

**MAMMALIAN SURVEYS OF TWO FORESTED AREAS, WITH DIFFERENT
DEGREES OF DISTURBANCE, IN PANAMA**

**CENSOS DE MAMÍFEROS EN DOS AREAS BOSCOSAS CON DIFERENTES
GRADOS DE PERTURBACIÓN, EN PANAMA**

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ABSTRACT

I calculated encounter rates, densities and biomass by strip censuses, for most species of non-volant forest mammals found in Gigante Peninsula, and compared them with those reported for Barro Colorado Island (BCI), both located in the Canal Zone in Panama. I found 29 species of non-volant mammals in Gigante. Encounter rates were 3.81 animals/km for diurnal and 2.60 animals/km for nocturnal censuses. There are more species of large mammals in BCI than in Gigante, and most species have higher densities in BCI, which is an older forest and has been protected against hunting for a longer time. The species missing in Gigante are mainly big game animals, better adapted to undisturbed forest and that have suffered from previous hunting. However, three young forest species are predominant in Gigante and their biomass compensates for the absent species and species with lower densities. Total biomass for selected species in Gigante was 18.98 Kg/ha, similar to that of BCI for the same species. White-tailed deer (*Odocoileus virginianus*) is one of the main components of biomass in Gigante, while it is almost extinct in BCI. I conclude that a young disturbed forest, with some degree of protection, may support a high mammalian biomass.

Key words: Censuses, mammals, Panama, moist Forest

RESUMEN

Por medio de censos visuales, se calcularon tasas de encuentros, densidades y biomasa para la mayoría de los mamíferos no voladores encontrados en la Península de Gigante, y se compararon con los datos reportados para la isla Barro Colorado (BCI), ambos situados en la Zona del Canal en Panamá. Se encontraron 29 especies de mamíferos no voladores en Gigante. Las tasas de encuentro fueron: 3,81 animales/km en los censos diurnos y 2,60 animales/km en los censos nocturnos. Hay más especies de mamíferos grandes en BCI que en Gigante, y la mayoría de las especies tienen densidades más altas en BCI, cuyo bosque es más antiguo y ha sido protegido contra la caza por más tiempo. Las especies que faltan en Gigante son principalmente animales grandes mejor adaptados a bosques primarios y que han sido objeto de caza anteriormente. Sin embargo, tres especies típicas de bosque secundario predominan en Gigante, y su biomasa compensa por las que allí faltan o que tienen bajas densidades. La biomasa total para una selección de especies en Gigante fue de 18,98 Kg/ha, la cual es similar a la reportada para las mismas especies en BCI. El venado de cola blanca (*Odocoileus virginianus*) es uno de los principales componentes en la biomasa total de Gigante, mientras que está casi extinto en BCI. Se concluye que un bosque secundario, con cierto grado de protección, podría mantener una alta biomasa de mamíferos.

Palabras clave: Censos, mamíferos, Panamá, bosque húmedo

INTRODUCTION

The mammalian communities of tropical lowland moist forests have been studied by several researchers in different parts of Central and South America. One of the topics studied has been the effects of the degree of disturbance and forest age on these mammalian communities. As a general observation, the higher diversity, density and biomass of forest mammals has been associated with older, better protected forest (Eisenberg and Thorington 1973; Eisenberg et al. 1979; Emmons 1984; Glanz 1982; Schaller 1983; Ochoa et al. 1988, Eisenberg 1989). However, it is difficult to find two adjacent study sites at the same chronological time, which differ only in the degree of disturbance and forest age. Hence, most of the comparisons have been done between sites located far away with likely different climatic or soil conditions, or in the same place but at two different historical moments.

In 1983 the Smithsonian Tropical Research Institute (STRI) initiated a forest mammals research project as part of a program named Alternatives to Destruction in Panama (Oca et al. 1988). As part of this project, two study sites were selected: one of them was Barro Colorado Island (BCI), which is one of the places where more research have been conducted in mammalian communities. Most mammals on this island are found at exceptionally high densities mainly due to the well protected mature forest and the lack of natural predators (Eisenberg 1980, 1989). The other study site is in Gigante Peninsula which is part of the mainland surrounding BCI and it supports different ecological conditions mainly due to different history of the site; these conditions still need to be described.

Both study sites are located within Barro Colorado Natural Monument (BCNM) in the Canal Zone of Panama and the type of vegetation there is tropical lowland moist forest. Gigante study site has an area of 58 ha and is limited by the shore of Lake Gatun and a wire fence. The area of BCI is 1,564 ha. Fig. 1 shows location of BCI and Gigante study site.

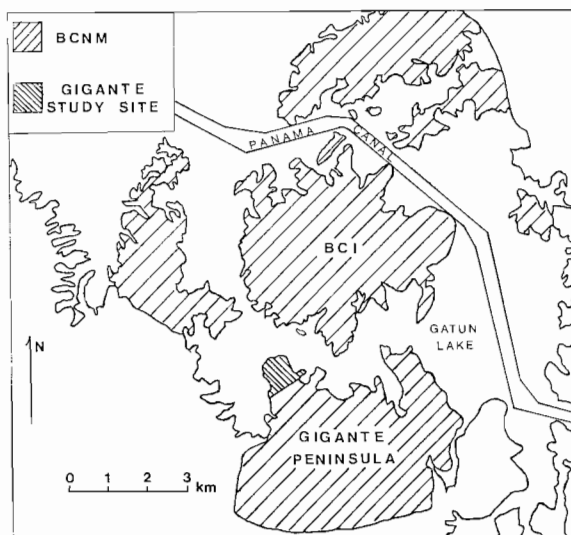


FIGURA 1. General location of BCI and Gigante study site within.

There are basic differences in the history of the two study sites. BCI forest is at least 120 years old and has been protected against hunting since it became a reserve in 1923, although effective vigilance began in 1965. Gigante habitat is mostly second growth forest 40-60 years old, with abundant figs and other second growth forest trees, and some crops planted close to the research laboratory. There was moderate hunting pressure in Gigante until 1979, when some protection against poaching began. Gigante has probably been better protected since 1983 when the lab and the fence were built.

In this report I present the results of mammal surveys conducted in Gigante from June 1986 to November 1987 and compare them with those found in BCI, with the objective of assessing the possible effects of forest age and degree of disturbance on the mammalian diversity, density and biomass in these two adjacent study sites.

METHODS

Strip Census

Strip censuses were conducted by walking slowly along the trails (average speed: 1.1 km/h for diurnal census and 1.0 km/h for nocturnal censuses), and recording every individual mammal or group detected (seen or heard). I looked for both terrestrial and arboreal animals, but the canopy was not as efficiently sampled as the ground. For each animal I recorded species, location, distance from the observer and perpendicular distance from the trail. I attempted to count the number of

individuals in groups of social terrestrial mammals. Diurnal censuses were conducted from 0700 to 1200 h and nocturnal censuses from 1900 to 2400 h. Only one observer was present during a census.

Census routes in Gigante were two concentric looping trails making a total of 6 km. On BCI, only diurnal censuses were conducted on about 11 km of trails, but since the area is very large, I combined my data with those provided by J. Wright and co-workers (unpub. data), through an ongoing project that began in 1987. Table 1 summarizes information about distance and the period of time censused in each place.

Tabla 1. Censuses conducted in Gigante and BCI

Site	No of Distance Time		
	Period	Censuses (k)	(h)
Gigante (day) (1)	10/86/87	66	173.2155.0
Gigante (day total)	6/86-11/87	122	333.0287.0
Gigante (night total)	6/86-2/87	38	107.2109.5
Gigante (night-day total)	6/86-11/87	160	440.2396.5
BCI (day total)	1/87-7/87	42	173.2162.8

(1) This period was used to calculate year-round encounter rates (ER) for diurnal species in Gigante.

The strip census allows the calculation of Encounter Rates (ER) defined as the number of animals detected per distance walked. In this paper, ER are reported as animals/km or groups/km depending on the species. The ER is a measure of relative abundance and does not represent absolute density, but it is useful to make comparisons among places and times.

I used two basic methods to estimate densities (animals/ha) in Gigante. The first one is by comparison of ER from Gigante with ER from BCI, where densities for most species are known, as follows:

$$D(g) = \frac{ER(g) \times D(BCI)}{ER(BCI)}$$

Where D(g) is density in Gigante, D(BCI) is density in BCI, ER(g) is encounter rate in Gigante and ER(BCI) is encounter rate in BCI.

Although I conducted censuses in BCI, most ER and densities for the island were taken from Glanz (1982). Glanz's ER are in animals/h, so I converted them to animals/km by dividing his figures by his average speed. When more recent or more reliable data were available about a particular species in BCI, I used it instead of that reported by Glanz. For instance, for the agouti I used the ER from my censuses and the density provided by Smythe (1978). For spiny rats, I used a combination of data from Glanz and Smythe.

For most species I found mean detection distance to be similar in BCI and Gigante. From this, I assumed equal detectability in both study sites in

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order to use the first method. However, for two common rodents agouti (*Dasyprocta punctata*) and squirrel (*Sciurus granatensis*), I found differences in detection distance between BCI and Gigante, and accordingly, correction factors were applied to calculate their densities. For the agouti, I obtained a ratio of 1.35 by dividing average detection distance in BCI by that on Gigante. This ratio was 1.28 for the case of squirrel. These ratios were then used as an indirect measure of differences in detectability. I calculated corrected ER by multiplying their observed ER times their respective ratios. Densities for these two species were then derived by comparing their corrected ER with BCI data (using equation 1).

Another correction to the first method was used with the coatis (*Nasua narica*). These social carnivores were recorded as either groups or single males. I estimated independent densities (as animals/ha) for groups and singles by comparison with equivalent data reported for BCI (Glanz 1982) using equation 1, but as the mean group size in Gigante (15.8 animals/group) is 1.66 times larger than that in BCI (9.5 animals/group), I multiplied this ratio times the group estimate in Gigante to get a corrected group estimate. Finally, I added together single and group estimates to get the total density.

The second method used was Kelker's estimation method described in Glanz (1982), from which density of a particular species is derived as:

$$D = \frac{N}{2PL}$$

Where D is density estimate, P is critical perpendicular distance, N is number of animals detected within the critical distance (P), L is distance walked.

The critical distance is the distance beyond which a significant proportion of animals is missed. My results led me to select this distance as 5 m on each side of the trail for all species. I did not

calculate Kelker's estimate for social animals.

The Kelker's estimate assumes that the observer is not missing any individuals within the strip censused, an unrealistic assumption for most forest mammals. The method, however, provides a safe minimum estimate. I used Kelker's estimate when there was not enough data to use the first method, or when particular characteristics of a species made it easily detectable.

Capture program

The capture program was conducted in Gigante from August 1986 to February 1987. I used 136 Tomahawk live-animal traps, 96 large (40' x 12.5' x 12.5') and 40 small (32' x 9.5' x 9.5') placed along the census trails covering most of the study site. I had four trapping sessions every month (one per week) making a total of 2,248 trap-nights. The bait used was dried corn and manioc root. In each session, I baited and set the traps at 1600 h and checked them the day after, at 1000 h. For the purpose of this paper, I used the capture results for the list of species in Gigante. Detailed results of this program will be published elsewhere.

RESULTS

Censuses

I detected a total of 3.81 animals/km in diurnal censuses, and 2.60 animals/km in nocturnal censuses in Gigante. ER and density estimates (product of the analysis of each species) are reported in Table 2. Details of the calculations for each species will be discussed in the next section.

A total of 29 species were found in Gigante. Table 3 shows a list of species not reported in Table 2 because either their encounters were too infrequent to calculate reliable ER and densities, or they were not seen during the censuses. As all genera reported in Tables 2 and 3 are monospecific in the study sites (except for *Felis*), I refer only to genera in the next Tables.

Tabla 2. Encounter rates (ER) and density (animals/ha) estimates for all species found in Gigante, with enough reliable information.

Species	TC	ER	Density
MARSUPIALIA			
<i>Didelphis marsupialis</i>	N	0.187	0.4670
<i>Caluromys derbianus</i>	N	0.056	0.2190
PRIMATES			
<i>Alouatta palliata</i>	D	0.548	0.8470
<i>Saguinus geoffroyi</i>	D	0.208	0.1910
EDENTATA			
<i>Tamandua mexicana</i>	D-N	0.015	0.0105
<i>Dasybus novemcinctus</i>	D-N	0.011	0.0457
LAGOMORPHA			
<i>Sylvilagus brasiliensis</i>	N	0.168	0.1120
RODENTIA			
<i>Dasyprocta punctata</i>	D	0.987	0.6062
<i>Agouti paca</i>	N	0.327	0.1890
<i>Proechimys semispinosus</i>	N	0.907	3.5992
<i>Sciurus granatensis</i>	D	0.831	0.7650
CARNIVORA			
<i>Nasua narica</i>	D	0.098	0.1680
<i>Potos flavus</i>	N	0.205	0.1120
<i>Bassaricyon gabbii</i>	N	0.065	0.0280
ARTIODACTYLA			
<i>Odocoileus virginianus</i>	D	0.266	0.1700
<i>Tayassu tajacu</i>	N	0.065	0.0620

TC = Type of census used to estimate ER: diurnal (D) or nocturnal (N) / ER = expressed as animals/km or groups/km for social animals (see text) / Density = given as animals/ha

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Table 3. Species present in Gigante, but not reported in Table 2.

Seen during censuses	Known to be present ^a
<i>Philander opossum</i>	<i>Metachirus nudicaudatus</i>
<i>Marmosa robinsoni</i>	<i>Hydrochaeris hydrochaeris</i>
<i>Cebus capucinus</i> ^b	<i>Coendou rothschildi</i>
<i>Aotus trivirgatus</i>	<i>Heteromys desmarestianus</i>
<i>Bradypus variegatus</i>	<i>Felis yagouaroundi</i>
<i>Choloepus hoffmanni</i>	<i>Eira barbara</i>
<i>Felis pardalis</i>	

^aSpecies found through the capture program or other observations.

^bwith *Cebus* monkeys were frequent, but I did not calculate an E.R. (see text).

Table 4 shows a comparison of ER of some selected genera between Gigante and BCI. The species composition is different in Gigante and BCI: more species are more abundant at BCI (block 1: 11 species) than species more abundant

at Gigante (block 3: 3 species). Also the total ER for diurnal mammals was 3.81 animals/km in Gigante, compared with 4.92 animals/km in BCI, or 1.29 times more encounters in BCI than in Gigante.

Table 4. Comparison of encounter rates (animals/km) for some selected genera in Gigante and BCI.

Genus	Gigante	BCI	Factor ^a	
<i>Tapirus</i>	0.000	0.006		
<i>Ateles</i>	0.000	present		
<i>Mazama</i>	0.000	0.276		
<i>Dasypus</i>	0.011	0.069	6.57	
<i>Tamandua</i>	0.015	0.089	5.90	
<i>Sciurus</i> ^b	1.063	2.500	2.35	Block 1
<i>Nasua</i>	0.098	0.223	2.27	
<i>Agouti</i>	0.327	0.690	2.11	
<i>Dasyprocta</i> ^b	1.333	2.750	2.07	
<i>Sylvilagus</i>	0.168	0.309	1.80	
<i>Tayassu</i>	0.065	0.098	1.50	
<i>Didelphis</i>	0.187	0.200		
<i>Caluromys</i>	0.056	0.049		Block 2
<i>Alouatta</i>	0.548	0.561		
<i>Potos</i> ^c	0.270	0.380		
<i>Proechimys</i>	0.907	0.504	1.81	
<i>Saguinus</i>	0.208	0.029	7.17	Block 3
<i>Odocoileus</i>	0.266	0.010	26.60	

^aRatio between both values (BCI and Gigante)

^bCorrected ER in Gigante (see text)

^cThese ER for Gigante and BCI are a combination of Potos and *Bassaricyon*

Block 1 = Species with ER 1.5 or more times higher at BCI

Block 2 = Species with similar ER in both places

Block 3 = Species with ER 1.5 or more times higher at Gig.1

A comparison of estimated densities and biomass for the major components of total biomass in Gigante and BCI is shown in Table 5. Unfortunately, I did not have an adequate method to estimate densities of sloths (*Bradypus* and *Choloepus*) and capuchin monkey (*Cebus*), which

are important components of total biomass in tropical moist forest (Eisenberg and Thorington 1973). Unit weights of each species were taken from Eisenberg and Thorington (1973), Eisenberg (1989) and my own data for *Dasyprocta* and *Proechimys*.

Table 5. Densities (animals/ha) and biomasses (kg/ha) for selected genera in Gigante and BCI.

GENUS	Weight ^a	Density Gigante	Biomass Gigante	Density BCI	Biomass BCI
<i>Agouti</i>	8.000	0.189	1.512	0.400	3.200
<i>Alouatta</i>	5.500	0.847	4.659	0.867	4.769
<i>Ateles</i>	5.000	0.000	0.000	0.010	0.050
<i>Bassaricyon</i>	1.300	0.028	0.036		
<i>Caluromys</i>	0.300	0.219	0.066	0.192	0.058
<i>Dasyprocta</i>	2.600	0.606	1.576	1.250	3.250
<i>Dasybus</i>	3.800	0.046	0.175	0.300	1.140
<i>Didelphis</i>	1.500	0.047	0.070	0.500	0.750
<i>Mazama</i>	29.000	0.000	0.000	0.019	0.551
<i>Nasua</i>	4.000	0.168	0.672	0.230	0.920
<i>Odocoileus</i>	40.000	0.170	6.800	0.006	0.240
<i>Potos</i>	2.500	0.112	0.280	0.190	0.475
<i>Proechimys</i>	0.400	3.599	1.440	2.000	0.800
<i>Saguinus</i>	0.500	0.191	0.096	0.025	0.013
<i>Sciurus</i>	0.300	0.765	0.230	1.800	0.540
<i>Sylvilagus</i>	0.800	0.112	0.090	0.064	0.051
<i>Tamandua</i>	4.000	0.011	0.044	0.050	0.200
<i>Tapirus</i>	180.000	0.000	0.000	0.006	1.080
<i>Tayassu</i>	20.000	0.062	1.240	0.089	1.780
TOTALS:	18.984	19.866			

^akg

^bReported density and biomass of *Potos* in BCI is really a mix of *Potos* and *Bassaricyon*

Encounter rates and densities for each species in Gigante

Marsupialia

For *Didelphis* and *Caluromys* I derived the density from BCI data using equation 1. The other marsupials present in Gigante are *Philander*, *Marmosa* and *Metachirus* (Table 3), but encounters with them during my nocturnal censuses were too infrequent to calculate ER and densities.

Primates

All species of monkeys were recorded as groups during my diurnal censuses, thus ER are given as groups/km. I assumed group sizes to be similar as those reported for BCI (Glanz 1982). Densities of howler (*Alouatta*) and tamarin (*Saguinus*) monkeys were derived from BCI data using equation 1. For capuchin monkeys (*Cebus*) I did not calculate ER or densities because groups of these monkeys moved very fast through the concentric census trails in Gigante, so the same group could be

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recorded several times during a census. Encounters with the nocturnal monkey *Aotus* were too rare to calculate ER or densities.

Edentata

Walking censuses are of little or no use to estimate densities of sloths, the diurnal *Bradypus* and nocturnal *Choloepus*, because they are so cryptic and motionless. Because the lesser anteater (*Tamandua*) and armadillo (*Dasybus*) are as easily detected during the day as during the night in Gigante, I used the total (day-night) distance walked to calculate ER. *Tamandua* is generally noisy when moving or foraging, and I unlikely underestimated its density by using Kelker's method. For *Dasybus*, I derived the density from BCI data using equation 1.

Lagomorpha

For the nocturnal cotton-tail rabbit (*Sylvilagus*), I used the Kelker's density estimate as a safe minimum.

Rodentia

For the agouti (*Dasyprocta*) and spiny rat (*Proechimys*) I used equation 1. The method used to calculate the corrected ER and densities in Gigante was already explained in the section of methods. Table 2 reports the observed ER while Table 4 reports the corrected ER for these two species. The density of the nocturnal paca (*Agouti*) was derived from BCI data using equation 1. For the other rodents reported in Table 3, I do not have adequate estimates in Gigante.

Carnivora

The method used to calculate indices and densities of coatis (*Nasua*) in Gigante was already explained in the section of methods. The figure reported in Table 2 for this species is a total ER, of which 60% corresponds to groups and 40% to singles. Because kinkajou (*Potos*) and olingo (*Bassaricyon*) are conspicuous nocturnal animals, Kelker's estimate was used. The other carnivores found, such as *Felis* spp. and *Eira*, live at densities too low to provide estimates.

Artiodactyla

Groups of collared peccaries (*Tayassu*) were seen more often at night than during the day, thus I computed the ER as groups/km using only nocturnal records. The density was derived from BCI data using equation 1. Encounters with groups were too few to calculate average group size, so I assumed it to be similar to BCI. White-tailed deer (*Odocoileus*) is seen more often by day than at night, thus I computed a diurnal ER. Density was calculated from BCI data using equation 1.

DISCUSSION

Three species present in BCI were not found in Gigante. They are tapir (*Tapirus*), brocket deer (*Mazama*) and spider monkey (*Ateles*). Spider monkeys have been reintroduced in BCI. *Tapirs* are big game mammals, they are shy and prefer undisturbed forest (Janzen 1983; Ochoa et al. 1988). The same applies to brocket deer (Branan et al. 1985). Previous human activities, including hunting, and the second growth type of vegetation, must be the best explanation for their absence in Gigante.

It has been noted that changes in the ecological complexity due to maturation of the forest, as well as the lack of large predators and hunting pressure, have promoted a steady raise of densities of several mammals in BCI in the last decades (Eisenberg et al. 1979; Glanz 1982; Emmons 1984). This could explain in part the higher densities in BCI of the species in block 1 (Table 4). Also most of the animals in this block are game species for local hunters: agouti (*Dasyprocta*), paca (*Agouti*), peccary (*Tayassu*), armadillo (*Dasybus*), rabbit (*Sylvilagus*), and coati (*Nasua*), while species in block 2 and 3 are not (except for *Odocoileus*).

The three species in block 3 are disturbed forest dwellers. Spiny rat (*Proechimys*) do better in closed understory typical of second growth forest (Emmons 1984). Tamarin monkeys (*Saguinus*) also prefer disturbed areas and plantations where they benefit from insects associated with crops (Moynihan 1970). And the white-tailed deer (*Odocoileus*), whose ER is 26.60 times higher at

Gigante, prefers open savanna or young forest (Brox 1984; Branan et al. 1985) In Gigante, I observed this deer frequently feeding on figs (*Ficus insipida*), which is a common species in young forest (Foster and Brokaw 1982) and is more abundant in Gigante than BCI (S. Williams, personal communication). Also, this deer is a big game species, but it has a high productivity (Eisenberg et al. 1979) and an excellent recovery potential in a suitable habitat (Leopold 1959) if overhunted, which may have been the case of Gigante before 1979. In BCI, the population of these three species (block 3) have declined probably due to the reduction of their suitable habitat (Eisenberg 1989).

These results could also support the theory of long-term changes, defined as the reduction in densities of some species together with the increase of others, which has been pointed out before (Glanz 1982, Eisenberg 1989), by looking to Gigante and BCI as the same type of biome at two different successional stages.

There are basic differences in biomass composition in both places (Table 5). The white-tailed deer (*Odocoileus*) has the highest biomass in Gigante (35% of the total biomass of selected species), while howler monkeys (*Alouatta*) are the most important in BCI. This agrees with Eisenberg et al. (1979) who state that the arboreal forms (sloths, monkeys) predominate in a mature forest like BCI, while terrestrial mammals predominate in second growth forest. However, howler monkeys were found to live at similar densities in BCI and Gigante. I think the abundance of fig trees in Gigante has favoured the presence of these monkeys. Also spiny rats (*Proechimys*) are more significant at Gigante, while pacas (*Agouti*) and agoutis (*Dasyprocta*) are more important in BCI.

This biomass comparison is partial (I am excluding sloths and capuchin monkeys), however, it is interesting to notice that although there are fewer species of large mammals, and densities in general are lower in Gigante, the total biomass of

selected species in both places are almost equal: 18.98 Kg/ha in Gigante and 19.86 Kg/ha in BCI. This is due to the higher contribution of white-tailed deer, whose biomass in Gigante is more than 4 times the combined biomass of tapir and brocket deer in BCI, two species that are absent in Gigante.

Although species richness is usually higher in a mature forest, due to its higher vertical complexity (August 1983; Eisenberg 1989), my results suggest that it is possible to attain high mammalian biomass in a disturbed young forest with some degree of protection. If properly managed, this biomass could be translated into productivity for human usage. More research is necessary to find out how productive a young forest could be.

The differences in mean detection distance between both study sites found for some common species, could be attributed to the more open understory in BCI, or the fact that animals are tamer in the island. Both reasons would provide better detectability in the island. More research is necessary in the development of adequate census methods for forest mammals. However, for most species I would recommend a combination of strip census with the appropriate correction for detectability. At least for some species, the mean detection distance seems to be useful as an indirect measure of detectability.

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