

The bat fauna of Lamanai, Belize: roosts and trophic roles

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ABSTRACT. Thirty-six of the 70 species of bats known from Belize were recorded from the area around Lamanai, Orange Walk County: two in roosts and 34 in about 680 mist net hours that produced 560 captures. Day roosts used by 35 of the species were located using radio-tracking (*Sturnira lilium*, *Platyrrhinus helleri*, *Centurio senex* and *Bauerus dubiaquercus*) or general searching for roosts (*Rhynchonycteris naso*, *Saccopteryx bilineata*, *Saccopteryx leptura*, *Diclidurus albus*, *Mimon bennettii*, *Micronycteris schmidtorum*, *Carollia brevicauda*, *Carollia perspicillata* and *Eptesicus furinalis*). Data on the day roosts of 23 other species were determined from the literature. Most species reported from Lamanai (19) roosted in hollows, while others used foliage (6), tents (3), sheltered sites (2), crevices (2), open sites (1), and a few species used more than one type of day roost (hollows and crevices (1); hollows and foliage (1); hollows, foliage and tents (1)). The fauna consisted of 13 aerial foragers, 9 gleaners, 11 fruit/leaf eaters, one trawler, one flower-visitor and one blood-feeder. In day roost use and foraging behaviour, the Lamanai fauna did not differ significantly from that of Paracou, French Guiana, but both these locations differed from the bat fauna of Kruger National Park, South Africa, in foraging behaviour.

KEY WORDS: diversity, faunal structure, radio-tracking

INTRODUCTION

The diversity of bats provides an opportunity to revisit a fundamental question that has long engaged ecologists (Klopfer 1962, Ricklefs 1979), namely, why are there so many species? Bats show a wide spectrum of species diversity, from one or two species in some faunas (e.g. Hawaiian Islands, Newfoundland) to

over 100 in others (e.g. Colombia, Costa Rica, Guyana). Roosts and food are two resources that could be limiting for bats and either or both may influence their diversity at any particular location (Altringham 1996, Findley 1993). What factors account for these differences?

The importance of day roosts to bats is well documented (Kunz 1982, Neuweiler 2000), reflecting in part the small size of most bats and their large surface area : volume ratios. Furthermore, the diversity of day roosts (hollows, crevices, foliage) used by bats, particularly by any one species (Altringham 1996, Gaisler 1979, Kunz 1982, Verschuren 1957) suggests a measure of opportunism in roost selection that sometimes coincides with differences in physiology and behaviour (Altringham 1996, Kunz 1982, Neuweiler 2000). Humphrey (1975) used data from the United States of America to demonstrate how increased variety of roosting situations (measured by topographic variation) was reflected by higher local diversity of bats, supporting the view that day roosts can be important determinants of bat faunas.

Outside the temperate areas which are dominated by taxa that eat mainly insects, bats fill a range of dietary roles including taking a wider range of animals beyond insects in addition to plant-visiting (eating leaves, fruit, nectar and pollen) and, in the neotropics, blood-feeding (Altringham 1996, Fenton 1992). The marked increase in the diversity of bats as one travels from temperate to tropical locations is a reflection of the increase in the numbers of insectivores as well as bats filling more trophic roles and a proliferation of animal-eating species beyond the temperate insectivorous model (Findley 1993, Wilson 1974). Animal-eating bats include those that are aerial-feeders, taking airborne prey, usually flying insects; gleaners, species taking prey from surfaces; and trawlers, usually taking prey from the water's surface (Altringham 1996, Fenton 1990).

While we are relatively well-informed about the general diets and approaches to foraging of most bats (Altringham 1996, Fenton 1990), the same is not true about the day roosts that they use. The small size of most bats (compared to other mammals) and their secretive nature partly accounts for the reality that we lack details of the day roosts used by perhaps 50% of the over 900 species of bats. For example, Simmons & Voss (1998) made strenuous efforts to search out the day roosts of bats in their study area in French Guiana, and still did not find the day roosts of over 50% of the 73 species they studied. Lack of information about roosts contributes to our general ignorance about the factors responsible for the diversity of bats.

We often find roosting bats by accident and such discoveries can change our view of the situations in which bats roost. So, we may believe that some specializations limit the spectrum of roosts available to some bats and thus their distribution. For example, Findley & Wilson (1974) proposed that the local abundance and distribution of *Thyroptera tricolor* Spix was limited by the availability of suitable roosts (furled, new leaves). But Allen & Barbour (1923)

and later Simmons & Voss (1998) also found *T. tricolor* roosting in dried, rolled leaves, expanding our view of what constitutes an appropriate roost for them.

The advent of radio-tracking which permits finding roosting bats in a more systematic fashion, considerably broadened our knowledge of both the day roosts used by bats and their patterns of roost-occupancy (reviewed by Lewis 1995). The discovery that many species frequently (sometimes almost daily) move between day roosts while others do not, has demonstrated that the impact of roosts on bat faunas can be much more complicated than one roost per bat or one type of roost per species (reviewed by Lewis 1995).

The purpose of our study was to document the bat fauna in the vicinity of Lamanai, Orange Walk County, Belize (17°45.848'N; 88°39.128'W) with reference to roosting and foraging behaviour. We used captures in mist nets and monitored echolocation calls in addition to searching and radio-tracking to prepare a list of the bats of Lamanai and associate species with roosts. The vegetation in our study area was tall broadleaf deciduous forest rich in lime-loving species adjoining cleared areas used in agriculture. The wet season typically lasts from June through October.

METHODS

Between us we made four separate trips to the study area (January, July and August 1999; January 2000) and used mist nets (all visits), monitoring echolocation calls (all visits), radio-tracking (January visits), and searching (all visits) to assess habitat use by foraging and roosting bats. We used 6 × 2, 9 × 2, 12 × 2 or 30 × 6 m mist nets set in (1) open areas, (2) waterside, (3) in trails and (4) along roads. The macro mist net was set perpendicular to clearings in forest (3 nights), under the tree canopy near Maya ruins (4 nights), adjacent to and over water (4 nights), along trails (4 nights) or along roads at the interface between forest and clearings (6 nights). We tended set nets continuously. One 12 × 2 m net set for one hour equals one net hour. In January 2000, the mist netting was supplemented by setting a Tuttle Trap (Tuttle 1974) in trails or flyways.

We used Anabat bat detectors with Anabat Zero Crossing Analysis Interface Module and Anabat 5 software installed in a DOS computer to monitor the echolocation calls of bats in the area. In January 2000, we supplemented the Anabat work with a QMC S200 bat detector operated with a Racal Store 4 D tape recorder running at 30 inches per second. Echolocation calls recorded in this way were analysed with Canary Version 2.1 software.

Captured bats were identified to species using a key prepared from the literature, museum specimens and Reid's (1997) field guide. We followed the classification proposed by Simmons & Geisler (1998), and the names for bats as presented in Wilson & Reeder (1993). In January 2000, we affixed radio transmitters to 12 bats of eight species: three *Platyrrhinus helleri* (Peters), two *Centurio*

senex Gray, two *Pteronotus parnellii* (Gray), one *Mimon bennettii* (Gray), one *Mormoops megalophylla* (Peters), one *Noctilio leporinus* (L.), one *Desmodus rotundus* (E. Geoffroy), and one *Bauerus dubiaquercus* Van Gelder (Table 1). While *D. rotundus* and *N. leporinus* received Holohil MD-2C transmitters, the other bats were tagged with Holohil BD-2 transmitters. Invariably, transmitters weighed less than 5% of the bats' body masses. To find and follow radio-tagged bats, we used two Lotek SRX400 Telemetry Receivers and two Communications Specialists Telemetry Receivers Model: R1000, all equipped with Lotek H (Model AN-ADH) antennae. One bat carrying an active transmitter by day in a roost equals one roost day. Bats carrying active transmitters and flying in forest were readily detectable at ranges of at least 2 km using the Lotek receivers, considerably less with the Communications Specialists Telemetry receivers. The range achieved for roosting bats varied with roost type, but was usually about 1 km with a Lotek when the roosts were in foliage.

We used pairs of receivers and observers in communication by walkie-talkie to locate the signals from the transmitters of roosting bats, making daily searches from the highest local points of land (Maya temples), roads and trails. Roost positions and distances between roosts were determined using a Garmin GPS 12 Personal Navigator, Software 4.55, accurate to the nearest 100 m. After locating a roost site, we used direct observation through binoculars or with the naked eye in an effort to see roosting bats. To document the times that radio-tagged bats emerged and their patterns of activity, we used the receivers situated atop the local height of land, the 'High Temple' (17°46.028'N; 88°39.154'W) in the Maya complex (*c.* 35 m above the general land level, *i.e.* sea level). Each receiver was programmed to scan each frequency of an active transmitter for 1 min, and this procedure was used from 18h00 to 0h00 on 17, 18 and 19 January.

In January in our study area sunset varied from 17h36 to 17h43.

RESULTS

In about 680 total mist net hours of sampling, we captured 560 bats in the Lamanai study area, representing 34 species. Two other species, located in their day roosts, also have been recorded from the area. The fauna, or at least the captures, are dominated by a few species (Figure 1a) and after reaching about 23 species, we have been slow to add additional ones by capture (Figure 1b). The fauna includes 13 aerial foragers (Mormoopidae (3), Vespertilionidae (9), Molossidae (1)), 1 trawler (Noctilionidae), 9 gleaners (Phyllostominae (8), Antrozoidae (1)), 11 fruit/leaf eaters (Phyllostomidae), as well as one nectar-feeder (Phyllostomidae) and one blood-feeder (Phyllostomidae). The species in most of these trophic categories tend to be smaller (body mass < 20 g), with only *N. leporinus*, *A. jamaicensis* Leach, *A. lituratus* (Olfers), and *D. rotundus* exceeding 30 g. We caught *Pteronotus parnellii*, *P. davyi*, *Myotis keaysii*, *M. elegans* and *Rhogeessa anaëus* in the Tuttle Trap.

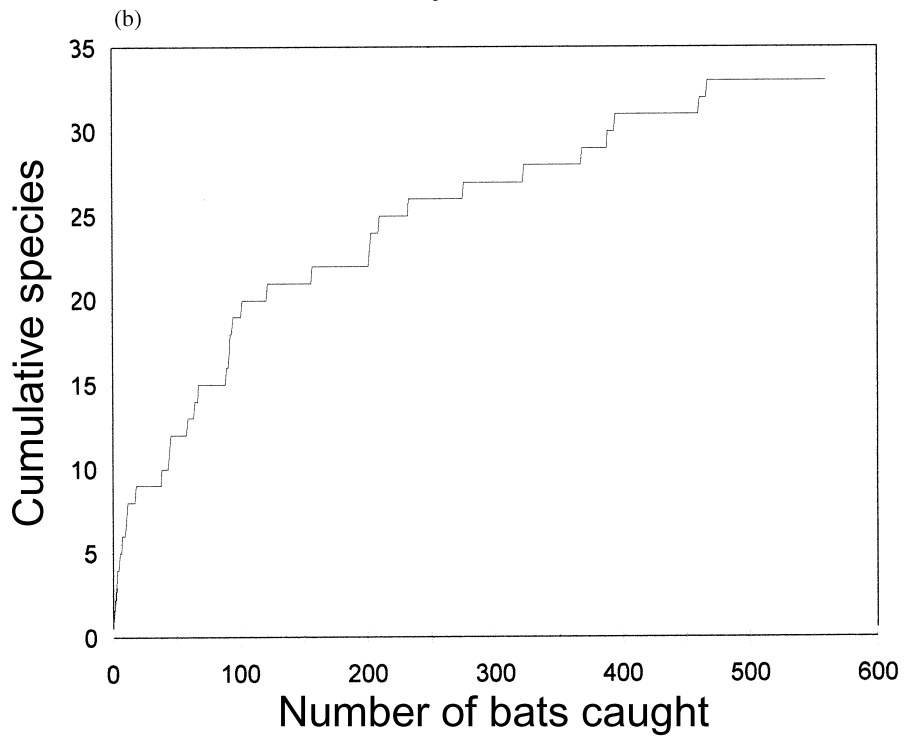
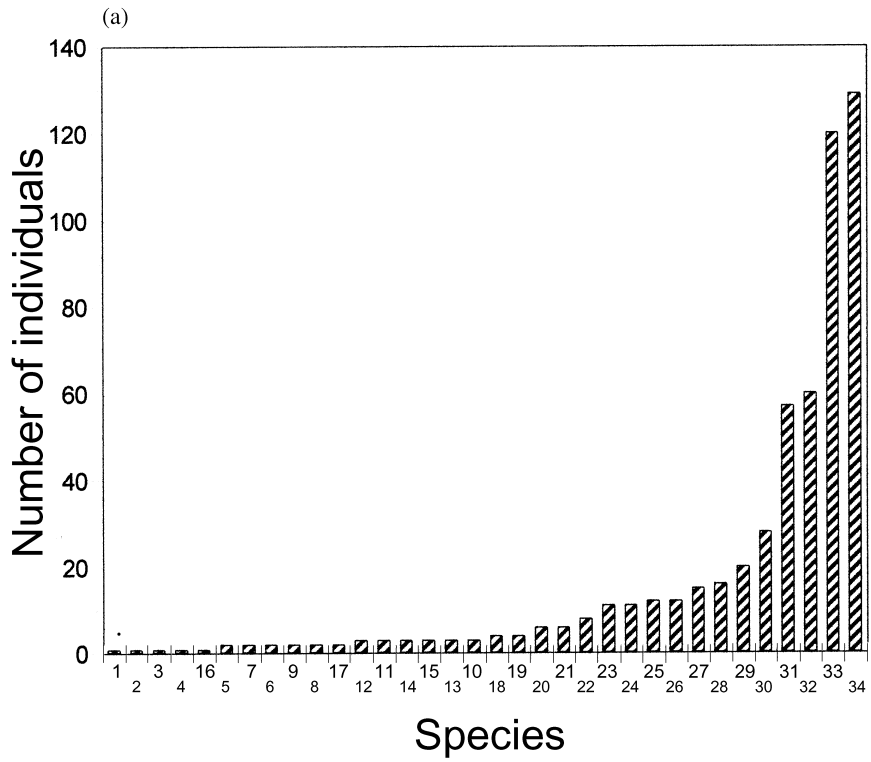
Table 1. Transmitters placed on bats, showing the species, age, sex, mass and forearm size (FA) of tagged bats. Also indicated is the date in January 2000 that the transmitter was applied and relative size of the transmitter (as a percentage of the bat's body mass).

Frequency	Weight of transmitter	Species	Age	Sex	Weight (g)	FA (mm)	%	Date applied	End date
173.103	0.63	<i>Platyrrhinus helleri</i>	a	m	16.8	40	3.75	10 –	12
173.123	0.64	<i>Centurio senex</i>	a	f	19.3	42.7	3.3	10 –	20
173.142	0.64	<i>Platyrrhinus helleri</i>	a	m	15.3	34.3	4.2	10 –	20
173.197	0.61	<i>Mimon bennettii</i>	a	m	25.2	55.7	2.4	14 –	20
173.224	0.6	<i>Mormoops megalophylla</i>	a	m	13.5	53.4	4.4	14 –	20
173.242	0.63	<i>Bauerus dubiaquercus</i>	a	m	15.7	50	4.0	14 –	20
173.265	0.64	<i>Pteronotus parnellii</i>	a	m	16.6	55.5	3.9	14 –	20
173.284	0.61	<i>Pteronotus parnellii</i>	a	m	17.2	56.6	3.6	14 –	20
173.302	0.62	<i>Centurio senex</i>	a	m	17.9	41.8	3.5	14 –	20
173.325	0.62	<i>Platyrrhinus helleri</i>	a	f	16.4	36.2	3.8	12 –	20
173.38	0.61	<i>Noctilio leporinus</i>	a	m	62	64.7	1	14 –	20
173.421	0.6	<i>Desmodus rotundus</i>	a	m	?	55	?	13 –	20

Table 2. Roosts used by specific bats. In the first part of the table we present the species and gender of tagged bats, along with the numbers of roosts used, the moves made between roosts, the distances involved and the tree species or vine tangles used as roosts. The data in the second part of the table do not come from individually tagged bats. Numbers in parentheses are number of trees followed by number of bats.

Species	Sex	Number of roosts	Number of moves	Distances (m)	Roosts
Part 1					
<i>Platyrrhinus helleri</i>	m	1	0	0	<i>Persea americana</i> (2 – 1);
	m	3	2	All < 100	<i>Acacia grandis</i> (3 – 1); <i>Guazuma ulmifolia</i> (2 – 1); <i>Dendropanax arboreus</i> (3 – 1)
	f	7	6	All < 100	<i>Stemmadenia donnell-smithii</i> (1 – 1); <i>Guazuma ulmifolia</i> (1 – 1); <i>Psidium guajava</i> (1 – 1); <i>Castilla elastica</i> (1 – 1); <i>Guazuma ulmifolia</i> (1 – 1); <i>Guazuma ulmifolia</i> (1 – 1)
<i>Centurio senex</i>	m	6	5	All < 100	<i>Ficus</i> spp. (3 – 1); <i>Swietenia macrophylla</i> (1 – 1); <i>Coccoloba cozumelensis</i> (1 – 1); <i>Vitex gaumeri</i> (1 – 1); <i>Swietenia macrophylla</i> (1 – 1); not found
	f	2	1	1,170	<i>Dendropanax arboreus</i> (1 – 1); <i>Ficus</i> spp. (4 – 1)
<i>Bauerus dubiaquercus</i>	m	1	0	0	<i>Swartzia cubensis</i> (5 – 1)
Part 2					
<i>Rhynchonycteris naso</i>					<i>Bucida buceras</i> ; <i>Bucida buceras</i> ; <i>Pachira aquatica</i>
<i>Diclidurus albus</i>	1				<i>Orbignya cohune</i>
<i>Micronycteris schmidtorum</i>	1				Unidentified hollow tree at water's edge

We located at least one day roost for 13 of the 36 species (Table 2), finding those of four species (*Sturnira lilium* (E. Geoffroy) (Fenton *et al.* in press); *P. helleri*, *C. senex* and *B. dubiaquercus*) only because individuals carried radio transmitters. But, radio transmitters do not guarantee finding day roosts, as five other species (*Noctilio leporinus*, *Mormoops megalophylla*, *Pteronotus parnellii*, *Mimon bennettii* and *Desmodus rotundus*) so tagged were not located in their day roosts in spite of persistent searching. Even though all of these radio-tagged individuals but *M. megalophylla* were active at night in the study area (as indicated



by changing bearings of signals from radio transmitters) we could not locate their roosts. In July and August 1999, a group of about eight *Mimon bennettii* roosted in a Chultun (underground Maya storage chamber), 1.3 km from where we caught and radio-tagged a *M. bennettii*. In July, nursing young were part of this colony. In January 2000, neither this Chultun nor another nearby (*c.* 500 m distant) harboured any day-roosting bats.

Other roosts were found by general searching or drawn to our attention by personnel of the Lamanai Outpost Lodge (Table 2). During the day, roosting *Saccopteryx bilineata* (Temminck) were commonly observed on walls under the eaves of some buildings at the Lodge, in a cistern or around the ruins of a sugar mill. A hollow tree (*Ceiba pentandra*) was used as a roost by a colony of *c.* 25 *S. leptura*. An unidentified hollow tree harboured one roosting *Micronycteris schmidtorum* Sanborn. A colony of about 20 *Eptesicus furinalis* (d'Orbigny) roosted in the space between a window frame and the wall in one of the Lodge buildings. During each of our visits to the area, two modern buildings at the museum complex at the Maya ruins housed colonies of *Glossophaga soricina* Pallas (*c.* 50) and *Carollia brevicauda* (Schinz) (*c.* 30), but both structures were bat-proofed in January 2000. It remains to be seen whether the bats continue to roost in these buildings.

We located three other roosts. Carlos Godoy drew our attention to a roosting *Diclidurus albus* Wied, while personnel from the Lodge showed us the locations of roosts used by *Rhynchonycteris naso* (Wied-Neuweid). While setting a mist net, one of us (JZ) disturbed a small vespertilionid roosting < 30 cm above the ground behind an old gear wheel at the ruins of a sugar mill. On four subsequent checks of the site, we did not find any more bats roosting there.

Radio-tagged individuals whose roosts we located provided a picture about the roosts used and the patterns of roost occupancy. Two species (*P. helleri* and *C. senex*) were similar in both respects and differed from *B. dubiaquercus*. We followed the three radio-tagged *P. helleri* for a total of 18 roost-days (Table 2). While one male used the same roost on two days, another male used three roosts in nine days, and the third, a female, a different roost on each of seven days. Radio-tagged individuals invariably roosted within or beneath tangles of vines and leaves. On one occasion we saw three individuals roosting together about 10 m above the ground beneath a disused bird's nest. The three bats

Figure 1. Two views of the bat fauna at Lamanai, the first (a) showing how the abundances of different species vary, the second (b) showing the cumulative numbers of species with bats captured. The species numbers for (a), are: *Bauerus dubiaquercus* - 1; *Trachops cirrhosus* - 2; *Micronycteris brachyotis* - 3; *Tonatia brasiliense* - 4; *Micronycteris schmidtorum* - 5; *Myotis keaysii* - 6; *Vampyressa pusilla* - 7; *Centurio senex* - 8; *Lasiurus ega* - 9; *Molossus ater* - 10; *Saccopteryx leptura* - 11; *Micronycteris microtis* - 12; *Artibeus watsoni* - 13; *Mimon bennettii* - 14; *Artibeus lituratus* - 15; *Mimon crenulatum* - 16; *Noctilio leporinus* - 17; *Mormoops megalophylla* - 18; *Tonatia evotis* - 19; *Eptesicus furinalis* - 20; *Uroderma bilobatum* - 21; *Myotis elegans* - 22; *Rhogeessa anaeus* - 23; *Desmodus rotundus* - 24; *Pteronotus davyi* - 25; *Saccopteryx bilineata* - 26; *Platyrrhinus helleri* - 27; *Carollia perspicillata* - 28; *Pteronotus parnellii* - 29; *Artibeus jamaicensis* - 30; *Carollia brevicauda* - 31; *Artibeus phaeotis* - 32; *Sturnira lilium* - 33; *Glossophaga soricina* - 34.

roosted with their noses together, their individual patterns of facial and dorsal stripes giving the impression of white lines radiating from a central point. The tangles usually involved vines associated with a variety of trees (Table 2). We followed the two radio-tagged *C. senex* for a total of 14 roost days (Table 2; male for 9 days, female for 5 days). The male used six roosts in 9 days, the female two roosts in 5 days. These bats also used tangles as day roosts and in spite of intensive searching of known roost tangles, we never saw one of them roosting. The roosts were 5–10 m above the ground and associated with a variety of trees (Table 2). The male *B. dubiaquercus* used the same hollow tree roost on each of 5 days (Table 2). The tree was 16 cm in diameter (breast height), and through the opening in the base we could see the roosting bat 1–1.5 m above the ground, apparently alone.

Radio-tagged bats also provided information about their patterns of habitat use and activity. *Platyrrhinus helleri* tended to leave their day roosts between 18h00 and 18h30 (mean 18h23) and typically interspersed short flights (fluctuating signals) with longer roosting periods (stationary signals). Over 1048 min of observation between 18h00 and 19h00 (61 min) and 18h00 to 00h00 (987 min) (spread over 4 nights), the radio-tagged female made 41 moves detectable from the High Temple, presumably associated with taking fruit and/or leaves. The radio-tagged males were active south of the temple complex and signals from their transmitters were not detectable from the High Temple. Most of the flight and roosting activity appeared to occur within the forested areas.

Radio-tagged *C. senex* left their day roosts on average at 18h32 (17:58 to 18:57) and spent much of the time until midnight relatively close to the High Temple (strong signals). In 2045 min of radio-tracking over three nights between 18h00 and 00h00, the two *C. senex* made a total of 109 moves, the female 62 and the male 47. Here, again, short flights (fluctuating signals) were interspersed with longer periods of roosting (stationary signals). Most of the flight and roosting activity appeared to occur within the forested areas.

Signals from the radio-tagged *Mimon bennettii* first appeared from the north and grew stronger as the bat approached the area of the temples. In three nights we were in contact with this bat for 651 min (between 18h00 and 00h00) and during this time the bat was mostly stationary, making only short flights (28 flights in 651 min). The radio-tagged *B. dubiaquercus* showed the same pattern of behaviour. Although this bat was netted at 18h05, on nights after capture and tagging it tended to leave the tree roost later (*c.* 19h00) and make only short flights. Signals from both of these species suggested that the tagged bats were active in the forested areas.

Radio-tagged *Pteronotus parnellii* typically flew into range between 18h15 and 18h30, on a steady bearing to the north. Signals from the transmitters on these bats were constantly changing bearings and fluctuating in strength, suggesting that the bats were flying while we were in contact with them. Once the bats were in the general area of the temples, the signals were from the east, apparently in the forested area. After tagging we only twice detected signals from

the radio-tagged *N. leporinus* and *D. rotundus* and were unable to locate the bats' day roosts.

Monitoring echolocation calls and direct observation indicated that *N. leporinus* and *R. naso* regularly foraged over the waters of the lagoon and tributary creeks even though these species were rarely (*N. leporinus*) or never (*R. naso*) caught in mist nets. Throughout the night we observed several individual bats foraging among insects attracted to lights at the lodge, and monitoring echolocation calls suggested that they were *Lasiurus ega* (Gervais), a species captured just twice. At the same time, monitoring echolocation calls suggested that *Eptesicus furinalis* also foraged over the lagoon, flying higher than either the *N. leporinus* or the *R. naso*. Along the trails at the Lodge itself, we often detected the echolocation calls of foraging *P. parnellii*, but did not detect these bats flying over the lagoon or near its edges. Monitoring echolocation calls at the edge of the lagoon indicated the regular presence of *Molossus ater* E. Geoffroy which produced distinctive, long, narrow-band echolocation calls (Fenton *et al.* 1998), but no other species.

DISCUSSION

Our sampling to 20 January 2000 at Lamanai indicated the presence of 36 of the 70 species of bats reported from Belize (McCarthy & Mendez 1998). We had first hand observations of the day roosts of 13 species, 35 when we include species for which roost data have been published from elsewhere (Table 3). In use of day roosts and in faunal structure based on size and trophic roles, the Lamanai fauna resembles that of Paracou, French Guiana (Simmons & Voss 1998) which has about twice as many species. In terms of numbers of species using different types of day roosts there are no significant differences between Lamanai and Paracou ($\chi^2 = 12.64$; $df = 10$; $P = 0.28$; $\chi^2 = 3.15$; $df = 9$; $P = 0.96$; if species for which there are no data are excluded). When the comparison of faunas includes the bats of Kruger National Park in South Africa (Smithers 1983), there are no significant differences in day roost types between the three areas ($\chi^2 = 18.65$; $df = 18$; $P = 0.42$ – excluding species for which there are no data) even though tent-making bats are absent from the African location.

Previous reports indicated that *P. helleri* uses a variety of roosts (Ferrell & Wilson 1991), from houses to hollow trees and palm foliage in Trinidad (Goodwin & Greenhall 1961) or culverts and caves in Mexico (Villa-R 1966). Our data on the roost sites of *C. senex* support the previous observation of these bats roosting in foliage (Jones *et al.* 1971, Rick 1968). The day roosts of *B. dubiaquercus* had not been previously reported (Engstrom *et al.* 1987).

In general our data on roost-occupancy by radio-tagged bats reflect the previously reported dichotomy between roost switching and roost fidelity (Lewis 1995). Like the foliage-roosting *Artibeus lituratus* and *Vampyrodes caraccioli* (Thomas) (Morrison 1980) and *Lasiurus borealis* (Müller) (Hutchinson & Lacki 2000), radio-tagged *P. helleri* and *C. senex* returned to foliage roosts in the same

Table 3. The species of the study area showing data on roost site selection either from this study and/or the literature. Species for which we found roosts in the study area are shown as +.

Species	Roost type	Roosts located/reported	Source
Emballonuridae			
<i>Diclidurus albus</i> +	foliage	under palm frond	this study, McCarthy (1987); Reid (1997)
<i>Rhynchonycteris naso</i> +	open	tree trunk/branch over water	this study, Simmons & Voss (1998), Plumpton & Jones (1992)
<i>Scaevoteryx bilineata</i> +	open/sheltered	sheltered areas, cistern	this study, Rick (1968), Yancey <i>et al.</i> (1998a), Simmons & Voss (1998), Reid (1997)
<i>Scaevoteryx leptura</i> +	open/sheltered	sheltered areas, trees vertical cavities – more exposed	this study, Simmons & Voss (1998), Reid (1997)
Noctilionidae			
<i>Noctilio leporinus</i>	hollows	hollows, trees, caves	Reid (1997), Hood & Jones (1984)
Mormoopidae			
<i>Mormoops megalophylla</i>	hollows	caves	McCarthy (1987), Rezsutek & Cameron (1993)
<i>Pteronotus daeyi</i>	hollows	caves, buildings	Adams (1989), Reid (1997)
<i>Pteronotus parnellii</i>	hollows	caves	Rick (1968), Herd (1983), Reid (1997)
Phyllostomidae			
<i>Artibeus jamaicensis</i>	tents, hollows, foliage	caves, trees	Reid (1997)
<i>Artibeus lituratus</i>	foliage	palm frond	Simmons & Voss (1998)
<i>Artibeus phaeotis</i>	foliage	under leaves, tents	Timm (1985)
<i>Artibeus vaosoni</i>	tents		Reid (1997)
<i>Carollia brevicauda</i> +	hollows	buildings, trees, caves, culverts	this study, Simmons & Voss (1998), Reid (1997)
<i>Carollia perspicillata</i> +	hollows	buildings, trees, caves, culverts	this study, Cloutier & Thomas (1992), Reid (1997)
<i>Centurio senex</i> +	foliage	tangles	this study, Rick (1968), Jones <i>et al.</i> (1971)
<i>Desmodus rotundus</i>	hollows	caves, trees, buildings	Greenhall <i>et al.</i> (1983)
<i>Glossophaga soricina</i> +	hollows	buildings, caves, trees, bridges	this study, Simmons & Voss (1998), Alvarez <i>et al.</i> (1991)
<i>Micronycteris brachyotis</i>	hollows	caves	Rick (1968), Medellín <i>et al.</i> (1985), McCarthy (1987), Reid (1997)
<i>Micronycteris microtis</i>	hollows	trees	Simmons & Voss (1998)
<i>Micronycteris schmidlorum</i> +	hollows	trees	This study
<i>Mimon hennetli</i> +	hollows	underground – Chulium; trees	this study, Rick (1968), Simmons & Voss (1998), Ortega & Arita (1997)
<i>Mimon crenulatum</i>	hollows	trees, buildings	Reid (1997)
<i>Platyrrhinus helleri</i> +	foliage	tangles, culverts, caves, buildings	this study, Goodwin & Greenhall (1961), Villa-R (1966)
<i>Sturnira litium</i>	foliage	vine tangles, tree hollows, palms	Fenton <i>et al.</i> (in press)
<i>Tonatia brasiliense</i>	hollows	in arboreal termite nests	Reid (1997)
<i>Tonatia evotis</i>	hollows	termite nests, building	Reid (1997)
<i>Trachops cirrhosus</i>	hollows	trees, logs	Rick (1968), Reid (1997)
<i>Uroderma bilobatum</i>	tents		Dickerman <i>et al.</i> (1981), Baker <i>et al.</i> (1987), Simmons & Voss (1998)
<i>Vampirosa pusilla</i>	tents		Reid (1997)
Vespertilionidae			
<i>Eptesicus furiatus</i> +	crevices	buildings, shutters, under bark	this study, Rick (1968), McCarthy (1987), Simmons & Voss (1998), Mies <i>et al.</i> (1996)
<i>Lasius ega</i>	foliage	mid rib of leaves, foliage	Kurita & Lehr (1995)
<i>Myotis elegans</i>	?		
<i>Myotis keaysii</i>	hollows	caves, trees	Reid (1997)
<i>Rhogeessa anaens</i>	hollows	trees, buildings	Reid (1997)
Antrozoidae			
<i>Bauerus dubiaquercus</i> +	hollows	tree	this study
Molossidae			
<i>Molossus ater</i>	crevices/hollows	buildings, caves, trees	Reid (1997), Renton <i>et al.</i> (1998)

general area day after day, but usually moved < 100 m between specific roost sites. In contrast, at Lamanai foliage-roosting *S. lilium*, like those using tree hollows or palm fronds, consistently used the same specific roost sites day after day (e.g. Fenton *et al.* 2000). In its roost fidelity, *B. dubiaquercus* resembled some other species that roost in hollows, repeatedly using the same roost, unlike others that often move between such roosts (reviewed by Lewis 1995).

The data on bats' day roosts at Lamanai together with published information (Table 3) generally support broad classifications of bats' day roosts. For example, Kunz (1982) proposed caves, crevices, tree cavities, as well as foliage and other external sites as the main categories of bats' day roosts. Our arrangement of day roosts of bats (Tables 3, 4) generally follows Kunz (1982) although we treat hollows as one category (whether in rock, trees or buildings) because so many species roost across this spectrum of structures (e.g. Table 3, see also Reid 1997, Simmons & Voss 1998). We also use the categories crevices and foliage, distinguishing tents from foliage, and the open roosting situations used by *R. naso* from the open yet more sheltered roost sites often used by other emballonurids such as *Saccopteryx* spp., *Peropteryx* spp. or *Centronycteris* spp. (Table 3 and Simmons & Voss 1998).

The day roost categories presented in Table 4 generally resemble those of Verschuren (1957) in that they consider the degree of isolation from the macrohabitat. But we have not considered the degree of bodily contact between roosting bats (not in contact versus in contact) or the setting (phytophilus, lithophilus and anthropophilus – Verschuren 1957). Our arrangement of bats' day roosts is closer to that of Gaisler (1979) who recognized free roosting sites; tree and other natural holes and crevices, underground cavities; buildings; and permanent versus temporary roosts.

Most species of bats at Lamanai and Paracou (and in Kruger National Park) roost in hollows, whether in rock, trees, or buildings, with foliage roosts a distant second or third; at least two species roost in foliage and in tents (Table 4). Roosts such as hollows and crevices that provide thermal benefits offer a clear advantage to bats as illustrated by the comparison of the growth rates of the young of foliage-roosting versus hollow-roosting bats (Koehler & Barclay 2000). Crevices are commonly used roost sites, while fewer species use more than one type of day roost (*A. jamaicensis* uses day roosts ranging from hollows in trees or caves to foliage and tents – Morrison 1979, 1980; Ortega & Arita 1999) or roost in the open (*R. naso*, *D. albus*). In *A. jamaicensis*, the use of a range of roosts coincides with differences in the social structure of roosting groups (Ortega & Arita 1999). A potential disadvantage of hollows as roosts is infestation by ectoparasites (Lewis 1996) but the real impact of this remains unknown.

Are roosts limiting factors for bats? Some evidence suggests that the answer is 'yes'. By collecting bats from roosts at Paracou and revisiting the roost sites and collecting other bats there, Simmons & Voss (1998) found that some roosts from which *Peropteryx kappleri* Peters were removed were then used by other

Table 4. A comparison of the day roost situations and foraging habits of bats at Lamanai (this study) and from Paracou, French Guiana (Simmons & Voss 1998), and Kruger National Park, South Africa (Smithers 1983).

	Numbers of species		
	Lamanai	Paracou	Kruger
Roosting			
hollows	19	27	12
foliage	6	7	2
sheltered	2	8	1
open	1	1	0
tents	3	4	0
crevices	2	1	3
hollows/crevices	1	4	6
hollows/foliage	1	1	1
hollows/foliage/tents	1	1	0
unknown	1	19	10
Foraging			
Aerial feeders			
< 10 g	8	14	19
11–20 g	4	7	7
> 20 g	1	5	7
Gleaners			
< 10 g	3	8	3
11–20 g	3	3	2
> 20 g	2	11	2
Fruit/leaves			
< 10 g	3	2	0
11–20 g	5	10	0
>20 g	3	5	2
Nectar			
c. 10 g	1	5	0
Blood			
c. 30 g	1	2	0

species (*Cormura brevirostris* (Wagner), *Peropteryx macrotis* (Wagner)), while at other roosts *Peropteryx leucoptera* Peters was replaced by *C. brevirostris*. Tents initially occupied by *Ectophylla macconnellii* were later used by *Rhinophylla pumilio* Peters and some hollows were simultaneously used by mixtures of species (e.g. *Rhynchonycteris naso*, *Glossophaga soricina*, *Carollia perspicillata*, *Macrophyllum macrophyllum* (Schinz), *Trachops cirrhosus* (Spix), *Micronycteris microtis* and *Mimon bennettii*), a common phenomenon when the roosts are large hollows (Kunz 1982).

As noted above, in terms of roost types used, there was no significant difference between the bat faunas at Lamanai, Paracou and Kruger National Park in South Africa. When this comparison is extended to the dietary roles, the Lamanai and Paracou faunas do not differ significantly in size and diet ($\chi^2 = 6.16$; $df = 10$; $P = 0.80$), but the Kruger fauna differs significantly from them both in both parameters ($\chi^2 = 32.78$; $df = 20$; $P = 0.036$), mainly because of the preponderance of small (< 10 g) and large (> 20 g) aerial insectivores there.

This difference suggests that the increase in bat diversity towards the equator (Wilson 1973, Wilson 1974) reflects diet more than roosting behaviour.

The evidence suggests that differences in foraging behaviour and diet may better explain the diversity of bats than the variety of day roosts used in any area.

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