrate conclusively the importance of capacity rules. First, our analysis used density estimates from numerous localities with presumably different resource availabilities. A statistical relationship between the amount of energy

presumed to be available and the average population density does not necessarily imply that capacity rules determine species densities in a specific area (see Brown 1984). Second, our analysis assumed that metabolic requirements scale predictably to body mass and that metabolic requirements, once body mass is accounted for, do not vary with diet. These assumptions are not completely realistic (see McNab 1983). A demonstration of capacity rules requires measuring both availability of energy and the specific metabolic requirements at a specified site.

Population densities of Neotropical mammals vary widely across locations (Eisenberg 1979; Freese et al. 1982; Emmons 1984), frustrating the attempt to describe the rules of community structure. Peters and Raelson, for instance, concluded that "none of the[ir] regressions are effective tools for the prediction of the abundance of individual populations" (1984, p. 515), because their analyses (like ours) were based on mean densities. This intraspecific variation in density, however, can also be an opportunity to test those same general rules. A number of recent studies have examined the relationship between intraspecific variation in density and the geographic distribution of species (e.g., Hanski 1982; Bock and Ricklefs 1983; Brown 1984). Brown's conclusion is in accord with our prediction: "species tend to occur relatively independently of most other species wherever environmental conditions are suitable, and local population densities are determined by the extent to which the local environment meets the requirements of individuals" (Brown 1984, p. 274). Another approach, if the niche requirements of a species are known, is to examine the relationship between resource availabilities and densities of that species. For example, capuchin, or *Cebus* monkeys, are frugivore-omnivores inhabiting a wide range of forest types from Nicaragua to Argentina. Based on our sample of 33 density estimates for the four *Cebus* species, it appears that densities are higher in undisturbed forest (mean = 14.8 individuals per km², $n = 17$) than in areas where there has been selective logging (mean = 9.3 individuals per km², $n = 16$), and higher in whitewater drainages (mean = 12.8 individuals per km², $n = 27$) than in blackwater drainages (mean = 9.0 individuals per km², $n = 6$). Fruit production is generally lower in selectively logged forests (Marsh and Wilson 1981) and in blackwater drainages (Janzen 1974). Although these mean densities did not differ significantly, these results suggest that *Cebus* population densities are related to fruit production in the forest. This prediction requires a field test at sites distinguished by their fruit production.

SUMMARY

The population densities of Neotropical mammalian species are predictably related to their body masses and diets. In interspecific comparisons, population densities generally declined with increasing body mass, and declined with body mass within each of seven specified dietary categories. In our regression analyses, body mass alone accounted for approximately half of the variation in density in the general case, and a greater proportion of the variation in five of the regressions within dietary categories. Pairwise comparisons using stepwise multiple regres-

sion indicated that adding diet as well as body mass significantly increased the proportion of variance explained. Finally, the magnitude of the effect of body mass on population density varied with dietary class.

These results indicate that, in general, larger-bodied species occur at lower densities than smaller-bodied species, and species with restricted diets and those at higher trophic levels occur at lower densities than species whose diet allows them access to a greater abundance of food resources. The decline in density with increasing body size is greater within some dietary categories than others. The results broadly support the hypothesis that population densities of species are determined by the potential resources, and ultimately energy, available to them in specified habitats.

ACKNOWLEDGMENTS

This work was inspired by the pioneering efforts of J. F. Eisenberg in establishing rules to account for the variation in tropical mammalian communities. He also provided from unpublished or obscure sources some of the body-mass and density estimates. To this unselfish professionalism we owe a great deal. For discussions and comments on earlier versions of this manuscript we thank J. Damuth, J. F. Eisenberg, B. McNab, T. T. Struhsaker, S. D. Webb, and two anonymous reviewers. This is contribution 6802 of the Journal Series, Florida Agricultural Experimental Station, and contribution 11 from the Program for Studies in Tropical Conservation.

APPENDIX

BODY MASS, DIET CLASSIFICATION, POPULATION DENSITY OF THE NEOTROPICAL MAMMAL SAMPLE

SPECIES	MEAN BODY MASS (g)	N_1	DIETARY CLASSIFI- CATION	POPULATION DENSITY		N_2
				Mean	SD	
MARSUPIALS						
<i>Caluromys derbianus</i>	1300	1	FO	13.4	9.4	2
<i>Caluromys philander</i>	300	1	FO	59.8	81.5	3
<i>Caluromysiops irrupta</i>	250	1	FO	10.0	—	1
<i>Didelphis marsupialis</i>	1041	6	FO	55.3	34.0	8
<i>Marmosa cinerea</i>	127	3	IO	25.0	15.0	3
<i>Marmosa fuscata</i>	60	1	IO	113.0	—	1
<i>Marmosa murina</i>	45	1	IO	43.0	—	1
<i>Marmosa noctivaga</i>	60	1	IO	15.0	—	1
<i>Marmosa robinsoni</i>	49	3	IO	123.5	113.5	4
<i>Monodelphis breviceaudata</i>	80	1	IO	63.0	—	1
<i>Metachirus nudicaudata</i>	400	1	IO	8.3	5.2	2
<i>Philander opossum</i>	400	3	IO	62.9	77.3	5
PRIMATES						
<i>Cebuella pygmaea</i>	122	2	IO	389.6	294.4	4
<i>Callithrix argentata</i>	380	1	IO	8.5	11.0	5
<i>Callithrix humeralifer</i>	380	1	IO	116.7	—	1

(continued)

APPENDIX (Continued)

SPECIES	MEAN BODY MASS (g)	N_1	DIETARY CLASSIFI- CATION	POPULATION DENSITY		N_2
				Mean	SD	
<i>Callithrix jacchus</i>	259	2	IO	133.0	—	1
<i>Saguinus nigricollis</i>	360	1	IO	17.4	2.6	2
<i>Saguinus fuscicollis</i>	364	3	IO	26.9	32.6	25
<i>Saguinus mystax</i>	517	3	IO	24.2	10.3	10
<i>Saguinus labiatus</i>	520	1	IO	15.9	8.9	6
<i>Saguinus imperator</i>	520	1	IO	42.3	66.4	4
<i>Saguinus midas</i>	500	1	IO	9.8	8.9	5
<i>Saguinus oedipus</i>	435	3	IO	51.4	35.7	2
<i>Saguinus leucopus</i>	440	1	IO	1.7	1.5	2
<i>Leontopithecus rosalia</i>	745	1	IO	4.6	—	1
<i>Aotus azarae</i>	873	4	FO	13.6	4.6	3
<i>Aotus lemurinus</i>	873	4	FO	63.0	28.2	4
<i>Aotus nigriceps</i>	873	4	FO	34.1	11.9	5
<i>Callicebus moloch</i>	1166	2	FO	15.4	15.0	14
<i>Callicebus torquatus</i>	1000	1	FO	16.5	13.1	4
<i>Pithecia hirsuta</i>	1800	1	FO	37.5	—	1
<i>Pithecia monachus</i>	1800	1	FO	5.1	2.7	8
<i>Pithecia pithecia</i>	1809	2	FO	5.1	4.1	6
<i>Chiropotes albinasus</i>	2847	1	FG	6.5	1.0	3
<i>Chiropotes satanas</i>	2986	2	FG	9.3	3.0	3
<i>Saimiri boliviensis</i>	800	1	FO	46.4	33.3	10
<i>Saimiri sciureus</i>	688	2	FO	62.3	62.8	8
<i>Cebus albifrons</i>	2005	2	FO	9.5	11.3	6
<i>Cebus apella</i>	3445	1	FO	12.4	11.2	21
<i>Cebus capucinus</i>	3250	1	FO	12.1	7.8	3
<i>Cebus olivaceus</i>	2900	1	FO	15.2	11.5	6
<i>Alouatta caraya</i>	6500	1	FH	42.2	53.8	6
<i>Alouatta palliata</i>	6679	4	FH	47.6	35.8	13
<i>Alouatta pigra</i>	6500	1	FH	12.0	7.4	4
<i>Alouatta seniculus</i>	6185	3	FH	29.3	34.5	27
<i>Ateles belzebuth</i>	7500	1	FH	9.1	5.3	3
<i>Ateles geoffroyi</i>	7500	1	FH	18.0	23.7	3
<i>Ateles paniscus</i>	7775	2	FH	11.3	8.8	7
<i>Lagothrix flavicauda</i>	10000	1	FH	7.3	6.0	4
<i>Lagothrix lagothricha</i>	10000	1	FH	10.3	6.4	5
<i>Brachyteles arachnoides</i>	13500	1	FH	5.0	1.2	4
EDENTATES						
<i>Bradypus tridactylus</i>	2400	3	HB	170.9	193.8	4
<i>Bradypus variegata</i>	3725	2	HB	438.3	317.1	4
<i>Choloepus didactylus</i>	4150	2	HB	57.5	17.8	2
<i>Choloepus hoffmanni</i>	9000	1	HB	133.7	46.5	3
<i>Cyclopes didactylus</i>	400	1	MY	15.4	19.2	3
<i>Tamandua mexicana</i>	4210	1	MY	5.2	.2	2
<i>Tamandua tetradactyla</i>	4560	5	MY	6.6	6.1	4
<i>Myrmecophaga tridactyla</i>	27000	6	MY	.1	.1	2
<i>Cabassous unicinctus</i>	4800	1	MY	.7	.7	2
<i>Tolypeutes matacus</i>	1066	2	MY	13.3	—	1
<i>Dasybus novemcinctus</i>	3544	16	IO	21.9	21.1	8
<i>Euphractus sexcinctus</i>	4350	2	IO	3.0	3.9	2
<i>Priodontes maximus</i>	39400	6	MY	.4	—	1

(continued)

APPENDIX (Continued)

SPECIES	MEAN BODY MASS (g)	N_1	DIETARY CLASSIFI- CATION	POPULATION DENSITY		N_2
				Mean	SD	
LAGOMORPHS						
<i>Sylvilagus brasiliensis</i>	1017	3	HZ	4.0	2.9	3
<i>Sylvilagus floridanus</i>	1025	2	HZ	35.0	—	1
RODENTS						
<i>Sciurus</i> spp.	338	5	FG	98.9	106.7	7
<i>Liomys</i> spp.	45	1	FG	720.0	141.4	2
<i>Heteromys</i> spp.	85	2	FG	438.7	630.0	4
<i>Akodon</i> spp.	40	3	FG	200.0	—	1
<i>Calomys</i> spp.	15	1	FG	400.0	0.0	2
<i>Neacomys</i> spp.	20	1	FG	400.0	—	1
<i>Oryzomys</i> spp.	48	6	FG	276.9	174.2	9
<i>Rhipodomys</i> spp.	90	2	FG	172.0	39.6	2
<i>Zygodontomys</i> spp.	50	1	FG	58.0	—	1
<i>Echimys</i> spp.	600	2	FG	73.5	89.5	3
<i>Proechimys</i> spp.	477	3	FG	334.5	256.6	6
<i>Sphiggurus insidiosus</i>	1000	1	FG	29.7	2.8	2
<i>Coendou bicolor</i>	5000	1	FG	6.3	4.7	3
<i>Coendou prehensilis</i>	3360	5	FG	43.5	34.9	3
<i>Myoprocta acouchy</i>	552	2	FG	8.6	6.5	2
<i>Dasyprocta leporina</i>	2167	3	FG	56.1	62.2	2
<i>Dasyprocta punctata</i>	3600	2	FG	19.7	21.0	8
<i>Agouti paca</i>	8227	12	FG	27.5	27.9	8
<i>Hydrochaeris hydrochaeris</i>	31500	7	HB	17.8	7.4	2
CARNIVORES						
<i>Nasua nasua</i>	3880	5	FO	15.1	13.2	7
<i>Potos flavus</i>	2490	3	FO	24.4	25.9	6
<i>Procyon cancrivorus</i>	10100	2	FO	3.8	4.5	4
<i>Procyon lotor</i>	8850	2	FO	10.0	—	1
<i>Conepatus semistriatus</i>	1700	2	FO	13.8	5.6	3
<i>Eira barbara</i>	3980	4	FO	1.0	.9	7
<i>Galictis vittata</i>	2910	2	CA	2.4	—	1
<i>Felis yagouaroundi</i>	5000	2	CA	.5	.6	3
<i>Felis pardalis</i>	10460	4	CA	.8	1.0	7
<i>Felis concolor</i>	37000	5	CA	.1	.1	3
<i>Panthera onca</i>	68750	7	CA	.1	.1	3
PERISSODACTYLS						
<i>Tapirus bairdii</i>	300000	5	FH	.5	0.0	2
<i>Tapirus terrestris</i>	148950	4	FH	1.6	2.6	6
ARTIODACTYLS						
<i>Tayassu tajacu</i>	17520	12	FH	11.9	14.9	10
<i>Tayassu pecari</i>	28550	8	FH	4.9	4.4	5
<i>Mazama americana</i>	26100	8	FH	10.5	13.1	7
<i>Mazama gouazoubira</i>	17350	2	FH	10.4	13.4	4
<i>Odocoileus virginianus</i>	40000	1	HB	2.8	2.4	10

NOTE.—The body-mass is in grams; the population density is the number per square kilometer. N_1 is the sample size of body-mass estimates; N_2 , the sample size of population-density estimates. FO, frugivore-omnivore; IO, insectivore-omnivore; FG, frugivore-granivore; FH, frugivore-herbivore; HB, herbivore-browser; MY, myrmecophage; HZ, herbivore-grazer; CA, carnivore. Information on body mass, diet, and population density of these species is available from the authors.

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