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INVENTORYING MAMMALS AT MULTIPLE SITES IN THE MAYA MOUNTAINS OF BELIZE

T. M. CARO,* M. J. KELLY, N. BOL, AND S. MATOLA

Department of Wildlife, Fish and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616 (TMC, MJK)
Las Cuevas Research Station, P.O. Box 410, Belmopan, Belize (NB)
The Belize Zoo, P.O. Box 1787, Belize City, Belize (SM)

Inventories of mammals in the Neotropics usually are derived from specimens recorded at a single site, about 25 km^2 in area, but this may not represent the diversity of the whole region. To illustrate this point, presence of 42 species of nonvolant mammals was recorded in the Chiquibul Forest Reserve, an area of subtropical wet forest in the Maya Mountains of western Belize. Data on diversity and abundance of mammals at that site were compared with 3 other sites in the Maya Mountains to determine how measurements varied with location of site. Of the nonvolant species, $<$33% were found at all 4 sites and $>$20% were found only at 1 site. Trapping success of researchers and densities of small mammals varied greatly between sites. Although number of species increased with research effort, the most extensively studied site did not encompass all mammalian diversity in the region. To obtain a representative mammalian inventory, effort should focus on sampling mammalian fauna at multiple sites, rather than increasing time at 1 site.

Key words: Belize, mammalian inventories, Neotropical diversity

Information on diversity and abundance of mammals in the Neotropics is central to understanding ecological processes (Fleming 1973), including population dynamics (O'Connell 1989), population demography (Torres-Contreras et al. 1997), and community structure of mammals (Asquith et al. 1997). Such information also is significant to conservation in that it can pinpoint areas of high diversity of mammals (Mares 1992) and help managers understand effects of habitat fragmentation (Lynam 1997; Malcolm 1997), selective logging (Eisenberg et al. 1979; Malcolm 1995), loss of top predators (Wright et al. 1994), and exploitation of mammalian fauna (Glanz 1991). Fortunately, the list of localities with data on diversity of species of mammals has increased considerably over the past decade and includes 10 well-studied localities (Voss and Emmons 1996). Data on abundance of mammals at these locations are less extensive. Comparative information from different locations is starting to give mammalogists the ability to make generalizations about patterns of mammalian diversity and to relate these patterns to gross ecological variables, such as elevation, rainfall, and vegetation (Gentry 1990; Voss and Emmons 1996).

As noted by Voss and Emmons (1996), data on abundance and diversity of mammals at a given locality usually are gathered at 1 localized site, about 25 km^2 in area. For logistic reasons such as proximity to a research camp, in many instances, data from each site are assumed to be representative of the protected area as a whole, or even of a whole region, especially in comparisons between geographic regions or countries (Eisenberg 1990; Emmons 1995;

* *Correspondent: tmcaro@ucdavis.edu*

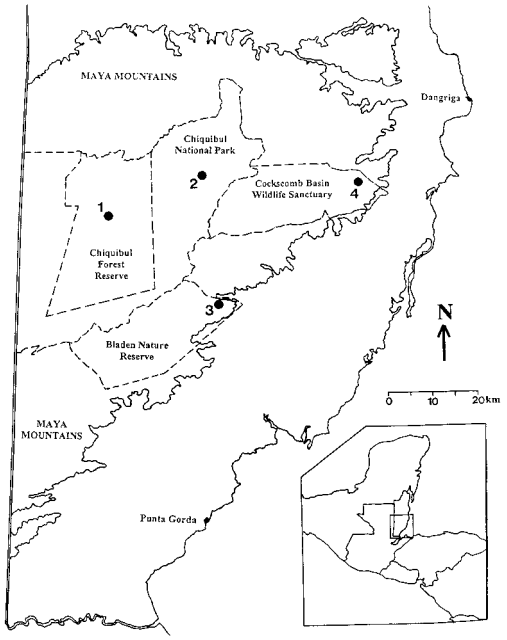

FIG. 1.—Location of the 4 study sites in the Maya Mountains of Belize. Continuous lines indicates the extent of the Maya Mountains, dashed lines denote boundaries of the 4 protected areas, and double lines show the international boundary. The coastal ports of Dangriga and Punta Gorda also are shown.

Voss and Emmons 1996). Unfortunately, sampling at what is effectively 1 place can lead to biases in data, including failure to record rare species or species with large home ranges that visit the research site infrequently, failure to observe species with specific habitat requirements that may be locally absent, and a reduced probability of noting competitively weak species that may only exist in heterogeneous habitats that are not present at the site.

We present information on diversity and abundance of mammals from 4 sites in the Maya Mountains of Belize to highlight how species diversity and densities of mammals change as different sites from the same ecosystem are included in a data set. Although these sites lie at varying elevations and have slightly different annual rainfall, they are close to each other (<55 km; Fig. 1), are situated in well-protected areas, and are all within a region widely regarded as a continuous ecosystem of lowland subtropical wet forest (Hartshorn et al. 1984). We present new information on diversity of mammals in Chiquibul Forest Reserve in western Belize and on abundance of small mammals from a recent trapping survey there. We compare this site with 3 other sites nearby; each of which might be taken as characterizing the Maya Mountains as a whole.

MATERIALS AND METHODS

The Chiquibul Forest Reserve, Cayo District, western Belize, is nested within the fully protected Chiquibul National Park (Fig. 1). The vegetation is a mosaic of deciduous semievergreen and deciduous seasonal forest with stands of pine (*Pinus*) in the northern sector (Wright et al. 1959). Some blocks of the Chiquibul Forest Reserve have been, and are still being, selectively logged for commercially important species such as mahogany (*Swietenia macrophylla*) and cedar (*Cedrela odorata*) on a >40-year rotational basis. Also, a large part of the Chiquibul Forest Reserve suffered losses of trees in Hurricane Hattie in 1961. Rainfall averages about 1,500 mm/year, with the rainy season starting in June and continuing through January. We prepared a list of medium-sized and large mammals based on observations made by N. Bol during 20 years (1979–1999) of working in and near the Chiquibul Forest Reserve, combined with information on small mammals caught by T. M. Caro and M. J. Kelly in live traps.

Small and medium-sized mammals were trapped <5 km from the Las Cuevas Research Station in the center of the Chiquibul Forest Reserve (1 in Fig. 1; 16°44′N, 88°59′W; elevation 500 m). Mammals were trapped in June and July 1999 at the onset of the rainy season but before heavy rains had begun. Small mammals were trapped using standard 23 by 8 by 8-cm Sherman traps or similar ones custom-made of galvanized wire mesh, except for a galvanized-aluminum plate door that was part of the floor until the door swung upward on closure (Emmons 1984). Traps were placed 15 m apart in a 7 by 7 grid and were set for 5 consecutive nights (Wilson et al. 1996). We set grids at 12 locations to obtain a representative sample of mammals

around Las Cuevas Research Station. Two grids were set <1 km from the station; 2 in each of 2 experimental plots that had been logged selectively for commercial hardwoods in 1995, and 2 in each of 2 adjacent control plots (Bird 1998; Mallory and Brokaw 1997); 6 in the 4 corners and midway along each long side of a 500 by 1,000-m (50-ha) forest population dynamics plot. Additionally, on the grid in the southwestern corner of this latter plot, we placed 49 medium-sized Tomahawk traps (40 by 13 by 13 cm or 40 by 17 by 17 cm) and 49 large Tomahawk traps (65 by 22.5 by 22.5 cm). We placed 1 trap from each of those categories alongside each custom-made small trap for 3 traps/station. We further rebaited 2 grids of custom-made small traps and the grid with 3 trap sizes a 2nd time, a week after the 1st round of trapping to sample a different phase of the moon at the same locations. That yielded 15 trapping sessions using small-trap grids (3,659 trapnights), 2 sessions using medium-sized Tomahawk traps (474 trapnights), and 2 sessions using large Tomahawk traps (474 trapnights). All traps were opened and baited with a piece of banana between 1530 and 1830 h and checked the next morning between 0600 and 0900 h. Captured mammals were identified with the works of Reid (1997) and Emmons and Freer (1990). To identify recaptures, small mammals were marked with numbered ear tags, and larger mammals (*Didelphis*) were marked with hair dye.

We calculated abundance of mammals by 3 measures: percent capture success (numbers of captures divided by number of trapnights); individual mammals caught per 100 trapnights (number of different individuals divided by number of trapnights × 100); densities of each species, calculated as number of different individuals divided by area covered by the grid (11,025 m^2) expressed as individuals per km^2. In each case, we present averages calculated across grids.

We compared identities of species found in 4 locations in the Maya Mountains and abundance of small mammals in 3 areas for which information was available. Those data came from the Cockscomb River Basin in the Cockscomb Basin Wildlife Sanctuary (Fig. 1) collected through sightings and trapping by Rabinowitz and Nottingham (1989) in 1983–1984 during 20 months. Data also came from the Raspaculo River Basin in the Chiquibul National Park collected by S. Matola through sightings during two 2-week expeditions in 1991 and 1993 (Rogers and Sutton 1991, 1994). Finally, data came from the Bladen Nature Reserve in 1994, 1995, 1997, and 1998 collected through sightings and trapping during 6 months (Caro et al., in press). Those 3 sites lay at similar low elevations of <600, 440, and 300 m, respectively. All received 1,500–3,000 mm of rain annually, with Bladen Nature Reserve receiving the most. In all cases, trapping was conducted from the end of the dry season to the beginning of the wet season.

RESULTS

By sight, 42 species of mammals were identified inside or near the Chiquibul Forest Reserve over a 20-year period (Table 1). The area was notable for the large number of carnivores. We captured 8 nonvolant species (*Marmosa mexicana, Philander opossum, Heteromys desmarestianus, H. gaumeri, Oryzomys couesi, O. alfaroi, Tylomys nudicaudus,* and *Ototylomys phyllotis*) with an average of 1.3 species/grid. Average percent capture success was 0.8% ± 0.6 *SD,* or 0.7 individuals/100 trapnights (n = 15 grids; 3,659 trapnights). Small traps yielded densities of 67, 6, 36, 6, 6, 12, 6, and 12/km^2, respectively, for the above species. With the middle-sized Tomahawk traps, we caught only 1 *H. desmarestianus* ($\bar{X}$ = 0.5 species/grid) with a trap success of 0.4% (n = 2 grids; 474 trapnights). With the large Tomahawk traps, we caught *Didelphis marsupialis* and *D. virginianus* ($\bar{X}$ = 1.0 species/grid) with an average trap success of 0.9% or 0.7 individuals/100 trapnights. Densities of those species were 91 and 45/km^2, respectively (n = 2 grids; 474 trapnights).

When species inventories from the 4 study sites in the Maya Mountains were collated (Table 1), 51 nonvolant mammals and 17 species of bats were found in the area. Number of chiropteran species in the Maya Mountains was underestimated because they only were trapped systematically in the Cockscomb Basin Wildlife Sanctuary.

Restricting analyses to nonvolant species,

TABLE 1.—Occurrence of mammals at 4 sites in Belize.

Order and species	Chiquibul Forest Reserve[a]	Raspaculo River Basin[b]	Bladen Nature Reserve	Cockscomb Basin Wildlife Sanctuary
Marsupialia				
Didelphis marsupialis	X		X	X
D. virginianus	X	X	X	
Chironectes minimus	X		X	X
Metachirus nudicaudatus	X			
Philander opossum	X	X	X	X
Micoureus alstoni	X		X	
Marmosa mexicana	X			X
M. robinsoni			X[c]	
Insectivora				
Cryptotis parva		X		
Xenarthra				
Tamandua mexicana	X		X	X
Dasypus novemcinctus	X	X	X	X
Cabassous centralis	X			
Chiroptera				
Rhynchonycteris naso		X		X
Balantiopteryx io			X	
Noctilio leporinus		X	X	X
Desmodus rotundus				X
Carollia perspicillata				X
C. brevicauda				X
Lonchorhina aurita				X
Glossophaga soricina				X
Sturnira lilium				X
Rhinophylla fischerae			X	
Artibeus lituratus				X
A. intermedius				X
A. phaeotis				X
A. watsoni				X
Thyroptera tricolor				X
Lasiurus ega				X
L. blossevillii				X
Primates				
Alouatta pigra	X	X	X	X
Ateles geoffroyi	X	X	X	
Rodentia				
Sciurus yucatanensis	X		X	X
S. variegatoides		X		
S. deppei	X	X	X	X
Orthogeomys heterodus	X			
O. hispidus		X		X
Heteromys desmarestianus	X		X	X
H. gaumeri	X			
Reithrodontomys gracilis				X
Oryzomys alfaroie	X			X
O. couesi	X	X	X	X
Sigmodon hispidus		X		X

TABLE 1.—Continued.

Order and species	Chiquibul Forest Reserve[a]	Raspaculo River Basin[b]	Bladen Nature Reserve	Cockscomb Basin Wildlife Sanctuary
Rodentia				
Tylomys nudicaudus	X		X	X
Ototylomys phyllotis	X		X	X
Nyctomys sumichrasti				X
Rattus rattus				X
Coendou mexicanus	X			X
Dasyprocta punctata	X	X	X	X
Agouti paca	X	X	X	X
Lagomorpha				
Sylvilagus brasiliensis	X			
Carnivora				
Urocyon cinereoargenteus	X		X	X
Nasua narica	X	X	X	X
Potos flavus	X		X	X
Mustela frenata	X		X	
Eira barbara	X	X	X	
Lutra longicaudus	X	X	X	X
Spilogale putorius	X			
Conepatus semistriatus			X	
Herpailurus yaguarondi	X			X
Puma concolor	X	X	X	X
Panthera onca	X	X	X	X
Leopardus wiedii	X			X
L pardalis	X	X	X[d]	X
Artiodactyla				
Tayassu tajacu	X	X	X	X
T. pecari	X		X	X
Tapirus bairdii	X	X	X	X
Mazama americana	X	X	X	X
Odocoileus virginianus	X		X	
Total number of species	42	22	33	35

[a] No attempt has yet been made to identify Chiroptera in Chiquibul Forest Reserve.
[b] No attempt was made to trap small mammals in the Raspaculo River Basin.
[c] Possibly *Marmosa mexicana.*
[d] Possibly *Leopardus wiedii.*

we found that number of species recorded increased with increasing time spent in the field (22 in 2 months in the Raspasculo River Basin, 33 in 6 months in the Bladen Nature Reserve, 35 in 20 months in the Cockscomb Basin Wildlife Sanctuary, and 42 in 20 years in the Chiquibul Forest Reserve). It is noteworthy that the site with the most recorded species, the Chiquibul Forest Reserve, contained only 82.4% of nonvolant species recorded for the Maya Mountains. Furthermore, a rather low percentage of species of mammals was recorded at all 4 sites (29.4%), and 21.6% were noted at 1 site only. Examining orders of mammals separately, it was clear that no site had all species of marsupials, rodents, or carnivores, suggesting that those taxa required inventorying at >1 site to obtain a complete picture of species diversity.

The most notable feature of trapping effort for small and medium-sized mammals

at the Chiquibul Forest Reserve, the Bladen Nature Reserve, and the Cockscomb Basin Wildlife Sanctuary was the difference in trapping success (Table 2). The Chiquibul Forest Reserve had a lower density than the other 2 sites for small traps and lower success than Bladen for large traps. That was reflected in low densities of small mammals in the Chiquibul Forest Reserve compared with the Bladen Nature Reserve and the Cockscomb Basin Wildlife Sanctuary, although the Chiquibul Forest Reserve had higher densities of *Didelphis.* The Cockscomb Basin Wildlife Sanctuary had lower densities of *Heteromys, Marmosa,* and *Oryzomys* than the Bladen Nature Reserve, but higher densities of *Tylomys* and *Ototylomys* combined.

Discussion

The Chiquibul Forest Reserve and its environs had a minimum of 42 species of nonvolant mammals. How does this number compare with other sites in the Neotropics? Because mammalian fauna of Central America is depauperate compared with South America, comparison with other Central American sites is most appropriate. Number of nonvolant species of mammals compares favorably with other intensively studied sites in Central America: 49 in Barro Colorado Island, Panama (Glanz 1991); 52 in La Selva, Costa Rica (Timm 1994; Voss and Emmons 1996); and 48 in Selva Lacondona, Chiapas, Mexico (Medellin 1994); sampled during 71, 34, and 10 years, respectively.

Trapping success around the Las Cuevas Research Station in the Chiquibul Forest Reserve (0.8%) was lower than at other sites in the Maya Mountains (Table 2) and other sites in Central America (e.g., the Gigante Peninsula, Panama, 4.2% for the wet and 7.3% for the dry season—McClearn et al. 1994). Because the number of trapnights was reasonably high, trapping was carried out during all phases of the moon, using banana bait that is known to be successful elsewhere (Caro et al., in press), and trapping was conducted during the onset of the rains when abundance of small mammals is high in the Maya Mountains (Rabinowitz and Nottingham 1989), analysis of our preliminary data suggests that this part of the Chiquibul Forest Reserve contains low densities of many species of small mammals. Nevertheless, rodents and marsupials were diverse, with 8 species captured (Table 2). We speculate that abundance of small mammals is low, but diversity is high. More data are needed to confirm this. As an aside, it is well documented that abundance of small mammals increases in selectively logged habitats in the tropics (Delany 1971; Malcolm 1995; Struhsaker 1997). Our findings suggest that effects of such logging may be lost within 25–40 years, which are, respectively, the times since Hurricane Hattie and selective logging was practiced in most of the area that we sampled.

Number and identity of species differed between sites in the Maya Mountains. For example, <33% of nonvolant species were found at all 4 sites, and about 20% were noted at 1 site only. These differences could result from differences in research effort, soils, vegetation, elevation, rainfall, or even the year in which sampling occurred (Bird 1998; Kelt et al. 1999; Rogers and Sutton 1994). Although there is no question that recorded diversity of species increased with time in the field, as found elsewhere (Voss and Emmons 1996), research effort did not seem to be the sole factor affecting diversity. We conclude this because, 1st, even the whole of Chiquibul Forest Reserve, which was sampled longer than any other site, contained only 82.4% of nonvolant mammals in the Maya Mountains. Second, diversity did not differ markedly between the 3 most intensively studied sites. Third, some species, such as the variegated squirrel (*Sciurus variegatoides*), were not found in the most-studied site but were found at other sites. We suspect that differences in topography, geology, and flora influenced whether certain small species, particularly rodents, were found in a given area. If so,

TABLE 2.—Percent trapping success and densities of species of mammals (per square kilometer) in 3 sites in the Maya Mountains, Belize; number of trapnights in parentheses.

	Chiquibul Forest Reserve[a] (3,659)	Bladen Nature Reserve[b] (4,236)	Cockscomb Basin Wildlife Sanctuary[c] (1,607)
Percent trapping success			
Small	0.8	6.5	5.2
Medium	0.4	0.7	
Large	0.9	4.3	
Density			
Marmosa mexicana	67		251
M. robinsoni		925	
Heteromys desmarestianus	37	6,836	1,004
H. gaumeri	6		
Tylomys nudicaudus	6	183	502[d]
Ototylomys phyllotis	12	270	
Oryzomys couesi	6	2,127	307[e]
O. alfaroi	12		
Sigmodon hispidus			167
Philander opossum	6		
Didelphis marsupialis	91	28	
D. virginianus	45	8	
Dasypus novemcinctus		2	

[a] Trapping in June and July.
[b] Trapping in March and June–August.
[c] Trapping in March–October.
[d] *Tylomys* and *Ototylomys* combined.
[e] Species of *Oryzomys* combined.

inventories of species based on extensive research restricted to the vicinity of a single research camp will not represent adequately the total list of species in the surrounding ecosystem.

Analysis of our data has demonstrated empirically that it is misleading to assume that data sampled at 1 site are representative inventories of Neotropical marsupials, rodents, and carnivores of an entire locality, as frequently is assumed in the literature. We advocate that research effort be geared toward sampling multiple sites, rather than simply increasing time spent at 1 site.

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