

## Home Range of *Dobsonia minor* (Pteropodidae): A Solitary, Foliage-roosting Fruit Bat in Papua New Guinea<sup>1</sup>

Frank J. Bonaccorso

National Museum and Art Gallery, P.O. Box 5560, Boroko, Papua New Guinea

John R. Winkelmann<sup>2</sup>

Department of Biology, Gettysburg College, Gettysburg, Pennsylvania 17325, U.S.A.

Elizabeth R. Dumont

Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003, U.S.A.

and

Katherine Thibault

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131, U.S.A.

### ABSTRACT

Lesser bare-backed bats (*Dobsonia minor* [Pteropodidae]) are solitary and roost in foliage of understory and subcanopy trees in lowland rain forest. These 70–90 gram frugivorous bats forage in primary and secondary forest and in abandoned gardens. At the Kau Wildlife Area in Papua New Guinea, movements ( $N = 1041$ ) of four males and four females fitted with radio transmitters were monitored for 1 to 18 months. Mean home range within 30-day sampling periods was 5.1 ha ( $N = 12$ ). There were no significant differences in home ranges by sex or by dry–wet season. Females, however, had significantly larger mean core-use areas than males ( $1.43 \pm 0.61$  and  $0.65 \pm 0.16$  ha, respectively). There was moderate overlap in home range and core-use areas among some simultaneously tracked animals. The long axes of home ranges varied from 150 to 1150 m and the mean was significantly larger in females. Individuals commuted from day roosts to multiple feeding areas, sometimes resulting in disjunct core-use areas and home ranges. Fruits of native *Ficus* species and the exotic shrub *Piper aduncum* were staple food items. *Piper aduncum* grew as dense clusters within early successional habitats, and individual plants ripened 5–20 fruits per night throughout the year. *Ficus* spp. grew in primary and secondary forest and fruited asynchronously, but individual trees produced tens to thousands of ripe fruits over 7 to 10 days. Three adult female *D. minor* were tracked over multiple periods spanning 2.5–18 months. Although each female continued to visit a core-use area containing *P. aduncum* throughout the study, turnover of other core-use areas reflected the ephemeral locations of fruiting fig trees.

*Key words:* bat; core-use area; day roost; *Dobsonia minor*; *Ficus*; foraging; home range; Papua New Guinea; *Piper aduncum*; radio telemetry.

SPACING AND MOVEMENTS OF CHIROPTERA are obtained by the availability and dispersion of food and day-roost resources (Humphrey 1975, Bradbury & Vehrencamp 1976, Winkelmann *et al.* 2000), as well as by life history dynamics such as the timing and scope of migration or reproduction (Humphrey & Cope 1976, Ceballos *et al.* 1997). Individuals of colonial species that roost in large assemblages undertake long commuting flights to reach food resources not depleted or dominated by conspecifics. Highly colonial species such as Brazilian free-tailed bats (*Tadarida brasiliensis*; Davis *et al.* 1962), gray-headed flying foxes (*Pteropus poliocephalus*; Spencer *et al.* 1991, Parry-Jones & Auger 1992), and southern long-nosed bats (*Leptonyc-*

*teris curasoae*; Sahley *et al.* 1993) commute distances of 15 to 50 km to their foraging areas. In contrast, bat species that are solitary or live in small groups (<15 individuals), particularly in tropical forests, often roost within 2 km of their foraging areas and incur minimal time and energy costs for commuting. Furthermore, in highly productive tropical rain forests such bats meet nutritional requirements within comparatively small foraging areas, usually 12 ha or less (Morrison 1978, 1980; Kalko *et al.* 1999; Winkelmann *et al.* 2000). In Panama, *Tonatia silvicola*, a gleaning insectivore, commuted 200–500 m from day roosts to foraging sites, the latter being 3–4 ha (Kalko *et al.* 1999). In the same study, the gleaning insect- and frog-eating bat *Trachops cirrhosus* roosted in small groups in tree hollows, and commuted 1200 m or less to foraging areas of ca 12 ha. In Panama, solitary males of the common fruit bat (*Artibeus jamaicensis*) roosted in foliage and commuted less than half

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<sup>2</sup> Corresponding author; e-mail: jwinkelmann@gettysburg.edu

the distance to food resources observed for harem males or females (*ca* 500 m) living in small groups inside tree hollows (Morrison 1978). Thus, both commuting distances and the dispersion and abundance of food resources strongly influence the size of the home range, defined in the seminal paper of Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young."

Although the study of home range is fundamental in animal natural history, wildlife management, and conservation biology, we know of only one study that documented home range using radiotelemetry for mammal species in Papua New Guinea (Sekharan & Miller 1995, Winkelmann *et al.* 2000). Our present study is the first to report on the foraging and commuting movements, home ranges, core-use areas, day-roost areas, and diet of the lesser bare-backed bat *Dobsonia minor* (Pteropodidae). This bat is a 70–90 g obligate frugivore that is common in lowland rain forests of New Guinea (Bonaccorso 1998). It is solitary at its day roosts within the foliage of understory and subcanopy plants, including palm trees and vine tangles.

Previously, we reported very small home ranges and the movement patterns of the 18 g fruit- and nectar-feeding bat *Syconycteris australis* (Winkelmann *et al.* 2000). We hypothesized that *D. minor* also would have small home ranges and commute short distances to feeding areas. We based this assumption on its solitary roosting habits and the annual abundance of bat-dispersed fruits such as figs and pipers within our study site.

## STUDY AREA

Our study was conducted at the Kau Wildlife Area, Madang Province, Papua New Guinea, during six intervals over a span of three years: 11 June–2 July 1997; 19 December 1997–8 January 1998; 20 June–7 July 1998, 14–18 December 1998; 9–21 April 1999; and 9 June–1 July 1999. Kau Wildlife Area (5°08'S, 145°46'E) is privately owned and managed by the Didipa Clan of Kau and Baitabag Villages, and forms an 800 ha reserve of lowland rain forest between 20 and 60 m elevation that includes primary, successional, and riparian forest (Fig. 1). The Biges and Kau Rivers and several small tributaries with permanent waterflow dissect this area of hills, plateaus, and valleys. Traditional, shifting vegetable and fruit gardens, and seral stages of abandoned gardens surround the wildlife area. Mean annual precipitation at nearby Nagada Harbor is 3460 mm (1994–1996). June through Au-

gust usually are the driest months and each receive less than 100 mm of rain.

Up to 155 tree species occur within 1 ha of primary forest at Kau (R. Kitchings, personal communication). Twenty-eight *Ficus* species have been recorded in Kau Wildlife Area (G. Weiblen, personal communication). In secondary forest greater than ten years of age at Kau, *Ficus hispidoidea* and *F. bernaysii*, are common gynodioecious species exploited for fruit by *D. minor*. In areas where abandoned gardens are returning to forest, *Piper aduncum*, introduced onto New Guinea only after 1940 (Kidd 1997), forms very dense stands until plants senesce at about ten years of age.

## MATERIALS AND METHODS

With a compass and transect line, we mapped 285 reference points along 5.6 km of interconnecting footpaths and creeks. Reference points were doubly marked with flagging and metal forestry tags. The total area mapped for this study encompassed 78 ha, including all the above described habitats.

Lesser bare-backed 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, England) for individual recognition. The bands passed through slits cut in the patagium on either side of the middle of the fifth metacarpal (modified from placement along the wrist described in Bonaccorso *et al.* 1976). Eight individuals were fitted with position-sensitive radio transmitters (PD-2CP models, Holohil Systems, Carp, Ontario, Canada). A change in pulse rate according to the orientation of the radio allowed us to determine whether the bat was flying or roosting. Flight also is indicated by rapid fluctuations in signal strength. Bats were transported in cloth bags by vehicle to our laboratory at Jais Aben Resort, a distance of 4.5 km. In the laboratory, transmitters were attached by collars sheathed with surgical tubing and stabilized at the back of the neck by Skinbond Surgical Cement (Smith and Nephew United, Largo, Florida). Complete transmitter and collar units weighed no more than 3.5 g (*ca* 4% of the body mass of *D. minor*) and had an expected battery life of either six or ten weeks. Radio-tagged animals readily drank a 15 percent honey-water solution before return transport and release near the site of capture. Bats fitted with radio collars were released within three hours of capture but were not monitored until the following night.

All bats fitted with radio collars were adults or



TABLE 1. Home range, Core-use area, and day-roost area of lesser bare-backed bats in Papua New Guinea.

Bat	Sex	Age class	Body mass (g)	Telemetry periods		Home range			CU area	Day roost	
				Mo/yr	Days <sup>2</sup>	N <sup>3</sup>	MAP 0.95 <sup>1</sup>	Axis <sup>4</sup>	MAP 0.50 <sup>1</sup>	N	Area <sup>1</sup>
A	male	subadult	76	June 1997	16	112	8.08	1150	0.89	9	0.07
B	male	subadult	78	June 1997	5	48	1.73	150	0.58	5	0.11
C	female	adult	74	January 1998	11	79	9.27	635	2.52	6	0.07
			80	April 1999	9	47	4.28	470	1.12	3	2.81
			88	June 1999	22	90	1.38	365	0.30	7	0.07
D	female	adult	99	January 1998	8	82	3.73	340	1.26	6	0.08
			102	June 1998	18	88	5.76	455	1.57	6	0.45
E	male	subadult	83	January 1998	16	92	3.11	395	0.52	6	0.03
F	female	adult	91	December 1998	6	62	5.87	780	1.51	3	0.00
G	female	adult	86	April 1999	13	73	5.94	710	1.47	7	4.03
			85	June 1999	23	138	9.39	905	1.69	13	1.00
H	male	adult	90	April 1999	9	51	2.55	435	0.61	3	0.12
			Means				5.09	566	1.17		1.49
			SD				2.77	280	0.63		1.31

<sup>1</sup> Units are hectares.

<sup>2</sup> Number of days that radiotelemetry positions were obtained.

<sup>3</sup> These values refer to the number of positions taken by radiotelemetry for an individual; values for home range, long axis, and CU are identical.

<sup>4</sup> Long axis of home range in meters.

feasible. We rarely lost radio contact with focal animals, except on the first night with a newly affixed radio, or when bats with large home ranges moved to a distant food patch. When radio contact was broken with a moving bat, contact usually was re-established within 20 minutes by walking toward the bearing of the disappearing bat. Bat movements between feeding patches often were predictable, so that we could anticipate movement into a new area. Communications via short-range voice radio (FRS-101 Radioshack, Fort Worth, Texas) between two observers facilitated the documentation of movements beyond the 300 m maximum reception range of a single observer.

We created a map of the study area (Fig. 1) and plotted positions for each bat on separate copies. Later, a grid was superimposed on the map, a zero intercept was chosen, and the X- and Y-coordinates were determined for each position. Map coordinates were entered into a Microsoft Excel database for each bat and were accessed and analyzed with Antelope home range software (J. Bradbury and S. Vehrencamp, pers. comm.). Following Wilkinson and Bradbury (1988), we used Anderson Fourier analysis (nonparametric) to calculate probabilistic values for home range ( $P = 0.95$ ), and core-use area ( $P = 0.50$ ) 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 by an individual bat,

based on a nonprobabilistic minimum convex polygon method (Odum & Kuenzler 1955; Wilkinson & Bradbury 1988). The latter method, although it overestimates use areas compared to 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  $t$ -tests.

## RESULTS

**HOME RANGE.**—One thousand and forty-one position determinations on four male and four female *D. minor* fitted with radio transmitters were used to calculate home ranges, core-use areas, and day-roost areas (Table 1). Females C, D, and G were recaptured once or twice and refitted with new radios, resulting in data for individual movements over multiple periods, each spanning from 5 to 30 days.

Home range for single periods of 30 days or less ( $HR_{30}$ ) varied from 1.4 to 9.4 ha ( $N = 12$ ; Table 1). The mean size of  $HR_{30}$ s for all individuals in this study was  $5.1 \pm 2.8$  ha. Although there were no significant differences ( $t$ -test) in  $HR_{30}$ s based on sex, age class (adult vs. subadult), or season (wet vs. dry), females had slightly larger  $HR_{30}$ s than males ( $5.7 \pm 2.7$  and  $3.9 \pm 2.9$  ha, respec-

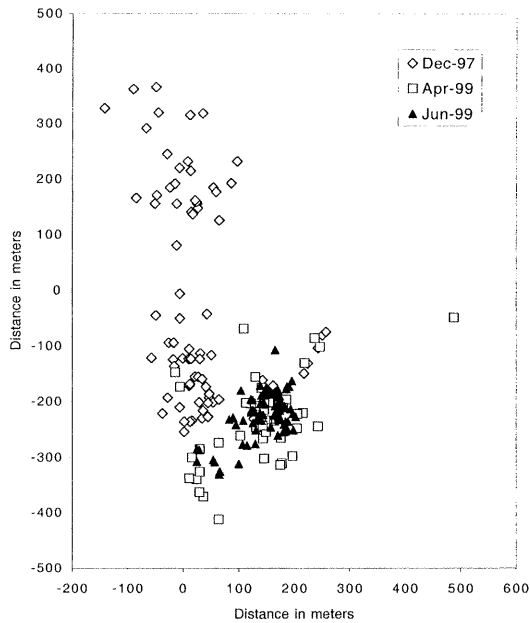


FIGURE 2. Home ranges of three individuals tracked simultaneously in April 1999.

tively). The mean long axis across HR<sub>30</sub>s for all bats was 565.8 m and the range was 150–1150 m. Females had significantly larger means of long axes ( $P = 0.02$ , two-tailed  $t$ -test assuming unequal variances) than males ( $652 \pm 225$  vs.  $248 \pm 202$  m, respectively).

Females C, D, and G were radio-tracked for multiple periods spanning 2.5–19 months, allow-

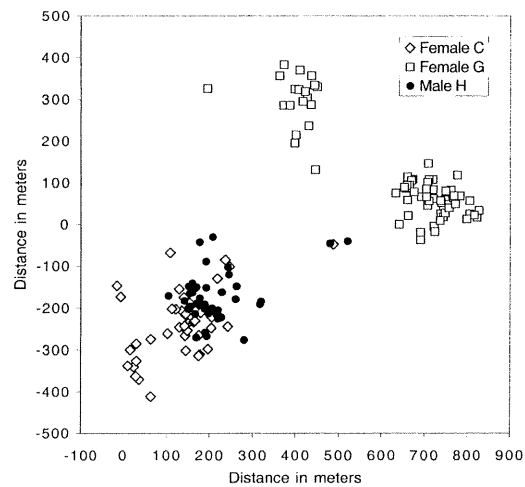


FIGURE 3. Home ranges (HR<sub>30</sub>s) of female C during three tracking periods.

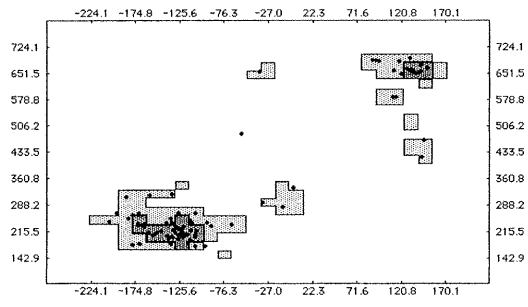


FIGURE 4. Antelope plot for male E. Total shaded areas are home range (MAP 0.95) and darker shaded areas are core-use area (MAP 0.50). The  $x$ - and  $y$ -axes are in meters, but are not to scale.

ing us to examine temporal flux in use-areas. Female C had HR<sub>30</sub> values of 9.3, 4.3, and 1.4 ha, respectively, in December 1997, April 1999, and June 1999 (Table 1). All three HR<sub>30</sub>s of this bat overlapped. The two core-use areas in 1999 overlapped with one another, but not with the core-use area in 1997 (Fig. 2). The cumulative home range (HR<sub>cum</sub>) over all tracking periods for female C was 11.8 ha. The HR<sub>30</sub> of female D increased from 3.7 ha in December 1997 to 5.8 ha in June 1998, retaining large portions of the HR<sub>30</sub> from the earlier period (Table 1). Female G also showed a large fluctuation in HR<sub>30</sub>, with values of 5.9 and 9.4 in April and June 1999, respectively; however, the primary core-use area was virtually identical over both time periods. Again, *P. aduncum* was the most abundant food plant in the primary core-use area of G. Thus, home range size and boundaries for an individual changed over periods that exceeded a month.

Some simultaneously monitored individuals showed moderate overlap in home range. The overlap in HR<sub>30</sub>s of male H and female C is depicted in Figure 3. Male A and male B also showed considerable concurrent overlap in home range. The overlap between the above pairs of bare-backed bats occurred at clusters of *P. aduncum* and at individual *Ficus* trees when figs were ripe. Unfortunately, we were unable to track more than three individuals simultaneously during our study.

CORE-USE AREA.—Females had a mean core-use area of  $1.4 \pm 0.6$  ha, and this was significantly larger ( $P = 0.002$ , two-tailed  $t$ -test with unequal variance) than the mean of males,  $0.7 \pm 0.2$  ha (Table 1). Core-use areas for some bats were fragmented into two or more disjunct areas as demonstrated for bat E (Fig. 4). Each core-use area represented

TABLE 2. *Commuting distances and group size of frugivorous bats from moist lowland tropical forests.*

Species	Body mass (g)	Group size	Mean, range of commuting distance (m)	Locality	Source
<i>Syconycteris australis</i>	17–22	1	484, 363–725	New Guinea	Winkelmann <i>et al.</i> 2000
<i>Nyctimene robinsoni</i>	30–50	1	506, 63–1012	Australia	Spencer & Fleming 1989
<i>Artibeus jamaicensis</i> (harem male and females)	35–50	6–12	590 ± 350 <sup>1</sup>	Panama	Morrison 1978
<i>A. jamaicensis</i> (bachelor males)	35–50	1	255 ± 155 <sup>1</sup>	Panama	Morrison 1978
<i>Dobsonia minor</i>	70–90	1	565, 150–1150	New Guinea	This study

<sup>1</sup> Standard error rather than range is presented.

either a day-roost area with surrounding flight activity, a feeding patch, or a heavily used flight corridor between roosts and feeding patches or between two feeding patches.

**DAY-ROOST AREA.**—All individuals in this study used compact day-roost areas (DRA) to which they returned before dawn. The mean DRA within a 30-day maximum sampling period (DRA<sub>30</sub>) was 1.49 ± 1.31 ha ( $N = 12$ ; Table 1). A DRA is subject to shift periodically. Case histories of DRA dislocation for three individuals illustrate this pattern.

Bat G used at least three disjunct day-roost areas over 2.5 months. On 15 April 1999, it abandoned its previous roost area and moved 600 m northwest. It used this new area for five consecutive days and shifted 200 m to the west on 20 April, but was back at the previous site on 21 April, the final observation for that period. On 9 June 1999, this bat occupied a roost near the one it used on 20 April, and continued to use this location through 1 July 1999, the final day of our observations. In contrast, female D used a compact DRA of 0.5 ha throughout our observations ( $N = 13$ ), which spanned nearly seven months during December and January 1997 and June 1998. Female C was located by radiotelemetry and accidentally flushed from its day roost located 1.5 m above ground, within a small palm tree (*Calyptrocalyx lauterbachianus*, Arecaceae). This bat immediately flew to an alternate roost 150 m to the south and used this area as its day roost for the next 11 days at which time observations ceased on 5 January 1998. Sixteen months later, female C was recaptured and fitted with a new radio; and on 18 April 1999, it used a day roost that was 310 m southeast of the January 1988 DRA. On 21 April 1999, this female, without disturbance by our observations moved its day roost 330 m southwest (about 600

m southwest of its day roost on 26 December 1997). Finally, this bat was radio-tracked from 9 to 30 June 1999 with the same active radio as in April and continued to roost ( $N = 7$  observations) in the DRA established on 21 April. This latter DRA<sub>30</sub> was 0.07 ha (Table 1).

**DIET.**—The seeds or pulp matrix from fruit in fecal samples were identified from animals netted in Kau. Four species of fruiting plants were identified in fecal material: two figs (*F. bernaysii* and *F. hispidioides*) an introduced piper (*Piper aduncum*) and the papaya (*Carica papaya*). *Ficus* spp. represented 55 percent, *P. aduncum* 36 percent, and *C. papaya* 9 percent of the plant taxa in 11 fecal samples.

## DISCUSSION

Lesser bare-backed bats occupied home ranges of 1.5 to 12.0 ha. Home range may overlap with one or more conspecifics. The mean home range was 5.1 ha for *D. minor*, and although small in comparison to records for central refuging bat species (Wilkinson & Bradbury 1988, Jong 1994, Robinson & Stebbings 1997), was similar to other solitary bats or bats that live in small colonies (Vehrencamp *et al.* 1977, Kalko *et al.* 1999, Winkelmann *et al.* 2000; Table 2).

A small home range is advantageous because it favors intimate knowledge of both fruiting patterns and habitat dynamics. In addition, shorter foraging routes conserve energy and minimize exposure to predators. One potential aerial predator at Kau is the sooty owl *Tyto tenebricosa* (Coates 1985).

Although we found no significant difference in home range between the sexes, females had significantly larger core-use areas, possibly reflecting additional nutritional requirements linked to reproduction and parental care. Parental care is solely the burden of female *D. minor*. Also, females have

larger long-axes across the home range than males at Kau. We believe that length of the long-axis across the home range potentially indicates longer commuting flights between day roosts and foraging areas. Females with non-volant juveniles too large to carry in flight must retain residence at a day roost until their offspring fledge, whereas males may switch day roosts in response to fluctuating food resource areas at any time.

Three lesser bare-backed bats were tracked during multiple periods spanning 19 months or less in both wet and dry seasons. *Piper aduncum* patches provided ripe fruits during all tracking periods and were the foci of all HR<sub>30s</sub>. In the Kau Wildlife Area a single, mature *P. aduncum* plant of 3 to 7 m height produced 5–20 ripe fruits per day throughout the year (FJB and JRW, pers. obs.). A single fruit including seeds, pith, fiber, and soluble components weighed 1.0–3.5 g, and several plants could feed one *D. minor* in a 24-hour period. Nonetheless, figs appeared to be equally important in the diet of *D. minor*, and *Ficus* species comprised a stable resource for bats. Individual trees, however, often were widely separated and fruited asynchronously, so that bat HR<sub>30s</sub> shifted in response to the fruiting patterns of the fig trees contained within them. We were able to locate trees with ripe figs by searching in areas indicated by radiotelemetry hot spots; these activity centers lasted only as long as the fruiting period of each tree. The nutritional content of fig fruits varies with species, but typically are high in calcium, amino acids, and fiber (Herbst 1986, O'Brien *et al.* 1998, Nelson *et al.* 2000, Wendeln *et al.* 2000). By feeding on a variety of highly productive fig species, as well as *P. aduncum*, *D. minor* can remain in energetic and nutritional balance within very small home ranges, despite competition in Kau from six other species of frugivorous bats.

Foraging movements of other similar-sized, fig-eating bats are compared to *D. minor* in Table 2. The distances of foraging movements for *D. minor* are remarkably similar to those of *Nyctimene robinsoni* in Queensland, Australia (Spencer & Fleming 1989) and *A. jamaicensis* in Panama (Morrison 1978). *Nyctimene robinsoni*, *A. jamaicensis*, and *D. minor* possess similar physical, ecological, and behavioral characteristics, including size (40–90 g mass), habitat selection (lowland rain forest), roost requirements (solitary or small groups roosting in foliage or tree hollows), and extensive reliance on fig fruits for food.

In addition, mean home range (HR<sub>30</sub>) of *D. minor* does not differ significantly (*t*-test) from the

mean home ranges of *S. australis* and *M. minimus* in Kau. These smaller (20 g) frugivore/nectarivores feed largely on fruits and/or blossoms that are clumped in space but stable in production throughout the year (Winkelmann *et al.* 2000).

All *D. minor* in this study used day-roost areas considerably smaller than their home ranges. Individuals monitored over long periods shifted day roosts to disjunct areas one or more times. Shifts in day-roost area sometimes are immediate responses to attack or close approach by a predator (including humans perceived as a predator), but also may occur spontaneously after a period of long use because accumulated guano and odors may cue predators. Usually more than one tree within a day-roost area was used.

In summary, within the Kau Wildlife Area, lesser bare-backed bats maintain home ranges that are somewhat fluid but include continuous use of some core-use areas. The solitary roosting habitats, the use of non-limiting foliage for the day roost, and the rich productivity of preferred food species permit very small home ranges. Most commuting flights between core-use areas are less than 600 m. The introduction during World War II of the weedy shrub *P. aduncum* to Papua New Guinea (Kidd 1997), its rapid spread along road and waterway margins, and the ability of *P. aduncum* to dominate abandoned human gardens (FJB and JRW, pers. obs.) no doubt have enriched the fruit resources available to *D. minor*. In addition, *F. hispidoides* and *F. bernaysii* are more abundant in successional habitats than in undisturbed habitats. It would be interesting to compare the *D. minor* population in Kau to one in forest that is unaffected by large-scale human disturbance and introduced plant species. Under such conditions, we predict that figs will be the dominant component of the diet, that home ranges will be larger and more fluid, and that population density of *D. minor* will be lower than in Kau. Finally, because of the abundance of *P. aduncum* in Kau, *D. minor* feeds less on other fruits. The impact of this dietary change on the dispersal of seeds of traditional food species and on the species composition of regenerating forests has yet to be assessed.

Presently, Papua New Guinea is undergoing extensive loss of forests from development including timber harvesting, plantation agriculture, and mining. The majority of the human population lives in remote rural areas and practices subsistence agriculture (Alcorn & Bechler 1993, Sekharan & Miller 1995) supplemented by gathering forest products (Batet *et al.* 1998) and hunting wildlife,

which includes even small bats and rodents (Busse *et al.* 1993; F. Bonaccorso, pers. obs.). Nonetheless, there is a strong conservation ethic among the people of Papua New Guinea, both at the “grassroots” level and within government agencies charged by the constitution of Papua New Guinea to protect its natural heritage (Bonaccorso, 1997).

Our study has demonstrated that individual *D. minor* require only *ca* 5 ha of forest to survive in lowland rain forest of northern New Guinea. This forest need not all be old growth, as all individuals in our study used a combination of primary and secondary forest, the latter with the exotic *P. aduncum* as a major food source. A mosaic of primary and secondary forest as well as active and abandoned gardens appears to benefit populations of the lesser bare-backed bat. As the human population continues to grow in Papua New Guinea, forest management policy that promotes the retention of small patches of old-growth forest in combination with clearing for gardens should be

sufficient to retain viable populations of common blossom bats (Winkelmann *et al.* 2000) and lesser bare-backed bats.

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