Mamm. biol. 66 (2001) 90–101
© Urban & Fischer Verlag
http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Diversity of mammals in the Bladen Nature Reserve, Belize, and factors affecting their trapping success

By T. M. Caro, Rachel Brock, and Marcella Kelly

Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California, USA

Receipt of Ms. 12. 11. 1999
Acceptance of Ms. 20. 04. 2000

Abstract

The presence of 33 non-volant mammal species was recorded in the Bladen Nature Reserve, an area of subtropical wet forest in south central Belize, as determined from walking transects and using Sherman and Tomahawk traps to capture mammals. Using trapgrids over 6 075 trapnights, the effects of trap design, bait, moon phase, logging, elevation, and proximity to a river on three measures of trapping success were examined systematically. Open wire mesh traps yielded somewhat higher trapping success than Sherman traps; oats and molasses produced higher trapping success than other kinds of bait; and trapping success was higher in selectively logged than in unlogged forest, and marginally higher at lower elevations and close to a river. Moon phase had no effect on trapping success. These results provide baseline data on mammal diversity in a relatively unexploited area of central America and, though preliminary, indicate which aspects of trapping technique need to be standardized when comparing species diversity and abundance across neotropical sites.

Key words: Mammals, trappability, diversity, Bladen, Belize

Introduction

Most ecological studies of neotropical mammals require data on species diversity and abundance. For example, questions about population dynamics (e.g., O'Connell 1989), population demography (e.g., Torres-Contrera et al. 1997), community structure (e.g., Asquith et al. 1997), and regions of mammal abundance (e.g., Mares 1992) all require information on the number of mammal species or their relative abundance in an area. Conservation studies similarly require data on diversity and abundance in order to understand the effects of habitat fragmentation (Lynam 1997; Malcolm 1997), loss of top predators (Wright et al. 1994; Terborgh et al. 1997), and mammal exploitation (Dirzo and Miranda 1991; Glanz 1991; Wright et al. 2000) on communities of mammals. In the neotropics data on mammal communities are growing (Voss and Emmons 1996) but they still come from only a handful of locations, the most notable of which are La Selva in Costa Rica (Timm 1994a), Los Tuxlas, Mexico (Estrada et al. 1994), Barro Colorado Island, Panama (Glanz 1990), Cosha Cashu, Peru (Janson and Emmons 1990) and near Manaus, Brazil (Malcolm 1990)

1616-5047/01/66/02-090 $ 15.00/0.

which limits our ability to make generalizations about how mammalian communities are organized.

As studies of mammals in the neotropics increase, and comparisons between areas become more feasible, researchers must standardize their techniques for estimating mammal abundance, or at least be aware of the biases inherent in different methods of mammal estimation (Wilson et al. 1996). We therefore investigated six different factors that influence trapping success outside the neotropics and might therefore be of importance elsewhere. Two of these were methodological factors (type of small mammal trap and characteristics of the bait) and four were ecological factors (phase of the moon, selective logging, elevation, and proximity to rivers).

Trap design can influence trapping success substantially in temperate regions (Sealander and James 1958) and this problem has been identified in at least one neotropical site (Woodman et al. 1996). We therefore compared measures of trapping success using hand-made wire mesh small mammal traps which could be seen through with standard Sherman traps which obscure visibility. It is also well known that baits can affect trapping success in temperate zones (e.g., Buchalczyk and Olszewski 1971). Although far less work has been carried out on this problem in the neotropics, preliminary evidence suggests that bait is not an important factor in mammal trapping (Woodman et al. 1996). Increased moonlight lowers trapping success in open habitats in temperate regions (Brown et al. 1988) because small mammals often show changes in activity in accordance with a reduction of predation risk from visually hunting aerial and terrestrial predators (Clarke 1983). Although moonlight is known to influence activity patterns of some tropical mammals (Fenton et al. 1977; Emmons 1987; Alkon and Saltz 1988), it has received little systematic attention in small neotropical mammal trapping studies. Selective logging has many influences on mammal community structure in tropical environments with arboreal mammal densities being lower (Eisenberg et al. 1979) and small mammal abundance being higher in logged sites (Kasenene 1984; Isabiyre-Basuta and Kasenene 1987; Malcolm 1995). Increased elevation has been found to change species diversity in some areas of the tropics (Rickart et al. 1991) while proximity to seasonally flooded areas close to rivers may alter species diversity and abundance in complex ways (Janson and Emmons 1990). Therefore the aim of this study is to investigate the diversity of species at a new site in the neotropics and to analyse factors affecting trapping success in this environment.

Material and methods

The study was conducted in and adjacent to the Bladen Nature Reserve in the Maya Mountains, Toledo District, Belize (Fig. 1). The reserve encompasses 350 km^2 of the watershed of the Bladen River between latitudes 16°36′18″ and 16°24′34″ N and longitudes 88°42′16″ and 89°04′51″ W. Elevation ranges from 50 to 1 000 m. Rainfall averages around 3 000 mm per annum or more; January to April are the driest months with rain starting from June onwards through November. Mean monthly temperatures range from 16 ° to 33 °C in Belize. Much of the reserve is composed of Coban formation limestone and volcanic rock. The reserve contains subtropical wet forest (Hartshorn et al. 1984) with the lowest parts, along the main flow of the river where we worked, supporting alluvial soils and tall broad-leaved forest. Most of the Bladen Nature Reserve is unlogged; selective logging has been practiced immediately outside its eastern border, however. The reserve is subject to unknown hunting pressure by local people for game meat.

The study was conducted during four periods of fieldwork: June and July 1994, June through August 1995, March 1997 and July 1998. Some rain fell in each of these periods but trapping was suspended under extremely wet conditions because we were concerned about hypothermia of captured individuals. All the work was conducted adjacent to the eastern entrance of the reserve, 1–3 km inside, and 0.5 km outside it.

Mammal diversity was assessed in three ways: through night and daytime walks in which observations and calls of mammals were noted, by in-

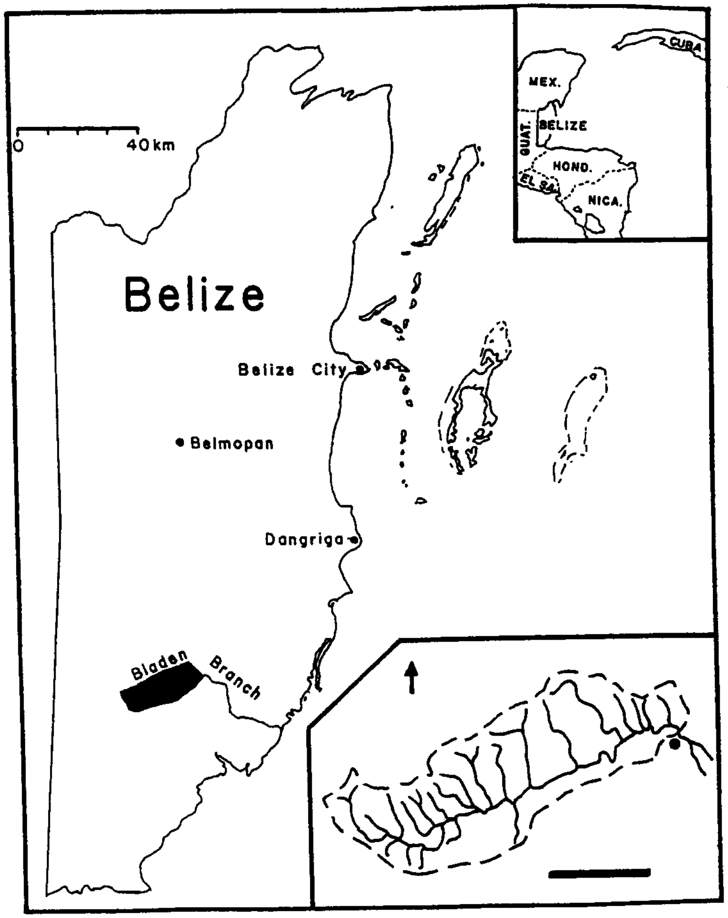

Fig. 1. Belize and the location of Bladen Nature Reserve (in black) in the country. Top right inset shows location of Belize in central America. Bottom right inset shows the boundary of Bladen Nature Reserve (dashed line) and the Bladen Branch River and its tributaries (solid lines). The entrance to the reserve is at Forest Hill shown as a black dot. Three 2 km transects were located (i) just inside the reserve boundary running south west to north east terminating at Forest Hill; (ii) between Forest Hill and the Richardson Creek (fifth tributary upstream from the entrance) confluence south and parallel to the Bladen River; (iii) and outside the reserve from and due north east of Forest Hill. All trapgrids within the reserve were set south of the Bladen River between Forest Hill and the second tributary upstream from the entrance. Trapgrids outside the reserve were set within 500 m of the reserve entrance. Black bar denotes 10 km; arrow shows north (adapted from Hartshorn et al. 1994).

terpreting mammal tracks in the mud, and through live trapping. Abundances of certain mammal species were estimated through repeat trapping using standard Sherman, custom-made small mammal traps, and three sizes of Tomahawk traps. We used the field guide of Emmons (1990) to identify mammals in the field. Two previous mammal surveys had been conducted in the Bladen (Brokaw and Lloyd-Evans 1987; The Nature Conservancy 1993).

We set up three 2 km transects that were walked at a pace of 1 km/hour. One was located within the reserve and followed an abandoned logging track that serves as the main road into the reserve; the second was further inside the reserve on the south side and parallel to the Bladen River; the third was located adjacent to but outside the Reserve in a selectively logged area. Night walks (N = 18) were conducted between 18.30 and 21.00 h and animals were spotted using flashlights; day walks (N = 28) took place between 05.30 and 07.30 h. Tracks of mammals were examined opportunistically and in specially prepared flats of mud, at the center at which was placed a commercial carnivore olfactory lure.

Small mammals were trapped using standard Sherman traps (23×8×8 cm), or traps of the same dimensions custom-made entirely out of galvanized wire mesh (by the late R. Schwab) save for a galvanized aluminum plate door that was part of the floor until the door swung upwards on closure (see also Emmons 1984). Traps were usually set in an 8×8 or 7×7 grid with traps 10 m apart; infrequently they were set along a transect precluding calculation of density. Grids of small mammal traps were baited either with a mixture of oats and molasses, with peanut butter, with green or ripe bananas, or with a medley of fruit consisting of apple, banana, and coconut mixed together. Ripe and green bananas were lumped together in bait analyses because green bananas quickly ripened in traps making it difficult to distinguish between the two. Traps were usually set on the flat valley floor of the reserve approximately 20–200 m from the Bladen River bank. In another protocol, trapgrids were set at higher elevations on the steep limestone slope bordering the floodplain approximately 50 and 100 m above the valley floor and 200–250 m from the river.

We set two types of Tomahawk traps (40×13×13 cm and 40×17×17 cm) which we termed middle-sized traps. These were usually set in a 6×8 grid with traps 50 m apart. Traps were baited either with oats and molasses, with green or ripe bananas, raisins, or a fruit found on the forest floor, Warre Cohune palm, *Astrocarynm mexicanum*. These traps were set approximately 50–450 m from the river. In one set of tests these traps were placed at a height of 1–2.5 m in trees and baited with oats and molasses in order to estimate squirrel abundance.

We also set large Tomahawk traps (65×22.5×22.5 cm) in a 6×8 grid with traps set 50 m apart. These were baited with either green or ripe bananas, *Astrocarynm mexicanum* fruit, commercial cat food or fresh fish; these latter two baits were combined in bait analyses since they both contained animal protein and smelled similar. In none of the trapping protocols were different baits run at the same time on either the same or different grids.

Traps were usually set for 5 consecutive nights although a small minority was set for fewer or more nights (range 1–7). Traps were set either in unlogged forest with a tall thick canopy and relatively open understory inside Bladen Nature Reserve, or in the area east of the reserve where selective logging allowed light to penetrate, producing a thicker understory of vegetation. Traps were opened and baited between 16.00 and 17.00 h and checked next morning between 06.00 and 09.00 h. Captured animals were individually marked by cutting small patches of fur since we were only interested in recaptures over a maximum of 7 days. Quarter of the moon was noted during each sequence of trapping; in some analyses traps set during the first and last quarter spanning the new moon, and then the second and third quarters spanning the full moon were combined.

We recorded number of species caught, percentage capture success, individual mammals caught/100 trapnights, and densities when traps were set in a grid square. Percentage capture success was the number of captures divided by the number of trapnights (i.e., number of traps multiplied by the number of nights on which they were set); individual mammals caught per 100 trapnights was the number of different individuals captured divided by the number of trapnights × 100; and densities were calculated by dividing the number of individuals captured by the area covered by the grid expressed as number of individuals/km^2. We took this area to be the dimensions of the grid plus 5 m either side (i.e., 70 m×70 m or 4900 m^2 in a 7×7 grid) because paucity of captures made it difficult to calculate maximum distance between captures of known individuals. We did not use mark-recapture techniques to estimate density because recapture rates were so low.

Data were analysed by comparing trapgrids although the number of trapnights that these represented is also presented for clarity. Non-parametric statistics were used as number of species was an ordinal measure, and captures/trapnight and individual mammals caught/100 trapnights produced too many zeroes (no captures) to justify normalizing the data required for parametric statistics. The use of non-parametric statistics made it difficult to control for confounding variables; instead we conducted a series of carefully controlled comparisons among grids by excluding variables that were found to be important in previous analyses even though these resulted in a reduction in sample sizes. α was set at 0.05; nevertheless p values lying between 0.1 and 0.05 are noted and discussed with appropriate caution.

Results

Captures

In this study, twenty eight species of non-volant mammals were identified inside and outside but within 0.5 km of the Bladen Nature Reserve, although two of these were equivocal identifications (Tab. 1). In our study all of these species except five, *Philander opossum*, *Urocyon cinereoargenteus*, *Conepatus semistriatus*, *Leopardus* sp., and *Panthera onca* were found inside the reserve; in a previous study conducted by the Rapid Ecological Assessment Team in 1993 a jaguar and a small felid had been identified inside Bladen (The Nature Conservancy 1993). Our results, combined with those of the two earlier surveys (Tab. 1), show that the Bladen area holds a minimum of 33 non-volant species including large predators such as *Felis concolor* and *Panthera onca*.

Employing small mammal traps, we captured five non-volant species, *Heteromys desmarestianus*, *Ototylomys phyllotis*, *Tylomys nudicaudus*, *Marmosa robinsoni*, *Oryzomys couesi* and an unknown species of bat with an average percentage capture success of 6.5% (sd ± 5.9), or 5.6 individuals/100 trapnights (sd ± 5.6) (n = 26 grids; 4236 trapnights). These traps yielded respective densities of 6836/km^2, 270/km^2, 183/km^2, 925/km^2 and 2127/km^2 for the five non-volant species (n = 18 grids; 3521 trapnights). With the middle-sized Tomahawk traps, we caught only two species, *Ototylomys phyllotis* and *Tylomys nudicaudas*. Trap success was low at 0.7% (sd ± 1.0), or 0.6 individuals/100 trapnights (sd ± 0.8) (n = 9 grids; 1354 trapnights). Density of these two species was 2/km^2 and 10/km^2, respectively (n = 5 grids; 1200 trapnights). With the large Tomahawk traps, we caught *Didelphis marsupialis*, *Didelphis virginianus*, *Dasypus novemcintus* and a *Tylomys nudicaudus* giving an average percentage trap success of 4.3% (sd ± 4.3), or 3.9 individuals/100 trapnights (sd ± 3.9) (n = 9 grids; 1218 trapnights). Density of these species was 28/km^2, 8/km^2, 2/km^2, and 2/km^2, respectively (n = 5 grids; 1152 trapnights). Excluding bats, we calculated a Shannon-Wiener index of 2.021.

Factors affecting trapping success

Type of trap: Compared to standard Sherman traps, custom-made wire mesh traps of the same dimensions caught marginally more terrestrial mammal species (n = 6; 20 grids, respectively; 618, 3618 trapnights, Means ($\bar{X}$s) = 1.0 (sd ± 0.9), 2.1 (sd ± 1.4) species, Mann-Whitney U test, z = –1.763, P = 0.078), demonstrated marginally higher percentage capture success ($\bar{X}$s = 2.2% (sd ± 3.0), 7.7% (sd ± 6.1) respectively, z = –1.951, P = 0.051), and caught a marginally greater number of individuals per trapnight ($\bar{X}$s = 2 (sd ± 3), 7 (sd ± 6) individuals/100 trapnights respectively, z = –1.830, P = 0.067).

Type of bait: For small mammal traps, there were significant differences in the number of species caught (n = 26 grids; 4236 trapnights, Kruskal-Wallis test, H = 11.444, P = 0.01), percentage trap success (H = 8.464, P = 0.037), and individuals captured/100 trapnights (H = 7.888, P = 0.048) depending upon the type of bait offered. On each measure, oats and molasses were most successful followed by green and ripe bananas combined, and then the fruit medley (Tab. 2). There were no significant differences between baits on measures of density,

Table 1. List of species of mammals in and immediately adjacent to Bladen Nature Reserve. 1994–1998 this study: Tp: trapped; O: observed; Tr: tracks; H: heard; I/O: inside or outside Bladen Nature Reserve. 1. refers to species noted by the 1993 Rapid Ecological Assessment Team (The Nature Conservancy 1993); 2. refers to species noted by the 1987 Manomet survey (Brokaw and Lloyd-Evans 1987). * species may have been *Marmosa mexicana*; + species may have been *Leopardus wiedii* (Margay).

Scientific name	Common name	Tp	O	Tr	H	I/O
Marsupilia						
Didelphis marsupialis	Common opossum	X				I
Didelphis virginianus 2	Virginia opossum	X				I
Philander opossum	Common gray four-eyed opossum		X			O
Chironectes minimus 1	Water opossum		X			I
Micoureus alstoni 1	Alston's wolly mouse opossum					
*Marmosa robinsoni**	Robinson's mouse opossum	X				I/O
Xenarthra						
Tamandua mexicana	Northern tamandua		X			I
Dasypus novemcinctus	Nine-banded long-nosed armadillo	X				I/O
Chiroptera						
Balaniopteryx io 1	Least sac-winged bat					
Noctilio leporinus	Greater fishing bat		X			I
?	Unidentified species	X				I
Primates						
Alouatta pigra 1	Mexican black howler monkey				X	I/O
Ateles geoffroyi 1, 2	Central American spider monkey		X			I
Carnivora						
Urocyon cinereoargenteus	Gray fox		X			O
Nasua narica 1	White-nosed coati				X	I
Potos flavus	Kinkajou		X			I
Mustela frenata 1	Long-tailed weasel					
Eira barbara 2	Tayra		X			I
Conepatus semistriatus	Striped hog-nosed skunk		X			O
Lontra longicaudus 2	Neotropical otter		X			I
Leopardus pardalis + 1	Ocelot			X		O
Puma concolor 2	Puma			X		I/O
Panthera onca 1	Jaguar			X		O
Perissodactyla						
Tapirus bairdii 1, 2	Baird's tapir			X		I/O
Artiodactyla						
Tayassu tajacu 1	Collared peccary					
Tayassu pecari 1, 2	White-lipped peccary				X	I/O
Mazama americana 1, 2	Red brocked deer		X			I/O
Odocoileus virginianus 1, 2	White-tailed deer					
Rodentia						
Sciurus yucatanensis	Yucatan squirrel	X				I
Sciurus deppei 1, 2	Deppe's squirrel		X			I
Heteromys desmarestianus	Forest spiny pocket mouse	X				I/O
Oryzomys couesi	Coues' rice rat	X				I/O
Tylomys nudicaudus 1	Naked-tailed climbing rat	X				I/O
Ototylomys phyllotis	Big-eared climbing rat	X				I/O
Agouti paca 1, 2	Paca			X		I/O
Dasyprocta punctata 1, 2	Central American agouti					

Table 2. Mean ($\bar{X}$) and standard deviation (sd) measures of trapping success in all small mammal traps separated by type of bait; round brackets refer to numbers of trapgrids or traplines, square brackets to the number of trapnights.

		Oats and molasses	Peanut butter	Bananas	Fruit medley
		(7) [1973]	(3) [502]	(14) [1461]	(2) [300]
Number of species	$\bar{X}$	3.1	0.7	1.6	1.0
	sd	0.9	0.6	1.2	1.4
Percentage trap success	$\bar{X}$	10.3	0.6	6.6	1.0
	sd	1.0	0.6	6.8	1.4
Individuals/100 trapnights	$\bar{X}$	7.5	0.6	6.5	0.4
	sd	1.3	0.6	6.8	0.6
		(7) [1973]	(1) [245]	(10) [1303]	
Individuals/km²	$\bar{X}$	8600	6100	12200	–*
	sd	14300	0	12400	

* traps were set in a line, rather than grid, so estimates of density are unavailable.

however. When analyses were restricted only to small mammal wire mesh traps, the number of species captured still differed significantly by type of bait (n = 20 grids; 3618 trapnights, H = 7.792, P = 0.02) although this was no longer the case for measures of percentage trap success and individuals/100 trapnights. There were no effects of bait for any measure in the medium-sized or large traps.

Moon phase: Considering either small, medium-sized or large traps, there was no effect of moon phase on number of species captured, percentage capture success, number of individuals caught/100 trapnights, or density either when quarters were analyzed separately or when quarters respectively spanning the new and full moons were combined.

Selective logging: Somewhat more individual mammals were captured in logged forest than in unlogged forest using small mammal traps (n = 11,15 grids, respectively; 956, 3280 trapnights, n = 8 (sd ± 7), 4 (sd ± 4) per 100 trapnights, Mann-Whitney U test, z = 1,664, P = 0.096) but there were no significant differences on the three other measures. Restricting analyses to the custom-made traps that were somewhat more effective in catching small mammals, we found that percentage capture success and individuals/trapnight were significantly greater in logged forest outside Bladen than in unlogged forest inside (n = 7,13 grids, respectively; 741, 2877 trapnights, $\bar{X}$s = 12.2% (sd ± 5.4), 5.3% (sd ± 5.1), z = 2.260, P = 0.024; $\bar{X}$s = 12 (sd ± 4), 4/100 trapnights (sd ± 6), z = 2.539, P = 0.011). In the Tomahawk traps, a slightly greater number of species was captured in the unlogged than in the logged forest in the medium-sized (n = 7,2 grids, respectively; 1312, 42 trapnights, $\bar{X}$s = 0.7 (sd ± 0.5), 0 (sd ± 0) species, z = 1.690, P = 0.091) and in the large traps (n = 7,2 grids, respectively; 1200, 18 trapnights, $\bar{X}$s = 2.0 (sd ± 1.0), 0.5 (sd ± 0.7) species, z = 1.869, P = 0.062).

Elevation: We obtained a marginally greater number of species, percentage capture success and number of individuals/100 trapnights on the valley floor than at higher elevations on the slope above the Bladen River (n = 24,2 grids, respectively; 3876, 360 trapnights, $\bar{X}$s = 2.0 (sd ± 1.3), 0.5 (sd ± 0.7) species, Mann-Whitney U test, z = 1.642, P = 0.1; $\bar{X}$s = 0.7% (sd ± 0.6), 0.3% (sd ± 0.4), z = 1.832, P = 0.067; $\bar{X}$s = 6.1 (sd ± 5.6), 0.3 (sd ± 0.4), z = 1.832, P = 0.067). Two of these three results still held after analyses were restricted to custom-made small mammal traps placed in unlogged areas only (n = 11 low and 2 higher elevation grids; 3258, 360 trapnights, $\bar{X}$s = 2.4 (sd ± 1.6), 0.5 (sd ± 0.7) species respectively, z = 1.610, P = 0.107; $\bar{X}$s = 6.3% (sd ± 5.0), 0.3% (sd ± 0.4) respectively, z = 1.781, P = 0.075; $\bar{X}$s = 4.7 (sd ± 3.5), 0.3/100 trapnights (sd ± 0.4) respectively, z = 1.781, P = 0.075). Tomahawk traps were not placed above the valley floor.

Proximity to the river: Finally, we compared traps Set within < 50 m of the river bank with those placed further away (50–200 m). Results showed that the number of species captured was marginally higher close to the river than further away from it (n = 11,11 grids, respectively; 2239, 1349 trapnights, $\bar{X}$s = 2.4 (sd ± 1.6), 1.2 (sd ± 0.9) species, Mann-Whitney U test, z = 1.793, P = 0.073) but there was no effect on percentage trap success or individuals/100 trapnights. When analyses were restricted to custom-made traps set on the valley floor in unlogged areas, however, proximity to the river resulted in greater numbers of mammals caught on all three measures (n = 8,3 grids next to and away from the river, respectively; 2103, 414 trapnights, $\bar{X}$s = 2.9 (sd ± 1.5), 1.0 (sd ± 1.0) species, z = 1.763, P = 0.078; $\bar{X}$s = 7.9% (sd ± 4.6), 1.9% (sd ± 2.8) trap success respectively, z = 2.041, P = 0.041; $\bar{X}$s = 5.7 (sd ± 3.2), 1.9 individuals/100 trapnights (sd ± 2.8) respectively, z = 1.837, P = 0.066).

Discussion

Captures

Bladen Nature Reserve and land immediately adjacent to it held a minimum of 33 species of non-volant mammals which is comparable to other central American sites. Rabinowitz and Nottingham (1989) documented 39 species of non-volant mammals in the Cockscomb basin which is almost adjacent to the Bladen; Medellin (1994) reported 48 species in Selva Lacondona, Chiapas, Mexico but these were compiled over 10 years as opposed to our 6 month total period; Timm (1994b) documented 50 species for La Selva in Costa Rica over 20 years; and Glanz (1990) reported 39 species on Barro Colorado Island, Panama, which had been studied for 13 years at the time.

Small mammal trapping success in Bladen (6.5%) was comparable to that in other neotropical wet forests such as Cockscomb. For example, trapping success in the Gigante Peninsula, Panama was 4.2% for the wet and 7.3% for the dry season (McClearn et al. 1994). In contrast to measures of mammal diversity, it is difficult to make many direct comparisons of species' densities with other sites as data for many of the same species are unavailable. *Didelphis* and *Dasypus* densities appeared low compared to Barro Colorado Island and south American sites (Glanz 1990), whereas *Marmosa* densities were higher than either at Barro Colorado or even Guatopo, Venezuela (Eisenberg et al. 1979). *Oryzomys* densities were extremely high in comparison to Barro Colorado, Guatopo, Cosha Cashu and Cabassou, French Guiana (Charles-Dominique et al. 1981; Glanz 1990) possibly because some traps were set in selectively logged habitats.

Factors affecting trapping success

There is a substantial literature on the effects of trap type on trapping success in temperate regions (e.g., Sealander and James 1958; Slade et al. 1993). The few studies that have been conducted in the neotropics have compared live traps to snap traps and found the latter to catch more species and individuals (Pizzimenti 1979; Woodman et al. 1996). The only studies to compare wire mesh and Sherman traps were conducted in temperate climates (Holdenreid 1954; O'Farrell et al. 1994). In both cases a greater proportion of captures was made using wire mesh traps and heteromyid rodents in particular were captured in mesh traps. O'Farrell et al. (1994) found that custom-made wire mesh traps captured two to three times more individuals than Sherman traps. Our results from the neotropics replicated these findings in that they showed marginally greater percentage success and individuals caught/100 trapnights in mesh traps. Clearly, comparisons of small mammal densities in the neotropics must take into account of whether traps are of mesh or box design.

There is also a considerable literature on the effects of baits on trap success but again mostly from temperate regions (e.g., Beer 1964; Slade et al. 1993; but see Laurance 1992) and it is well known that rolled oats and peanut butter is a very effective bait in capturing terrestrial mammals in this part of the world. Although very few comparisons have been reported for the neotropics, Woodman et al. (1996) found no differences in captures using suet or peanut butter in tropical forest in south-eastern Peru. In contrast, we found that oats and molasses caught more species, generated greater trap success, and captured more individuals/100 trapnights than other baits, with peanut butter producing poorest results. In addition, there are many other baits that include animal protein that we did not use. It therefore appears premature to suggest that bait has little influence on trapping in the neotropics.

In contrast to many studies in deserts of North America (e.g., Price et al. 1984), phase of the moon had no effect on measures of trapping in this study. Possibly, the thick canopy obscured the moon to such an extent that little light penetrated to the forest floor.

It is well documented that small mammal abundance is greater in selectively logged habitats in temperate regions (e.g., Monthey and Southiere 1995) as well as in the tropics (Delany 1971; Struhsaker 1997). For example, Malcolm (1995) showed that terrestrial mammal abundance, richness and diversity were all greater in pasture and young secondary forest than in continuous forest north of Manaus. Our results are consistent with his findings in that percentage success and number of individuals captured was greater in areas that had been logged outside the reserve than inside it. In addition, we caught a greater variety of species, principally marsupials, outside the reserve. There may be many reasons for these associations including a more abundant and predictable insect prey base (Malcolm 1995), increased seed abundance stemming from increased vertical vegetation density (Monadjem 1997), or even reduced threat of predation (da Fonesca and Robinson 1990) but these were not investigated.

Studies that have looked into the effects of elevation on small mammals have often found different results. For example, abundance increased with elevation in a tropical rainforest in the Philippines but species richness did not change (Heaney et al. 1989). In contrast, in a temperate rainforest in Chile, number of species, number of individuals, and species diversity all declined with increased elevation (Patterson et al. 1989). We found a marginally reduced number of species, trapping success, and number of individuals at higher elevations although trapping effort was relatively low off the valley floor. In addition, we caught a somewhat greater number of species, had somewhat greater success, and captured somewhat more individuals per trapnight near the river than farther from it. Taking these two results together, there appeared to be a gradient of decreasing small mammal diversity and abundance as one progressed away from the Bladen River and up the slope. Whether these findings reflect differences in humidity, soil drainage or type, or habitat structure remains unresolved.

Our findings are necessarily preliminary because we chose to examine a large number of factors which reduced our sample size. Nevertheless, they highlight the importance of carefully selecting the type of trap and type of bait in trapping studies of neotropical mammals. They also point to the differences that may be expected in estimating mammal abundance and diversity in areas with different logging regimes, elevations and proximity to rivers in neotropical habitats. As such, they reinforce the necessity of standardizing techniques when comparing species abundance and diversity across neotropical sites.

Acknowledgements

We thank The Forestry Department and Belize Audubon Society for permission to work in the Bladen Nature Reserve and Raphael Manzanero and John Pinello for important assistance. We thank Jake and Kelly Marlin for permission to work in the Belize Foundation for Research and Environmental Education (BFREE). This work was supported by two University of California faculty research grants and a President's undergraduate fellowship as well as funding from San Francisco State University. Work was conducted under UC Davis Animal Care and Use Protocols. We thank Deirdre Doherty, Dave Drouillard, Chris Gregory, Beth Johnstone, Tom McNamara, Jeremy Mull, Megan Templeton, and Susan Woofsy for logistical help in the field; Ron Cole, Jake and Kelly Marlin, and Dirk Van Vuren for loaning and storing equipment; Steven Brewer, Doug Kelt, Marcel Rejmanek, and Dirk Van Vuren for discussions; and Sabine Schmid-Holmes for translating the summary into German.

Zusammenfassung

Diversität von Säugern im Bladen Naturreservat, Belize, und Faktoren, die einen Fangerfolg beeinflussen

Im Bladen Naturreservat, einem subtropischen Feuchtwaldgebiet, wurde durch Zählungen an Transekten und unter Einsatz von Sherman- und Tomahawk-Lebendfallen das Vorkommen von 33 Säugetierarten festgestellt. In insgesamt 6 075 Fallennächten wurden Einfluß von Fallendesign, Köder, Mondphase, Holzeinschlag, Höhenlage und Nähe eines Flusses auf Fangerfolg systematisch untersucht. Drahtgitterfallen hatten etwas größeren Fangerfolg als Sherman-Fallen, Haferflocken und Molasse erzielten größeren Fangerfolg als andere Köder, Fangerfolg in Wald mit selektivem Holzeinschlag war größer als in Wald ohne Einschlag und er war etwas größer in höher gelegenen Gebieten und näher an einem Fluß. Die Mondphase hatte keinen Einfluß auf Fangerfolg. Die Resultate liefern Basisdaten über die Säugetiervielfalt in einem relativ unerforschten Gebiet Zentralamerikas und geben an, wenn auch nur vorläufig, welche Aspekte im Fangdesign standardisiert werden sollten, um einen Vergleich der Artenvielfalt zwischen verschiedenen neotropischen Studiengebieten zu ermöglichen.

References

Alkon, P. U.; Saltz, D. (1988): Influence of season and moonlight on temporal activity patterns of Indian crested porcupines (*Hystrix indica* Kerr). J. Mammalogy 69, 71–81.

Asquith, N. M.; Wright, S. J.; Clauss, M. J. (1997): Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78, 941–946.

Beer, J. R. (1964): Bait preferences of some small mammals. J. Mammalogy 45, 632–634.

Brokaw, N. V. L.; Lloyd-Evans, T. L. (1987): The Bladen Branch wilderness. Manomet Bird Observatory, Mass.

Brown, J. S.; Kotler, B. P.; Smith, R. J.; Wirtz, II, W. O. (1988): The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76, 408–415.

Buchalczyk, T.; Olszewski, J. L. (1971): Behavioural response of forest rodents against trap and bait. Acta Theriol. 18, 277–292.

Charles-Dominique, P.; Atramentowicz, M.; Charles-Dominique, M.; Gerard, H.; Hladik, A.; Hladik, C. M.; Prevost, M. F. (1981): Les mammiferes frugivores arboricoles nocturnes d'une foret guyanaise: inter-relations plantes-animaux. Revue Ecologie (Terre et Vie) 35, 341–435.

Clarke, J. A. (1983): Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behav. Ecol. and Sociobiol. 13, 205–209.

Delany, M. J. (1971): The biology of small rodents in Mayanja forest, Uganda. J. Zool. (London) 165, 85–129.

Dirzo, R.; Miranda, A. (1991): Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: Plant-Animal Interactions: Evolutionary

Ecology in Tropical and Temperate Regions. Ed. by P. W. Price, T. M. Lewinsohn, G. W. Fernandez, and W. W. Benson. New York: John Wiley and Sons. Pp. 273–287.

Eisenberg, J. F.; O'Connell, M.; August, P. V. (1979): Density, productivity, and distribution of mammals in two Venezuelan habitats. In: Vertebrate Ecology in the Northern Neotropics. Ed. by J. F. Eisenberg. Washington, DC: Smithsonian Institution Press. Pp. 187–207.

Emmons, L. H. (1984): Geographic variation in densities and diversities of non-flying mammals in Amazonia. Biotropica 16, 210–222.

Emmons, L. H. (1987): Comparative feeding ecology of felids in a neotropical forest. Behav. Ecol. and Sociobiol. 20, 271–283.

Emmons, L. H. (1990): Neotropical Rainforest Mammals: a Field Guide. Chicago: Univ. Chicago Press.

Estrada, A.; Coates-Estrada, R.; Meritt Jr, D. (1994): Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxlas, Mexico. Ecogeography 17, 229–241.

Fenton, M. B.; Boyle, N. G. H.; Harrison, T. M.; Oxley, D. J. (1977): Activity patterns, habitat use, and prey selection by some African insectivorous bats. Biotropica 9, 73–85.

Fonesca, G. A. B. da; Robinson, J. G. (1990): Forest size and structure: competitive and predatory effects on small mammal communities. Biol. Conserv. 53, 265–294.

Fleming, T. H. (1973): The number of rodent species in two Costa Rican forests. J. Mammalogy 54, 518–521.

Glanz, W. E. (1990): Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? In: Four Neotropical Rainforests. Ed. by A. W. Gentry. New Haven, Connecticut: Yale Univ. Press. Pp. 287–313.

Glanz, W. E. (1991): Mammalian densities at protected versus hunted sites in central Panama. In: Neotropical Wildlife Use and Conservation. Ed. by J. G. Robinson and K. H. Redford. Chicago: Univ. Chicago Press. Pp. 163–173.

Hartshorn, G. S.; Nicolait, L.; Hartshorn, L.; Bevier, G.; Brightman, R.; Cal, J.; Cawitch, A.; Davidson, W.; Dubois, R.; Dyer, C.; Gibson, J.; Hawley, W.; Leonard, J.; Nicolait, R.; Weyer, D.; White, H.; White, C. (1984): Belize: Country Environment Profile. A Field Study. Belize City, Belize: Robert Nicolait and Associates.

Heaney, L. R.; Heideman, P. D.; Rickart, E. A.; Utzurrum, R. B.; Klompen, J. S. H. (1989): Elevational zonation of mammals in the central Philippines. J. Trop. Ecol. 5, 259–280.

Holdenreid, R. (1954): A new live-catch rodent trap and comparison with two other traps. J. Mammalogy 35, 267–268.

Isabirye-Basuta, G.; Kasenene, J. M. (1987): Small rodent populations in selectively felled and mature tracts of Kibale forest, Uganda. Biotropica 19, 260–266.

Janson, C. H.; Emmons, L. H. (1990): Ecological structure of the nonflying mammal community at Cosha Cashu Biological Station, Manu National Park, Peru. In: Four Neotropical Rainforests. Ed. by A. W. Gentry. New Haven, Connecticut: Yale Univ. Press. Pp. 314–338.

Kasenene, J. M. (1984): The influence of selective logging on rodent populations and the regeneration of selected tree species in the Kibale forest, Uganda. Trop. Ecol. 25, 179–195.

Laurance, W. F. (1992): Abundance estimates of small mammals in Australian tropical rainforest: a comparison of four trapping methods. Wildlife Res. 19, 651–655.

Lynam, A. J. (1997): Rapid decline of small mammal diversity in monsoon evergreen forest fragments in Thailand. In: Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed. by W. M. Laurance and R. O. Bierregaard, Jr. Chicago: Univ. Chicago Press. Pp. 222–240.

Malcolm, J. R. (1990): Estimation of mammalian densities in continuous forest north of Manaus. In: Four Neotropical Rainforests. Ed. by A. W. Gentry. New Haven, Connecticut: Yale Univ. Press. Pp. 339–357.

Malcolm, J. R. (1995): Forest structure and the abundance and diversity of neotropical small mammals. In: Forest Canopies. Ed. by M. D. Lowman and N. M. Nadkarni. San Diego: Academic Press. Pp. 179–197.

Malcolm, J. R. (1997): Biomass and diversity of small mammals in Amazonian forest fragments. In: Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed. by W. M. Laurance and R. O. Bierregaard, Jr. Chicago: Univ. Chicago Press. Pp. 207–221.

Mares, M. A. (1992): Neotropical mammals and the myth of Amazonian biodiversity. Science 255, 976–979.

McClearn, D.; Kohler, J.; McGowan, K. J.; Cedeno, E.; Carbone, L. G.; Miller, D. (1994): Arboreal and terrestrial mammal trapping on Gigante peninsula, Barro Colorado Nature Monument, Panama. Biotropica 26, 208–213.

Medellin, R. A. (1994): Mammal diversity and conservation in the Selva Lacondona, Chiapas, Mexico. Conserv. Biol. 8, 780–799.

Monadjem, A. (1997): Habitat preferences and biomasses of small mammals in Swaziland. Afr. J. Ecol. 35, 64–72.

Monthey, R. W.; Soutriere, E. C. (1995): Responses of small mammals to forest harvesting in northern Maine. Canad. Field Nat. 99, 13–18.

O'Connell, M. A. (1989): Population dynamics of neotropical small mammals in seasonal habitats. J. Mammalogy 70, 532–548.

O'Farrell, M. J.; Clark, W. A.; Emmerson, F. H.; Juarez, S. M.; Kay, F. R.; O'Farrell, T. M.; Goodlett, T. Y. (1994): Use of a mesh live trap for small mammals: are results from Sherman live traps deceptive? J. Mammalogy 75, 692–699.

Patterson, B. D.; Meserve, P. L.; Lang, B. K. (1989): Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. J. Mammalogy 70, 67–78.

Pizzimenti, J. J. (1979): The relative effectiveness of three types of traps for small mammals in some Peruvian rodent communities. Acta Theriol. 24, 351–361.

Price, M. V.; Waser, N. M.; Bass, T. A. (1984): Effects of moonlight on microhabitat use by desert rodents. J. Mammalogy 65, 353–356.

Rabinowitz, A.; Nottingham, Jr, B. G. (1989): Mammal species richness and relative abundance of small mammals in a subtropical wet forest of Central America. Mammalia 53, 217–226.

Rickart, E. A.; Heaney, L. R.; Utzurrum, R. C. B. (1991): Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Phillipines. J. Mammalogy 72, 458–469.

Sealander, J. A.; James, D. (1958): Relative efficiency of different small mammal traps. J. Mammalogy 39, 215–233.

Slade, N. A.; Eifler, M. A.; Gruenhagen, N. M.; Deavelos, A. L. (1993): Differential effectiveness of standard and long Sherman live-traps in capturing small mammals. J. Mammalogy 74, 156–161.

Struhsaker, T. T. (1997): Ecology of an African rainforest: logging in Kibale and the conflict between conservation and exploitation. Gainesville: Univ. Florida Press.

Terborgh, J.; Lopez, L.; Tello, J.; Yu, D.; Bruni, A. R. (1997): Transitory states in relaxing landbridge islands. In: Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. Ed. by W. F. Laurance and R. O. Bierregaard, Jr. Chicago: Univ. Chicago Press. Pp. 256–274.

The Nature Conservancy (1993): Rapid ecological assessment of the Bladen Nature Reserve, October 1993.

Timm, R. M. (1994 a): The mammal fauna. In: La Selva: Ecology and Natural History of a Neotropical Rainforest. Ed. by L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn. Chicago: Univ. Chicago Press. Pp. 229–237.

Timm, R. M. (1994 b): Mammals. In: La Selva: Ecology and Natural History of a Neotropical Rainforest. Ed. by L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn. Chicago: Univ. Chicago Press. Pp. 394–398.

Torres-Contreras, H.; Silva-Aranguiz, E.; Marquet, P. A.; Camus, P. A.; Jaksic, F. M. (1997): Spatiotemporal variability of rodent subpopulations at a semiarid neotropical locality. J. Mammalogy 78, 505–513.

Voss, R. S.; Emmons, L. H. (1996): Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. Bull. Amer. Mus. Nat. Hist. 230, 1–115.

Wilson, D. E.; Cole, F. R.; Nichols, J. D.; Rudran, R.; Foster, M. S. (1996): Measuring and Monitoring Biological Diversity: Standard Methods for Mammals. Washington DC: Smithsonian Institution Press.

Woodman, N.; Timm, R. M.; Slade, N. A.; Doonan, T. J. (1996): Comparison of traps and baits for censusing small mammals in neotropical lowlands. J. Mammalogy 77, 274–281.

Wright, S. J.; Gompper, M. E.; DeLeon, B. (1994): Are large predators keystone species in neotropical forests? The evidence from Barro Colorado island. Oikos 71, 279–294.

Wright, S. J.; Zeballos, H.; Dominguez, I.; Gallardo, M. M.; Moreno, M. C.; Ibanez, R. (2000): Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conserv. Biol. 14, 227–239.

Authors' address:
T. M. Caro, Rachel Brock, and Marcella Kelly, Department of Wildlife, Fish and Conservation Biology, 1 Shields Avenue, University of California, Davis, CA 95616, USA
(e-mail: tmcaro@ucdavis.edu)