

# A Preliminary Analysis of a Neotropical Mammal Fauna

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## ABSTRACT

The abundance and biomass of species of nonvolant mammals on Barro Colorado Island are estimated and compared with data from other areas. The edentates, particularly the sloths, are shown to be dominant elements in neotropical forests. The sloths and howler monkeys together constitute more than 50 percent of the biomass of mammals, emphasizing the importance of the forest canopy. The bulk of the mammalian biomass is maintained by species which are browsers or frugivores and browsers. The total energy consumption of each species is estimated and the metabolic rate of the whole mammalian fauna is judged to be between 3000 and 4000 kilocalories per hectare per day on Barro Colorado Island.

THE OBJECTIVE of this paper is to assess the biomass and the numbers of different mammalian species in a defined area of neotropical forest. For almost a decade we have been concerned with this assessment and with defining the trophic structure of the major species of nonvolant terrestrial mammals within a neotropical rainforest ecosystem. It is most important to determine the biomass and the trophic role of each major species for the following reasons:

(1) These data are necessary for determining the food consumption and the role in nutrient cycling of mammalian populations.

(2) They provide a measure of the success of different species and orders of mammals within an ecological context. The biomass per taxon is a different and perhaps better measure of ecological dominance than is the more conventional measure of number of species or genera per higher taxon in a given geographic area.

(3) The information forms the necessary basis for comparison with mammalian faunas elsewhere: in different habitats and geographic areas within the neotropics, in other tropical areas, and in non-tropical habitats.

(4) Numerical data from one area are essential for studies of population fluctuations. The tropics are not the stable equitable environments they were once thought to be, and thus we must examine the effects of climatic fluctuations on mammalian populations.

(5) It is imperative to consider the biomass and trophic roles of mammalian species in any efforts to conserve them in their native habitats or elsewhere. Reserves and parks must be large enough

for mammals to maintain self-perpetuating breeding populations. The adequacy of such reserves can only be determined when we know the densities and fluctuations of mammalian populations supported by tropical habitats.

Within a mature tropical rainforest the undergrowth is often sparse and, aside from the fruits, leaves, and other litter which fall from the crowns of trees, most of the plant productivity is either locked in the trunks and root systems or produced and stored in the crowns of the trees themselves. The low biomass estimates for terrestrial mammals in tropical ecosystems were pointed out some years ago by Bourliere (1963). As the result of extensive research on mammalian populations in Ceylon, Eisenberg, Muckenhirn, and Rudran (1972) called attention to the importance of arboreal herbivores in the tropical rainforests of the Old World. The unsuspected abundance of folivorous primates in Old World rainforests was established for the first time. The theoretical implications of the important biomass contribution of arboreal forms in tropical rainforests were amplified in the publication by Eisenberg and McKay (1973) and reiterated by Bourliere (1972).

In the neotropics, the howler monkey (*Alouatta*) is a frugivore which also consumes a great deal of foliage and, in some respects, appears to occupy an ecological niche comparable to that occupied by the Old World langurs and colobus monkeys (*Presbytis* and *Colobus*). The trophic structure of primate populations on Barro Colorado Island has been clarified through the work of Hladik and Hladik (1969). An examination of the presumed density of howlers on Barro Colorado suggested that they

had not reached a density commensurate with those observed for folivorous primates in the Old World tropics (see Eisenberg, Muckenhirn, and Rudran 1972).

It occurred to us that the true folivore niche in the New World tropics could well be partly occupied by the tree sloths (*Bradypus* and *Choloepus*). On the strength of this hypothesis, a research project was launched in 1970 by G. G. Montgomery and M. Sunquist aimed at clarifying the abundance, activity, and feeding patterns of sloths on Barro Colorado Island (Montgomery and Sunquist 1973). The major results of this work are in preparation, but the conclusions may be summarized here: Sloths are the most numerically abundant large mammal on Barro Colorado Island and account for the bulk of the mammalian biomass. Thus when the combined biomass of sloths and howler monkeys is considered, the arboreal herbivores constitute the major populations of mammals on Barro Colorado Island.

**An estimate of mammalian biomass in Surinam:** During the establishment of a reservoir behind the Afobaka Dam in Surinam, a large lowland area was flooded. A rescue operation was conducted and has been described in a book by Walsh and Gannon (1967) which includes an appendix of all mammals recovered during the rescue operation. From their data, it is possible to calculate the numerical abundance and relative biomass contribution of each species recovered (table 1). Of course, we do not know from what area the sample is drawn nor do we know its bias. We assume, however, that it is biased in favor of larger mammals and that most of the smaller forms either went unnoticed during the rescue operations or did not long survive swimming from flooded areas to high ground.

In spite of the unknown biases associated with these data, we consider them very informative. The two sloths, *Bradypus* and *Choloepus*, constitute 23 percent of the biomass, while *Alouatta* is another 6 percent. Thus these three arboreal herbivores total 29 percent of the biomass. *Tapirus* and *Mazama* account for another 42 percent of the biomass. Since tapirs and deer were the largest and most conspicuous (in the water) of the animals rescued, we believe this figure is an overrepresentation of their contribution to the mammalian biomass. Other informative data are the estimates of the biomass of *Dasypus* 9 percent and *Coendou* 7 percent. These values are higher than we expected and suggest that armadillos and porcupines constitute larger percentages of the mammalian biomass in the neotropics than is generally conceded.

A comparison with the mammalian biomass on

**Barro Colorado Island:** In table 2 we present an analysis of the mammalian populations of Barro Colorado Island as we presently understand them. The densities of marsupials and small rodents are not based upon actual trapping on Barro Colorado but rather are extrapolations from studies carried out on the Panamanian mainland by Fleming (1971, 1972). Other bases for the estimates of population densities are cited by species below.

An examination of table 2 will indicate that we do not have any accurate census data for *Coendou*, *Tamandua*, *Dasypus*, and many of the carnivores from Barro Colorado. As noted above, the data from Surinam suggest that *Coendou* and *Dasypus* are significant contributors to the mammalian biomass. This possibility means that the total biomass estimate of Barro Colorado may actually equal only some 80 percent of the possible total. Compensating for this, we have compared the percent contribution to biomass of those genera common to the Surinam and Barro Colorado samples in table 3. Since the generic composition is not completely equivalent between the two areas, only 80 percent of the Surinam biomass is compared with 95 percent of the known calculated biomass for Barro Colorado. Bearing in mind that this 95 percent representation in table 3 from Barro Colorado is based on perhaps as little as 80 percent of the total, the correspondence between the two samples is remarkably close.

In both areas the sloths constitute a large portion of the biomass, although the percentage attributed to *Bradypus* is three times as large for the BCI estimate as that found in Surinam. A glaring discrepancy is the underrepresentation of the tapir (*Tapirus bairdii*) and the brocket (*Mazama*) on Barro Colorado, which may result from the isolation of the island or from poaching in the past. Or, as suggested above, the tapir biomass from Surinam may be an overestimate. Barro Colorado has a higher percentage of caviomorph rodents than was found in Surinam. This situation may result from a smaller than normal predator complement on the island. The primate data from the two areas compare favorably.

After comparing the Surinam and Barro Colorado data, we suspect that the density of *Coendou*, *Dasypus*, and *Tamandua* is much higher on Barro Colorado than previously realized. This is an important hypothesis to test because *Coendou* and *Dasypus* could be extremely influential components of the ecosystem, playing significant roles in the consumption and cycling of nutrients.

The total biomass of mammals rescued in Surinam is about two-thirds the estimated biomass of terrestrial mammals on Barro Colorado. Barro Colorado is 15 km<sup>2</sup> (Woodring 1958) in area and, pre-

TABLE 1. Nonvolant terrestrial mammals recorded from rescue operation in Surinam (Walsh and Gannon 1967).

	n	% N	Average <sup>a</sup> weight (kg)	Biomass (kg)	% Biomass
<b>MARSUPIALIA<sup>b</sup></b>					
<b>Didelphidae</b>					
<i>Didelphis marsupialis</i>	151	1.8	1.8	271	.59
<i>Metachirus nudicaudatus</i>	85	1.0	1.8	153	.33
<i>Caluromys philander</i>	28	.34	1.3	36	.07
<b>EDENTATA</b>					
<b>Bradyrodidae</b>					
<i>Bradyrodus tridactylus</i>	2104	27.7	3.2	6732	14.7
<i>Choloepus didactylus</i>	840	10.1	4.3	3612	7.9
<b>Myrmecophagidae</b>					
<i>Tamandua tetradactyla</i>	261	3.1	4.0	1044	2.2
<i>Cyclopes didactylus</i>	161	1.9	.4	64.4	.14
<b>Dasypodidae</b>					
<i>Dasypus novemcinctus</i>	1051	12.7	4.0	4204	9.2
<i>Priodontes giganteus</i>	7	<.1	55.0	385	.84
<i>Euphractus sexcinctus</i>	3	<.04	4.9	14.9	<.1
<b>PRIMATES</b>					
<b>Hapalidae</b>					
<i>Saguinus midas</i>	14	.17	.56	58	.12
<b>Cebidae</b>					
<i>Alouatta seniculus</i>	479	5.7	5.5	2634	5.7
<i>Saimiri sciureus</i>	32	.38	.93	29.6	<.1
<i>Cebus capucinus</i>	3	.04	2.6	7.8	<.1
<b>RODENTIA</b>					
<b>Erethizontidae</b>					
<i>Coendou prehensilis</i>	927	11.2	2.6	2414	5.3
<i>Coendou insidiosus</i>	518	6.2	1.0	518	1.13
<b>Hydrochoeridae</b>					
<i>Hydrochoerus hydrochoerus</i>	1		50.0	50	.1
<b>Dasypodidae</b>					
<i>Myoprocta acouchi</i>	247	2.9	.6	148	.3
<i>Dasypodactylus agouti</i>	226	2.7	2.0	452	.98
<i>Cuniculus paca</i>	147	1.7	8.0	1176	2.5
<b>Echimyidae</b>					
<i>Echimyus chrysurus</i>	104	1.2	.8	83.2	.18
<b>CARNIVORA</b>					
<b>Canidae</b>					
<i>Canis familiaris</i>	7	.08	7.0	49	.1
<b>Procyonidae</b>					
<i>Potos flavus</i>	67	.8	2.5	167.5	.36
<b>Mustelidae</b>					
<i>Tayra barbara</i>	2		4.0	8.0	
<b>Felidae</b>					
<i>Felis pardalis</i>	13	.15	12.0	156	.34
<i>Felis wiedii</i>	1		5.0	5	
<i>Felis domestica</i>	1		1.5	1.5	
<i>Panthera onca</i>	3	.03	55.0	165	.36
<b>PERISSODACTYLA</b>					
<b>Tapiridae</b>					
<i>Tapirus terrestris</i>	36	.44	262	9432	20.6
<b>ARTIODACTYLA</b>					
<b>Tayassuidae</b>					
<i>Tayassu tajacu</i>	71	.85	23	1633	3.5
<b>Cervidae</b>					
<i>Mazama</i> sp.	671	8.1	15	10,065	21.92
<b>Total</b>	<b>8261</b>			<b>45,769</b>	

suming the Surinam recovery area was only moderately hunted, we estimate that the Surinam animals were recovered from a total area of similar size. The mammalian biomass of Barro Colorado is calculated to be 4400 kg/km<sup>2</sup> on the basis of table 2 or 5300 kg/km<sup>2</sup> if the biomass total of table 2 is 20 percent low. These figures are similar to those from other tropical areas (see Eisenberg and McKay 1973). The only available comparison in the neotropics is derived from the data of Odum (1970), who found an animal biomass estimate of roughly 11,800 kg/km<sup>2</sup> (dry weight) or about 39,300 kg/km<sup>2</sup> wet weight of which less than 700 kg/km<sup>2</sup> is from vertebrates. These data were obtained from studies on Puerto Rico where the vertebrate biomass is extraordinarily low due in part to the depauperate nature of the vertebrate fauna (see Odum 1970, Sections I-1 and I-216).

These estimates of the biomass of mammals on Barro Colorado and in Surinam should not be construed to mean that mammals are evenly distributed throughout the forest. Rather, the local distribution and abundance of mammals reflects the distribution of available resources, which do not have a regular distribution and are probably not randomly distributed either. The distribution of major fruit trees dramatically affects the distribution and movements of many mammals and seems to determine seasonal patterns of use of an area for decades, if not longer.

Our data clearly show persistent patterns of habitat utilization by *Alouatta*, *Cebus*, *Nasua*, and *Tayassu*. In 1959, Carpenter's team located howler monkeys at 44 locations on Barro Colorado Island (Carpenter 1965). While conducting censuses between 1964 and 1970, Eisenberg visited 41 of these locations and relocated howlers at 30 of them. In any given census period, 13 to 19 troops were located within 100 m of a locality designated by Carpenter for 1959. In 1973, Thorington mapped the distribution of all fig trees, a major resource of *Alouatta*, throughout most of the home range of the "laboratory troop" of howlers. This map has been compared with maps of the movement of *Alouatta* troops in this area in 1955 (Altmann 1959), 1964, 1967, 1972, and 1973 (data collected by Thorington and collaborators). The patterns of usage of the forest are persistent and clearly reflect the distribution of the fig trees. We do not argue that the same troops of *Alouatta* are involved in these temporal compar-

<sup>a</sup> Average weights are computed from zoo specimens when suitable field weights have not been recorded. *Tapirus*, *Tayassu*, and all primates have had their weights adjusted to conform to subadult and juvenile weights. In no case are maximum weights employed.

<sup>b</sup> Nomenclature unchanged from Walsh and Gannon, 1967. *Mazama* includes *M. americana* and *M. gouazoubira*.

TABLE 2. Nonvolant terrestrial mammals recorded from Barro Colorado Island during the interval 1964 to 1971<sup>a</sup> (nomenclature from Handley 1966).

	n	% N	Weight (kg)	Biomass (kg)	Biomass %	Diurnal	Nocturnal	Terrestrial	Scansorial	Arboreal	Trophic speciality
<b>MARSUPIALIA</b>											
<b>Didelphidae</b>											
<i>Caluromys derbianus</i>	?	-----	-----	-----	-----		+			+	Frugivore/carnivore
<i>Marmosa robinsoni</i>	825	3.0	.06	49.5	<.1		+			+	Frugivore/insectivore
<i>Philander opossum</i>	400	1.4	1.4	560.0	.8		+		+		Frugivore/carnivore
<i>Metachirus nudicaudatus</i>	?	-----	-----	-----	-----		+			+	Frugivore/carnivore
<i>Didelphis marsupialis</i>	1050	3.7	1.0	1050.0	1.5		+		+		Frugivore/carnivore
<i>Chironectes minimus</i>	?	-----	-----	-----	-----		+	+			Piscivore/crustaceivore
<b>PRIMATES</b>											
<b>Cebidae</b>											
<i>Aotus trivirgatus</i>	50?	.1	.8	40.0	<.1		+			+	Frugivore/insectivore
<i>Alouatta palliata</i>	1000	3.6	5.5	5500.0	8.3	+				+	Frugivore/brower
<i>Cebus capucinus</i>	250	.9	2.6	650.0	.9	+				+	Frugivore/omnivore
<i>Ateles geoffroyi</i>	14	.05	5.0	70.0	<.1	+				+	Frugivore
<b>Callitrichidae</b>											
<i>Saguinus geoffroyi</i>	50	.1	.8	40.0	<.1	+				+	Frugivore/insectivore
<b>EDENTATA</b>											
<b>Myrmecophagidae</b>											
<i>Tamandua tetradactyla</i>	?	-----	-----	-----	-----	+	+			+	Anteater
<i>Cyclopes didactylus</i>	?	-----	-----	-----	-----		+			+	Anteater
<b>Bradypodidae</b>											
<i>Bradypus infuscatus</i> <sup>b</sup>	11,400	41.0	2.8	31,920	48.0	++	+			+	Brower
<i>Choloepus hoffmanni</i> <sup>b</sup>	2800	10.0	3.5	9800	14.7		+			+	Brower
<b>Dasypodidae</b>											
<i>Dasypus novemcinctus</i>	?	-----	-----	-----	-----	+	++	+			Insectivore/omnivore
<b>LAGOMORPHA</b>											
<b>Leporidae</b>											
<i>Sylvilagus brasiliensis</i>	Not recorded since 1964			-----	-----		+	+			Brower
<b>RODENTIA</b>											
<b>Sciuridae</b>											
<i>Microsciurus alfari</i>	?	-----	-----	-----	-----		+			+	Frugivore/granivore
<i>Sciurus granatensis</i>	300	1.0	.25	75.0	.12		+			+	Frugivore/granivore
<b>Heteromyidae</b>											
<i>Heteromys desmarestianus</i>	1000?	3.6	.1	100.0	.15		+	+			Frugivore/granivore
<b>Cricetidae</b>											
<i>Oryzomys capito</i>	} 3000	10.8	.07	210.0	.3		+	+			Frugivore/granivore
<i>Oryzomys concolor</i>						+		+	Frugivore/granivore		
<i>Oryzomys bicolor</i>						+		+	Frugivore/granivore		
<i>Tylomys panamensis</i>						+		+	Frugivore/granivore		
<i>Zygodontomys microtinus</i>	?	-----	-----	-----	-----	+	+			+	Frugivore/granivore
<b>Muridae</b>											
<i>Rattus rattus</i>	?	-----	-----	-----	-----		+		+	+	Frugivore/granivore
<i>Mus musculus</i>	?	-----	-----	-----	-----		+	+		+	Frugivore/granivore
<b>Erethizontidae</b>											
<i>Coendou rothschildi</i>	?	-----	-----	-----	-----		+			+	Frugivore/brower
<b>Dasyproctidae</b>											
<i>Agouti paca</i>	500	1.8	8.0	4000.0	6.0		+	+			Frugivore/brower
<i>Dasyprocta punctata</i>	1400	5.0	2.0	2800.0	4.2	+		+			Frugivore/granivore
<b>Echimyidae</b>											
<i>Proechimys semispinosus</i>	3000	10.8	.8	2400.0	3.6		+	+			Frugivore/granivore
<i>Diplomys labilis</i>	?	-----	-----	-----	-----		+			+	Frugivore/omnivore

CARNIVORA

Procyonidae									
<i>Procyon lotor</i>	?	.....	.....	.....	.....	+	+	+	Frugivore/carnivore
<i>Nasua nasua</i>	600	2.1	3.0	1800.0	2.7	+	+	+	Frugivore/carnivore
<i>Potos flavus</i>	?	.....	.....	.....	.....	+	+	+	Frugivore/omnivore
<i>Bassaricyon gabbii</i>	?	.....	.....	.....	.....	+	+	+	Frugivore/carnivore
Mustelidae									
<i>Eira barbara</i>	?	.....	.....	.....	.....	+	+	+	Frugivore/carnivore
Felidae									
<i>Felis pardalis</i>	?	.....	.....	.....	.....	+	+	+	Carnivore
PERISSODACTYLA									
Tapiridae									
<i>Tapirus bairdii</i>	8	<.1	300.0	2400.0	3.6	+	+	+	Browser
ARTIODACTYLA									
Tayassuidae									
<i>Tayassu tajacu</i>	100	.3	23.0	2300.0	3.5	++	+	+	Frugivore/omnivore
Cervidae									
<i>Odocoileus virginianus</i>	10?	.1	40	400.0	.6	+	+	+	Browser
<i>Mazama americana</i>	20?	<.1	15	300.0	.4	+	+	+	Browser
Total	27,777			66,465 kg or 4431 kg/km <sup>2</sup>					

<sup>a</sup> *Heteromys*, *Oryzomys*, and *Zygodontomys* probably present. *Oryzomys* not identified to species with certainty for BCI.

<sup>b</sup> *Bradypus* and *Choloepus* estimates from Montgomery and Sunquist (1973).

sons, although they probably are, but rather we emphasize that the resources have a stable distribution in the forest which leads to a replicability of the distribution of howler troops.

Similarly, our data show persistent distributions of troops of *Cebus*, *Nasua*, and *Tayassu* between 1964 and 1973. For instance, during censusing periods between 1964 and 1970 Eisenberg located coati troops within the core areas of the three bands studied by Kaufmann in 1959-60. Again the argument is strongly reinforced that the distribution of resources in Barro Colorado Island has changed little in the last 10 years and that these resources are exploited in a predictable fashion by mammalian populations.

We also recognize that mammalian populations are not static in the tropics. In fact, our censusing data over the years indicate some population trends. During the seven years, agoutis (*Dasyprocta*) and squirrels (*Sciurus*) increased in number. The number of *Cebus* may possibly have declined. The other species do not show any consistent trends, or present problems of interobserver reliability, or were noted with such infrequency as to permit no valid comparisons.

**Volant mammals:** The preceding analyses do not treat an important element of the neotropical mammalian fauna, the Order Chiroptera. Bats are abundant and ubiquitous in the neotropics. Handley (1966) records 100 species of bats from Panama. Handley (unpublished) lists 60 species recorded from the Canal Zone, of which 34 have been found

on Barro Colorado Island. The trophic structure of neotropical bats has been analyzed by MacNab (1971) who finds that of approximately 70 species native to Surinam, 37 percent are frugivorous and nectarivorous, 50 percent insectivorous and carnivorous, and 4 percent sanguivorous. The percentages are similar in Panama. For the 100 species listed by Handley (1966), we have used Wilson's (1973)

TABLE 3. Biomass contributions for selected genera.

Genus	Barro Colorado Island		Surinam	
	Contributed biomass (kg)	% of estimated total biomass <sup>a</sup>	Contributed biomass (kg)	% of total <sup>b</sup>
<i>Didelphis</i>	1050	1.3	558	.59
<i>Bradypus</i>	31,920	40.0	6732	14.7
<i>Choloepus</i>	9800	12.3	3612	7.9
<i>Alouatta</i>	5500	6.8	2634	5.7
<i>Saguinus</i>	40	<.1	58	.12
<i>Cebus</i>	650	0.8	8	<.1
<i>Agouti</i>	4000	5.0	1176	2.5
<i>Dasyprocta</i>	2800	3.5	452	.98
<i>Proechimys</i> <sup>c</sup>	2400	3.0	83	.18
<i>Tapirus</i>	2400	3.0	9432	20.6
<i>Tayassu</i>	2300	2.8	1633	3.5
<i>Mazama</i>	300	<.4	10,065	22.0
Total	63,160		36,443	
	represents 95% of the tabulated total or 76% of the estimated total		represents 80% of the known total	

<sup>a</sup> Percentage calculated from a postulated total of 79,758 kg or 5317 kg/km<sup>2</sup> which is 20% higher than the known total of 66,465 kg as tabulated in table 2 (see text).

<sup>b</sup> Percentage calculated from the recorded total of 45,769 kg as quoted in table 1.

<sup>c</sup> *Echimyis* from Surinam.

trophic role values to calculate that 3 percent are carnivorous, 1 percent piscivorous, 3 percent sanguivorous, 13 percent are foliage gleaners, 39 percent are aerial insectivores, 32 percent are frugivorous, and 9 percent are nectarivorous. Handley (1967) discusses preliminary data concerning the ecological separation of insectivorous bats as a function of their flying height in the forest. Fleming, Hooper, and

Wilson (1972) relate trophic specializations to the breeding cycles of neotropical bats with rather good results. Hence, the analysis of neotropical bat faunas is proceeding, but at present data on abundance or biomass are simply not available. Knowledgeable specialists estimate that the biomass of bats exceeds that of all other mammals in neotropical forests. We doubt that this supposition is true and think the illusion results from the rapid movement and large range of bats. They are numerous, but they are small. Referring to Odum (1970), we hypothesize that the bat biomass is not more than 10 percent of the total biomass of nonvolant mammals.

TABLE 4a. *Strip census results.*<sup>a</sup>

Genus	Diurnal and crepuscular sightings							
	Eisenberg				Thorington			
	1964		1965		1970		1971	
Number <sup>b</sup>	%	Number	%	Number	%	Number	%	
<i>Alouatta</i> <sup>c</sup>	25	25	13	19	27	28	17	18.3
<i>Cebus</i>	26	26	17	25	14	14	4	4.3
<i>Saguinus</i>	4	4	5	7.5	4	4	1	1.1
<i>Bradypus</i>	1	1	1	1.5	6	6	1	1.1
<i>Dasybus</i>	0	0	0	0	2	2	3	3.2
<i>Nasua</i>	8	8	5	7.5	7	7	4	4.3
<i>Dasyprocta</i>	10	10	9	13.4	23	23	29	31.2
<i>Sciurus</i>	6	6	5	7.5	8	8	33	35.5
<i>Sylvilagus</i>	2	2	0	0	0	0	0	0
<i>Tayassu</i>	8	8	7	10.4	4	4	0	0
<i>Tamandua</i>	7	7	3	4.5	1	1	0	0
<i>Eira</i>	1	1	2	3.0	0	0	0	0
<i>Mazama</i>	1	1	0	0	0	0	0	0
<i>Odocoileus</i>	0	0	0	0	0	0	1	1.1
	99		67		97		93	
	Based on 55 hours		Based on 27 hours		Based on 43 hours		Based on 30 hours	

<sup>a</sup> *Ateles* was not included since it was the object of intensive study by Eisenberg.

<sup>b</sup> In group living species, e.g., *Alouatta*, *Cebus*, *Nasua*, *Saguinus*, *Tayassu*, one sighting equals the sighting of one or more animals in the same group, thus groups are treated as one to balance comparisons with solitary species.

<sup>c</sup> In 1965, *Alouatta* troops were counted only once and the same troop was not counted on subsequent days; this lowers the count. The same criterion was applied to no other species.

TABLE 4b. *Strip census results.*

Genus	Nocturnal sightings			
	Eisenberg		Thorington	
	1964 and 1965		1971	
	Number	%	Number	%
<i>Didelphis</i>	8	29	13	22
<i>Philander</i>	2	7	3	5
<i>Choloepus</i>	1	3.5	2	3
<i>Dasybus</i>	1	3.5	8	14
<i>Potos</i> or <i>Bassaricyon</i>	1	3.5	5	8
<i>Dasyprocta</i>	0	0	2	3
<i>Agouti</i>	3	10	7	12
<i>Diplomys</i>	0	0	3	5
Misc. small rodents	2	7	5	8
<i>Caluromys</i>	0	0	6	10
<i>Chironectes</i>	0	0	1	1.5
<i>Aotus</i>	2	7	2	3
<i>Proechimys</i>	2	7	0	0
<i>Tamandua</i>	1	3.5	0	0
	23		57	
	Based on 21 hours		Based on 55 hours	

An evaluation of census techniques: We have described and reviewed various techniques useful for censusing tropical mammals (Eisenberg, Santiapillai, and Lockhart 1970; Eisenberg and Lockhart 1972; Thorington 1972). Numerous other discussions of censusing techniques exist and will not be repeated here.

In 1964, 1965, 1970, and 1971 we conducted visual censuses along the trails of Barro Colorado Island, totaling 155 daylight hours and 66 hours at night, biased toward times of greatest mammalian activity. Table 4 (a and b) summarizes the results of the sightings, and table 5 compares their rank order of abundance with those of the Surinam data and the Barro Colorado estimates from tables 1 and 2. From these comparisons we conclude that most of the large diurnal mammals on Barro Colorado are easily censused visually. However, the cryptic, arboreal sloth *Bradypus* is vastly underestimated. The nocturnal animals are not as easily censused by our techniques. We believe the arboreal forms *Coendou* and *Choloepus* are grossly underestimated, but that many of the terrestrial forms are seen in approximate proportion to their abundance. We conclude that visual-strip censuses can give useful data about the relative abundance of diurnal terrestrial mammals such as *Dasyprocta*, *Nasua*, and *Tayassu*, and diurnal arboreal forms such as *Sciurus*, *Alouatta*, and *Cebus*.

## PROBLEMS OF CENSUSING PARTICULAR SPECIES

### A. DIURNAL ARBOREAL FORMS

(1) The three-toed sloth, *Bradypus infuscatus*: This species has been studied by Montgomery and Sunquist on Barro Colorado Island, who have found it may reach a density of 7.6 animals per hectare. Assuming an adult weight of 2.8 kg, this is a biomass of almost 2130 kg/km<sup>2</sup>. It would appear that *Bradypus* exists at the highest numerical density of any large, arboreal mammal and is therefore a sig-

TABLE 5. Rank order of abundances.<sup>a</sup>

Surinam	BCI estimate	Diurnal			
		1964	1965	Censuses	
				1970	1971
<i>Bradypus</i>	<i>Bradypus</i>	<i>Cebus</i>	<i>Cebus</i>	<i>Alouatta</i>	<i>Sciurus</i>
<i>Alouatta</i>	<i>Dasyprocta</i>	<i>Alouatta</i>	<i>Alouatta</i>	<i>Dasyprocta</i>	<i>Dasyprocta</i>
<i>Tamandua</i>	<i>Alouatta</i>	<i>Dasyprocta</i>	<i>Dasyprocta</i>	<i>Cebus</i>	<i>Alouatta</i>
<i>Myoprocta</i>	<i>Nasua</i>	<i>Tayassu</i>	<i>Tayassu</i>	<i>Sciurus</i>	<i>Cebus</i>
<i>Dasyprocta</i>	<i>Sciurus</i>	<i>Nasua</i>	<i>Nasua</i>	<i>Nasua</i>	<i>Nasua</i>
<i>Tayassu</i>	<i>Cebus</i>	<i>Tamandua</i>	<i>Saguinus</i>	<i>Tayassu</i>	<i>Dasyprocta</i> <sup>b</sup>
---	<i>Tayassu</i>	<i>Sciurus</i>	<i>Sciurus</i>	<i>Saguinus</i>	---
Surinam	BCI	Nocturnal			
		Eisenberg	Censuses		
				Thorington	
<i>Dasyprocta</i>	<i>Choloepus</i>	<i>Didelphis</i>		<i>Didelphis</i>	
<i>Coendou</i>	<i>Proechimys</i>	<i>Proechimys</i>		<i>Dasyprocta</i>	
<i>Choloepus</i>	<i>Didelphis</i>	<i>Agouti</i>		<i>Agouti</i>	
<i>Coendou</i>	<i>Agouti</i>	---		<i>Caluromys</i>	
<i>Didelphis</i>	<i>Phyllander</i>				
<i>Agouti</i>	---				
<i>Echimyis</i>	---				

<sup>a</sup> Animals  $\geq 250$  gm.

<sup>b</sup> Number of sightings becomes less than three times after *Dasyprocta*.

nificant component in the cycling of materials in the rainforest ecosystem (Montgomery and Sunquist 1973).

In spite of its high density, the animal is so cryptic that it is rarely seen and impossible to census visually. However, three-toed sloths descend to the ground to defecate every five to eight days. Each digs a small hole at the base of a tree with its tail and deposits its feces in it. A hole may be used in common by a mother and her young. By sweeping the forest litter one can find these fecal deposits and from their abundance estimate the density of sloths (see Montgomery and Sunquist 1973). This is the only valid indirect censusing technique for *Bradypus* available to an observer on foot.

(2) The howler monkey, *Alouatta palliata*: Censused by direct counts, the howler monkey is probably the second most numerically abundant diurnal arboreal mammal on Barro Colorado Island. With an average density of .7 per hectare and with an average adult weight of 5.5 kg, the biomass approximates 400 kg/km<sup>2</sup>. Censusing techniques for *Alouatta* have been described elsewhere (Carpenter 1934; Collias and Southwick 1952; Thorington 1972).

(3) The white-throated capuchin monkey, *Cebus capucinus*: Data from Oppenheimer (1968) indicate that the *Cebus* monkey on Barro Colorado Island exists at a moderate density of .17 individuals per hectare; this may be a low estimate. Their biomass would be approximately 44 kg/km<sup>2</sup> assuming an average adult weight of 2.6 kg. In walking surveys Eisenberg found *Cebus* troops almost as frequently as troops of howler monkeys, which are four times as abundant. This situation would appear to result

from two factors: First, *Cebus* frequently emit alarm calls upon sighting a terrestrial observer, which makes them very conspicuous. Secondly, *Cebus* troops move rapidly through the forest and have home ranges almost 10 times larger than those of howler troops (Oppenheimer 1968; Chivers 1969). Thus, the probability of seeing the same troop several times on separate surveys is increased and the density of troops is overestimated.

(4) The spider monkey, *Ateles geoffroyi*: This species was introduced on Barro Colorado Island in 1962 and has grown from an established group of 5 adults to 14 animals as of September 1972. Spider monkeys have large home ranges, and troops frequently divide into subunits. Thus, one of the problems in censusing spider monkeys is to obtain accurate troop counts by recognizing all members of the same troop. Only patient work can ensure that troop composition has been worked out and all animals have been counted (Eisenberg and Kuehn 1966; Klein 1972).

(5) The rufous-naped tamarin, *Saguinus geoffroyi* or *Saguinus oedipus geoffroyi*: In a mature tropical rainforest, *Saguinus* exists at rather thin densities, since it appears to be adapted to second-growth conditions or forested areas near natural clearings (Moynihan 1970). In recent years, the *Saguinus* population on BCI has declined. We do not have a reliable estimate but judge that there are fewer than 50 animals on the island at present. We saw them infrequently during our censuses (4% of all sightings).

Marmoset groups are easy to locate by the scolding chirps they give when they see an individual on

foot. They will also respond to the calls of an isolated marmoset or imitations of their calls. A caged marmoset can attract any marmoset troop within hearing range; however, this range probably is less than 200 yards.

(6) The lesser anteater, *Tamandua tetradactyla*: This animal appears to be active both during the day and at night. It may be encountered on the ground or observed in the trees; hence, its categorization with respect to activity rhythm and location is somewhat ambiguous. During walking surveys on BCI, *Tamandua* accounted for only 4 percent of mammal sightings. Compared with the Surinam data this is a lower than expected density. We would expect it to be at the same density as *Cebus* on Barro Colorado unless the termite fauna of the island differs significantly from that of Surinam. We know *Tamandua* is moderately abundant in a tropical rainforest, but as yet we have no adequate censusing technique.

## B. ARBOREAL NOCTURNAL FORMS

(1) The two-toed sloth, *Choloepus hoffmanni*: This species is cryptic and almost entirely nocturnal in habits (Sunquist and Montgomery 1973), which render it almost impossible to census directly. An indirect method of censusing utilizing a modified pellet count was developed by Montgomery and Sunquist (1973). Their preliminary studies suggest that the two-toed sloth has a larger home range than the three-toed sloth and that it exists at roughly one-fourth the density of the three-toed sloth, with a biomass of 650 kg/km<sup>2</sup>. The data from Surinam differ only slightly, suggesting that *Choloepus* exists at approximately 40 percent of the density of *Bradypus*. Thus *Choloepus* constitutes a significant proportion of the total biomass of arboreal mammals.

(2) The prehensile-tailed porcupine, *Coendou*: The species *C. rothschildi* occurs on BCI, but its nocturnal habits render it very difficult to census. Males produce a distinctive strong odor which we have detected in the forest, but an olfactory census has not yet been devised. The data from Surinam suggest that *Coendou* exists at a density equal to two-thirds that of *Bradypus*. If this is true on Barro Colorado, then porcupines comprise a significant part of the arboreal mammalian biomass on the island.

## C. DIURNAL TERRESTRIAL OR SEMI-TERRESTRIAL FORMS

(1) The common agouti, *Dasyprocta punctata*: The density of this species on BCI may be estimated from the data of Smythe (1970 a, b) as roughly one animal per hectare. If we assume 2 kg to be

the average weight of an adult, then the biomass estimate would approximate 200 kg/km<sup>2</sup>. Thus, *Dasyprocta* is the most numerically abundant diurnal, terrestrial mammal, as was also indicated by the walking surveys.

The agouti is conspicuous because it barks when it sees an observer and continues to bark as it retreats. This anti-predator strategy makes it easy to census by walking transects. The animals tend to live paired but travel separately; hence, they do not show any particular clumping tendency.

(2) The coatimundi, *Nasua nasua*: The coati on BCI is a dominant member of the mammalian community and was studied definitively by Kaufmann (1962). Our density estimates are based on Kaufmann's data. We assume an average home range of 40 hectares for a female band of 8 animals. Allowing overlap in home ranges and accounting for the mostly solitary males, we estimate the average density to be 0.4 animals per hectare. This is half the agouti density, which is approximately the frequency with which we encountered them in the forest.

We believe that coatis are amenable to a transect census. They are noisy in the forest. They have squeaking contact notes, and the mothers give a warning squeak when they notice an observer. Thus they are easy to detect in a transect. A rough index of abundance might also be achieved by keeping count of tracks and by determining the relative abundance of agouti and coati tracks.

(3) The collared peccary, *Tayassu tajacu*: This species is active in part at night but certainly active enough during the day to be censused by foot surveys. Bands often give away their position by barking as they flee. Contact frequency with peccaries was at about the same as that for coatis during the walking surveys by Eisenberg (7%). However, their density is probably only a sixth that of the coati because their greater conspicuousness and larger home range increases the probability for repeated contact with the same band. Computing frequency of tracks along transects might be a useful index to estimating the abundance of this species.

(4) The brocket and white-tailed deer, *Mazama* and *Odocoileus*: During walking surveys on BCI, Eisenberg noted *Mazama* only twice and did not see any *Odocoileus*; however, Montgomery and Thorington report occasional sightings of *Odocoileus*. These deer may well be studied by transect walking if special attention is paid to tracks and if survey plots are set up adjacent to the transects which are cleared bi-weekly of all fecal material. Relative abundance of these deer species could then be estimated in a manner similar to that employed in Ceylon by Eisenberg, Santiapillai, and Lockhart (1970).



#### D. NOCTURNAL TERRESTRIAL FORMS

(1) The spiny rat, *Proechimys semispinosus*: Utilizing the data from Fleming (1971) and Smythe (1970a), we consider *P. semispinosus* to be the most numerically abundant nocturnal small mammal on BCI, probably existing at a density of more than 2 per hectare. However, its biomass contribution (1.6 kg per hectare) is not large due to the small size of the animal. The only effective way to estimate *Proechimys* abundance is a trap-mark-release program, such as that used by Fleming. This same technique could well be applied to the other small rodents which probably exist at reasonable numerical densities but do not contribute significantly to the biomass.

(2) The nine-banded armadillo, *Dasypus novemcinctus*: We have no firm estimate of the numerical density of this species on BCI. However, it was the second most abundant mammal in Thorington's nocturnal counts, and its burrows are common. The data from Surinam suggest that *Dasypus* may exist at a numerical density roughly half that of the three-toed sloth. If so, it would be a significant contributor to terrestrial mammalian biomass. The best census technique of which we know is a capture-mark-release program in which the animals are banded on the tails with colored electrical tape. An index of abundance could be obtained by counting burrows along transects.

(3) The paca, *Agouti paca*: According to Smythe (1970a), this species lives in pairs like *Dasyprocta* but with a home range almost three times as large. We calculate from the estimates of Smythe that paca may contribute biomass at the level of 2.7 kg per hectare on BCI, which makes it a significant component of the terrestrial mammalian fauna. The paca is nocturnal, much quieter and more cryptic than *Dasyprocta*, and therefore it is much more difficult to census directly. If the abundance of the agouti could be estimated by walking surveys, and a ratio of paca tracks to agouti tracks could be obtained, then the abundance of the paca could be related to agouti density.

(4) The common opossum, *Didelphis marsupialis*: The opossum is reasonably abundant on BCI and is both arboreal and terrestrial. In nocturnal censusing, we encountered it most frequently. The data from Surinam suggest that it exists at roughly half the density of the agouti. This species could also be censused by recording tracks on a transect and relating their abundance to those of agouti tracks.

(5) Baird's tapir, *Tapirus bairdii*: Baird's tapir has been repeatedly reintroduced and is firmly established on BCI. Most of the individuals are known

and named. It has proven difficult if not impossible to introduce new specimens to the island since the intruders are generally attacked by the resident male. This circumstance strongly suggests that members of a given "community" know one another although they do not form cohesive social groupings. Tapir density is very difficult to estimate, but track counts might again prove useful. The data from Surinam suggest it exists at half the density of the peccary, but this may be an overestimate. Even at low numerical densities, the tapir is an important contributor to terrestrial mammalian biomass.

#### CONCLUSIONS AND DISCUSSION

In this paper we have examined the importance of the various species of mammals in a neotropical forest, as judged by the biomass of each. The impact of these species on the forest ecosystem can be viewed in terms of their trophic specializations and their location in the forest. Utilizing the biomass data, as set forth in tables 1 and 2, we offer two biomass pyramids in figure 1, which provide this viewpoint. From 40 percent (Surinam) to 70 percent (BCI) of the mammalian biomass is maintained by the arboreal species. Browsers and grazers, both terrestrial and arboreal, account for 65 percent (Surinam) to 53 percent (BCI) of the total biomass; and combination feeders on fruits and browse account for 15 percent (Surinam) to 25 percent (BCI) of the total. The pyramids conform in shape to similar figures published for the Old World tropics (Hendrichs 1972; Schaller 1972; Eisenberg and Lockhart 1971). Fleming's (1973) analysis of trophic diversity is not directly comparable with ours, both because he included bats and because his unit of analysis was the species not biomass.

We have taken our biomass estimates and computed from them an estimate of the energy consumption of the different taxa (table 6). This estimate is given in kilocalories per hectare per day and is computed from the estimated basal metabolic rates of average-sized individuals of each species. The basal metabolic rates were computed as 70 Kcal/kg<sup>3/4</sup> per day (Kleiber 1961) and the figures for *Bradypus* and *Choloepus* were reduced by 51 and 34 percent, respectively (Goffart 1971).

These figures are only first approximations of the rates of energy consumption by different mammals in the neotropics and hence of the importance of these in nutrient cycling, but we find them informative. The sloths, *Bradypus* and *Choloepus*, are obviously the most important consumers in the canopy and together may use more than four times as many kilocalories as the howler monkeys. We calculate that these three genera account for more than half

the energy consumed by the total fauna of nonvolant mammals. The rodents account for 23 percent of

TABLE 6. *Metabolic rates per hectare for species of mammals on Barro Colorado Island.*<sup>a</sup>

Taxon	Average weight (kg)	Kcal/H/day	% of total Kcal
<i>Marmosa</i>	.06	4.6	.3
<i>Philander</i>	1.4	24.	1.5
<i>Didelphis</i>	1.0	49.0	3.0
<i>Aotus</i>	.8	1.9	.1
<i>Alouatta</i>	5.5	170.	11.
<i>Cebus</i>	2.6	24.	1.5
<i>Ateles</i>	5.0	2.2	.1
<i>Saguinus</i>	.8	1.9	.1
<i>Bradypus</i>	2.8	560.	36.
<i>Choloepus</i>	3.5	220.	14.
<i>Sciurus</i>	.25	4.9	.3
<i>Heteromys</i>	.10	8.3	.5
<i>Oryzomys</i>	.07	19.0	1.2
<i>Agouti</i>	8.0	110.	6.9
<i>Dasyprocta</i>	2.0	110.	6.9
<i>Proechimys</i>	.8	120.	7.4
<i>Nasua</i>	3.0	64.	4.0
<i>Tapirus</i>	300.	27.	1.7
<i>Tayassu</i>	23.	49.	3.0
<i>Mazama</i>	15.	7.1	.5
<i>Odocoileus</i>	40.	7.4	.5

<sup>a</sup> See text for bases of estimates. Calculations assume two significant digits.

all estimated basal energy consumption. The three genera, *Agouti*, *Dasyprocta*, and *Proechimys*, are the most important terrestrial mammals in considerations of nutrient cycling on Barro Colorado Island. The large mammals, *Tapirus*, *Tayassu*, *Odocoileus*, and *Mazama*, are relatively insignificant consumers of energy accounting for less than 6 percent of the total, approximately the same as the marsupials. Because of their high rates of metabolism, the small rodents and marsupials are potentially significant consumers, and hence it is important to obtain better estimates of their biomass. The same argument applies equally well to the Chiroptera.

The total mammalian population which we have estimated on Barro Colorado consumes energy at the basal rate of 1600 kilocalories per hectare. The actual rate of consumption is greater than this, and the total energy consumption of nonvolant mammals on BCI probably lies between 3000 and 4000 kilocalories per hectare per day.

Obviously much more work needs to be done on populations of tropical mammals. Data on the numbers, biomass, and energy consumption of mammals must be collected from many different areas and many different habitats for comparison. This

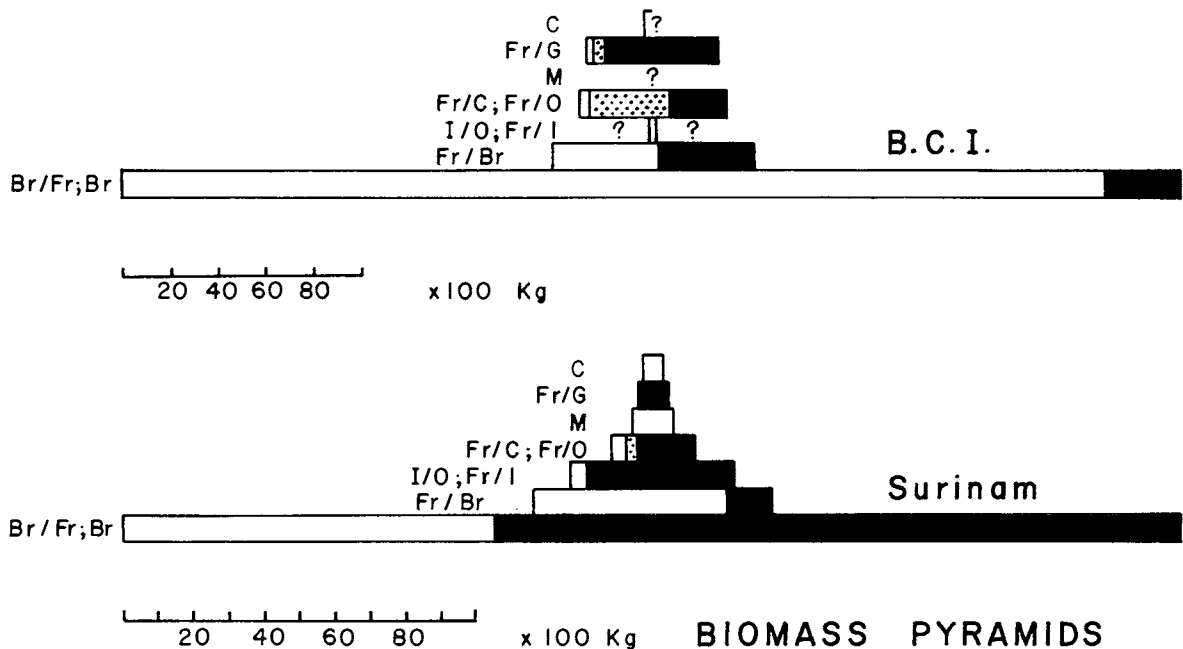


FIGURE 1. Biomass pyramids for Barro Colorado Island and Surinam. Br/Fr = primary browser, secondary frugivore; Br = browser; Fr/Br = primary frugivore, secondary browser; I/O = primary invertebrate consumer and secondary omnivore; Fr/I = primary frugivore, secondary insectivore; Fr/C = primary frugivore, secondary carnivore; Fr/O = primary frugivore, secondary omnivore; M = Myrmecophage; Fr/G = primary frugivore, secondary granivore; C = carnivore. Black bars indicate terrestrial component. Stippled bars indicate scansorial component. White bars indicate arboreal component. Question marks refer to incomplete censusing for three trophic levels on Barro Colorado Island.

procedure will require refinement of censusing techniques, which is also obligatory for collecting data on the population dynamics of many species. It is important to obtain this information, because it is basic to an understanding of population fluctuations and the long-term dynamics of survival of mammalian species in the tropics. Only with such data is it possible to predict the minimal sizes of populations consistent with wise conservation practices, and thereby to establish the minimal sizes of reserves and parks for maintaining the diversity of the neotropical mammalian fauna.

Finally, our analysis emphasizes the dominance of the Edentata in the neotropics. This is not clear from faunal lists because a small number of species are involved. The Edentata, according to the Surinam data, account for 36 percent of the terrestrial mammalian biomass. The Panama data confirm this dominance with sloths alone accounting for more than 50 percent of the estimated mammalian biomass on BCI.

The Edentates seem to have evolved three types of feeding specializations, two of which concern very stable, predictable resources. The family Bradypodidae is specialized as an arboreal browser, thus utilizing a predictable and extensive resource. The family Myrmecophagidae includes both arboreal and terrestrial forms, highly specialized for feeding on ants and termites. A significant part of the animal biomass is tied up in ants and termites (Odum 1970), and the niche is apparently an extremely

stable one in the tropics. The Dasypodidae are somewhat generalized, although showing many specializations within the family. *Dasypus novemcinctus* is a generalized feeder occupying an insectivore-omnivore niche.

The Edentates are definitely holding their own as a dominant mammalian order in the neotropics in spite of the fact that this realm has been invaded since the Pliocene by successive waves of other eutherian immigrants (Simpson 1969). The Edentata together with the Marsupialia exhibit the longest evolutionary history of any surviving mammalian group in the neotropics. Evidently in their long-term occupancy of arboreal browsing and myrmecophagus niches in the neotropics they have become sufficiently specialized to withstand competition from subsequent immigration. The ecological dominance of this order in the neotropics is unique and comparable to the ecological dominance of the order Marsupialia in the rainforests of the York Peninsula in Australia (Harrison 1962).

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