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Original investigation

Low density of small mammals at Las Cuevas, Belize

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Abstract

Small mammal (< 1 500 g) diversity and density were examined by grid trapping in four trapping sessions over a 2 year time period in a Belizean moist forest in Central America. During 10 829 trap-nights, 96 individuals of 13 species were trapped. The 3 most common species, *Marmosa mexicana*, *Heteromys desmarestianus* and *Ototylomys phyllotis* accounted for 68% of mammals (< 200 g) captured, while *Didelphis marsupialis* dominated captures of mammals > 200 g. Trap success increased with litter fall across grids. Trap success and density tended to be higher at the onset of the dry season. More females were breeding and more animals were in poor body condition at the onset of the wet season. Across studies using grid trapping in the neotropics, diversity and density were positively related to trapping effort. Despite this effect, small mammal densities at Las Cuevas were 2.7 per ha for mammals < 200 g, among the lowest in the neotropics. *Didelphis* densities had a negative effect on densities of all other small mammals across studies; however, this relationship was driven largely by our study. A combination of poor soil, high *Didelphis* densities, and high predator densities is hypothesized for such low densities of small (< 200 g) mammals in our study.

Key words: *Didelphis,* small mammals, diversity, density

Introduction

A primary goal of the mammalian ecologist in the tropics is to assess species richness and abundance (Janson and Emmons 1990; Malcolm 1988, 1990; O'Connell 1989; Robinson and Redford 1986). While data on richness or diversity are now becoming widely available (Voss and Emmons 1996), data on abundance or density is lacking. As noted by Mares and Ernest (1995), most studies estimating densities use strip censusing or trap lines (Fonseca and Kieruff 1988; Emmons 1984; Glanz 1990; Janson and Emmons 1990; Lacher et al. 1989; Malcolm 1988, 1990; Robinson and Redford 1989). Grid trapping, however, is preferred for estimating densities (Davis and Winstead 1980; Otis et al. 1978; Wilson and Anderson 1985) because other methods may have little bearing on actual population densities for small nocturnal mammals in dense forest (Davis and Winstead 1980; Otis et al. 1978). For example, Emmons (1982) noted that her strip census method yielded only about 50% of *Proechimys* obtained by grid trapping. Therefore, we use extensive grid trapping to estimate

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abundances in this study. Lack of data on mammal densities is worrying given that tropical rainforests are the richest terrestrial ecosystems on the planet and are undergoing rapid human-induced change resulting in the current species-extinction crisis (Cuarón 2000).

Nevertheless we do know that mammalian diversity and density in the neotropics is correlated with seasonality, productivity, vertical and horizontal habitat structure (August 1983; Ceballos 1989) habitat variety and abundance of large predators (Janson and Emmons 1990). Additionally, several studies have suggested that larger small mammals such as *Didelphis* sp. affect densities of other small mammal species through competition (Miles et al. 1981) or predation (Fleming 1972; Eisenberg and Thorington 1973). In this study we present new data on trap success, diversity, density, and community composition of terrestrial and scansorial small mammals (< 1 500 g) in a neotropical moist forest of Belize, Central America.

Material and methods

The Chiquibul Forest Reserve, Cayo District, western Belize, is nested within the Chiquibul National Park. The vegetation is a mosaic of deciduous semi-evergreen and deciduous seasonal forest on limestone with abundant ramon, bullhoof, sapote, copal, cedar, and fiddlewood (Wright et al. 1959). Stands of pine (*Pinus*) occur in the northern sector on granite bulges. 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 a loss of trees in Hurricane Hattie in 1961. Rainfall ranges from 1 524–2 032 mm/year with the rainy season starting in June and continuing through December. This study was conducted within 10 km of the Las Cuevas Research Station in the center of the Chiquibul Forest Reserve (16°44′ N 88°59′ W; elevation 500 m) an area classified as Subtropical Lower Montane Moist (SLMM) zone (Hartshorn et al. 1984).

We trapped small mammals (< 1 500 g) in June and July of 1999 and 2000 at the onset of the rainy season, and in January of 2000 and 2001 at the onset of the dry season. Small mammals were trapped using standard 23 × 8 × 8 cm Sherman traps or similar ones custom-made of galvanized wire mesh, except for a galvanized-aluminum plate door that swung upward on closure. Traps were placed 15 m apart in a 7 × 7 grid and were set for 5 to 7 consecutive nights (Wilson et al. 1996) on the ground.

In 1999 we set grids in 12 different locations to obtain a representative sample of mammals around Las Cuevas Research Station (Caro et al. 2001). Additionally, on one grid in the southwestern corner of a 50 ha forest-population-dynamics plot, we placed 49 medium-sized Tomahawk traps (40 × 13 × 13 cm or 40 × 17 × 17 cm) and 49 large Tomahawk traps (65 × 22.5 × 22.5 cm). We placed 1 trap from these 2 categories within 2 meters of each custom-made small trap for 3 traps per station in that grid only. Four of the 12 grids, including the 3-trap grid, were trapped for 10 days in 2 separate 5 day periods in June and then July of 1999 while the other 9 grids were trapped for 5 days. This yielded 16 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) in 1999.

In 3 more trapping sessions in 2000 and 2001, we trapped in the same locations for the aforementioned 4 grids, including 3-trap grid, and additionally added one grid of small traps near the Monkey Tail River approximately 8 km from the station house for a total of 6 174 trap nights in these 3 trap sessions. All traps were opened and baited with a piece of banana between 15.30 and 18.30 h and checked the next morning between 06.00 and 09.00 h. Captured mammals were identified using Reid (1997) and Emmons (1997). To identify recaptures, small mammals were marked with numbered ear tags, and larger mammals (*Didelphis* sp.) were marked with red hair dye.

We calculated percent trap success (numbers of captures, including recaptures, 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 hectare, and diversity calculated as the number of different species caught per grid. We present averages calculated across grids. We used one-way analysis of variance to determine if percent trap success, density, or diversity varied more between seasons than between grids within a season. Additionally we used student's t-tests to determine if there were signifi-

Table 1. Descriptions of habitat variables measured within a 2 m radius of each trap station

Name	Description
litter	percent cover
herbs	cover of herbaceous plants = 0.5 m tall
shrubs	cover of herbaceous or woody plants between 0.5 m and 2 m tall
canopy	cover of overstory trees
	For the above 4 measures numerical values were recorded as follows: 0 = < 10% cover, 1 = 10–30% cover, 2 = 30–50% cover, 3 = 50–70% cover, 4 = 70–90% cover, 5 = 90–100% cover
logs	presence or absence of downed logs = 60 cm diameter
holes	presence or absence of holes in the ground or in logs
brush	presence or absence of tangled vines, lianas, and root mats
slope	slope of the ground around trap
	For the above 4 measures presence or absence was scored as follows: 0 = none, 1 = some, 2 = many

cant differences in these measures between seasons (averages and variances presented). We also used t-tests to examine whether or not trap type had any influence on percent trap success, density, or diversity. To determine how length of trapping session influenced our findings, we calculated trap success, number of individuals caught, and cumulative number of species caught, as a function of the number of days spent trapping.

We calculated sex ratios for each trapping session and determined female reproductive condition by the presence of enlarged nipples. Additionally we noted poor body condition as the presence of ticks, botflies, or a thin straggly coat. Proportion breeding and proportion in poor condition were then compared between seasons and between species. Additionally, we present the densities of each species caught during the different seasons.

In 1999 vegetation data were taken for 13 grids. At each trap station, we scored the amount of litter, herbs, shrubs, and canopy cover on a 6 point scale (CARO 2001), and we scored the presence of logs, holes, brush, and slope on a 3 point scale (Tab. 1). While we did not catch enough animals to examine microhabitat associations of each species, we were able to obtain an overall estimate of vegetation characters for each grid by averaging our vegetation measures over all trap stations within each grid. These estimates were then compared to our measures of trap success, density, and diversity for these grids using forward stepwise regression (NEDER et al 1990). Variables were permitted to enter and remain in the model when F-values were deemed appropriate (i. e. F = 4.0 to enter and F = 3.9 to remove – NEDER et al. 1990). All tests were performed in Stat-View 1994 – SAS Inst. Inc.

Lastly, we compared our densities of small mammals to those from other studies in the Neotropics. We limited our comparisons to those studies using grids, rather than traplines or visual line transects to determine densities, and we examined, through linear regression whether or not density or diversity was influenced by trapping effort. Additionally, since *Didelphis* sp. can decrease trap success of other species (FONSECA and ROBINSON 1990), we separated out densities of *Didelphis* sp. in these studies and regressed them against the densities of all other small mammals captured to determine if *Didelphis* numbers are associated with the densities of the rest of the small mammal community.

Results

Small mammals of the Chiquibul Forest Reserve

We trapped 96 individuals of 13 species 137 times in 10 829 trap nights. The average percent trap success varied by season rather than between grids within a season (Fig. 1; F = 8.19, d. f. = 4, 26, P = 0.0002) as did the average small mammal density (F = 4.57, d. f. = 4, 26, P = 0.006) and average diversity (F = 4.78, d. f. = 4, 24, P = 0.0056). In parti-

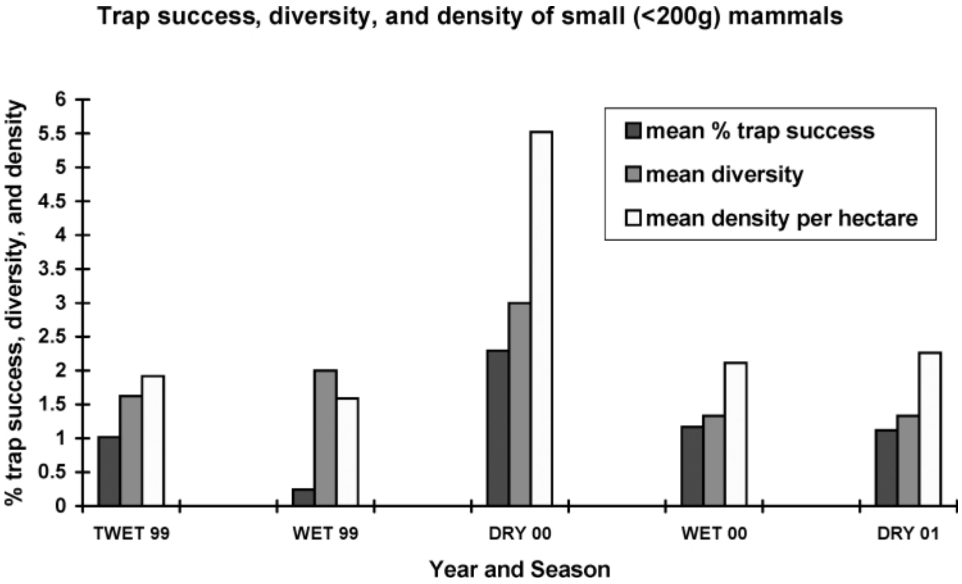

Fig. 1. Percent trap success, diversity, and density averaged across grids in different seasons. WET 99 through DRY 01 represent 5–6 grids all trapped in the same locations each trapping session, while TWET 99 represents 8 grids in different locations but in similar habitat. WET refers to the trapping sessions at the onset of the wet season in June/July of years 1999 and 2000 while DRY refers to trapping sessions at the onset of the dry season in January of 2000 and 2001.

cular, the onset of the dry season of 2000 had higher trap success per grid (2.29% ± 1.02) than any other season (Fig. 1.; Tab. 2; for all t-tests $P = 0.019$). Only the WET 99 had lower average trap success than all other periods (for t-tests all $P < 0.023$), likely due to 2 of the 5 grids capturing zero animals.

Average density of small mammals for DRY 00 was also higher than all other periods (Fig. 1, for all t-tests $P < 0.016$). DRY 2000 diversity was also higher per grid than all other trapping periods (for all t-tests $P < 0.012$) except for WET 99 ($P = 0.22$).

Within each trapping period, there were no differences in trap success between small wire mesh traps and small sherman traps (Fig. 2; for all t-tests $P = 0.089$), which differs from previous studies showing higher success with wire mesh traps (O'Farrell et al. 1994; Caro et al. 2000). While there were not enough grids of medium- and large-sized tomahawk traps to test statistically for differences, no consistent pattern of trap success was found in the present data (Fig. 2). However, large traps caught substantially more *Didelphis* in the last trapping session at the onset of the dry season 2001 (Tab. 2).

The average percent trap success per day and the number of new individuals caught per day was relatively constant from day 1 to 5 for all grids of small traps (Tab. 3) although more *Marmosa mexicana* were captured on day 5 than any other day. For the grids set for more than 5 days (4 grids in DRY 00 and 5 grids in DRY 01) there was a substantial increase in trap success and new individuals captured on day 7 for small traps (Tab. 3). In particular there was a jump in the numbers of *Oryzomys* sp. captured on the 7th day of trapping. Averaged across all grids, the cumulative number of species increased throughout the 7 day censuses without appearing to reach a distinct asymptote (Fig. 3), a common pattern noted in numerous other studies in the neotropics (Voss and Emmons 1996).

Table 2. Species densities per ha for Las Cuevas, Belize averaged across grids (n = number of 7X7 grids)

Species < 200 g	season TWET99 n = 8	WET99 n = 5	DRY00 n = 6	WET00 n = 6	DRY01 n = 6	average
Marmosa mexicana	0.57	0.45	2.04	0	1.45	0.90
Marmosa robinsoni	0.34	0.23	0	0	0	0.11
Heteromys desmarestianus	0.34	0.73	1.36	0.3	0.45	0.64
Heteromys glaucomys	0	0.18	0	0	0	0.04
Ototylomys phyllotis	0.11	0.18	1.06	1.51	0	0.57
Tylomys nudicaudus	0.11	0	0.15	0.3	0	0.11
Oryzomys sp.	0.34	0	0.73	0	0.36	0.29
Reithrodontomys gracilis	0	0	0.18	0	0	0.04
Philander opossum	0.11	0	0	0	0	0.02
sum	1.92	1.77	5.52	2.11	2.26	2.72

Species > 200g	n = 1	n = 1	n = 1	n = 1	
Sciurus deppei	0	1.81	0	1.81	0.91
Didelphis marsupialis	1.81	1.81	0.91	4.5	2.26
Didelphis virginianus	0.91	0	0	0	0.23
sum	2.72	3.62	0.91	6.31	3.39
all species < 200 g and > 200g	4.49	9.14	3.02	8.57	6.11

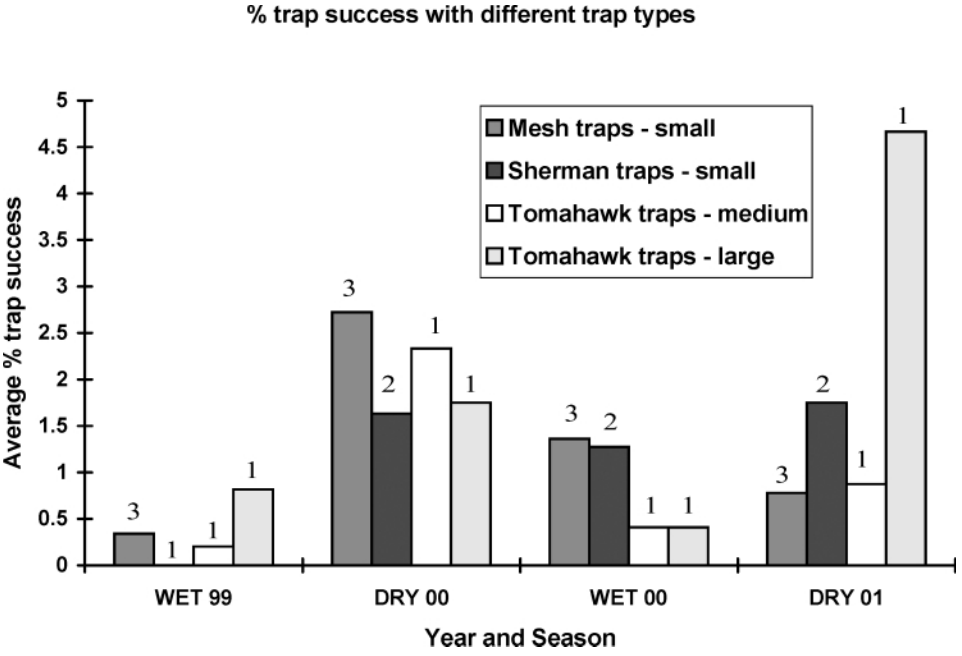

Fig. 2. The effect of trap type on trapping success in different seasons. The numbers above the bars represent the number of 7 × 7 grids trapped during the census period.

Table 3. Number of captures by species by day for Las Cuevas, Belize, summed across all grids

Species	Day of trapping							
	1	2	3	4	5	6	7	Totals
Marmosa mexicana	4	5	6	2	10	2	4	33
Marmosa robinsoni	1	1	3	1	0	0	0	6
Heteromys desmarestianus	5	3	1	6	3	0	5	23
Heteromys glaucomys	0	0	0	0	1	0	0	1
Ototylomys phyllotis	1	3	5	3	4	2	4	22
Tylomys nudicaudus	2	1	1	0	2	1	0	7
Oryzomys sp.	1	1	0	2	2	1	5	12
Reithrodontomys gracilis	0	0	0	0	1	0	0	1
Philander opossum	0	0	0	0	1	0	0	1
Sciurus deppei	0	1	0	0	1	0	2	4
Didelphis marsupialis	3	4	5	8	3	2	1	26
Didelphis virginianus	0	0	0	0	1	0	0	1
total individuals	17	19	21	22	29	8	21	137
% trap success (small traps)	0.99	1.11	1.22	1.28	1.74	1.81	4.76	
% trap success (*Didephis*)	1.22	1.63	2.04	3.26	1.63	2.04	1.02	
% trap success (*Sciurus*)	0	0.41	0	0	0.41	0	2.04	

The small mammal species most commonly caught during the study were *Marmosa mexicana*, *Heteromys desmarestianus*, and *Ototylomys phyllotis* (Tabs. 2, 3). In large traps, *Didelphis marsupialis* was commonly caught. There was a tendency to catch more males in this study as sex ratio over all captures was 1 : 1.56. More females were lactating at the onset of the wet season (67–80%) than at the onset of the dry (0–27%) and likewise more individuals were in poor condition at the onset of the wet season (22–38%) than at the onset of the dry (0%). In WET 99 numerous species were lactating including: *H. desmarestianus*, *H. glaucomys*, *M. mexicana*, *O. phyllotis*, and *D. marsupialis*, while in WET 00 we found only *O. phyllotis* to be lactating, however, this was the principal species we caught during this trap session. Only one dry season (DRY 00)

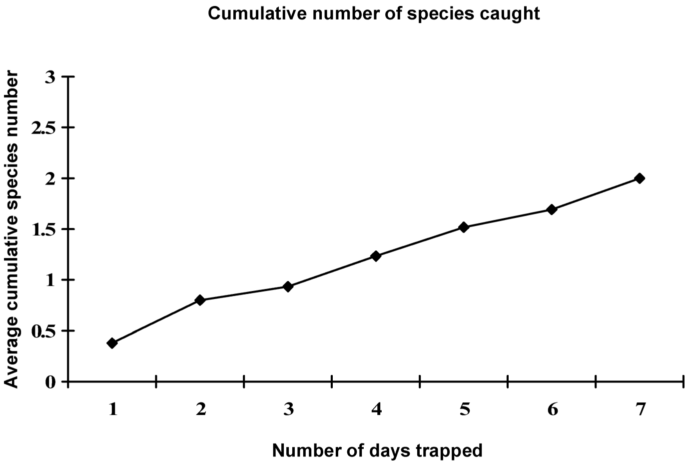

Fig. 3. The effect of number of days spent trapping on the cumulative number of species caught. Each data point represents an average accumulation of new species over all grids for each day.

had a lactating female of *O. phyllotis*. Most small mammals have a lifespan of one year or less. This was reflected in our study where we had only one recapture (*O. phyllotis*) between 6 month census periods and none from one year to the next.

Additionally it should be noted that we captured both *M. mexicana* (weight $\bar{x} = 35.92$ g; n = 25) and *M. robinsoni* ($\bar{x} = 113.3$ g; n = 6). Previously, no Central American location was known to have more than a single species of *Marmosa* (Voss and Emmons 1996).

Stepwise linear regression selected only the amount of holes as the best predictor of percent trap success. However, amount of holes was highly positively correlated with numerous other vegetation parameters including herb cover, shrub cover, logs, and brush, indicating that this variable is influenced by

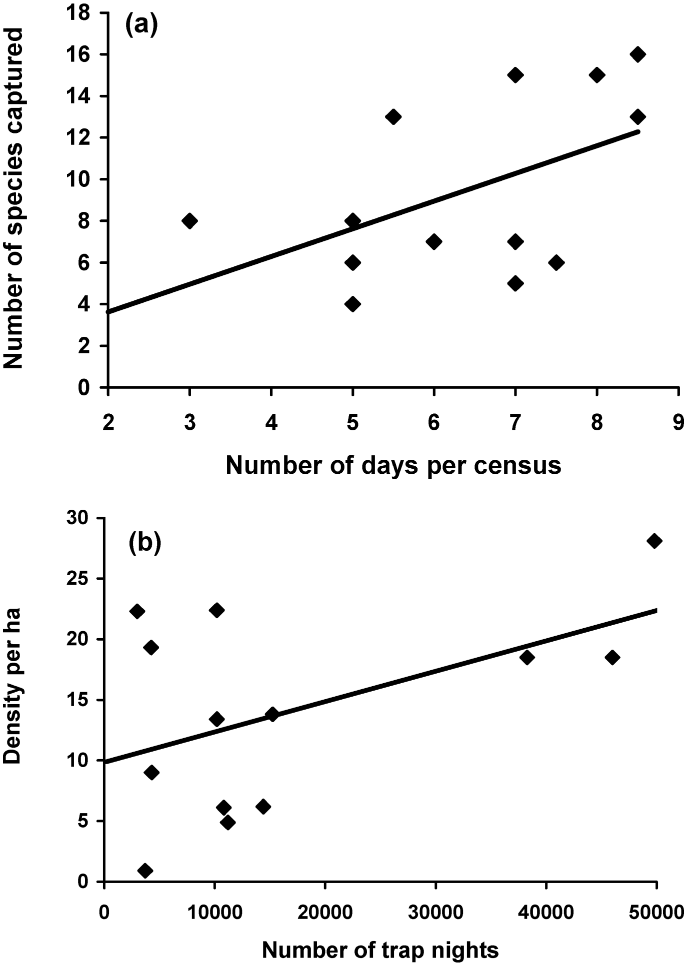

Fig. 4. a) The effect of trapping effort on diversity of species caught across neotropical studies using grid trapping. Three studies from table 4 were excluded from the analysis because they presented data on only a portion of species captured (Bergallo and Magnusson 1999; Emmons 1982) or were conducted on tiny islands (Adler and Beaty 1997) b) The effect of trapping effort on density of species per hectare across neotropical studies using grid trapping. Three studies from table 4 were excluded from the analysis because densities for an unknown portion of the small mammal community were presented (Aguilera 1999; Bergallo 1994; Emmons 1982).

the amount of vegetation and hence not a good predictor in its own right. After elimination of holes from the data set, stepwise regression chose only the amount of litter as the best predictor of trap success ($y = 0.95x - 1.44$, $r = 0.55$, $P = 0.05$). No habitat measures were statistical predictors of diversity or density of small mammals.

Comparisons to other neotropical studies

Very few studies using grid trapping present trap success and densities for the entire small mammal community. Table 4 summarizes those that we found including thorough studies that present densities for only a few species. In the Chiquibul, overall trap success for small mammals was 1.3% which is very low in comparison to other studies, including one study within the same country < 55 km away (Rabinowitz and Notingham 1989). Our density per hectare (6.1) was also low, although similar to what Fleming (1973) found for tropical rainforest in Costa Rica. Only the dry forest of Masaguaral Venezuela, had lower trap success and density than ours (August 1983). If we subtract species greater than 200 g, then our densities of < 200 g mammals is 2.7, equivalent or lower than August's (1983) study.

Excluding those studies from table 4 with insufficient data, we found that trapping effort affected estimates of density and diversity of the small mammal community (Tab. 4). All regressions of diversity and density were positively related to trapping effort, whether it was number of grids, days, months, or trapnights used. Only two, however, were significantly related and only marginally so (Fig. 4). The more days trapped per census, the higher the diversity of species caught ($y = 1.331x - 0.964$; $r^2 = 0.259$; $P = 0.07$) and more trapnights can lead to higher density estimates ($y = 0.0003x + 9.84$; $r^2 = 0.251$; $P = 0.08$). The fact that only 2 regressions were marginally significant is perhaps not surprising, given the variety of habitats surveyed and varying methods used in the studies.

Six studies in table 4 presented densities of individual species trapped and from those we separated out the densities of small mammals for comparison to the reported densities of *Didelphis* sp., especially the common opossum, *Didelphis marsupialis.* While we found *Didelphis* to have a marginally significant negative affect on other small mammals ($y = -4.33x + 17.71$; $r^2 = 0.555$; $P = 0.089$) this relationship, is based on only 6 data points and was driven by our study which had very high densities of

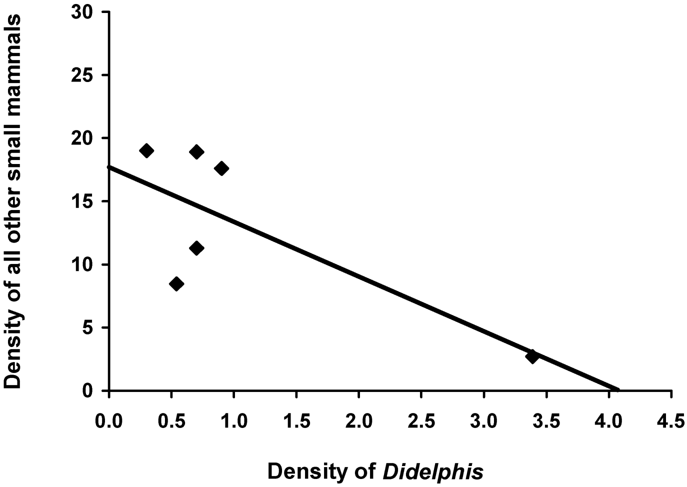

Fig. 5. The effect of *Didelphis* sp. densities on densities of all smaller mammals in 6 different neotropical studies. Data is from those studies in table 4 with *Didelphis* sp. densities listed.

Table 4. Comparisons of small mammal densities across neotropical sites that used grid trapping. (a) chose median for analysis, (b) months are not necessarily in succession, (c) values for *Proechimys* sp. only, (d) breeding season densities averaged over all islands. *Proechimys semispinosus* accounts for nearly the entire small mammal community, (e) median of 1.0–3.6, (f) possibly more captured but only 4 presented, (g) calculated from average monthly densities divided by grid area of 8.8 ha, (h) value for *Liomys salvini* only, however, *L. salvini* accounts for 96% of small mammal population, (i) value for *Heteromys desmarestianus* only, however, *H. desmarestianus* accounts for 94% of small mammal population, (j) sum of all averages for individual species presented in original study, (*) densities now calculated correctly after a mistake in previous publication

site	habitat	# grids	# days per census (a)	# months censused (b)	# trap nights	trap success (%)	# species trapped	density per ha	*Didelphis* density	study
4 Islands of Gatun Lake – Panama	tropical moist forest	4	4	60	46 000	7.0	1 (c)	18.5 (d)		ADLER and BEATY (1997)
Turiamo, Aragua, Venezuela	semi-deciduous seasonal forest	1	7	20	50 400	–	5	2.3 (c,e)		AGUILERA (1999)
Masaguaral, Venezuela	deciduous dry tropical forest	1	5	16	11 200	1.0	6	4.9		AUGUST (1983)
Masaguaral, Venezuela	deciduous dry tropical forest	1	5	6	3 725	1.0	4	0.9		AUGUST (1983)
Jureia-Itatins Research Station, Brazil	tropical rain forest	1	3	14	4 307	15.1	8	9	0.54	BERGALLO (1994)
Cardosa Island, San Paolo State, Brazil	coastal plain – montane tropical rainforest	2	2	20	9 600	–	4 (f)	3.9 (g)		BERGALLO and MAGNUSSON (1999)
Bladen Nature Reserve, Belize	tropical wet forest	3	5	6	4 236	3.8	8	19(*)	0.3	CARO et al. (2000, 2001)
Cocha Cashu, Peru	subtropical rainforest	2	4–5	4	1 908	–	2 (c)	3.14 (c)		EMMONS (1982)
Panama	lowland moist forest	1	8–9	12	10 200	15.7	13	13.4	0.7 (a)	FLEMING (1970, 1975)
Panama	lowland dry forest	1	8–9	12	10 200	15.7	16	22.4	0.7 (a)	FLEMING (1972)
La Pacifica, Costa Rica	dry tropical forest	1	4–10	14	15 246	–	7	13.8 (h)		FLEMING (1973, 1974 a, b, 1975)
Finca La Selva, Costa Rica	tropical rainforest	1	4–10	14	15 246	–	9	6.2 (i)		FLEMING (1973, 1974 a, b, 1975)
The Cerrado Province, Brazil	riprian gallery forest surrounded by grassland	3	4–10	14 4	49 810	–	15	28.1 (j)		MARES and ERNEST (1995)
Guatopo, Venezuela	premontane humid forest	1	7–9	23	38 270	6.0	15	18.5 (j)	0.9	O'CONNELL (1989)
Cockscomb Basin Belize	subtropical wet forest	10	6	7	2 987	5.2	7	22.3		RABINOWITZ and NOTTINGHAM (1989)
Chiquibul Forest Reserve, Belize	tropical moist forest	5–13	4 – 7	4	10 829	1.3	13	6.1	3.5	this study

Didelphis in comparison to other small mammals (Fig. 5). This relationship merits further attention.

Discussion

Small mammal community

In our study, small mammal trap success, density, and diversity varied seasonally and were significantly higher at the onset of the dry season in 2000 than all other times. Food availability (e. g. fruit, seeds, and arthropods) is considered a major factor influencing community diversity and abundance (Rosensweig 1995). Generally, in neotropical forests, fruit production coincides with the onset of the rainy season (Smythe 1970). Additionally, insect and arthropod abundance reaches a peak at the dry-rainy transition (Janson and Emmons 1990; Bergallo and Magnusson 1999). Numerous studies have shown that tropical small mammals time their reproductive activity and produce young (or more young) during the time period when food availability is highest (Adler and Beaty 1997; Bergallo 1994; Bergallo and Magnusson 1999; Fleming 1971; 1973; Glanz et al. 1982; Gliwicz 1984; Davis 1945). Overall population density then, follows an annual trend, reaching a peak at the end of the season of resource abundance, (i. e. usually the end of the wet season) (Alder 1994, 1998; Fleming 1971; Gliwicz 1984). While we did not collect data directly on food availability, the forest area at Las Cuevas follows the same general pattern of rainy season fruit production. Our study corroborates these finding as more females were breeding at the onset of the both wet seasons (1999, 2000) and the highest density occurred at the onset of dry season 2000, the end of the season of high food availability.

During the season of resource scarcity, mortality exceeds fecundity (Adler 1998). Our lower densities at the onset of the wet season were likely due to censusing survivors of the period of low food availability. Indeed in our study, between 22–38% of small mammals captured at the end of the dry season were in poor body condition while all appeared healthy at the end of the wet.

Conversely, higher densities at the end of the wet season could stem from higher trapability of mammals due to lower food availability as noted in other studies (Rudd 1979; Adler and Lambert 1997; Adler et al. 1999). In support of this second idea, we did not trap significantly more animals at the end of the wet season in January 2001 than at the onset of the wet season 2000. This was most likely due to a lengthened rainy season caused by hurricane Keith and hence a longer period of food availability. Tree species that normally in bloom by January, such as quamwood (*Schizolobium* sp.) had not yet flowered.

The small mammal (< 200 g) community was dominated by 3 species: *M. mexicana* (25 individuals), *H. desmarestianus* (23), and *O. phyllotis* (17). Fleming (1975) has shown that small mammal communities are usually numerically dominated by one to three species. In fact, in his Costa Rican wet forest study (Fleming 1973), *H. desmarestianus* accounted for 94% of the total rodents trapped. In this study, the 3 most dominant species accounted for 68% of the total number of individuals captured, very close to the average (69%) of numerous other studies (Fleming 1975). However, no one species of the top three was captured consistently more than the other two over the 2 year time period. *M. mexicana* was caught more at the onset of the wet season 1999 and onset of dry 2001, while there were more *H. desmarestianus* trapped at the onset of the dry 2000 and *O. phyllotis* completely dominated captures at the onset of the wet 2000.

We did not use understory or canopy traps in this study. In the central Amazon, there was little difference between richness and abundance of small mammal fauna between ground and understory trapping (Malcolm 1991). Additionally, Malcolm and Ray (2000) have shown that small mammal diversity and abundance are significantly higher on the ground, but that certain species such as *Caluromys philander* will only be caught in the understory or canopy and that others, such as *Philander opossum* are more abundant in the canopy (Malcolm 1991). We therefore accept that our *P. opossum* densities may be an underestimate and that there may be species we miss by only trapping on the ground.

Preliminary assessment of low density

While mammal diversity was high in our study, trap success and density were very low compared to other studies. Explanations for our low density of neotropical small mammals fall primarily into 4 categories: sampling error, poor soil, competition, and predation. While we only sampled intensively for 4 times separated by 6 month intervals, we used numerous grids sampled over many days per census with a high number of trapnights. We also timed our censuses to periods that should have produced two possible extremes in density: the end of the season of high food availability (DRY 00, DRY 01) and the end of the season of low food availability (TWET 99, WET 99, WET 00). However, given that small mammal populations are prone to large fluctuations both with-in and between years (August 1983; Emmons 1984; Malcolm 1990), we can not completely rule out sampling error without a year-round study.

Janzen (1974) suggested that animal biomass should be lower on nutrient poor tropical soils because plants (both seed and vegetative parts) should be heavily defended with toxic secondary chemicals. Support for this hypothesis comes from Eisenberg (1979) who showed that primate number and diversity were low on poor soils in Venezuela and Guyana, while Freese et al. (1982) reported higher primate densities in the fertile floodplain forest than adjacent uplands. Additionally, Emmons (1984) has shown soil fertility and undergrowth density to be positively correlated with species densities. While the area surrounding Las Cuevas Research Station is generally poor limestone soil, our preliminary vegetation analysis found no correlation with amount of understory cover (e. g. shrubs, herbs, or vine tangles) and small mammal abundance. The scale of this analysis, however, may be too course to discern vegetative differences important to small mammals (see August 1983). Litter fall perhaps represents a coarse measure of food availability and therefore its positive relationship to trap success in this study might be expected.

One of our grids placed near the Monkey Tail River, sampled for 3 periods had a higher average density of small mammals (8.2) than other grids. Similarly small mammal abundances were higher near a river in the Bladen Nature Reserve in the Maya Mountains (Caro et al. 2001). Soil near rivers may have higher nutrients as a result of periodic flooding and hence primary productivity may be higher. Data on soil fertility is not available for most sites examined in this study. Nonetheless, Masaguaral has rich soil and the lowest small mammal density of any site (August 1983). Soil type and proximity to rivers at Las Cuevas deserve further attention.

Didelphis sp., and particularly *D. marsupialis*, the common opossum, is perhaps the most generalist and versatile neotropical small mammal (Hershkovitz 1969). Diet and spatial use overlaps with almost all small mammals of communities where it exists (Miles et al. 1981). Young are weaned at 70–100 g and as independent foragers, they overlap in size with adults of other species in the community (Fonseca and Robinson 1990). As they increase in size, they can act as predators killing the young of other small mammals (Fleming 1972; Eisenberg and Thorington 1973). While we did not note common opossums disturbing the small mammal traps, other studies have reported frequent trap disturbance and killing of captured small mammals in traps by *D. marsupialis* (Rood 1963; Fleming 1972). In addition, Fonseca and Robinson (1990) have shown that presence of *D. marsupialis* decreased the trapping success of other small mammal species. However, this effect was primarily noted in small and medium sized forest plots where predators of *D. marsupialis* were absent (Fonseca and Robinson 1990). Similarly, small isolated forest fragments lacking predators at Los Tuxtlas were dominated by common opossums (Estrada et al. 1994).

The average *D. marsupialis* density in our study was 3.5 per ha, whereas the range for all other studies reporting densities from grid trapping was much lower at 0.3–0.9. The density of common opossums accounted for 55% of the total density of all small mammals at Las Cuevas compared to only 3–6% at other study sites. What is surprising and in contrast to previous studies, is that Las Cuevas is a large, undisturbed forest with a complete host of predators (Caro et al. 2001). In fact predators of small mammals were commonly seen on grids. In 3 of 4 trapping sessions, tayras were seen on or near grids and one tayra was responsible for killing two *D. marsupialis* in traps by pulling the legs through the wire and eating them as noted in another study (Fonseca and Robinson 1990). Additionally a margay was seen on one grid, an ocelot in the general vicinity of another, and large cats, especially jaguar, and their sign are often seen on the road near the research station. This ecosystem seems unusual in having very low densities of small mammals (< 200 g), high densities of *Didelphis*, and potentially, high densities of carnivore predators.

Our analysis did not show unequivocally that small mammal densities were negatively related to *Didelphis* densities across different study sites. Perhaps the high density of *D. marsupialis* is responsible for the extremely low densities of all other small mammals at this study site while other factors account for low densities of small mammals at other sites. Numerous studies have implicated predators as responsible for low densities of all small mammals including low densities of *Didelphis* (August 1983; Emmons 1984, 1987; Fleming 1974; Terborgh 1988). It is therefore unclear why predators do not keep *Didelphis* numbers low at Las Cuevas.

This study elucidates the difficulties in disentangling the various factors thought to influence the diversity and abundance of the small mammal community in the neotropics. Perhaps the combination of poor soil, high density of *Didelphis*, and high predator abundance are responsible for such low densities of all small mammals (< 200 g) in this study.

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Zusammenfassung

Geringe Dichte kleiner Säuger in Las Cuevas, Belize

Die Vielfalt und Dichte kleiner Säugetiere (< 1 500 g) wurde in einem Regenwald in Belize, Zentral-Amerika, durch eine Fallennetzanordnung in 4 Fangperioden über 2 Jahre untersucht. Sechsundneunzig Tiere aus 13 Arten wurden in 10 829 Fallennächten gefangen. *Marmosa mexicana*, *Heteromys desmarestianus* und *Ototylomys phyllotis* waren die 3 häufigsten Arten und nahmen 68% aller gefangenen Säuger (< 200 g) ein, wogegen *Didelphis marsupialis* den Fang der Säuger > 200 g do-

minierte. Fangerfolg nahm mit Laubfall zu und war, ebenso wie Dichte, am Anfang der Trockenheit höher. Mehr Weibchen waren am Anfang der Regenzeit tragend und mehr gefangene Tiere waren in schlechter körperlicher Kondition. Mehrere Studien, die Fallennetzanordnungen in den Neotropen benutzten, haben gezeigt, daß Vielseitigkeit und Dichte in positiver Wechselbeziehung zu Fangbemühungen stehen. Trotz dieses Effekts fanden wir eine Dichte von 2,7 Tieren/ha bei Säugern < 200 g, eine der niedrigsten Dichten in den Neotropen. Die Dichte von *Didelphis* hatte eine negative Wechselwirkung zur Dichte aller anderen Säuger in mehreren Studien; dieser Befund wurden jedoch hauptsächlich durch unsere Studie beeinflußt. Eine Kombination von schlechten Böden und hoher Dichte von *Didelphis* und Raubtieren könnte für die niedrige Dichte aller anderen Säuger verantwortlich sein.

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