

Consistency and variation in the bat assemblages inhabiting two forest islands within a neotropical savanna in Bolivia

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Abstract: Neotropical bats occupy a large variety of trophic niches, and represent locally abundant, species-rich communities. As such they are highly suited as a model group for the study of temporal and spatial dynamics of animal communities. However, despite this important research potential, data on the dynamics and turnover rates of Neotropical bat communities are lacking. We here study both aspects for bats inhabiting two natural forests surrounded by savanna in Bolivia. Over a period of 8 y, both bat communities showed high rates of species turnover. As predicted, species relying on fluctuating food resources were more likely to be absent in particular years, whereas species relying on more predictable food supplies were present in all years.

Key Words: chiroptera, community, Neotropics, turnover

INTRODUCTION

Since the early development of theoretical models in ecology (MacArthur & Wilson 1967), the temporal and spatial dynamics of animal communities have attracted the interest of many population biologists (Cornell & Lawton 1992, Fox 1990, Nichols *et al.* 1998). While the total number of species belonging to a community is often relatively constant in time, species composition is likely to change as some populations become extinct and are replaced by others (Russell *et al.* 1995, Wright 1985). Despite this intrinsic importance, detailed information on temporal and spatial patterns in community structure is scarce (Davis *et al.* 1999, Laurance & Bierregaard 1997, Morris 1990). Moreover, the available data are strongly biased towards birds (Boulinier *et al.* 2001, Holmes & Sherry 1986, Howlett *et al.* 2000, Karr *et al.* 1990, Terborgh *et al.* 1990, Thiollay 1994, Williamson 1983) and rodents (Brown & Heske 1990, Fox 1990, Lynam 1997), two groups for which substantial ecological and behavioural information is available and that can be captured fairly easily.

However, other groups such as Neotropical bat species are equally suited for the development of community ecological theory, for two reasons: (1) they represent a species-rich community; and (2) they occupy a large variety of trophic niches (Arita 1997, Crome & Richards 1988,

Humphrey *et al.* 1983, Willig & Moulton 1989). Several studies have demonstrated high diversity of bats in the Neotropics, with single sites hosting up to 70 species (Brosset *et al.* 1996, Handley *et al.* 1991, Koepcke 1987, Lim & Engstrom 2001, Medellín 1993, Patterson *et al.* 1996, Timm *et al.* 1989). Such diversity can be achieved and maintained mostly through an intricate partitioning – both temporally and spatially – of the available resources, and both processes are assumed to be major factors structuring Neotropical bat communities (Arlettaz *et al.* 1997, Bonaccorso 1979, Findley & Black 1983, Fleming 1986, Fleming *et al.* 1972; Heithaus *et al.* 1975, Kalko 1997, Willig 1986). Neotropical bats are further recognized as important regulators of complex ecological processes such as seed dispersal, pollination and as control of insect populations (Bonaccorso 1979, Fenton *et al.* 1992, Findley 1993, Fleming *et al.* 1972, Humphrey *et al.* 1983, LaVal & Fitch 1977, Medellín 1993, Ochoa 2000, Wilson 1973). Yet, despite their importance, little is known of the dynamics of Neotropical bat communities, especially over longer time periods (see Kalko *et al.* 1996).

Bonaccorso (1979) showed that in tropical ecosystems the great variety of food items available year-round together with habitat heterogeneity might explain the abundant number of bat species. Moreover, species relying on food resources that change over time might be more likely to be absent in particular years, probably due to temporal availability of the preferred food resource. Here we report on an 8-y study of temporal variation in bat communities inhabiting two forest islands within a

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neotropical savanna. Because species that rely on food resources that change dramatically between seasons (especially fruit and insects) are more likely to be absent in particular years, we specifically test the hypothesis that turnover rates differ between trophic guilds. We further examine the consequences of species dynamics on shaping the community in the two natural forest islands.

STUDY SITE

We studied bats in the Espiritu Wildlife Refuge (EWR), a seasonally flooded savanna interspersed with small forest islands located in the central north of the Llanos de Moxos, Beni, Bolivia (66°24'W, 14°8'S) (Hanagarth 1993). We sampled individuals at the two largest forest islands from which we had consistent information over a long period of time, Espiritu Viejo (12 ha) and Espiritu (7 ha) during August 1992, August 1995 and August 2000. This month was selected as representative of the dry season and results and discussions should be viewed as results of that season only. Collecting bats in both seasons is extremely difficult due to extensive flooding in the area. The distance between Espiritu and Espiritu Viejo is sufficiently large (> 4 km) to assume that the two islands constitute independent sampling units. Both forests had comparable vegetation structure with typical evergreen species (e.g. *Ficus* and *Cecropia*) and open undergrowth due to extensive grazing (Beck 1983) that was consistent throughout the study period. Baseline ecological data of the study area were presented in Aguirre (1994).

METHODS

Sampling

We used a standardized method described by Medellín (1993) and adjusted to the savanna ecosystem (Aguirre 1996) that allows us to have a good representation (>80%) of the community living there. To sample bats, we set five 6-m mist nets at ground level in the forest. To avoid habituation, nets were moved to different locations every second day at least 5 m away from the previous place. During each capture session (5–10 nights), mist nets were opened at dusk (18h30) and closed after midnight (02h00). Upon capture, bats were identified using field keys (Aguirre & Anderson 1997, Anderson 1997) (Table 1). A sample of bats was preserved as museum voucher specimens and deposited at the Colección Boliviana de Fauna of the Museum of Natural History of La Paz.

To examine whether the sampling scheme was adequate to quantify species compositions, we calculated the cumulative number of captured species (Moreno & Halffter 2000) for each forest island in relation to the number of capture sessions (Figure 1). To eliminate the influence of

the order in which nights were added to the total, we computed 1000 randomized species accumulation curves with the program EstimateS 5 (Colwell 1999, Colwell & Coddington 1994) and fitted the reordered data with a linear dependence model based on the equation: $S = (a/b)(1 - e^{-bt})$, where S is the species richness of the community at time t , a represents the rate of increase, b is species accumulation and a/b is the predicted asymptote. This equation permits an estimation of the total number of species in the community and is recommended for situations where the taxon is well known or the study area is relatively small and could reach an asymptote over a finite period of time (Soberón & Llorente 1993). The completeness of our inventory was assessed by calculating the proportion of the maximum number of species (asymptote) registered at the end of sampling. The model fitted well in all cases ($r^2 > 0.89$) and we obtained more than 80% of the total fauna for every year showing that our bat communities were well sampled allowing us further comparisons (Table 2). Accumulation curves differed between years, both in Espiritu ($F_{2,18} = 4.35$; $P = 0.028$) and Espiritu Viejo ($F_{2,16} = 29.7$; $P < 0.001$). The number of species collected per night did not differ between years in any of the forest islands (Espiritu: $F_{2,18} = 0.62$ and $P = 0.54$; Espiritu Viejo: $F_{2,18} = 0.94$; $P = 0.41$). We therefore conclude that our capture data accurately reflect the species compositions in the forest islands of Espiritu and Espiritu Viejo.

Analysis of species abundance and turnover

We constructed rank-abundance curves (Magurran 1988) to examine species abundance data for each of the three study years (after \log_{10} -transformation of the number of individuals per species). To estimate temporal variation in species composition, we applied a turnover rate (Diamond 1969, Mühlberg 1993) by calculating $T = (J+E)/(S_1+S_2)$, where J is the number of species found in the second but not in the first year of each time interval over which temporal variation was studied (i.e. 1992–1995 and 1995–2000), E the number of species found in the first but not in the second year, and S_1 and S_2 the total number of species during both years. Values of turnover rate vary from none (0) to complete turnover (1). This index is similar to the 'beta turnover' by Wilson & Schmida (1984) and the 'apparent turnover' index by Russel *et al.* (1995). In a first analysis, we calculated turnover rates for all species pooled by forest island. In a second analysis, we grouped species into trophic guilds according to observations of their diet in the study area (Aguirre 1994) and available literature data (Bonaccorso & Humphrey 1984, Kalko *et al.* 1996, Willig 1986, Willig *et al.* 1993). We thereby excluded the following cases: (1) species belonging to guilds that comprised a single member only (i.e. carnivor-

Table 1 Species of bats captured in the two largest forest islands of Espiritu Wildlife Refuge. The nomenclature follows Anderson (1997) and species within each family of bats are ordered alphabetically. Ia¹ = aerial insectivores; Ig² = gleaning insectivorous; P = piscivorous; F = frugivorous; S = sanguivorous; N = nectarivorous; O = omnivorous; C = carnivorous

	Acronym	Trophic guild	Espiritu			Espiritu Viejo		
			1992	1995	2000	1992	1995	2000
Emballonuridae								
<i>Peropteryx kappleri</i>	PK	Ia				1		
<i>Peropteryx macrotis</i>	PM	Ia					1	
<i>Saccopteryx bilineata</i>	SB	Ia					1	1
Noctilionidae								
<i>Noctilio albiventris</i>	NA	Ia	4	4	18	6	3	4
<i>Noctilio leporinus</i>	NL	P			26	3	3	
Phyllostomidae								
<i>Artibeus jamaicensis</i>	AJ	F		4	21	12	4	8
<i>Carollia perspicillata</i>	CP	F	4			4	7	2
<i>Chiroderma salvini</i>	CS	F	1					
<i>Desmodus rotundus</i>	DR	S				6	2	3
<i>Glossophaga soricina</i>	GS	N	6	10	7	1		
<i>Mimon crenulatum</i>	MC	Ig					8	5
<i>Micronycteris minuta</i>	MI	Ig				2		5
<i>Phyllostomus discolor</i>	PD	O	1				3	14
<i>Phyllostomus elongatus</i>	PE	O			5	5	18	
<i>Phyllostomus hastatus</i>	PH	O		3	3	5		
<i>Platyrrhinus lineatus</i>	PL	F	9	9		3	8	
<i>Sturnira lilium</i>	SL	F			1			7
<i>Tonatia sylvicola</i>	TS	Ig			2			5
<i>Vampyrum spectrum</i>	VS	C					1	
Vespertilionidae								
<i>Eptesicus furinai</i>	EF	Ia			1	11		
<i>Myotis albescens</i>	MA	Ia		1	5			
<i>Myotis nigriceps</i>	MN	Ia	31		2	2		
<i>Myotis simus</i>	MS	Ia			1	1	1	
Molossidae								
<i>Molossus molossus</i>	MM	Ia		1	18	1		
<i>Molossus rufus</i>	MR	Ia		1	1			
<i>Molossops temminckii</i>	MT	Ia	1					

¹ Hunting for insects while flying in open space.

² Hunting for insects over the foliage or on the ground

ous, nectarivorous and piscivorous species); and (2) species that were sampled only once (i.e. most of the insectivorous species that forage on very open areas or high above the canopy of the forest islands such as all the species belonging to the families Molossidae and Emballonuridae, as well as the fruit-eating *Chiroderma salvini*). After exclusion, the following four guilds were retained: frugivores (four species), omnivores (three species), gleaning insectivores (three species) and aerial insectivores (five species). To test whether turnover rates differed between trophic guilds, we performed mixed regression analysis (in SAS 612; Littell *et al.* 1996) with turnover rate (arcsine-transformed) as dependent variable, trophic guild as fixed effect and forest island as random effect. We added period as fixed effect to correct for the unequal length of the time intervals over which turnover rates were calculated (see above). Degrees of freedom were approximated by the method of Satterthwaite (Verbeke & Molenberghs 1997). We performed a *post hoc* test (Tukey-Kramer) to detect which guilds, if any, significantly differed in turnover rates.

RESULTS

Species composition and abundance

We captured a total of 387 individuals belonging to 26 species of bat (Table 1). Of these, 22 species were captured in Espiritu Viejo and 18 species in Espiritu. Despite the high number of species in Espiritu Viejo, more individuals were captured in Espiritu (211 vs. 176 in Espiritu Viejo), mainly due to the high number of *Myotis nigriceps* (31) (in 1992) and of *Noctilio leporinus* (26 individuals) (in 2000). When pooling aerial and gleaning insectivorous species, a higher number of individuals was captured in Espiritu (101) than Espiritu Viejo (57), whereas the latter forest island held a higher number of insectivorous species (13 species against 9 in Espiritu). Forty-two per cent of bat species captured in Espiritu belonged to the guild of aerial insectivores (i.e. vespertilionids, molossids and *Noctilio albiventris*). In Espiritu Viejo they comprised 36% of the overall community. Together with the carnivorous bat (*Vampyrum spectrum*), two species of gleaning insectivorous bats (*Mimon crenulatum*, *Micronycteris*

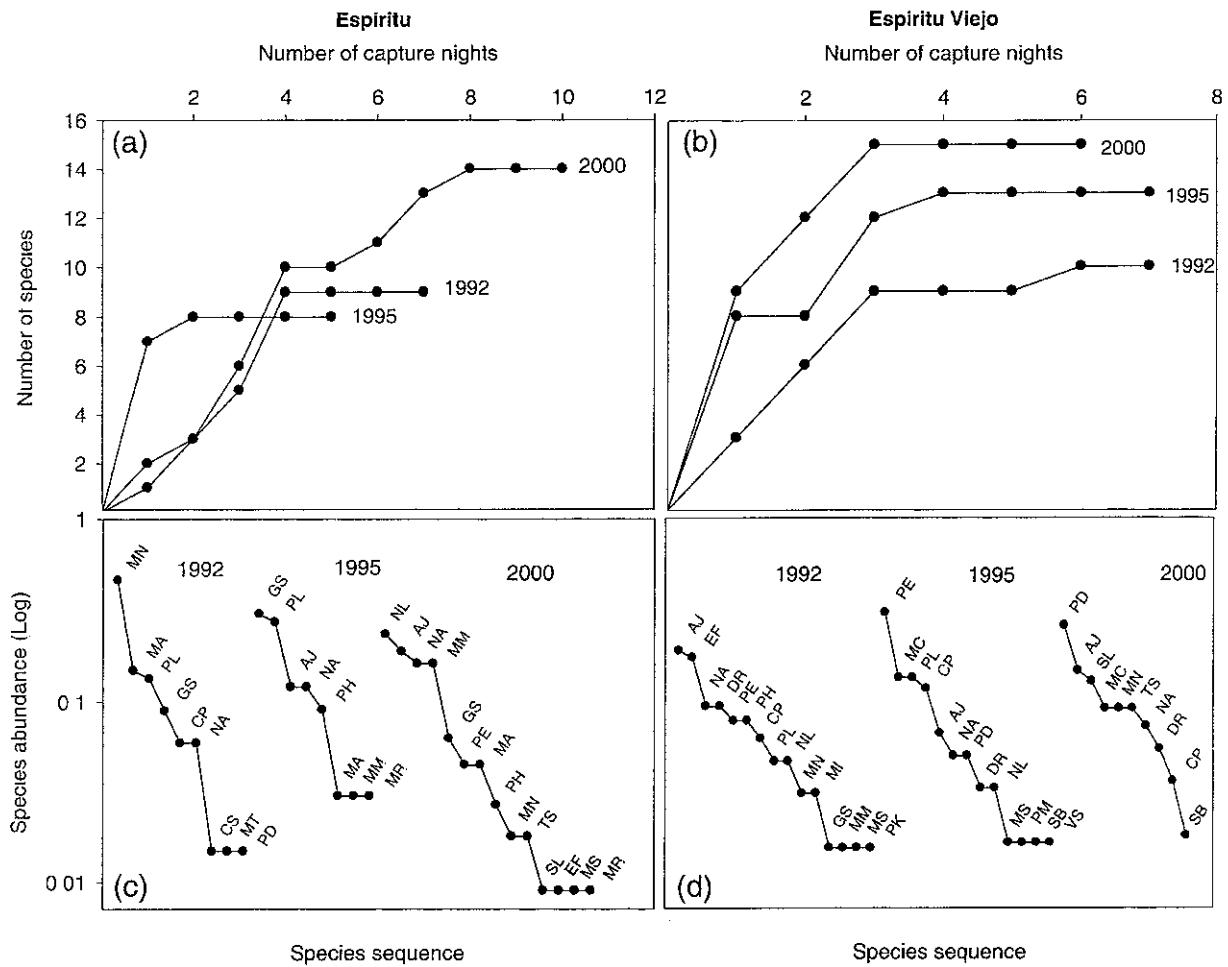


Figure 1 Accumulation curves (a, b) and rank–abundance distributions (c, d) of 26 bat species during three study periods in two neotropical forest islands. Species acronyms are explained in Table 1

Table 2. Number of captured species per forest fragment per year, where *a* and *b* are parameters of the linear dependence model *a/b* is the predicted asymptote. *r*² is the coefficient of determination (Soberón & Lorente 1993).

Forest island	Year	Total species observed	<i>a</i>	<i>b</i>	<i>a/b</i>	<i>r</i> ²	Per cent of the asymptote recorded
Espiritu	1992	9	7.03	0.69	10.1	0.93	87.7
	1995	8	6.53	0.68	9.6	0.89	82.9
	2000	14	7.10	0.45	15.7	0.97	89.3
Espiritu Viejo	1992	15	12.2	0.73	16.7	0.91	89.8
	1995	13	12.4	0.87	14.2	0.96	91.7
	2000	10	9.88	0.92	10.8	0.94	92.9

minuta) were found in Espiritu Viejo only, while another gleaning insectivorous species (*Tonatia sylvicola*) was found in both forests islands. Omnivorous species were more common in Espiritu Viejo in number of individuals (45 compared to 12 in Espiritu).

Species turnover

For all bat species pooled, turnover rates were 0.53 (period 1992–1995) and 0.36 (1995–2000) in Espiritu and 0.43 (1992–1995) and 0.69 (1995–2000) in Espiritu Viejo

Table 3 Turnover rates per trophic guild in two forest islands of Espiritu Wildlife Refuge. S = total species richness combined for all years; G insectivorous = gleaning insectivorous; A insectivorous = aerial insectivorous (see text for details)

Bat guild	S	Turnover rate			
		Espiritu Viejo		Espiritu	
		1992–1995	1995–2000	1992–1995	1995–2000
Frugivorous	4	0	0.33	0.5	0.5
Omnivorous	3	0.5	0.33	1	0.33
G insectivorous	3	1	0.5		1
A. insectivorous	5	0.33	0.33	0.2	0.43

Within the forest-dwelling species, frugivores were more stable (mean turnover rate \pm SE: 0.43 ± 0.13) than omnivores (0.64 ± 0.13) and gleaning insectivores (0.97 ± 0.15), while aerial insectivorous species showed the lowest turnover rates (0.42 ± 0.13). Turnover rates differed significantly between trophic guilds ($F_{3,10} = 4.14$; $P = 0.0378$; Table 3), whereas the factors 'period' and 'forest island' did not explain additional variation (period: $F_{1,10} = 2.88$; $P = 0.12$; forest island: $\chi^2_1 = 0.00$; $P = 1.0$). *Post hoc* comparisons showed significant differences in turnover rate between frugivores and gleaning insectivores ($P = 0.049$), and between gleaning and aerial insectivores ($P = 0.045$).

DISCUSSION

The suite of bat species analysed in this paper represents a large fraction (*c.* 70%) of the community described for Llanos de Moxos (Aguirre *et al.* 1996; Table 1). The total number of species in EWR (37) follows the same pattern of species richness found for other similar habitats in South America (Bernard *et al.* 2001, Ibañez 1981, Willig 1986) but is less species-rich than forested habitats (Lim & Engstrom 2001, Patterson *et al.* 1996). Most of the captured species belong to the family of New World leaf-nosed bats (Phyllostomidae), which are generally strongly associated with forested areas (Fenton *et al.* 1992). A smaller proportion belong to the family of free-tailed bats (Molossidae), which are known to forage in open and uncluttered areas high above the canopy (Kalko 1997). It is important to notice, however, that these results are showing the structure of the bat community inhabiting this savanna during the dry season.

While the overall species richness was high, the total numbers of individuals captured was low for most species. The latter was reflected by the long tails of the rank-abundance curves (Figure 1), indicating that for several species no firm conclusions on their actual abundance could be drawn (Murray *et al.* 1999). This was true for all species of the Molossidae and Emballonuridae, probably as a result of the broken canopy of the forest islands (Cosson *et al.* 1999). Gaps in the canopy occasionally attract bats from both families while foraging, and subsequently allow small numbers to be captured (Crome & Richards 1988, Medellín *et al.* 2000). Other species for

which numbers may have been underestimated include some of the vespertilionids (*Myotis albescens*, *Myotis simus* and *Eptesicus furinalis*) and phyllostomids (*Chiroderma salvini*, *Glossophaga soricina*, *Phyllostomus hastatus*, *Sturnira lilium* and *Vampyrus spectrum*). For other species, however, their position in the tails of the species rank-abundance curves may reflect their 'true' rare status, but such species mostly do not significantly contribute to community assemblages (see Willig 1986 for similar conclusions when characterizing Caatinga and Cerrado biomes).

Bat communities in Espiritu and Espiritu Viejo were characterized by high rates of species turnover, sometimes of a complete change of species. Abundant species in the first sampling year were either present in low numbers or completely absent during subsequent years (e.g. *Myotis nigricans*). Similarly, species that were absent early in the study became abundant later (e.g. *Noctilio leporinus*). As expected, species relying on food resources that change over time (e.g. fruits) were more likely to be absent in particular years, probably due to temporal availability of the preferred food resource (Bonaccorso 1979). In contrast, species relying on more permanent (predictable) food supplies (such as aerial insects) were present all years. The high turnover in gleaning insectivores suggests that forest islands in EWR do not contain sufficient food to allow permanent residency. The more stable species composition of frugivorous bats, on the other hand, might have resulted from the fruiting of high numbers of fig trees during August in the three study years. As bat communities were sampled during 1 mo per year only, it is likely that short-term fluctuations in food availability caused even higher turnover rates, i.e. within 1-y periods (Bonaccorso 1979, LaVal & Fitch 1977).

Several studies have demonstrated that species richness in large (> 12 ha) man-made forest fragments is very high but that fragmentation affects most of the bat species that depend on pristine habitats. These forest-interior species (mostly gleaning insectivorous bats such as those from the genus *Tonatia* or *Micronycteris*) will be replaced by more general and opportunistic fruit-eating bat species living in semi-open areas such as *Artibeus jamaicensis*, *Carollia perspicillata* or *Sturnira lilium* (Estrada *et al.* 1993, Fenton *et al.* 1992, Medellín *et al.* 2000). On the other hand, Brosset *et al.* (1996) found that deforestation lowers

species richness favouring the presence of opportunistic frugivorous phyllostomid species. In the case of natural forest islands of Espiritu, a high number of bat species exploit those habitats over time but with very few individuals per species. Only one opportunistic species (*Artibeus jamaicensis*) is very common in the forest islands analysed in Espiritu but the low numbers of others (such as *Carollia perspicillata*, *Sturnira lilium* or the nectarivorous bat *Glossophaga soricina*) is remarkable. Cosson *et al.* (1999) found that fragmentation affects understory frugivores (*Carollia perspicillata* and *Sturnira lilium*) and that they are more sensitive than canopy frugivores (*Artibeus jamaicensis*). Instead of those opportunistic frugivorous species in the savanna, omnivorous bats (all from genus *Phyllostomus*) are very high in numbers and occurring every year. From all of these observations we can conclude that natural forest fragments in the savanna of Espiritu (i.e. forest islands ≤ 12 ha) are likely to follow the same patterns as those described for large fragments. The study of natural forest islands embedded in a savanna matrix might be important to understand the response of bats in man-made fragmented tropical landscapes.

The turnover results in this work could be viewed as a complex compound of estimations that might be reflecting variance in bats present year to year in a given fragment, variance between years in forest phenology and variance in number of catchable species. It is important to notice, however, that even with these limitations, this study wants to pose a novel approach to the study of bat communities and its importance to understand their structure in the long term.

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