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Bat community structure at Iwokrama Forest, Guyana

BURTON K. LIM[1] *and* MARK D. ENGSTROM

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada, M5S 2C6

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ABSTRACT. With 86 species, Iwokrama Forest in central Guyana has the highest reported bat biodiversity for a protected area in the world. Using standardized capture data for 73 of these 86 species, we document community structure of bats in terms of species diversity, relative abundance, gross biomass, feeding guilds, vertical stratification and a trophic–size niche matrix. Based on faunal surveys in 1997, with similar amounts of effort in the forest canopy and at ground level, the greater fruit-eating bat (*Artibeus lituratus*) was by far the most ecologically dominant species in terms of frequency of capture and biomass. In total, frugivores comprised 70% of the species diversity and 78% of the biomass. The most common species of bat were fully partitioned in a resource niche matrix of size and trophic guild when vertical stratification was included as a variable. We conclude that resource partitioning and species packing differentially affect relative size in tropical bats, and are better summarized and analysed in three dimensions.

KEY WORDS: biomass, feeding guilds, niche matrix, relative abundance, species diversity, vertical stratification

INTRODUCTION

Few studies have documented community structure of bats in lowland tropical rain forest sites in South America. In comparison to some non-volant mammals, bats have been more difficult to investigate because of a combination of factors including flight, nocturnal behaviour, larger and shifting home ranges, and high species diversity coupled with relative taxonomic uncertainty for some groups. In addition, few field studies of bat diversity have made a concerted effort to survey the canopy for bats because of logistical difficulties in sampling. Exceptional studies, however, employed canopy netting including Handley (1967) in Amazonian Brazil, Bonaccorso (1979) in Panama, Ascorra *et al*. (1996) in Peru and Simmons & Voss (1998) in French Guiana.

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[1] To whom correspondence should be addressed.

Species diversity and relative abundance are commonly used to assess the composition and importance of species within an area. A good measure of the ecological impact of organisms on the ecosystem is to determine the biomass for species and feeding guilds. Although there are many interrelated factors involved in determining bioenergetics such as basal metabolic rate, body size, feeding behaviour and ecological parameters, the general premise is that larger animals require more food and space so therefore will have a greater impact on the environment than smaller animals. There have been several studies on the community biomass of non-volant mammals in the neotropics (Eisenberg & Thorington 1973, Eisenberg *et al*. 1979, Janson & Emmons 1990, Peres 1999) but we are aware of only one study where total bat community biomass was calculated (Pirlot 1964).

As with other organisms, most field studies of bats are concerned with autecology or the survey of alpha- or gamma-level taxonomic diversity. There have been, however, a few studies on bat community structure based on the trophic–size niche matrix developed by McNab (1971) using the common bats from Trinidad (Goodwin & Greenhall 1961). Delineation of cells within this matrix, however, was coarse and subjective because the food habits of many species are incompletely known. Size classes were also arbitrarily chosen with the range of each successive size class doubled to account for the logarithmic phenomenon of many more smaller species of bat than larger ones. Despite these deficiencies, niche matrices have proven informative in summarizing bat community structure at two localities in the Panama Canal Zone and one in western Costa Rica (Fleming *et al*. 1972), on Margarita Island and the northeastern mainland of Venezuela (Smith & Genoways 1974), at three sites in Costa Rica (LaVal & Fitch 1977), and two semi-arid communities in northeastern Brazil (Willig 1986).

The objective of this study is to characterize bat community structure of one of the most completely inventoried sites in the neotropics, namely Iwokrama Forest in central Guyana (Lim *et al*. 1999, Lim & Engstrom 2001) by biomass, vertical stratification, and trophic–size niche, in addition to species diversity and abundance. Biomass studies of mammalian communities have not included estimates for bats, and the community organization of bats based on a niche matrix has not been thoroughly evaluated for a lowland wet tropical forest site in South America. We test McNab's (1971) two-dimensional feeding guild–body size niche matrix, wherein he predicted that only one common species should occupy each cell in the matrix, but expand it to include the spatial dimension of vertical stratification.

The progressive urgency associated with shrinking tropical rain forests makes it increasingly important to characterize the community structure of bats to assess their ecological impact on the environment as seed dispersers, pollinators, and controllers of insect populations in mature forest. For example, in Guyana, the seeds of many plants are thought to be dispersed by fruit-eating bats (Polak 1992) but which species and how are unknown.

In terms of species diversity, bats are usually the dominant group of tropical mammals, typically accounting for over half of the total number of species at any one site. Basic biological information such as food resources are not known for most species so their role and impact on the ecosystem is likewise unknown. Changes in community structure, species diversity, and relative importance of individual species may also serve as important indicators of environmental change. Species richness and community structure of bats should, therefore, be considered in plans for sustainable use and conservation.

STUDY SITE

Iwokrama Forest is located in central Guyana on the northeast coast of South America (Figure 1). This protected area is unique in the region because the government of Guyana in 1989 offered it to the British Commonwealth Secretariat to establish an economically viable but environmentally sound sustainable

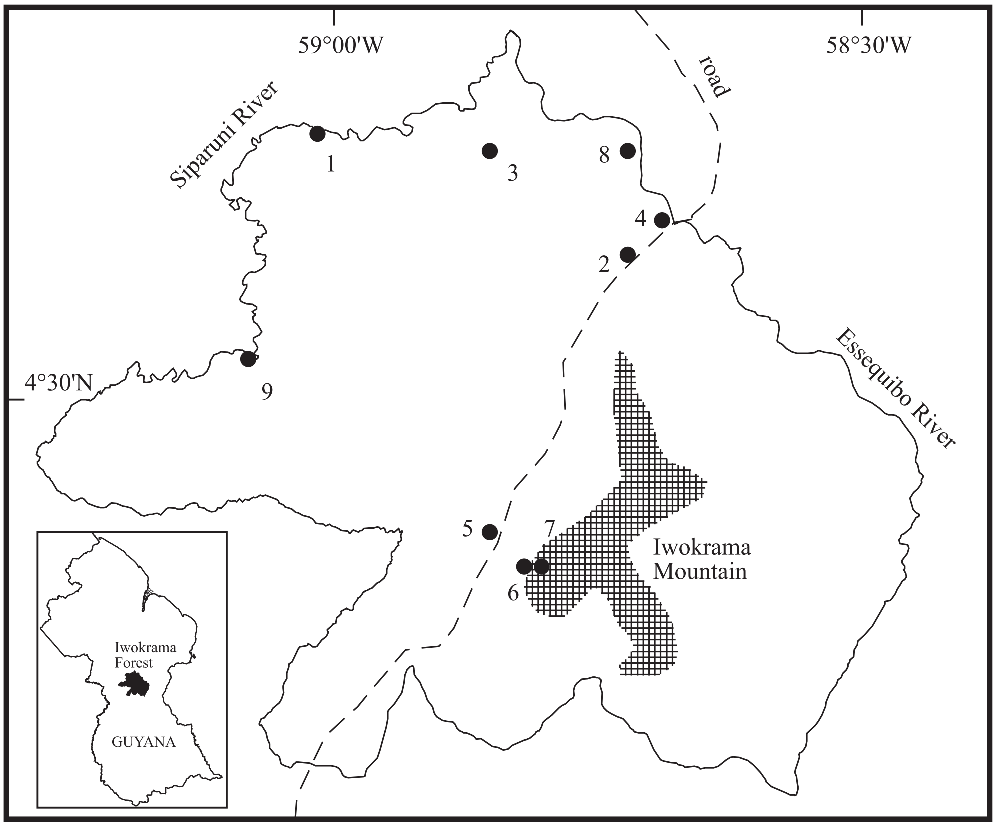

Figure 1. Map of Iwokrama Forest showing the 1997 mammal survey sites (circles), road (dashed line) and the dominant topographic feature, Iwokrama Mountain (hatching). The inset map indicates the location of Iwokrama Forest within Guyana. The localities are as follows: (1) Pakatau Falls, (2) 3-Mile Camp, (3) Clearwater Camp, (4) Iwokrama Field Station, (5) 38-Mile Camp, (6) Cowfly Camp, (7) Gorge Camp, (8) Turtle Mountain and (9) 'S' Falls.

management and conservation programme. The first phase of the Iwokrama programme involved a site resource survey (Hawkes & Wall 1993) and the second phase was to include an inventory of the biological diversity. For the second phase, we conducted surveys of mammals during the dry seasons from 9 March to 12 April 1997, in conjunction with the University of Kansas, and from 3 October to 21 November 1997. The data presented in this paper stem from these two field trips. As part of a larger project on the biodiversity and conservation of mammals in Guyana (Engstrom & Lim, in press), we also conducted fieldwork in the Iwokrama Forest area in October 1990, July 1994 and July 1995. The only other bat survey was carried out from July to September 1992 by Smith & Kerry (1996). Based on these field studies, 86 species of bat have been recorded from sites in Iwokrama Forest, giving it the highest reported diversity for any protected area in the world (Lim *et al*. 1999, Lim & Engstrom 2001).

Iwokrama Forest includes 3600 km^2 of pristine mixed lowland forest with a closed canopy to about 30 m. The eastern and northern boundaries are formed by the Essequibo and Siparuni Rivers respectively with smaller tributaries forming most of the southwestern boundary. A 70-km all-season road bisects Iwokrama Forest from the northeast to the southwest. The predominate topographic feature is the granitic Iwokrama Mountains in the south-central region which protrudes about 800 m above the surrounding lowlands which are approximately 100 m above sea level. The average annual rainfall is approximately 2500 mm with two wet seasons from May to August and December to January. Although there are different habitat types ranging from low mountains to alluvial plains to swampy areas, all of Iwokrama Forest is essentially covered by mixed lowland wet rain forest. No single tree species dominates but the canopy trees *Chlorocardium rodiei*, *Carapa* spp. and *Catostemma* spp. are found throughout at differing abundances (Hawkes & Wall 1993). A field station is situated on the Essequibo River in the northeast with an access road 2 km from the main road, and several field camps have been established in different habitat types. Our surveys were conducted at nine of these sites (Figure 1): (1) Pakatau Falls, (2) 3-Mile Camp, (3) Clearwater Camp, (4) Iwokrama Field Station, (5) 38-Mile Camp, (6) Cowfly Camp, (7) Gorge Camp, (8) Turtle Mountain and (9) 'S' Falls. The sites have been described in greater detail in reports on the first occurrence of bat species new to the fauna of Guyana (Lim *et al*. 1999, Lim & Engstrom 2001).

METHODS

Although we collected in Iwokrama Forest on previous occasions, data on community structure come from the 1997 surveys because therein we standardized field methods and made sustained efforts in canopy netting. This effort resulted in the capture of 73 species of bat (Appendix 1) during these surveys, although 86 in total are documented from Iwokrama Forest (Lim & Engstrom

2001). Taxonomy and species identification follow Lim *et al*. (1999), and Lim & Engstrom (2001). Voucher specimens are deposited at the Royal Ontario Museum, the University of Kansas Natural History Museum, and the Centre for the Study of Biological Diversity at the University of Guyana.

We used large mist nets, 30 m long × 10 m high, hoisted into the middle to upper canopy in a variety of situations including dense forest, over streams and over roads. Standard nets of 2.6 m in height and lengths of 6 and 12 m were deployed to a maximum height of 3 m above the ground in typical understorey settings such as across trails and streams, along the edges of clearings, and near roosts and fruiting trees. Mist nets were supplemented with four-bank harp traps measuring 1.4 m wide × 1.7 m high. These were placed along trails and streams that acted as natural funnels but their success in bat captures was incidental. During our first field season in 1997, nets were opened for the first half of the evening (approximately 17h30 to 23h30), whereas during the second field season, nets were typically run throughout the whole night (17h30 to 05h30). The determination of vertical stratification per species is based on six nights of trapping during the first field trip and 40 nights from the second field trip. Effort was calculated as the length of time a trap was deployed and expressed as m^2 h. For example, one short net opened all night contributed 187.2 m^2 h of effort (2.6 m × 6 m × 12 h).

Vertical stratification was classified into five categories based on the number of captures in ground-level nets and harp traps, expressed as a percentage of total captures. A species was classified as a strict understorey specialist if 100–80% of its captures were within 3 m of ground-level, predominately understorey specialist with 79–60%, stratified forest generalist with 59–40%, predominately middle to upper canopy specialist with 39–20%, and strict middle to upper canopy specialist with 19–0% of captures near ground-level. Gross biomass was calculated from the average mass of individuals kept as voucher specimens multiplied by the total number of individuals captured for each species.

A niche matrix was constructed based on the feeding guilds as used by LaVal & Fitch (1977) and body size as indicated by average mass as originally proposed by McNab (1971). Species found at Iwokrama Forest but not in Costa Rica (LaVal & Fitch 1977) are assigned the same feeding guild (aerial insectivore, gleaning insectivores, nectarivores, frugivores, omnivores, carnivores, sanguinivores) as their congeners. The lightest bat recorded during the 1997 survey was *Rhynchonycteris naso* with an average mass of 3.9 g. Thus small size category for bats was defined as an average mass of 3–5 g, medium–small as 6–10 g, medium as 11–19 g, medium–large as 20–36 g, large as 37–69 g, and very large as 70–134 g. Note that the range within each successive size class has doubled (i.e. 2 g, 4 g, 8 g, 16 g, 32 g, 64 g). This follows the suggestion that a size factor for mass of approximately two (1.26^3) can differentiate sympatric species using similar food resources (Hutchinson 1959, McNab 1971). Others (LaVal & Fitch 1977, Smith & Genoways 1974, Willig 1986) have used forearm length as a measure of size because it is more commonly and accurately recorded than body mass, but we concur with LaVal & Fitch (1977) who expressed reservations about the use of forearm length. The problem is exemplified by the gleaning insectivores caught at Iwokrama Forest: *Mimon crenulatum* has an average forearm length (48 mm) similar to *Tonatia carrikeri* (49 mm) but a much smaller mass (12 g versus 24 g, respectively) and presumably less ecological impact per individual in terms of resource consumption.

A species was considered common during the 1997 survey in absolute terms if it was captured more than 80 times, or considered the commonest species within a trophic–size cell if its frequency was twice as high as the second most frequently caught bat and it was captured at least 10 times.

RESULTS

Species diversity, abundance, biomass, feeding guilds

During the 1997 mammal surveys of Iwokrama Forest, there were 79 nights of trapping. A total of 2117 bats representing 73 species (see Appendix 1) was captured after 495 136 m^2 h of effort. The ratio of effort in the canopy to the understorey was similar (46%:54%) suggesting that the vertical sampling of bats was relatively unbiased in terms of magnitude of effort. Over half (53%) of the species were caught 10 or less times (Figure 2) whereas the five most

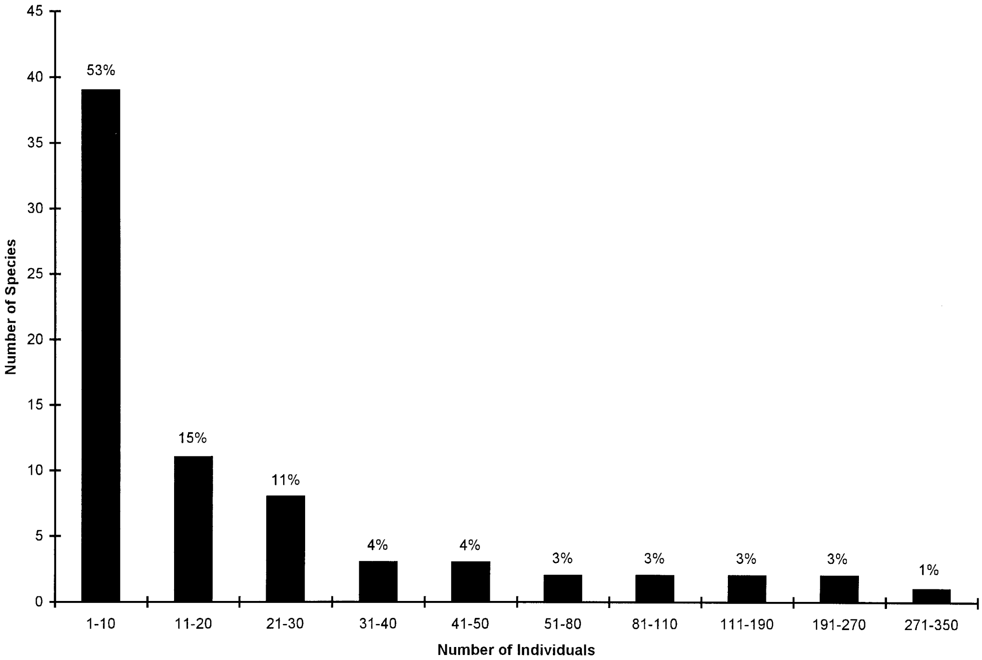

Figure 2. Histogram of the number of bat species documented by the number of individuals during the 1997 faunal survey of mammals at Iwokrama Forest, Guyana. Note the left skewness indicating that there are many species represented by a few individuals and a few species represented by many individuals.

abundant species (*Artibeus lituratus, Carollia perspicillata, A. obscurus, A. planirostris* and *Pteronotus parnelli*, in decreasing order) accounted for about half of the total captures. The 20 highest ranking species represent 27% of the diversity but account for 82% of the abundance.

This skewed distribution of abundance is more pronounced if gross biomass is considered. The 20 highest ranking species accounted for 92% of the total biomass (Figure 3). *Artibeus lituratus*, the most abundant species and the third largest bat based on mean body mass, accounted for almost one-third (32.3%) of the total bat biomass. For gross biomass, the five most abundant species are also the top contributors (69.5%) with the exception that the order of the three intermediate species is reversed. Thirty-four species (47%) had a biomass contribution of less than 100 g each.

Similar trends are also evident for feeding guilds. Although not the most speciose (29%), frugivores are the dominant bats in terms of number of individuals caught (70%) and gross biomass (78%; Figure 4). Aerial insectivores comprise 34% of the species diversity but only 13% of the number of individuals and 8% of the gross biomass. None of the remaining five feeding guilds account for more than 6% of the captures and in total comprise only 17% of the number of individuals caught, although they account for 37% of the species diversity. In terms of gross biomass, omnivores (7%) rival aerial insectivores but the remaining guilds account for only 8% in total.

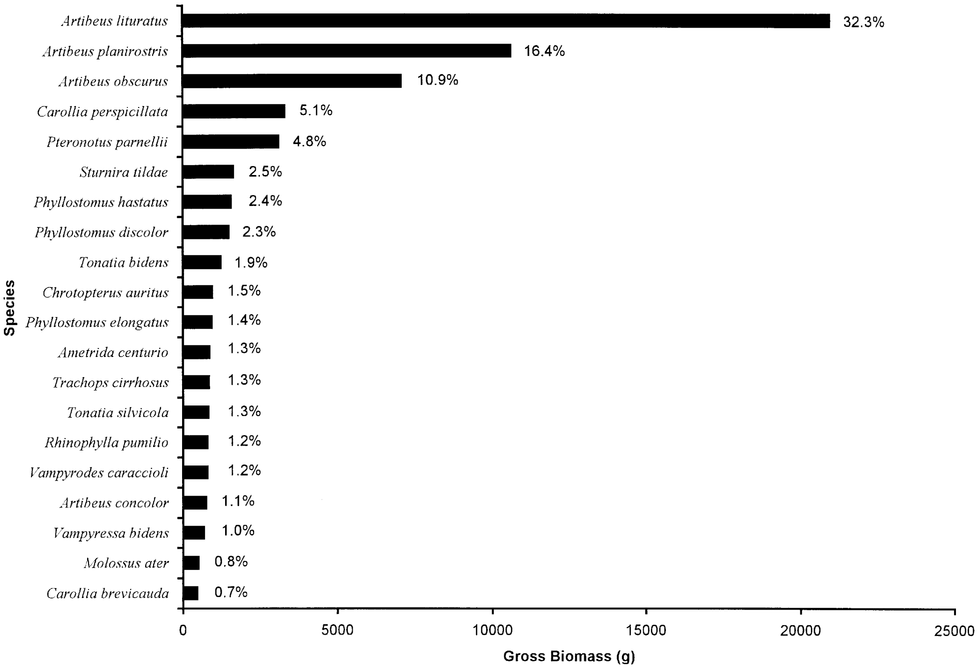

Figure 3. Histogram of the total biomass (g) for the 20 commonest species of bat documented during the 1997 faunal survey at Iwokrama Forest, Guyana. The three most ecologically dominant species are large fruit-eating bats belonging to the genus *Artibeus*.

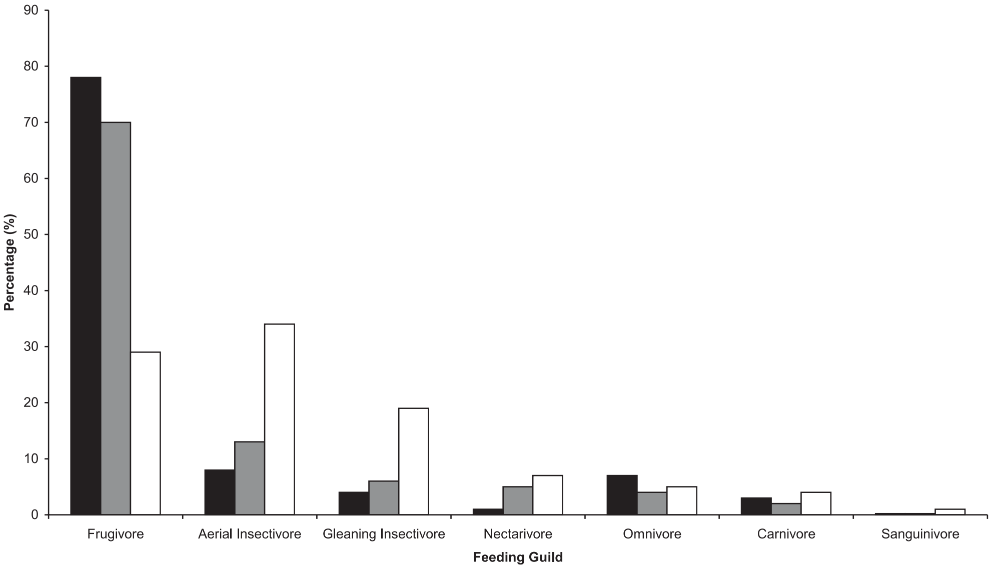

Figure 4. Graph of the seven different feeding guilds documented during the 1997 faunal survey at Iwokrama Forest, Guyana. A solid black bar is the percentage of gross biomass represented by each feeding guild, grey shading is the percentage of individuals representing each feeding guild and a white bar is the percentage of species represented by each feeding guild.

The four most abundant species (*Artibeus lituratus, Carollia perspicillata, A. obscurus* and *A. planirostris*) are all fruit-eaters (Appendix 1) and the only bats captured at all nine study sites. *Vampyressa pusilla*, a species only recently documented from Guyana (Lim & Engstrom 2001), is the only fruit-eating bat among 21 species (29%) considered rare (captured once or twice). Twelve of these rare species are aerial insectivores, six are gleaners, one is a nectarivore (*Anoura geoffroyi*) and one is a carnivore (*Vampyrum spectrum*).

Vertical stratification

Twelve species of bat (16%) were classified as middle to upper canopy specialists (Appendix 1) with nine of these species caught only in canopy nets, albeit they all are represented by small sample sizes. Six species (8%) were defined as predominantly middle to upper canopy bats which represented the less diverse group. The second largest group was the stratified forest generalists represented by 20 species (27%). Seven species (10%) were considered predominantly understorey bats. The largest group includes 28 species (38%) that we designated as understorey specialists. Nineteen of these species were caught only in ground-level traps but most of these were represented by small sample sizes. If we ignore the rare species caught less than five times, the rank order of diversity for the different canopy levels changes. The strict middle to upper canopy specialists comprised the fewest species (9% of the remaining 44 species) suggesting that many of the apparent canopy specialists were comparatively rare, at least in our study. Predominately middle to upper canopy specialists comprised 11% of the total species, the stratified forest generalist were now the most speciose at 36%, the predominately understorey specialists accounted for 14%, and the strict understorey specialists represented 32%.

Trophic–size niche

Half of the 42 potential feeding guild/body mass cells in the niche matrix for Iwokrama Forest bats were occupied (Table 1). The three carnivorous species are of different size classes. Omnivores also occupy three size classes with *Phyllostomus hastatus* averaging twice the mass of the other three species. These smaller species differ by about 10 g from one another (Appendix 1). None of them is particularly common, although *P. discolor* was captured in high numbers at one site where it was apparently feeding on flowers. Within the 37–69-g size class, although not common in absolute numbers, *Phyllostomus elongatus* was captured four times as often as *Phylloderma stenops*.

There are seven species of small frugivores, with *Ametrida centurio* and *Rhinophylla pumilio* being the most abundant. Interestingly, except for two species of *Artibeus*, the small fruit bats are all from different genera. A similar trend is seen in the next frugivore size class, wherein seven genera are represented and only one (*Carollia*) has two species. The only common species in this cell is *C. perspicillata*. The next size class is composed of four species all from different genera with *A. obscurus* the commonest. The two largest frugivores both belong to the same genus (*Artibeus*) and both are common. Although *A. planirostris* was captured in high numbers at one site, *Artibeus lituratus* was consistently common at all sites surveyed.

Nectarivores fall into two size classes and each species represents a different genus. *Anoura geoffroyi* was the only medium-sized species. The four smaller species are of similar size with *Choeroniscus minor* the only uncommon species. *Lonchophylla thomasi* and *Glossophaga soricina* are both moderately common and widespread in Iwokrama Forest whereas *Lionycteris spurrelli* is not as widespread but can be locally common.

Gleaning insectivores are divisible into four size classes. Although separated into two different classes by definition, the four smallest species have an average mass within a 2-g range and all are *Micronycteris*. Until recently (Simmons 1996, Simmons & Voss 1998), these four taxa were assigned to two species and

Table 1. Food-size niche matrix for bats captured at Iwokrama Forest, Guyana during a faunal survey in 1997. A number in parentheses indicates the number of common or relatively abundant species within that cell.

Feeding Guild	Average body mass (g)					
	<6	6–10	11–19	20–36	37–69	>69
Aerial insectivores	8 (1)	6 (1)	6 (1)	5 (1)		
Gleaning insectivores	2	5	3 (1)	4 (1)		
Nectarivores		4 (3)	1			
Frugivores		7 (2)	8 (1)	4 (1)	2 (2)	
Omnivores				1	2 (1)	1
Carnivores				1	1	1
Sanguinivores				1		

basic ecological and behavioural data are unavailable. Such data are required to explain the unusual situation of four similar-sized congeners in sympatry. The next three smallest gleaners are represented each by different genera, however, two (*Glyphonycteris* and *Trinycteris*) were only recently split from *Micronycteris* (Wetterer *et al*. 2000). The 11–19-g category has three species from different genera including *Mimon crenulatum*, *Micronycteris hirsuta* and *Lampronycteris brachyotis* of which the last also was previously included in *Micronycteris* (Wetterer *et al*. 2000). The latter two species were each caught only once while the former was caught 11 times. The largest size class for gleaners includes four species, of which the smallest is *Glyphonycteris daviesi*, another species split from *Micronycteris* (Wetterer *et al*. 2000). The three largest are *Tonatia* with *T. carrikeri* and *T. saurophila* similar in size. The former was not very common whereas the latter was caught over twice as many times as the next most abundant, and the largest gleaning insectivore, *T. silvicola*.

Aerial insectivores include some of the smallest bats with eight species averaging under 6 g. They each belong to a separate genus except the three species of *Myotis*. Although none of these species was commonly captured, in Guyana colonies up to about 20 *Myotis* are known to roost in tree hollows and crevices. The river bat (*Rhynchonycteris naso*) is the smallest and also the only abundant species in this cell; it is regularly seen in colonies of 10–20 individuals roosting on trees overhanging streams.

The 6–10-g size class is occupied by six species from different genera. Although marginally abundant, *Saccopteryx bilineata* accounted for over half of the total captures in this guild-size class. The next largest class is also represented by six species from separate genera. The most abundant, *M. molossus*, roosts in large colonies throughout its neotropical distribution. The largest aerial insectivores include five species which again belong to different genera. The most abundant was *Pteronotus parnellii* which was commonly caught flying in the forest understorey. This is in contrast to *Noctilio albiventris* which roosts in small to large colonies in tree hollows and usually forages over water. The other three species are free-tailed bats which typically forage above the forest canopy or in open areas. Of these three, *Molossus rufus* roosts in large groups although few were caught.

For the overall feeding guild and body mass niche matrix, 14 of the 21 cells are occupied by more than one species. Of these 14 cells, seven are composed of species from different genera (see Table 1 and Appendix 1). Note also the absence of large insectivores and nectarivores (upper right of Table 1) and small omnivores, carnivores and sanguinivores (lower left of Table 1).

DISCUSSION

Biomass and ecological dominance

The bat community at Iwokrama Forest is composed of a few species that are abundant and many species that are rare (Figure 2). This log-normal distribution of abundance is typical for mammal communities including, for example, the bats at La Selva in Costa Rica (LaVal & Fitch 1977, Wilson 1990). *Artibeus lituratus* was the commonest species (14.9%) during our survey (Figure 3) and was almost 50% more abundant than the next most frequently caught bat (*Carollia perspicillata*). Its ecological dominance was even more accentuated when gross biomass was taken into account. *Artibeus lituratus* represented almost one-third (32.3%) of the total bat biomass. For comparison with neotropical non-volant mammals, it was estimated that the single most dominant species in the Afobaka Dam Reservoir in Suriname (Eisenberg & Thorington 1973, Walsh & Gannon 1967) was the pale-throated three-toed sloth (*Bradypus tridactylus*), an arboreal herbivore, in terms of numbers (27.7%) and the tapir (*Tapirus terrestris*), a terrestrial herbivore, in terms of single species biomass (20.6%). The two most dominant species in the Tucuruí Dam Reservoir of the lower Amazon in Brazil (Mascarenhas & Puorto 1988, Peres 1999) were the red-handed howler monkey (*Alouatta belzebul*), an arboreal frugivore and herbivore, with 19% of the total captures and 26% of the total biomass, and the brown-throated three-toed sloth (*Bradypus variegatus*) with 28% and 23%, respectively. For Barro Colorado Island in Panama (Eisenberg & Thorington 1973, Montgomery & Sunquist 1975, Peres 1999), the two most dominant species in terms of biomass were the mantled howler monkey (*Alouatta palliata*) and brown-throated three-toed sloth.

For bat feeding guilds in Iwokrama Forest, not surprisingly, frugivores are overwhelmingly dominant in terms of abundance (70%) and gross biomass (78%). This is in contrast to non-volant mammals in the neotropics where herbivores comprise over half of the biomass at sites in Suriname, lower Amazonian Brazil, Panama, and a seasonally flooded forest in Brazil (Eisenberg & Thorington 1973, Peres 1999). In non-flooded upper Amazonian sites, however, arboreal frugivores comprise the largest portion of the non-volant mammal biomass. The arboreal frugivores represented 42% of the biomass in the terra firme forest of Urucu in Brazil, whereas the arboreal folivores comprised a paltry 4% (Peres 1999). Similarly, the alluvial forest of Cocha Cashu in Peru was composed of 40% arboreal frugivores and 15% arboreal herbivores (Janson & Emmons 1990, Peres 1999).

Although five species of neotropical bats have been documented to feed on leaves (Bernard 1997), there have been few direct observations of leaf consumption (Kunz & Diaz 1995, Zortea & Mendes 1993). Herbivory is a feeding guild that seemingly has not been overly exploited by bats, however, it has been suggested that folivory may be more common and widespread, especially in frugivores to supplement the low amounts of protein in fruit (Kunz & Diaz 1995). Folivory in bats may be underestimated because of the difficulty with observing them feeding at night and identifying liquid fractionations of leaves in the stomach or faecal samples (Kunz & Diaz 1995). However, the ecological dominance of frugivores in terms of relative abundance and biomass is still undeniable for bat communities in the neotropics.

Our study of Iwokrama Forest is the most comprehensive evaluation of bat community biomass. The only other summary of biomass is for two habitats in northwestern Venezuela reported by Pirlot (1964). He documented 10 species of bat in gallery forest and a nearby plantation with similar levels of biomass in both habitats, although the species composition and abundances at the two sites were not similar. For non-volant mammals, biomass has been expressed per unit area (kg km^{-2}) to facilitate comparisons between localities (Eisenberg *et al*. 1979). Densities of large mammals can be estimated by observations or indirect signs of their occurrence, and population densities of smaller non-volant mammals can be estimated by trapping. Density estimates for bats, however, are few, and it is difficult to incorporate data from bats into reports of mammalian biomass. The few exceptions include *Thyroptera tricolor*, with densities estimated as 22 individuals ha^{-1} on the Osa Peninsula of Costa Rica (Findley & Wilson 1974), densities of six species of frugivores were reported from Santa Rosa in Costa Rica (Fleming 1988), and *Artibeus jamaicensis* was estimated to occur at a density of 2 ha^{-1} on Barro Colorado Island in Panama (Leigh & Handley 1991). Although there are no density estimates for the 86 species of bat known from Iwokrama Forest, we have estimated relative abundances derived from our standardized trapping methods.

Several studies on neotropical bats, however, provide some basis for comparison with our data. On Barro Colorado Island (Handley *et al*. 1991), for example, the frugivore *Artibeus jamaicensis* was numerically the most abundant species in 1979, representing 60% of total captures, and was over seven times as common as *A. lituratus*, the next most frequently caught bat. Clearly, given its proportionately large size (47 g), *A. jamaicensis* would comprise over 60% of the bat biomass in this community. Handley *et al*. (1991) relied exclusively on understorey netting, however, the high abundance of *A. jamaicensis* on Barro Colorado Island was also found by Bonaccorso (1979) who incorporated canopy netting, and was later re-confirmed by Kalko *et al*. (1996). At another site with data from canopy netting (Paracou, French Guiana; Simmons & Voss 1998), an understorey frugivore *Carollia perspicillata* accounted for 36% of the captures and was over five times as abundant as the next most frequently caught bat, a canopy aerial insectivore *Molossus molossus* (7%). In terms of biomass, *C. perspicillata* is still dominant at Paracou despite its moderate body size with almost three times the total biomass as the next most dominant species, *Phyllostomus elongatus*, an omnivore. Interestingly, the ecological impact of the three large species of *Artibeus* at Paracou is moderate compared to Iwokrama Forest and Barro Colorado Island.

Community composition and resource partitioning

Summarizing community organization using the niche matrices of McNab (1971) was criticized because they 'obscure more information than they reveal' (Willig 1986:151). Willig (1986) expressed three primary concerns which we will discuss below: (1) the majority of niche cells are unoccupied, (2) some cells are occupied by more than one species, and (3) the size categories are arbitrary and may obscure size differences within or between adjacent cells. We suggest that the perceived shortcomings of the trophic–size niche matrix approach can be improved by increasing the number of spatial dimensions with other ecological parameters including vertical stratification as suggested by Fleming *et al*. (1972).

(1) Unoccupied cells in a relatively well-inventoried community should not pose a major concern because these niches may actually be filled by other organisms or there may be physiological factors constraining plasticity in body size and feeding guilds (Smith & Genoways 1974). For example, we do not expect to find a truly carnivorous 3-g bat because there would be no vertebrate prey for it to consistently catch. In addition, a cell may be unoccupied because of an extinction or local extirpation event.

(2) Other ecological factors will need to be explored or refined to account for more than one common bat in a niche cell. For example, vertical stratification will be directly addressed later in the study with our data from Iwokrama Forest. As more information is accumulated on feeding habits, the extent of resource competition will be better understood. For instance, as mentioned in Willig's (1986) study of a semi-arid region in northeastern Brazil, *Phylloderma discolor* and *Trachops cirrhosus* occupy the same cell in the Caatinga. *Trachops cirrhosus* is usually considered a frog-eating specialist but also takes other vertebrates and insects whereas *P. discolor* is truly omnivorous, feeding on nectar, pollen, fruit and insects. Thus their dietary overlap is minimal.

(3) The arbitrary assignment of size ranges is necessarily unavoidable if only for comparative purposes between sites. Geographic variation is known for many bats so conceivably a species could be at the higher end of one size range and the lower end of the next larger size range at two different localities. However, this situation can still result even in statistical groupings, such as 95% confidence limits, as seen in *Anoura geoffroyi* for Willig's (1986) data. The main point of interest is not the exact range of measurements as dictated by a mathematical constant (e.g. Hutchinson 1959) but the species that comprise a generalized trophic–size niche (e.g. McNab 1971).

Based on ecological interactions summarized by the two parameters of body size and food habits, McNab (1971) hypothesized that a bat community would be organized with only one common bat occupying each trophic-size cell. At Iwokrama Forest, this was generally true, however, 3 of the 21 occupied cells had more than one common species of bat (Table 1). As others have suggested (Fleming *et al*. 1972, McNab 1971), factors such as vertical stratification and possibly activity patterns may account for additional spatial and resource partitioning in complex mainland tropical forest communities. For example, there are three species of small nectarivores occupying the same niche cell at Iwokrama Forest. However, when vertical stratification is taken into account, these taxa are differentiated into a strict understorey specialist (*Lonchophylla thomasi*), predominately understorey specialist (*Lionycteris spurrelli*) and stratified forest generalist (*Glossophaga soricina*). In addition to increasing sample sizes with long-term monitoring surveys, studies on diet and habitat use are needed to test this hypothesis of nectarivore stratification.

For the largest frugivores, *Artibeus planirostris* was common but not nearly as abundant as *A. lituratus*, and there was a 10-g difference between their mean body masses. Based on vertical stratification, *A. planirostris* was considered a predominantly understorey specialist and *A. lituratus* was a stratified forest generalist with slightly more captures in the canopy than understorey. We regard these categorizations as reliable because of the large sample sizes. An analysis of diet would confirm whether these differences translate into a real resource partitioning. Incidentally, *A. planirostris* has been considered as conspecific with *A. jamaicensis* (Handley 1987, 1989), which was well-studied on Barro Colorado Island in Panama (Handley *et al*. 1991), but we consider them separate species (Lim 1997, Lim & Wilson 1993).

Although *Ametrida centurio* was the most abundant small frugivore, almost half of its captures were from a single net set across a stream in terra firme forest for two nights. The reason for this high density was unknown but an abundance of food, suitable roosts, or concentrations due to mating behaviour may have contributed to its local abundance. In this size class, however, *Rhinophylla pumilio* is the common fruit bat found in most areas. Heterogeneous patterns of local abundance, therefore, should be considered when examining community structure and the partitioning of resources. Some species may only have a restricted spatial or temporal impact on ecological interactions. At a single study site, they may be dominant but for the larger community as a whole their effect may be greatly reduced. *Ametria centurio* was classified as a strict understorey specialist by our vertical stratification method, however, excluding the one abundant site, the proportion of captures in the middle canopy increased. If the high number of captures in the one highly successful ground-level net were discounted, it would be classified as a predominately understorey specialist like *R. pumilio*.

Besides vertical stratification, other ecological factors to consider in bat resource partitioning and competition include the availability of suitable roosts and roost specialization (Tamsitt 1967), foraging behaviour (Fenton *et al*., in press), and food adaptability such as the ability to switch from soft to hard fruits (Dumont 1999).

Taking into account all species captured in 1997, of the 14 cells occupied by more than one species, half are composed of species from different genera. For the other seven multi-occupied cells, only one genus has more than one species in each multi-occupied cell. Although we have not employed an ecomorphological approach, we predict that the species within cells composed of unique genera will be evenly distributed in multivariate space (e.g. Findley 1993) suggesting further ecological partitioning within the guild–size niche. This is in contrast to the overall community ecomorphology which is characterized by many similar closely packed species in community-wide multivariate space and a few distinctive outliers (Findley 1976). Those cells with congeneric species are more difficult to explain but slight differences in size or shape may reflect dietary differences. Some of these species are uncommon or contribute minimally to overall biomass and consequently their competition for resources may be ecologically negligible.

In Iwokrama Forest, the fruit-eater *A. lituratus* is the most ecologically dominant bat in terms of relative abundance and total biomass. The bat community structure of the common species can be organized into three dimensions by including vertical stratification in the feeding guild and body mass niche matrix of McNab (1971).

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APPENDIX 1

The 73 species of bat caught in the 1997 faunal survey of Iwokrama Forest, Guyana ordered by number captured, and including average mass, total biomass, feeding guild, and the percentage captured in understorey traps (calculated from six nights during the first field season and 40 nights during the second field season). For a full list of the 86 species of bat documented at Iwokrama Forest, see Lim & Engstrom (2001). The abbreviations under Family are Em = Emballonuridae, Ml = Molossidae, Mr = Mormoopidae, No = Noctilionidae, Ph = Phyllostomidae, Th = Thyropteridae and Ve = Vespertilionidae. The codes for feeding guild are as follows: A = aerial insectivore, C = carnivore, F = frugivore, G = gleaning insectivore, N = nectarivore, O = omnivore and S = sanguinivore. A species was classified as a strict understorey specialist if 100–80% of its captures were within 3 m of ground-level, predominately understorey specialist with 79–60%, stratified forest generalist with 59–40%, predominately middle to upper canopy specialist with 39–20%, and strict middle to upper canopy specialist with 19–0%.

Species	Family	No. captured	Average mass (g)	Biomass (g)	Feeding guild	% in understorey traps
Artibeus lituratus (Olfers, 1818)	Ph	314	67	21009	F	46
Carollia perspicillata (Linnaeus, 1758)	Ph	216	15	3316	F	81
Artibeus obscurus Schinz, 1821	Ph	199	36	7176	F	64
Artibeus planirostris (Spix, 1823)	Ph	198	56	11133	F	64
Pteronotus parnelli (Gray, 1843)	Mr	137	22	3072	A	90
Ametrida centurio Gray, 1847	Ph	105	8	850	F	86

Species	Family	No. captured	Average Mass (g)	Biomass (g)	Feeding guild	% in under-storey traps
Rhinophylla pumilio Peters, 1865	Ph	88	9	792	F	74
Sturnira tildae de la Torre, 1959	Ph	63	26	1618	F	44
Vampyressa bidens (Dobson, 1878)	Ph	52	13	667	F	57
Tonatia saurophila Koopman & Williams, 1951	Ph	49	25	1218	G	22
Phyllostomus discolor Wagner, 1843	Ph	44	34	1507	O	14
Artibeus gnomus Handley, 1987	Ph	41	10	416	F	33
Artibeus concolor Peters, 1865	Ph	38	19	739	F	50
Carollia brevicauda (Schinz, 1821)	Ph	37	12	457	F	97
Lionycteris spurrelli Thomas, 1913	Ph	34	9	298	N	70
Lonchophylla thomasi J. A. Allen, 1904	Ph	30	7	214	N	93
Glossophaga soricina (Pallas, 1766)	Ph	27	8	226	N	58
Rhynchonycteris naso (Wied-Neuwied, 1820)	Em	26	4	102	A	96
Phyllostomus elongatus (E. Geoffroy, 1810)	Ph	24	39	930	O	100
Vampyrodes caraccioli (Thomas, 1889)	Ph	24	33	790	F	13
Tonatia silvicola (d'Orbigny, 1836)	Ph	23	35	811	G	79
Molossus molossus (Pallas, 1766)	Ml	22	12	268	A	95
Trachops cirrhosus (Spix, 1823)	Ph	21	36	763	C	100
Chiroderma villosum Peters, 1860	Ph	20	22	444	F	44
Artibeus cinereus (Gervais, 1856)	Ph	20	11	213	F	50
Phyllostomus hastatus (Pallas, 1767)	Ph	19	85	1621	O	9
Chiroderma trinitatum Goodwin, 1958	Ph	19	14	274	F	31
Uroderma bilobatum Peters, 1866	Ph	17	16	280	F	50
Platyrrhinus helleri (Peters, 1866)	Ph	17	14	238	F	57
Molossus ater E. Geoffroy, 1805	Ml	16	31	497	A	50
Chrotopterus auritus (Peters, 1856)	Ph	15	63	939	C	80
Saccopteryx bilineata (Temminck, 1838)	Em	14	9	119	A	40
Mesophylla macconnelli Thomas, 1901	Ph	12	8	96	F	80
Mimon crenulatum (E. Geoffroy, 1810)	Ph	11	12	127	G	100
Noctilio albiventris Desmarest, 1818	No	9	29	259	A	100
Tonatia carrikeri (J. A. Allen, 1910)	Ph	9	24	220	G	33
Molossops neglectus Williams & Genoways, 1980	Ml	8	11	88	A	0
Eumops hansae Sandborn, 1932	Ml	7	15	108	A	50
Pteronotus personatus (Wagner, 1843)	Mr	7	8	58	A	100
Phylloderma stenops Peters, 1865	Ph	6	44	262	O	50
Trinycteris nicefori (Sanborn, 1949)	Ph	6	9	54	G	50
Saccopteryx leptura (Schreber, 1774)	Em	6	6	33	A	50
Micronycteris minuta (Gervais, 1856)	Ph	5	7	35	G	50
Micronycteris megalotis (Gray, 1842)	Ph	5	5.8	29	G	75
Desmodus rotundus (E. Geoffroy, 1810)	Ph	4	25	101	S	100
Choeroniscus minor (Peters, 1868)	Ph	4	10	40	N	0
Vampyressa brocki Peterson, 1968	Ph	4	10	39	F	50
Micronycteris microtis Miller, 1898	Ph	4	6	24	G	33
Myotis albescens (E. Geoffroy, 1806)	Ve	4	5	19	A	100
Sturnira lilium (E. Geoffroy, 1810)	Ph	3	18	55	F	67
Cynomops paranus (Thomas, 1901)	Ml	3	14	43	A	33
Peropteryx macrotis (Wagner, 1843)	Em	3	5	14	A	0
Pteronotus gymnonotus Natterer, 1843	Mr	2	13	26	A	100
Lasiurus atratus Handley, 1996	Ve	2	12	24	A	50
Glyphonycteris sylvestris (Thomas, 1896)	Ph	2	9	18	G	100
Vampyressa pusilla (Wagner, 1843)	Ph	2	9	17	F	50
Centronycteris maximiliani (Fischer, 1829)	Em	2	5	11	A	0
Micronycteris brosseti Simmons & Voss, 1998	Ph	2	5	10	G	50

Species	Family	No. captured	Average Mass (g)	Biomass (g)	Feeding guild	% in under-storey traps
Myotis nigricans (Schinz, 1821)	Ve	2	5	10	A	100
Vampyrum spectrum (Linnaeus, 1758)	Ph	1	135	135	C	0
Cynomops abrasus (Temminck, 1827)	Ml	1	27	27	A	0
Nyctinomops macrotis (Gray, 1840)	Ml	1	21	21	A	0
Glyphonycteris daviesi (Hill, 1964)	Ph	1	20	20	G	100
Lampronycteris brachyotis (Dobson, 1879)	Ph	1	14	14	G	100
Anoura geoffroyi Gray, 1838	Ph	1	14	14	N	100
Micronycteris hirsuta (Peters, 1869)	Ph	1	12	12	G	100
Tonatia brasiliense (Peters, 1866)	Ph	1	10	10	G	100
Molossus sp.	Ml	1	10	10	A	100
Cormura brevirostris (Wagner, 1843)	Em	1	8	8	A	0
Lasiurus blossevillii (Lesson & Garnot, 1826)	Ve	1	6	6	A	100
Peropteryx leucoptera Peters, 1867	Em	1	6	6	A	100
Myotis riparius Handley, 1960	Ve	1	5	5	A	100
Thyroptera tricolor Spix, 1823	Th	1	4	4	A	0
Total		2117		65115		