

## HOME RANGE AND TERRITORIALITY IN THE LEAST BLOSSOM BAT, *MACROGLOSSUS MINIMUS*, IN PAPUA NEW GUINEA

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Least blossom bats, *Macroglossus minimus* (Pteropodidae), were monitored by radiotelemetry in lowland rainforest for up to 22 days in Kau Wildlife Area, Madang Province, Papua New Guinea. Based on 1,502 radiotelemetry positions, mean home range for 18 individuals was  $5.8 \text{ ha} \pm 4.6 \text{ SD}$ , and mean core-use area was  $1.5 \pm 1.3 \text{ ha}$ . The mean long axis of the home ranges was  $495 \pm 258 \text{ m}$ . Activity hotspots were associated with flowering bananas, the primary food resource of least blossom bats at Kau. During the day, *M. minimus* roosted singly in subcanopy or canopy foliage and showed fidelity to a day-roost area. Mean day-roost area was  $0.5 \pm 0.4 \text{ ha}$ . Adult males appeared to exclude conspecifics from rich, compact feeding territories in primary forest. Overlap in home range occurred primarily in gardens and between subadults and other bats.

Key words: core-use area, day-roost area, *Musa*, radiotelemetry

Knowledge of home range, spatial movements, and foraging habits of rainforest animals is an invaluable asset in planning the conservation of biodiversity in developing tropical nations. Although Papua New Guinea includes large areas of undisturbed rainforest and ranks among the 15 highest national concentrations of “megadiversity” (sensu—Mittermeir et al. 1997), few studies of mammalian spatial requirements have been undertaken in the region (Bonaccorso et al. 2002; Salas 2002; Winkelmann et al. 2000). It is particularly important to understand the resource requirements of species that perform crucial ecological functions such as pollination or seed dispersal of ecologically or economically important plant species.

The least blossom bat, *Macroglossus minimus*, is the smallest member (16–21 g) of the family Pteropodidae (Old World fruit bats) in the South Pacific region. It occurs on continents, large islands, and small is-

lands of Malaysia, Thailand, Indonesia, Papua New Guinea, Australia, the Solomon Islands, and the Philippines. This distribution results from its ability to cross narrow Pleistocene water gaps and from a plasticity of energy that permits it to maintain populations on very small islands (Bonaccorso and McNab 1997). *M. minimus* is an important pollinator of mangroves (*Sonneratia*) and native bananas (*Musa*) throughout its large distribution in Australasia (Bonaccorso 1998; Lekagul and McNeely 1977; Payne et al. 1985; Strahan 1995) and is also associated with bananas in Borneo (Payne et al. 1985).

In Papua New Guinea, *M. minimus* is ubiquitous from sea level to 1,200 m elevation, and it is the most common bat where domestic bananas are abundant in traditional gardens (Bonaccorso 1998; Flannery 1995). However, *M. minimus* is reported to be common only in coastal mangroves in Malaysia, where it feeds principally on the blossoms of *Sonneratia*,

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whereas *M. sobrinus* is abundant in inland forests and is considered to be a banana specialist (Start and Marshall 1976). Similarly, in Sumatra *M. sobrinus* reportedly visits and pollinates the flowers of *Musa acuminata halabanensis* (Itino et al. 1991).

Our radiotelemetry study of the least blossom bat, *M. minimus*, in lowland rain-forest of Papua New Guinea is part of a larger project on the spatial and temporal movements of small pteropodids. This includes similar studies of *Syconycteris australis* (Winkelmann et al. 2000), *Dobsonia minor* (Bonaccorso et al. 2002), and ongoing research on *Nyctimene albiventer* and *Melonycteris melanops*. Mist-netting and radiotelemetry were used to investigate home range, core-use area, territoriality, day-roost area, and foraging behavior of *M. minimus*.

#### MATERIALS AND METHODS

*Study area.*—Our study was undertaken at the Kau Wildlife Area, Madang Province, Papua New Guinea, during 6 time periods: 14–24 June 1997, 20 June–7 July and 13–19 December 1998, 9–21 April and 15–30 June 1999, and 28 May–22 June 2000. Kau Wildlife Area (5°08'S, 145°46'E) is privately owned and managed by the Didipa Clan of Kau and Baitabag villages. It forms an 800-ha reserve at elevations between 20 and 65 m. Mean annual precipitation at nearby Nagada Harbor is 3,460 mm (1994–1996). June through August are the driest months in most years and usually receive <100 mm of rain each. The Biges and Kau rivers (and several small tributaries with permanent water flow) dissect this area of hills, plateaus, and valleys (Fig. 1).

The study area consists of primary forest, bordered by a complex mosaic of traditional gardens, primary forest remnants, and forest in various stages of regeneration. Up to 155 tree species may occur in a single hectare of primary forest at Kau (R. Kitchings, pers. comm.). Wild bananas are common along streams and smaller drainage courses and in tree-fall light gaps. In disturbed habitats, wild bananas survive within the forest remnants, usually in small ravines. Domestic bananas are cultivated in gardens and often persist in abandoned plots during early

stages of forest regeneration. Other potential food resources for nectar bats include papaya flowers in gardens, heliconias in forest light gaps, and flowers of bat-pollinated forest trees such as *Syzigium*.

*Radiotelemetry.*—Least blossom bats were captured in mist nets; weight (g), sex, age class, and forearm length (mm) were recorded. Each bat was fitted with a color-coded plastic band (A. C. Hughes, Hampton Hill, Middlesex, United Kingdom) for individual recognition. The band passed through 2 slits cut in the patagium on either side of the forearm (Bonaccorso et al. 1976). Bats were fitted with position-sensitive radiotransmitters (MD-2CP model, Holohil Systems, Carp, Ontario, Canada). Twenty-two bats were fitted with radiocollars: 14 adult males, 4 adult females, 2 subadult females, and 2 subadult males. Age class was based on the degree of closure of epiphyseal growth plates of the phalanges (Kunz et al. 1996). At the time the radios were affixed, all females were nonreproductive. The transmitters emitted 2 pulses/s when the bat roosted with the head downward, or 1 pulse/s when the body of the bat was horizontal, relative to the ground (usually indicating flight). Additionally, we could detect flight from modulation of the signal strength caused by the whipping motion of the trailing transmitter antenna. Bats were transported a distance of 4.5 km in cloth bags by vehicle to our laboratory at Jais Aben Resort (formerly Christensen Research Institute). At the laboratory, transmitters were attached by collars and stabilized at the back of the neck by Skinbond Surgical Cement (Smith and Nephew United, Largo, Florida). The collar consisted of wire that ran through a channel in the potting material. The exposed portions of the wire were covered by small-gauge tygon tubing, and the ends of the wire were fastened by a crimp and trimmed to remove sharp points. Complete transmitter and collar units weighed 1.5 g (about 7–8% of the body mass of *M. minimus*). We chose a somewhat larger unit size to increase battery life while retaining the position-sensitive function that makes it easier to determine if the bat is flying or roosting. In a flight cage, bats with radios did not differ from bats without radios in activity pattern, flight duration, or feeding behavior. Radios were equipped with batteries that had expected lives of either 6 or 10 weeks. Radiotagged animals readily drank 15% honey-water solution to satiation before be-

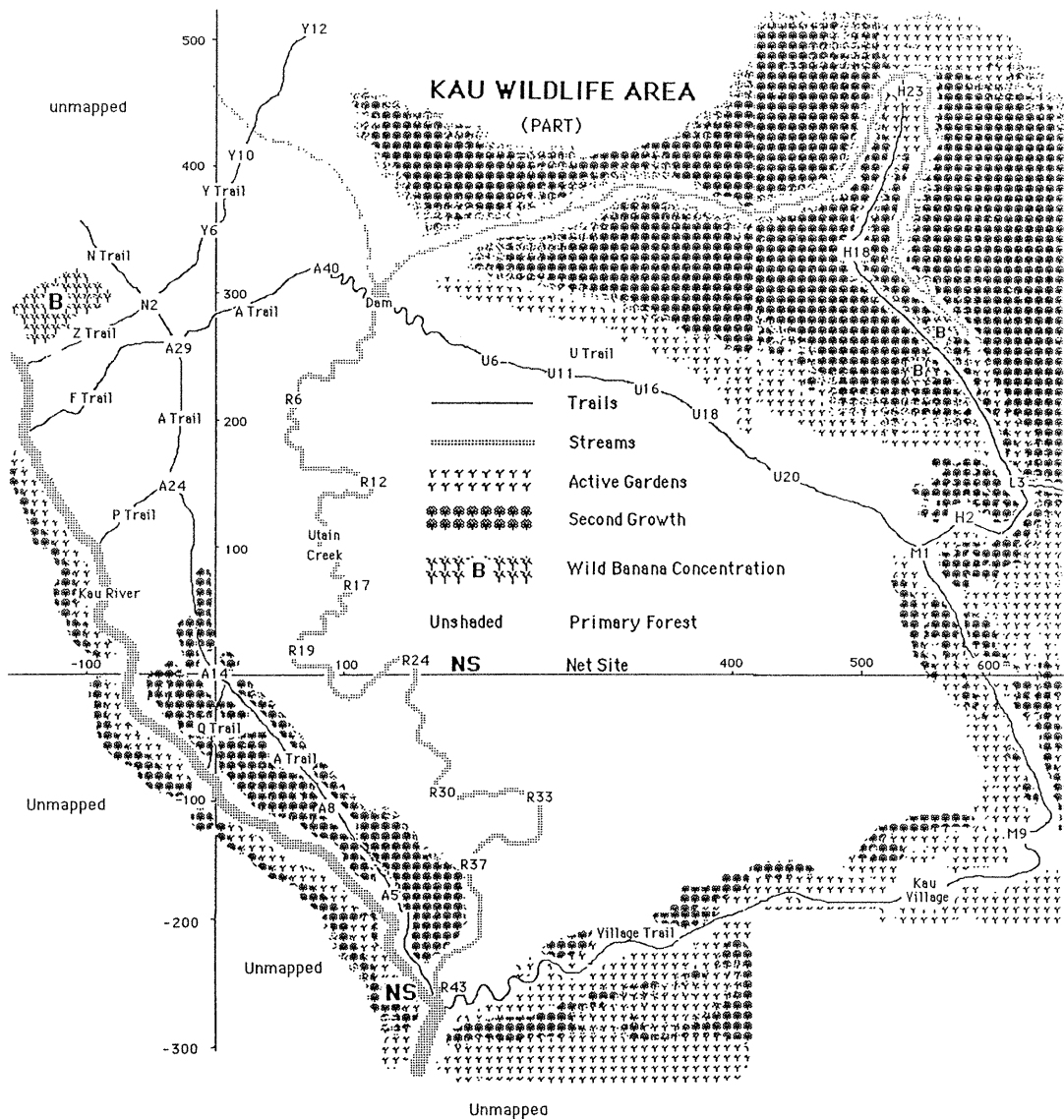


FIG. 1.—Kau Wildlife Area, Papua New Guinea, with reference points used in radiotracking, in mist-netting, and to locate food resources and habitats. Scales for axes are in meters and are identical to those in Figs. 2 and 3 to permit cross-referencing.

ing returned to site of capture. Bats fitted with radiocollars were released within 3 h of capture but were not monitored until the following night.

Output from the transmitters was monitored with 2 TRX 2000S tracking receivers (Wildlife Materials, Carbondale, Illinois) and 3-element Yagi antennas. Tracking stations were established at map reference points usually within 20–150 m of activity centers for each bat (foraging patches, commuting lanes, or day roost).

Receivers were moved as necessary to improve reception or to record multiple bearings on a stationary bat. Bearings were taken with a handheld compass (Suunto, Helsinki, Finland) and were read to the nearest degree. Also, time, signal strength, and gain setting (from gradations added by us to the gain dial of the receiver) were recorded with each bearing. Many positions were determined by triangulation when a bat was stationary long enough for bearings to be

sighted from 2 or more reference points. Other positions were calculated from single bearings along which distance was estimated from signal strength and gain (Law and Lean 1999; Winkelmann et al. 2000). Relationship of signal strength to distance was experimentally calibrated in the study area at standardized gain settings. With practice, single-bearing position determination was equivalent to triangulation in accuracy ( $\pm 15$  m for most instances that were cross-checked). We rarely lost radio contact with a focal animal once its foraging pattern was determined. When radio contact was broken with a moving bat, contact usually was reestablished within 20 min by walking toward the bearing of the disappearing bat. Walkie-talkies (FRS-101, Radioshack, Fort Worth, Texas) were used to coordinate simultaneous radiotracking by 2 operators.

A map of the study area with a superimposed zero intercept and a grid of  $x$ - and  $y$ -coordinates (Fig. 1) was created from 296 reference points along approximately 6 km of interconnecting footpaths and creeks. The total area mapped for this study encompassed 80 ha. Map coordinates were entered into a database for the radio positions determined for each bat and were analyzed with Antelope home-range software (available at <http://www.nbb.cornell.edu/neurobio/jbsv@downloads/programs.html>—J. Bradbury and S. Vehrencamp, pers. comm.). Following Wilkinson and Bradbury (1988), we used Anderson Fourier analysis (nonparametric) to calculate minimum-area probabilities (MAPs) for home range (MAP = 0.95) and core-use area (MAP = 0.50) for each bat. In addition, we calculated day-roost area, defined as the total area encompassed by the resting positions in foliage used during daylight hours for each bat, based on a nonprobabilistic minimum convex polygon method (Odum and Kunzler 1955; Wilkinson and Bradbury 1988). This latter method, although it overestimates use areas compared with the Andersen Fourier method, was chosen because of the small sample sizes and small total day-roost areas.

All numerical results are reported as means and standard deviations. Means for sex, age class, or season were compared for statistically significant differences ( $P < 0.05$ ) using  $F$ -tests.

## RESULTS

Eighteen *M. minimus* were tracked for 6–24 nights. Only 4 females were successfully

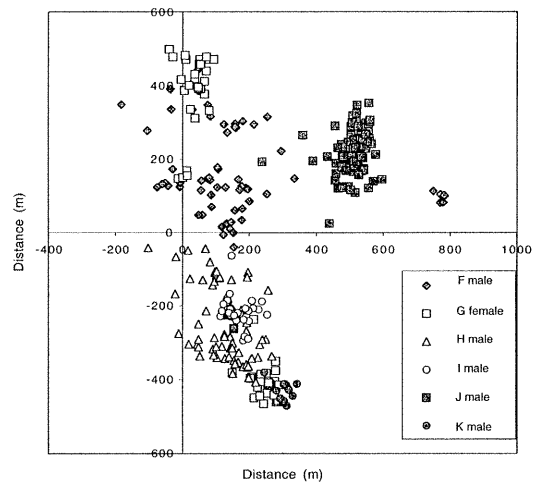


FIG. 2.—Radiotelemetry positions of 6 *Macroglossus minimus* tracked during overlapping time periods in 1999. Total area of plot is 168 ha. Bats are identified by letter and by sex. Sub-adult male K was tracked for only 1 night ( $n = 14$ ) and was excluded from home-range analysis.

radiotracked. Home ranges of bats tracked in 1999 and 2000 are shown in Figs. 2 and 3. Radio contact was lost with 3 additional females on the 1st night of tracking. Sub-adult male K was tracked for 1 night ( $n = 14$ ) before it disappeared. This bat was included in Fig. 2 but was excluded from Table 1. Home ranges occupied sequentially by 3 adult males are shown in Fig. 4.

Home ranges varied from 0.6 to 15.1 ha (Table 1). The size of home range was not correlated with the number of telemetry positions ( $r = -0.19$ ,  $d.f. = 16$ ,  $P > 0.05$ ). Mean home range (MAP = 0.95) was 5.8 ha, and there were no significant differences by sex ( $t$ -test: 2 sample, unequal variances,  $P = 0.98$ ). Core-use areas (MAP = 0.50) ranged from 0.1 to 4.0 ha (Table 1) and represented 15–33% of the home range of any individual. Core-use areas of all individuals contained at least 1 clump of bananas having at least 1 active inflorescence.

Day-roost areas (Table 1) of individuals with sample sizes  $\geq 4$  ranged from 0.03 to 1.62 ha and comprised 1.3–36.5% of the home range. The mean day-roost area was

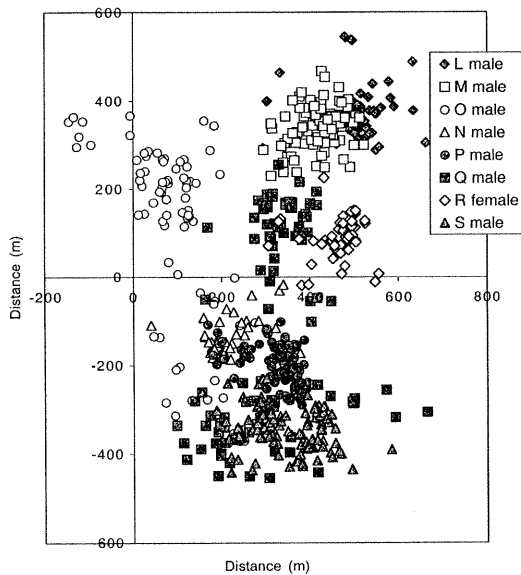


FIG. 3.—Radiotelemetry positions of 8 *Macroglossus minimus* tracked during overlapping time periods in 2000. Total area of plot is 120 ha. Bats are identified by letter and by sex.

0.5 ha. Males and females did not differ significantly in home range, core-use area, or day-roost area. Day-roost areas of bats tracked concurrently did not overlap and were separated by  $\geq 30$  m, except in 1 case where on different nights 2 bats occupied day roosts separated by 10 m (Fig. 5).

Least blossom bats selected day roosts in closed canopy forest, and in most cases this was in larger stands of primary forest. We were unable to see roosting bats with binoculars, even when roost trees were located by radiotelemetry. Adult males established day roosts within or adjacent to feeding patches. Two females (A and G) commuted to foraging areas in disjunct portions of the home range that were 800 and 1,000 m from their day roosts.

Visual observations provided direct evidence of visits by *M. minimus* to banana flowers in our study area. For example, 3 visits in rapid succession by a radiocollared bat (D) to 1 domestic banana inflorescence were seen by one of us (FJB). Despite evidence for strong reliance on banana nectar,

under some circumstances soft fruits might be nutritionally important. A single fecal sample collected from *M. minimus* contained the seeds of *Piper aduncum*. Some captive *M. minimus* refused *P. aduncum* fruits, but other individuals ate the tiny drupes with a combination of chewing motions and tongue extensions. To our knowledge, this is the first evidence of frugivory in *M. minimus*.

#### DISCUSSION

*Macroglossus minimus* coexists in Kau with at least 8 other pteropodid species. Three of these species also were radiotracked during the 7-year period of our study (Bonaccorso et al. 2002; Winkelmann et al. 2000). Mean home ranges (MAP = 0.95) for *S. australis*, *Dobsonia minor*, and *N. albiventer* were 5.5, 5.1, and 5.1 ha, respectively. Thus, despite differences in diet and in body mass (18–90 g), these solitary, foliage-roosting bats all had home-range sizes similar to that of *M. minimus* (5.8 ha).

At Kau, only *S. australis* is an important competitor of *M. minimus* (Winkelmann et al. 2000). *M. minimus* and *S. australis* are similar in body length and skull length. Nonetheless, maximum observed tongue extension in captives was 30.8 mm in *M. minimus* and 24.3 mm in *S. australis* (Winkelmann and Goedeke 2000). This capability, along with greater reduction of the incisors, suggests that *M. minimus* is more reliant on nectar than is *S. australis*.

In addition, our netting and radiotelemetry data provide indirect evidence that banana flowers are the primary food source for *M. minimus* and a secondary food source for *S. australis*. Often, clusters of activity data were recognized on the working maps, and these locations were investigated in the field. All such activity hotspots for *M. minimus* proved to be wild or domestic banana patches, but *S. australis* hotspots also included fruits such as *Ficus bernaysii* and *P. aduncum* (Winkelmann et al. 2000). Although our netting was not designed to sample habitats, netting results confirm an

TABLE 1.—Minimum-area probabilities (MAPs) for home range (MAP = 0.95) and core-use area (MAP = 0.5), long axis of home range (Axis), and minimum convex polygon (MCP) day-roost area of least blossom bats in Papua New Guinea. Sample size ( $n$ ) is the number of radiotelemetry data points in each data set. Day-roost data sets with  $n < 4$  were not included in the calculation of mean day-roost area.

Bat	Sex, age	Home range and core-use area			Day-roost area		Study date	
		$n$	MAP 0.95 (ha)	Axis (m)	MAP 0.5 (ha)	$n$		MCP (ha)
A	F, adult	31	9.66	945	3.22	5	0.61	June 1997
B	M, adult	102	2.53	330	0.59	8	0.13	June 1997
C	F, adult	85	4.56	360	1.22	11	0.80	June 1998
D	M, adult	117	4.50	435	1.22	6	0.20	Dec 1998
E	M, adult	64	7.30	372	2.06	10	0.62	Apr 1998
F	M, adult	63	13.10	947	4.02	6	0.40	June 1999
G	F, subadult	52	6.72	1,020	1.82	3		June 1999
H	M, adult	66	6.69	485	1.94	6	0.09	June 1999
I	M, adult	64	0.60	233	0.09	3		June 1999
J	M, adult	117	2.30	350	0.54	13	0.84	June 1999
L	M, adult	113	1.85	374	0.19	5	0.03	June 2000
M	M, adult	107	3.43	226	0.69	6	0.61	June 2000
N	M, adult	46	2.08	377	0.42	4	0.77	June 2000
O	M, adult	80	14.56	826	3.00	7	1.62	June 2000
P	M, adult	100	2.53	340	0.52	7	0.07	June 2000
Q	M, adult	103	15.11	577	3.78	11	0.70	June 2000
R	F, subadult	55	1.89	260	0.44	7	0.07	June 2000
S	M, subadult	113	4.07	457	1.18	9	0.44	June 2000
$\bar{X}$			5.75	495	1.50		0.50	
$SD$			4.55	258	1.26		0.42	

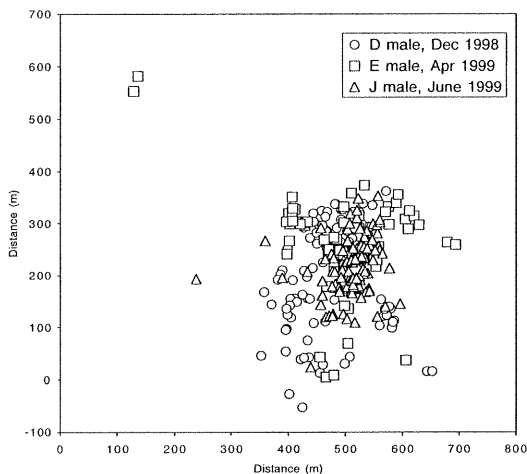


FIG. 4.—Radiotelemetry positions of 3 adult males that sequentially occupied an area that included 2 stands of wild bananas.

association of *M. minimus* with banana plants. Of the 27 *M. minimus* netted in Kau from 1994 to 2000, 20 (74.1%) were captured along garden trails in the immediate vicinity of domestic banana plants. In contrast, of the 83 *S. australis* captured during the same time period, 74 (89.2%) were netted along forest trails or streams, often in close proximity to fruiting *Piper* or *Ficus* plants. Nets were not set in patches of wild banana (*Musa*) because they usually were located in difficult terrain and because their inflorescences were often 5–6 m above the ground.

In Kau, home ranges of adult males were stable for the duration of tracking ( $\leq 24$  days). No adult male abandoned one home range and established another, and none permanently disappeared from radio contact during a tracking period. All bats with which we lost contact were subadult males

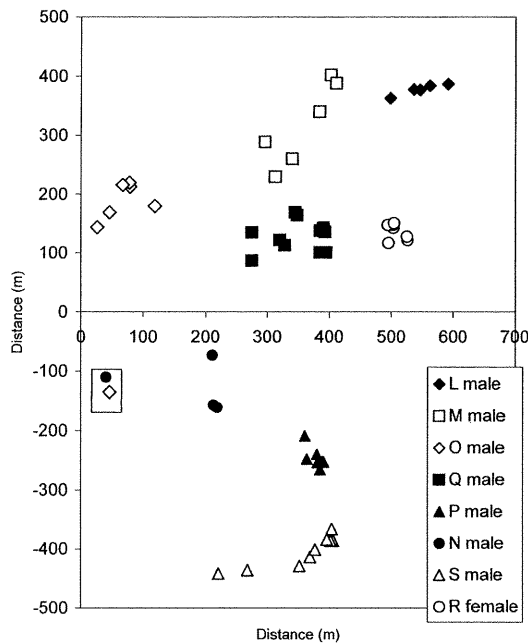


FIG. 5.—Day-roost positions of 7 male and 1 female *Macroglossus minimus* in 2000. Roost areas of individual bats were nonoverlapping, with the exception of 2 roost sites (in rectangle) that were occupied by males N and O on different nights.

or females. Mean home-range sizes for *M. minimus* were from 0.6 to 15.1 ha (Table 1). We believe that the high variance in this parameter reflects differences in the distribution of food resources and that it might also reflect differences in the social status of male bats. In our study, home ranges calculated by the minimum convex polygon method were 81% larger than the MAP = 0.95 home ranges generated by Antelope's Fourier analysis. Fourier analysis eliminates extreme outliers in the data set and recognizes disjunct areas where activity patterns are strongly polymodal. We believe that home ranges calculated in this way more accurately reflect the foraging activity of the bats and thus represent the portion of the total area most likely to be defended by territorial individuals.

All *M. minimus* occupied several different day-roost sites within their home ranges; thus, home-range size did not seem to

be inflated by limited roost-site availability. However, because all bats roosted in forest, or in forest remnants, those that commuted to gardens to feed tended to have larger home ranges.

Both wild and domestic bananas were abundant in the study area. Wild banana patches occurred in ravines and along stream banks in primary forest. Patch-sizes usually ranged from 1–2 mature plants (pseudostems) to >24 plants. One patch of wild bananas (*Musa*) occupied about 0.3 ha and contained about 60 mature plants, with at least 12 active inflorescences (Fig 1). This site was the core-use area of male B in 1997. On the other hand, domestic bananas were widely scattered among other crop plants. Thus, bats that fed in gardens had larger foraging areas and commuted  $\leq 1,000$  m to and from their forest roost areas. Female G in 1999 and males Q and O in 2000 exemplified this pattern. Movements of these 3 bats were highly predictable. Each night, after a few minutes of initial activity around the roost site, each bat flew directly to its garden foraging area.

In contrast, most bats with small home ranges ( $\leq 3$  ha) did not forage in gardens. Adult male I had the smallest home range (0.6 ha) in our study. Its home range included both domestic and wild bananas at the confluence of the Kau River and Utain Creek. Male L was unusual in that it was active in both gardens and forest ravines where domestic and wild bananas and *P. aduncum* were numerous. Seeds of *P. aduncum* in a fecal sample from male L indicate that these fruits might have been a significant part of the diet of this bat.

If bats were distributed randomly or according to resource patterns, we would expect extensive overlap in the home ranges of individuals. The most striking aspect of *M. minimus* home ranges is that they overlapped very little (Figs. 2 and 3). Despite exceptions discussed below, the home-range patterns suggest that individuals usually avoid one another during flight activity and at day roosts. Of 127 roost site records

for 18 bats, there was only 1 case in which 2 bats (males N and O, in 2000) had a single pair of slightly overlapping roost sites that were occupied on different nights (Fig. 5).

In 1999, the 5 simultaneously tracked adult males had home ranges that were essentially contiguous (Fig. 2). In 2000, 4 of the 6 adult males tracked had contiguous home ranges in forest with little overlap in foraging areas (Fig. 3). Significant overlap occurred only in gardens or between adults and subadults.

During our study only 3 females were tracked for more than 2 nights. Adult female A, monitored in 1997, roosted in primary forest within 10 m of adult male B. The home range of B was centered on a large patch of wild bananas, which it left only occasionally. Despite proximity to this rich nectar supply, female A commuted 800 m to a foraging area in secondary forest and gardens. Subadult female G, tracked during 1999, roosted in primary forest and commuted 1,000 m to forage in gardens, even though other gardens with domestic bananas were closer to her roost. Along the way, she passed through or around the home ranges of 3 adult males.

We suggest that in Kau, *M. minimus* are territorial, but the details of their social organization remain unknown. It is not clear if territories in volant mammals are as well-defined as in terrestrial species. In the latter, precise boundaries often are delineated by semipermanent scent marks (Ralls 1971). *M. minimus* males have prominent sternal glands (Hood and Smith 1984) that produce a musky odor. Although the function of these glands is unknown, it is possible that males with adjacent territories recognize one another by scent. Despite the stability of territories over short durations ( $\leq 24$  days), differences in the development of the sternal gland in nominal adult males might indicate flux in reproductive status and in territorial defense.

Many megachiropterans are highly vocal. *M. minimus* and *S. australis* emit similar

audible vocalizations during encounters with conspecifics in flight cages. We have heard these vocalizations in the field and assume that they occur in an agonistic context. Even though these bats do not echolocate, the possibility that ultrasonic communication plays a role in social behavior should not be disregarded.

Although vision might allow early detection of an intruder, scent is the most likely means by which a territory holder could recognize its neighbors or discriminate among intruders by age, sex, and reproductive status. Regardless of the mechanisms and rigor of territorial defense, at an estimated flight speed of 10 m/s, a bat flying directly through the territory of another is unlikely to be intercepted, even if detected.

Despite our contention that in Kau, *M. minimus* are territorial, certain violations of space occurred. These were of 3 kinds: (1) forays by individuals well outside their usual foraging area, (2) overlap of foraging areas of 2 or more bats, and (3) aggregations of  $\leq 7$  bats at a specific site along the Kau River. All these extraterritorial excursions might have reproductive as well as alimentary consequences.

Many bats made occasional long flights (6–22 min) well outside their areas of usual activity. The functions of these “probing forays” might include locating temporally variable food resources. In *Artibeus jamaicensis*, Morrison (1979) considered long, erratic flights away from feeding trees to be “searching flights” that allowed assessment of ripening fruit crops. *M. minimus* may exhibit similar behavior to locate new food resources. As a possible case in point, on 1 occasion male F flew 600 m to forage in gardens well outside its core-use area.

Another potential result of probing forays is that a vacant territory would be detected quickly by neighboring bats or by subadults without territories. A probable example of this is the sequential occupation of the same area by adult males D (December 1998), E (April 1999), and J (June 1999). These 3 bats had nearly identical territories centered

on 2 large patches of wild bananas (Fig. 4). In June 1999, we located the radio of male E on the ground, still broadcasting. The condition of the radio and its crumpled antenna suggested that it had been ingested and eliminated by a predator. By this time adult male J was the occupant of the former home range of male E.

Most bats had minor overlap with neighbors. For example, in 1999, adult male P was active in the vicinity of a wild banana patch within the territory of adult male N. The location of the latter at the time was unknown. In 2000, adult male M made a single incursion that lasted several minutes into the territory of adult male L, while the latter was at least 100 m away. Also in 2000, adult males O and Q had minor overlap in the garden portions of their foraging areas. At the same time, the foraging areas of Q and subadult male S exhibited the greatest overlap of any 2 bats in our study. We believe that there are 2 reasons for this. First, the home range of subadult male S was almost entirely in gardens. We suggest that garden foraging areas are less likely to be rigorously defended because the resources are more diffuse than those in forest and because bats active in these open areas are more vulnerable to predators. Second, subadults are likely to have unstable foraging areas, and their incursions might evoke less rigorous responses from territorial adults.

On 3 occasions we had multiple catches of *M. minimus* in a single net at the same site along the Kau River. The river is about 15 m wide, and its banks support numerous patches of wild and domestic bananas. The net was set parallel to the river and along second-growth vegetation; thus, bats that simply used the river as a flyway would not have been caught. On each occasion there were open flowers on 2 banana inflorescences within 3 m of the net. Two of the netted bats were adult males, 1 was a subadult male, and 1 was a subadult female. In 2000, a net in the same location caught 5 males and 2 females within a 15-min period. Three of these bats were caught while

other *M. minimus* vocalized as they were being removed from the net. Three weeks later the same site yielded 4 adult male *M. minimus*, none of which had been caught before. Two of the 1999 bats and 4 of the 2000 bats had territories within 100 m of this capture site.

During our project in Kau (1994–2000), other nets set across Utain Creek and across paths adjacent to patches of wild or domestic bananas caught no more than 2 *M. minimus* in any given night. The river net site was not particularly rich in food, nor were there other bananas within 25 m of the net. Thus, it does not seem likely that food was the primary attraction. Instead, we suggest that sites such as this one, along natural flyways, might be social information centers.

Much remains to be learned about the reproductive behavior of *M. minimus*. The association of adult males with clumped, defensible food plants might indicate a mating system based on resource defense polygyny. In this case, male reproductive success would be dependent on territorial defense and on the attractiveness of that territory to estrous females. Because reproduction is not seasonal in *M. minimus* (Hood and Smith 1989), male sexual activity, the vigor of territorial defense, and the degree of development of the sternal gland (Hood and Smith 1984) all might be cyclic or episodic. On the other hand, social information centers might facilitate sexual competition among males and mate choice by females. In this case, male reproductive success would not be directly dependent on territorial defense.

The lowland rainforests of Kau, and Papua New Guinea in general, are extremely productive and support a complex community of fruit- and nectar-feeding pteropodid bats. It is intriguing that several species of pteropodids including *M. minimus* are thriving in close proximity to human villages, in part due to plants cultivated (bananas) or introduced (*P. aduncum*) by humans. *Homo sapiens* and bats have coexisted in Papua New Guinea for 35,000 to

50,000 years (Summerhayes 2000; P. Swadling, pers. comm.). Thus, land-management schemes supporting permanent, viable populations of pteropodid bats in rainforests juxtaposed to human settlements should be achievable in Papua New Guinea.

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#### LITERATURE CITED

- BONACCORSO, F. J. 1998. Bats of Papua New Guinea. Conservation International, Washington, D.C.
- BONACCORSO, F. J., AND B. K. McNAB. 1997. Plasticity of energetics in blossom bats (Pteropodidae): impact on distribution. *Journal of Mammalogy* 78:1073–1088.
- BONACCORSO, F. J., N. SMYTHE, AND S. R. HUMPHREY. 1976. Improved techniques for marking bats. *Journal of Mammalogy* 57:181–182.
- BONACCORSO, F. J., J. R. WINKELMANN, E. R. DUMONT, AND K. THIBAUT. 2002. Foraging movements and home range of *Dobsonia minor* (Pteropodidae): a solitary, foliage roosting fruit bat in Papua New Guinea. *Biotropica* 34:127–135.
- FLANNERY, T. F. 1995. *Mammals of New Guinea*. Comstock/Cornell, Ithaca, New York.
- HOOD, C. S., AND J. D. SMITH. 1984. Histology of a sexually dimorphic integumentary gland in *Macroglossus lagochilus* (Chiroptera: Pteropidae). *Journal of Mammalogy* 65:1–9.
- HOOD, C. S., AND J. D. SMITH. 1989. Sperm storage in a tropical nectar feeding bat, *Macroglossus minimus* (Pteropidae). *Journal of Mammalogy* 70:404–406.
- ITINO, T., M. KATO, AND M. HOTTA. 1991. Pollination ecology of the two wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*: chiropterophily and ornithophily. *Biotropica* 23:151–158.
- KUNZ, T. H., C. WEMMER, AND V. HAYSEN. 1996. Sex, age, and reproductive condition of mammals. Pp. 279–290 in *Measuring and monitoring biological diversity: standard methods for mammals* (D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, eds.). Smithsonian Institution Press, Washington, D.C.
- LAW, B. S., AND M. LEAN. 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. *Biological Conservation* 91:201–212.
- LEKAGUL, B., AND J. A. MCNEELY. 1977. *Mammals of Thailand*. Sahakarnbhat, Bangkok, Thailand.
- MITTERMEIER, R. A., P. R. GILL, AND C. G. MITTERMEIER. 1997. *Megadiversity: earth's biologically wealthiest nations*. CEMEX, Mexico City, Mexico.
- MORRISON, D. W. 1979. Foraging ecology and energetics of the neotropical fruit bat *Artibeus jamaicensis*. *Ecology* 59:716–723.
- ODUM, E. P., AND E. J. KUNZLER. 1955. Measurement of territory and home range size in birds. *Auk* 72:128–137.
- PAYNE, J., C. M. FRANCIS, AND K. PHILLIPS. 1985. *A field guide to the mammals of Borneo*. Sabah Society, Kota Kinabalu, Sabah, Malaysia.
- RALLS, K. 1971. Mammalian scent marking. *Science* 171:443.
- SALAS, L. 2002. The comparative ecology and behavior of the mountain cuscus (*Phalanger carmelitae*), the silky cuscus (*Phalanger sericeus*), and the coppery ringtail (*Pseudochirops cupreus*) at Mt. Stolle, Papua New Guinea. Ph.D. dissertation, University of Massachusetts, Amherst.
- START, A. N., AND A. G. MARSHALL. 1976. Nectarivorous bats as pollinators of trees in West Malaysia. Pp. 141–150 in *Tropical trees: variation, breeding and conservation* (J. Burley and B. T. Styles, eds.). Linnean Society symposium series no. 2. The Linnean Society of London, London, United Kingdom.
- STRAHAN, R. 1995. *The mammals of Australia*. Reed Books, Chatswood, New South Wales, Australia.
- SUMMERHAYES, G. 2000. *Lapita interaction*. Australian National University, Canberra, Australia.
- WILKINSON, G. S., AND J. W. BRADBURY. 1988. Radiotelemetry: techniques and analysis. Pp. 105–124 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- WINKELMANN, J. R., F. J. BONACCORSO, AND T. L. STRICKLER. 2000. Home range of the southern blossom bat, *Syconycteris australis*, in Papua New Guinea. *Journal of Mammalogy* 81:198–204.
- WINKELMANN, J. R., AND E. E. GOEDEKE. 2000. Observations of tongue function and feeding behavior of captive *Macroglossus minimus* and *Syconycteris australis* (Pteropodidae). *Bat Research News* 41:150.

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