ASIA LIFE SCIENCES 2(2): 215-222, 1993
The Asian International Journal of Life Sciences

Vertical stratification of bats in a Philippine rainforest[1]

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To sample the bat community in a lowland rainforest on Luzon Island, Philippines, mist nets were set in the subcanopy (3-16 m high) at a ground-level (0-3 m high). A total of 1325 bats was netted.

Subcanopy nets caught an average of 15 bats per net-night, the highest capture rate yet reported for nets in tropical forest (except at roost sites and over water). The suborder Megachiroptera represented 95% of captures in subcanopy nets but only 25% of captures in ground-level nets; the suborder Microchiroptera accounted for the remainder. Although subcanopy nets were set in natural forest gaps whereas ground-level nets were set under closed canopy, the difference in the representation of megachiropterans in net captures at the two vertical strata suggests that megachiropteran activity is substantially higher in the subcanopy. The vertical distribution of their food, primarily fruit, could account for such a pattern.

KEY WORDS : bats, Chiroptera, community ecology, Megachiroptera, Microchiroptera, rainforest, stratification, Philippines

INTRODUCTION

The most common method of sampling bat communities involves capturing bats with mist nets set at ground-level (*e.g.* Bonaccorso 1979, Fleming *et al.* 1972, Laval & Fitch 1977, Wolton *et al.* 1982). One potential drawback of ground-level mist netting is that inferences concerning bat community composition apply only to bats in the lower strata of forest (Fleming 1986, Fleming *et al.* 1972, Francis 1989, Heideman & Heaney 1989, Wolton *et al.* 1982). The bat community in the subcanopy or canopy may in fact differ in representation of species or in abundance.

Three previous studies in tropical forest compared captures in nets raised into the subcanopy or canopy with those in ground-level mist nets (Bonaccorso 1979, Gaskell

[1]Paper presented at a symposium entitled, "Philippine Vertebrates: a symposium on their preservation and conservation", held at the Institute of Forest Conservation, College of Forestry, University of the Philippines Los Baños, College, Laguna on April 21-23, 1993.

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Received 02 September 1993; Accepted 10 October 1993.
 Printed in the Philippines

1984, Handley 1967). All three studies found substantial differences in representation of species between captures in ground-level and higher level nets.

In the Philippines, previous studies on bats involving mist netting did not use raised nets and therefore only sampled the space 0-5 m above the ground (*e.g* Catibog-Sinha 1987, Heaney *et al.* 1989, Heideman & Heaney 1989, Mudar & Allen 1986). In order to better understand the Philippine bat community, netting should be conducted at different heights. I set mist nets at subcanopy level (3-16 m high) to make inferences about the use of the subcanopy by bats in a Philippine rainforest.I used samples from ground-level nets (0-3 m high) to make comparisons.

STUDY AREA

The study was conducted from January to August 1989 within a 330 ha area of second growth forest (14 °09'N 121 ° 13'E) within Makiling Forest Reserve. The study area is located on the northeastern face of Mt. Makiling, Luzon Island, Philipines. Mt. Makiling is a dormant volcano with an elevation of 1143 m at the peak. Elevation within the study area ranges from 200 to 500 m. The topography is characterized by ridges and valleys, with few level areas. Four major creeks drain the study area. Despite variation in the annual pattern of rainfall on Mt. Makiling, in most years a wet season and a dry season can be identified. In 1989, the annual rainfall was 2055 mm. The wettest months were from May to October, when the monthly rainfall always exceeded 200 mm (mean monthly rainfall = 284 mm). The six other months of the year received less than 120 mm of rain (mean monthly rainfall = 59 mm). Mean monthly temperature ranged from 25 to 29° C.

The forest canopy is about 25 m high in valley levels and on slopes and is slightly lower on the tops of ridges. Dominant tree species include *Nephelium mutable* Bl. (Sapindaceae), *Celtis luzonica* Warb. (Ulmaceae), *Parashorea malaanonan* (Blco.) Merr. (Dipterocarpaceae), *Diplodiscus paniculatus* Turcz. (Tiliaceae), *Ficus variegata* Bl. (Moraceae), *Palaquium foxworthyi* Merr. (Sapotaceae), *Chisocheton pentandrus* (Blco.) Merr. (Meliaceae), *Bischofia javanica* Bl. (Euphorbiaceae), *Alstonia macrophylla* Wall. *ex* DC (Apocynaceae), and *Shorea contorta* Vidal (Dipterocarpaceae) (Quimbo *et al.* 1980). Palms and rattans (*Calamus* spp.) are common in the understory.

The study area had been selectively logged in the early 1900s and around World War II, but had recovered well, as evidenced by the relatively closed canopy, and the fact that trees with diameters greater than 1 m were not rare. No agricultural clearings were present within the study area.

METHODS

Bats were captured in 0.35 mm mesh monofilament mist-nets. Subcanopy nets, each consisting of two 6 m by 2 m nets, one strung above the other, were raised by a pulley system (modified from Dejonghe & Cornuet 1983; Figure 1, see appendix for description) to sample the space 3-16 m above the ground. Subcanopy nets were hoisted in natural gaps in the forest (10-20 m in diameter) usually caused by treefalls. Subcanopy nets were selectively placed in sites expected to be most productive, such as gaps on the crests of ridges (Heideman & Heaney 1989). One to five subcanopy nets were set within each of 12 sites, each containing at least one gap. Ground-level nets (6 x 2 m and 12

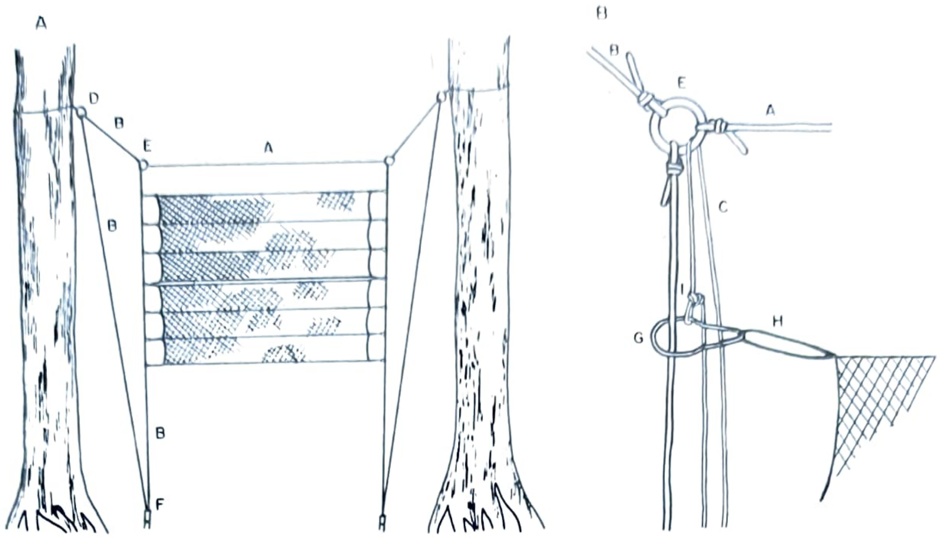

Figure 1. a) Diagram of subcanopy net system. The hoisting ropes have been omitted for clarity. b) Detail of rope ring and net.

x 2 m) were strung between pairs of small trees to sample bats flying 0-3 m above the ground. Most ground-level mist nets were set under closed canopy. Nets were usually left open from 1800-0530 h but were closed during periods of rain; nets were checked at 30 min to 2 h intervals. Every bat that was captured was identified to species, sex, and age. Body weight, forearm length, and reproductive condition were likewise recorded. Identifications follow Ingle and Heaney (1992).

Between January 29 and 6 February 1989 bats were trapped with ground-level nets at two sites on three nights. From April to August 1989 nets were set in 12 sites selected by locating randomly chosen coordinates within the study area and then finding a nearby gap in which subcanopy nets could be set. Each of these 12 sites was trapped for three or four consecutive nights. Ground-level nets were set in three sites, whereas subcanopy nets were in all 12 sites. The total netting effort was 87.5 subcanopy net-nights and 27 ground-level net-nights. A net-night was defined as one 12 m net or two 6 m nets open $\geq$ 10 h during the night. A half-net was one 6 m mist net open for $\geq$ 10 h. Net-nights when nets were open $\leq$ 10 h were excluded from the analysis. The difference in the netting scheduling and effort between ground-level and subcanopy nets was because this study was incidental to a study on the fruit bat community (Ingle 1992). Initial results indicated that raised nets had higher net success for fruit bats, and therefore most nets were then raised.

RESULTS

A total of 1313 bats was caught in subcanopy nets ($\bar{x}$ = 15.0 bats per net-night); 12 bats were caught in ground-level nets ($\bar{x}$ = 0.44 bat per net-night) (Table 1). All six megachiropteran species and 10 of the 13 microcheropteran species captured were caught in higher numbers per net-night in subcanopy nets than in ground-level nets. Captures in subcanopy nets consisted of 95% megachiropterans and 5% microcheropterans. In contrast, captures in ground-level nets consisted of 25% megachiropterans and 75% microcheropterans. *Ptenochirus jagori*, a 70 g bat, accounted for 81% of all megachiropterans captured in subcanopy nets.

Table 1. Species, numbers of bats caught, and number of captures/net-night in ground-level (0-3 m high) nets (27 net-nights) and subcanopy (3-16 m high) nets (87.5 net-nights) on Mt. Makiling, Philippines, from January to August 1989.

Species	Total captures 0-3 m	Total captures 3-16 m	Captures / net-night 0-3 m	Captures / net-night 3-16 m
Megachiroptera				
Ptenochirus jagori	1	1012	0.04	11.6
Cynopterus brachyotis	0	192	0	2.20
Macroglossus minimus	2	21	0.07	0.24
Haplonycteris fischeri	0	13	0	0.15
Eonycteris spelaea	0	6	0	0.07
Rousettus amplexicaudatus	0	4	0	0.05
All megachiropterans	3	1248	0.1	14.3
Microchiroptera				
Rhinolophus subrufus	0	26	0	0.30
Pipistrellus javanicus	0	12	0	0.14
Hipposideros diadema	0	8	0	0.09
Rhinolophus arcuatus	3	6	0.1	0.07
Myotis muricola	1	5	0.04	0.07
Megaderma spasma	4	0	0.1	0
Philetor brachypterus	0	2	0	0.02
Rhinolophus macrotis	0	2	0	0.02
Rhinolophus rufus	0	1	0	0.01
Rhinolophus virgo	0	1	0	0.01
Hipposideros obscurus	0	1	0	0.01
Myotis horsfieldii	0	1	0	0.01
Murina cyclotis	1	0	0.04	0
All microchiropterans	9	65	0.3	0.85
All bats	12	1313	0.4	15.0

DISCUSSION

Typical capture rates for ground-level mist nets in tropical habitats are 1-3 bats per net-night in Africa (Findley & Wilson 1983, Wolton *et al.* 1982), and 3-6 bats per net-night in Latin America (Findley & Wilson 1983). For Asia few netting studies with information on capture rates in intact forest are available. Netting in several habitat types in Negros and Leyte Islands, Philippines, Heaney *et al.* (1989) had much higher netting success in disturbed habitats (agricultural areas mixed with secondary forest or urban areas; average net success = 6-11 bats/net-night) than in intact forest (less than 5 bats/net-night). In a multi-year study in submontane dipterocarp forest at 850-1200 m elevation on Negros and Leyte Island, Heideman & Heaney (1989) caught an average of 6.0 bats per net-night in ground-level nets that were selectively placed in areas in which the subcanopy was relatively open. In lowland rainforest in Peninsular Malaysia and Borneo, Francis (1989) reported net capture rates of 0.13 bat per net-night. His nets were placed in a regularly-spaced grid pattern instead of being placed selectively; this sampling scheme may have been responsible for his low capture rate. The average capture rate in the present study of 15 bats per net-night for subcanopy nets is higher than any previously reported capture rate in tropical forest, except when netting was conducted at bat roosts or over bodies of water. However, direct comparisons of capture rates are problematical. Although most studies express capture rates in bats per net-night, the units "net" and "night" do not have standard definitions. Nets come in several sizes and often net sizes are not reported. A "night" could mean leaving the nets open for any number of hours; descriptions of methods often do not contain this information. Not withstanding the difficulty of comparing capture rates between studies, the difference between the capture rate of subcanopy nets in the present study and capture rates previously reported is so great that it is unlikely to be due solely to unreported differences in net size or night length. Other factors, such as the number of bats in the area, their flying and foraging habits, and the specific height and locations in which nets were set are more likely to account for the high capture rate of subcanopy nets in the present study.

The thirty-fold difference between capture rates of subcanopy nets and ground-level nets in the present study illustrates a pronounced effect of net placement on the bat sample netted. Nets were placed at either ground-level or in the subcanopy, and under closed canopy or in a gap. Because most canopy nets were set in gaps and most ground-level nets were set under closed canopy the effect of net height on capture rate could not be separated from the effect of canopy cover. Both factors may be important but only further work can determine their relative effects.

In Papua New Guinea and in Sulawesi, Indonesia, Gaskell (1984) caught about 50 times as many fruit bats in canopy nets (seven bats per net-night) than in nets set below at ground level. However, in a study in the New World on Barro Colorado Island, Panama, overall capture rates did not differ significantly between nets set at ground-level (0-3 m) and nets in the subcanopy (3-12 m) directly abobe the ground-level nets (X^2 test of data in Bonaccorso 1979). Based on the few studies using raised nets, predictions cannot be made on whether raised nets in any given location will result in higher capture rates. However, for reasons to be discussed later, I hypothesize that raised nets are more likely to increase capture rates in Old World locations than in New World locations.

As with the difference in capture rates, differences in composition of captures in subcanopy and ground -level nets in the present study cannot be attributed conclusively to net height due to the confounding factor of canopy cover (*i.e*, gap or closed canopy). Studies in which either canopy cover or net height were varied alone indicate that both factors affect foraging or flying activity by bats. Crome and Richards (1988) examine the foraging activity of insectivorous microchiropterans in an Australian rainforest by monitoring their echolocation calls in 0.03-0.07 ha gaps created by selective logging and under adjacent closed canopy. Nine of the 12 species they detected foraged in only one of the two inhabitats. Fruit removal experiments in Costa Rican rainforest indicate that fruit bats are more likely to forage upon fruit along man-made trails than upon fruit inside the forest (Palmerim & Etheridge 1885). Like gaps, trails are openings in the vegetation with canopy cover either reduced or absent.

Studies in which nets were placed both at ground-level and in either the subcanopy or canopy above indicate that species differ in their utilization of different vertical strata. For 11 of 31 species nettted in Panama, capture frequencies of ground-level (0-3 m high) and subcanopy (3-12 m high) nets differed significantly (Bonaccorso 1979). In

Amazonian forest in Brazil,capture frequencies of four of the five species of which at least 10 individuals were netted differed significantly between canopy nets and ground-level nets (X^2 test of data in Handley 1967).

In these studies in Panama and Brazil, diet was strongly related to the levels at which bat species were most frequently captured. In Panama, of the six species commonly caught in subcanopy nets, five were frugivorous stenodermines, which forage on fruits of canopy and subcanopy trees. Of the five species commonly caught in ground-level nets, four were phyllostomines that glean insects from vegetation and the ground (Bonaccorso 1979). In the Brazilian Amazon, stenodermines comprised a substantially higher proportion of total captures in canopy nets than in ground-level nets. Carollinines, which feed on fruits usually within 3 m of the ground (Bonaccorso 1979), tended to be caught in higher proprtions in ground-level nets than in canopy nets (Handley 1967).

In the present study the composition of subcanopy and ground-level nets could not be compared at the species level because of the low number of ground-level captures. At the suborder level, however, representation differed dramatically,and may be linked to diet. Megachiropterans, which comprised 95% of subcanopy net captures but only 25% of ground-level captures, are exclusively herbivorous and feed mainly on fruits (Marshall 1985); all the microchiropterans captured were primarily insectivorous. Fruit was confined mainly to the subcanopy and canopy (pers. obs.); insects may be distributed more evenly among different vertical strata (see Sutton 1989, Sutton *et al.* 1983). Like the bats in the present study, tropical forest birds in New Guinea and Australia appear to be similarly stratified: frugivores are confined mainly to the canopy, whereas insectivores and mixed diet frugivores/insectivores use a much broader range of vertical strata (Frith 1984, Bell 1982).

Unlike Old World fruit bats (Megachiroptera), many New World fruit bats (Phyllostomidae: Stenoderminae, Carollinae, Glossophaginae, and Phyllonycterinae) augment their diet with insects (Gardner 1977), and therefore might be expected to have a more even vertical distribution. A further reason to expect a substantial representation of New World fruit bats at ground-level is the presence of a groundstory frugivore guild (Carollinae) (Bonaccorso 1979). It is known whether this guild has a counterpart in the Old World bat community (Francis 1990).

The limited information on vertical stratification in New World fruit bats supports this prediction. In Panama, fruit bats made up only slightly more of the total catch in subcanopy nets (92%) than in ground-level nets (81%) (Bonaccorso 1979). In the Amazon, Handley (1967) netted almost equal proportions of fruit bats in ground-level (94%) and canopy nets (97%). Further work is necessary to obtain a clearer picture of the spatial use of the habitat by bats in sites in both Old and New Worlds, and now it relates to diet.

The results of the present study indicate that subcanopy nets can be very effective at increasing the number of captures of fruit bats. The differences in the composition of captures between subcanopy and ground-level nets indicate that interpretations of bat community composition based on mist-netting at only one vertical level should be limited to this level. Although use of subcanopy nets will add to our knowledge of bat community composition, ground-level and subcanopy nets still leave the canopy and the space above it unsampled, and caution is still necessary in interpreting capture data.

ACKNOWLEDGEMENTS

I thank A. Manamtam, D. Balete, and S. Salazar for assistance in the field, and H.-W. Yuan for drawing the figure. J. Hayes, L. Heaney, P. Heideman, J. Hermanson, M. Ishii-Eiteman, A. Marshall, D. McClearn, M. Richmond, A. Wilkinson, and an anonymous reviewer provided helpful comments on earlier drafts. The Institute of Forest Conservation, University of the Philippines Los Baños, kindly permitted me to work within the Makiling Forest Reserve. Fieldwork was supported by the Haribon Foundation for the Conservation of Natural Resources and the New York Cooperative Fish and Wildlife Research Unit, U.S.A.

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APPENDIX

Description of subcanopy net system.

The subcanopy net system was set between two trees 10-14 m apart. The space between the trees had to be clear from the ground to the height at which the nets were to be hoisted.

The hoisting system consisted of four 2.5 cm diameter metal 0-rings and five length of rope: one top rope (A) equal in length to the nets; two support ropes (B), each 2.5 times as long as the height to which the nets would be raised; and two hoisting ropes (C) of the same length as the support ropes. All ropes were of braided nylon. The support ropes were 0.7 cm in diameter and the top and the hoisting ropes were 0.5 cm in diameter.

Each tree was climbed (either unaided or with climbing spikes) so that a ring (tree ring=D) could be either tied or nailed to the trunk. A support rope (B) was threaded through each tree ring (D). Both ends of each support rope (B) were tied to a ring (tree ring=E). Each end of the top rope (A) was tied to a rope ring (E). A hoisting rope (C) was threaded through each rope ring (E) and its ends were tied together thus forming a loop. The top rope (A) was hoisted by pulling on the support ropes (B), which were then anchored to the ground directly below the rope rings (E) by tying them to a tree root, small sapling, or stake (F).

The two 6 m by 2 m nets were attached to the support ropes (B), one above another, by metal shower curtain rings (G). The curtain rings (G) were clipped around the support ropes (B) and one curtain ring (G) was threaded through each net shelf loop (H). Each shower curtain ring also threaded through one of the 5 cm loops (I) tied in the hoisting rope (C). These loops (I) were spaced the depth of a net shelf apart. The nets could be raised or lowered by means of the hoisting ropes.