HOME RANGE, ROOST SWITCHING, AND FORAGING AREA IN A PHILIPPINE FRUIT BAT (*PTENOCHIRUS JAGORI*)*

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Abstract. We show that roost switching in the musky fruit bat, *Ptenochirus jagori*, is probably determined by the spatially changing availability of fruit resources. We investigated the roosting behavior and foraging movements of this frugivorous bat species in a Philippine lowland rainforest with the help of radiotelemetry. Five male and five female *P. jagori* were triangulated and followed for up to four months. Single individuals mostly roosted in primary forest trees. Both sexes changed their day roosts at variable intervals (range 8 to 72 days). This data is the first of its kind for pteropodid bat species solitarily inhabiting tree cavities. Roost-related home ranges of individuals ranged from 8.4 to 30.9 ha with no significant difference between the sexes. Range spans of home ranges varied from 533 to 1589 m. Each bat typically visited several foraging areas every night and showed high fidelity to these sites during the occupancy of a particular day roost. These core-use areas represented 18 to 55 % of the home ranges and contained at least one fruiting tree. The predictability of foraging movements in a night, together with a preferential direction of home range geometry, indicate some kind of "trap-lining" behavior which reduces travel distances and energy cost. *Accepted 19 September 2001.*

Key words: *Core-use area, day roost, foraging, home range, musky fruit bat, Philippines,* Ptenochirus, *roost switching, telemetry.*

INTRODUCTION

The frugivorous musky fruit bat, *Ptenochirus jagori*, belongs to the Old World bats (Pteropodidae). It roosts solitarily in tree cavities or in small groups in caves (Mickleburgh *et al.* 1992). *P. jagori* inhabits disturbed areas as well as primary forest but is absent from sites more than a kilometer from forest or forest patches (Heideman & Heaney 1989). *P. jagori* is the most abundant fruit bat species within our study site (Luft 1998, and below). The species' diet comprises fruit of at least 45 different plant species, nectar of two species, and leaves of seven species (Luft 1998). We carried out radio-telemetry studies of *P. jagori* in order to gain an insight into home range size and foraging area. Of particular interest was the roost switching of this species since the reasons for such behavior are still unclear (Fenton *et al.* 1985).

STUDY AREA AND METHODS

The study was conducted around Sibaliw (11° 49 N, 121° 58 E), Province of Aklan, Philippines. This area is located on the Northwest Peninsula of Panay Island at an average elevation of 450 m a.s.l. and is do-minated by the island's last low-elevation primary forest sites partly intersected by secondary growth. The telemetry study was undertaken from February 1999 to September 2000 including both wet and dry seasons.

Bats were captured in the early night hours using mist nets. Five adult male and five adult female (including one pregnant) *P. jagori* were radio-tagged. Two bats received model PD-2C transmitters (Holohil Systems Ltd., Woodlawn, Ontario, Canada). The other eight bats were fitted with modified model PD-2 transmitters. A backpack built of shrink tube was glued onto a stainless steel bead necklace using epoxy. The transmitter was mounted on top of the backpack using epoxy as well. During the course of the study two individuals had been able to turn the necklace around and bite it off (the bats were recaptured carrying only the necklace and the saddle). The total mass of the transmitter was 4.9 g (less than 6 % of the body mass). The transmitter had an expected range of 400–500 m and a battery life of 16 weeks. Due to the very hilly topography of the study area the range often dropped to 200 m. We used two TRX-1000S receivers (Wildlife Materials, Carbondale, Illinois, USA) and collapsible 3-element Yagi antennae (Titley Electronics, Ballina, NSW, Australia).

We used triangulation in order to determine radiolocations. Bearings were taken at short time

intervals (every five min.). For our data analysis, circumstances dictated a tracking period of roughly 11 days for each bat (11.5 ± 4.8 d). Day roost occupancy was checked weekly. We chose the nonprobabilistic minimum-convex-polygon method to calculate home range and core-use area. Home range is defined as minimum area probability (MAP) = 0.95, and core-use area as MAP = 0.5 (Odum & Kuenzler 1955, Wilkinson & Bradbury 1988). Centers of activity within the foraging areas were determined by calculating harmonic mean fixes (Spencer & Barrett 1984). The distance between these centers of activity and the day roost was calculated. Data analysis was done using the software program RANGES V (ITE, Wareham, Dorset, UK). Results are reported as x̄ ± SD. Means for the sexes were compared for statistical significance ($P < 0.05$) using Student's t-test (S). Analysis of variance (ANOVA) was used when examining the distances between old and new roosts.

RESULTS

P. jagori mostly roosted in primary forest trees; only one of 16 roosts was in a secondary forest patch; one bat roosted in a cave and another one on a sheltered rock face. The pattern of day roost fidelity was diverse. Seven bats of both sexes changed their day roosts 1.07 times per month (range 8 to 72 days), the other three stuck to their roosting tree as long as we could pick up transmitter signals (range 99 to 127 days). Of three bats which changed their day roosts regularly, all the roosts could be found. The distances between old and new roosts were rather similar and showed no significant difference (ANOVA: F = 0.16; 3,5 df; $P > 0.9$). For example, male 168 changed its roosts across distances of 511, 444 and 523 m; it did so at a mean interval of 18 days. Female 349 switched roosts across distances of 536 and 574 m every 41.5 days, while in female 928 distances between old and new roosts were 136, 100, 474 and 413 m (with roost switching every 35 days).

Our observations indicate that one *P. jagori* switched day roosts in order to minimize travel distances to foraging areas. From the start of tracking (11 February 2000) female 349 occupied roost 1 (Fig. 1).

It fed mainly on fruits of *Ficus benjamina* (foraging areas FA1 and 3), but included three other *Ficus* species (Moraceae) in its diet as well. Travel distances from day roost 1 to FA1 and FA3 were 475 and 606 m respectively. At the time the *F. benjamina* tree in FA1 no longer bore ripe fruits, the bat changed its
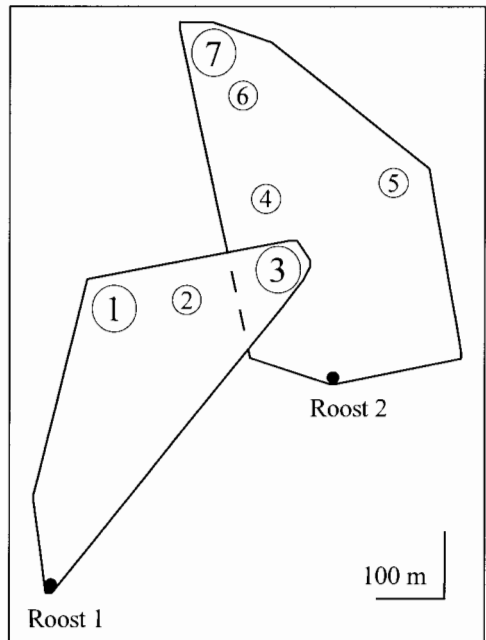

FIG. 1. Home ranges (95 % MAP) and foraging areas (arabic numerals in circles) of female 349 before and after roost switching. Foraging areas containing *Ficus benjamina* trees (see text) are highlighted by larger circles. Note that the home range was calculated separately for each occupied roost.

roost (verified on 15 March 2000). Roost 2 was found ro lie closer to a new foraging area (bat in FA7 first monitored on 13 March 2000) which contained three *F. benjamina* trees bearing ripe fruits. Reconnaissance flights in order to find new food sources seemed to be rare (unpubl. observ.). Since we did not track rhe female 349 every night it might have discovered FA7 shortly before 13 March 2000 and changed its roost within the next days. By occupying the new roost, female 349 reduced not only the travel distance to FA7 but also that to FA3; this latter tree ripened later than that in FA1 and was still visited after roost switching. Distances from roost 1 to FA3 and FA7 were 606 m and would have been 885 m respectively, but were only 170 and 583 m after roost switching.

Individual home ranges varied from 8.4 to 30.9 ha (Table 1). Mean home ranges were 18.2 ± 6.3 ha for males (N = 5), and 17.1 ± 9.0 ha for females (N = 5). There was no significant difference in mean

TABLE 1. Minimum area probabilities (MAP) and range spans of home range of musky fruit bats in Panay, Philippines. 349-1 and 349-2 denote occupied roosts 1 and 2 respectively.

Bat number	sex	age	n	95% MAP [ha]	50% MAP [ha]	Span [m]
149	F	Adult	19	19,9	4,7	672
389	F	Adult	29	8,4	3,0	533
349-1	F	Adult	36	10,2	5,6	817
349-2	F	Adult	33	14,9	9,1	654
928	F	Adult	32	16,2	5,5	801
709	F	Adult	30	30,9	9,2	1367
168	M	Adult	21	20,0	4,8	1589
190	M	Adult	35	23,0	12,7	1314
131	M	Adult	33	24,6	10,4	865
747	M	Adult	27	10,1	3,5	557
848	M	Adult	29	13,1	2,3	591

home range size between the sexes (S: $P > 0.5$). The only pregnant individual we tagged, female 709, had the largest home range of all tracked bats (Table 1).

Male *P. jagori* (Table 1) showed larger mean range spans than did females (983 ± 454 m compared to 838 ± 317 m); however, this difference was also not significant (S: $P > 0.5$). The bats spent most of their time near to feeding sites with one to several fruiting trees. The core-use areas (Table 1: 50 % MAP) of all tagged *P. jagori* ranged from 2.3 to 12.7 ha, representing 18-55 % of the momentary home ranges.

Mean core-use areas did not differ significantly between the sexes (S: $P > 0.5$).

Both male and female *P. jagori* visited several small-sized foraging areas (usually < 1 ha) each night and commuted between them. For short periods the direction and sequence of foraging movements was predictable. Male 848, for example, sequentially moved to the same four foraging areas on at least two consecutive nights, as did male 190 to at least three FAs on three consecutive nights. Female 389 sequentially visited the same two FAs for seven conse-

TABLE 2. Distance between day roost and centers of foraging areas (FA) of musky fruit bats in Panay, Philippines. AF and AM denote females and males respectively. AF349-1 and AF349-2 indicate occupied roosts 1 and 2 respectively.

Bat ID	Distance between day roost and FA centers [m]						
	FA1	FA2	FA3	FA4	FA5	FA6	FA7
AF149	202	318	452	633	–	–	–
AF389	20	202	485	–	–	–	–
AF349-1	475	497	606	–	–	–	–
AF349-2	–	–	170	285	298	520	583
AF928	132	255	590	605	801	–	–
AF709	430	594	1349	–	–	–	–
AM168	41	377	798	1072	–	–	–
AM190	385	417	645	710	999	1308	–
AM131	355	551	552	750	–	–	–
AM747	72	170	233	247	277	–	–
AM848	57	196	202	345	–	–	–

cutive nights. The mean number of foraging areas visited per tracking period (see study area and methods) was 4.6 ± 0.9 for males and 3.8 ± 0.8 for females (Table 2). All bats visited at least two different foraging areas every night.

On average females tended to travel about as far to foraging areas as did males (486 ± 203 m vs. 454 ± 243 m; S: $P > 0.5$). Interestingly, day roosts of all but two bats were positioned in one corner of their home ranges. Moreover, the home ranges often had a conspicuously elongate shape.

DISCUSSION AND CONCLUSIONS

To account for roost switching behavior one could assume a change in the distribution of ripe fruits, predator avoidance, competition over tree cavities, and changes in the nature of the roost through, e.g., parasitism (Morrison 1980, Kunz 1982, Fenton 1983, Fenton et al. 1985). Many frugivorous bat species studied so far failed to move their roosts to minimize commuting costs during foraging (Bradbury 1977; Morrison 1978b, 1980; Fenton et al. 1985). Hall (1983) stated that individuals of the pteropodid bat species *Nyctimene robinsoni* (a solitarily roosting species, mostly in primary forest, with a body mass of ca. 50 g) can be locally abundant at a food resource but then disappear. Thus individuals are likely to change their roosting and/or feeding sites opportunistically as availability of food in an area changes (Hall 1983). In their study, Spencer & Fleming (1989) found that *N. robinsoni* was rather site-faithful, thus indirectly supporting Hall's (1983) statement. A high density of fruiting figs during their two months tracking period probably accounted for the sedentary behavior. The same authors indicated that some bats changed their dayroost locations more frequently, but left open why they did so.

Our observations suggest that roost switching might be influenced by spatial changes in the availability of food resources and, by implication, the tendency to minimize travel costs. In the case of female 349, roost switching and the ripening of *F. benjamina* trees (the fruits of which it obviously preferred to other figs) in a new foraging area coincided. We did not monitor the ripening state of the *F. benjamina* trees in FA7 before female 349 visited this foraging area. However, we know that the fruits had newly ripened since overripe fruits fall on the forest floor in large numbers. This was not the case when we checked the trees after the roost switch.

Furthermore, the abundance of trees with cavities in our study site makes it unreasonable to assume that a lack of available roosting trees determined the direction of the roost switch.

To our knowledge data on the roost switching frequency of pteropodid bat species living in tree cavities are not available. Individuals of *P. jagori* moved to new roosts at variable intervals. This indicates that the roost switch is probably determined by the change in the distribution of ripe fruits.

In *P. jagori* there is no significant difference in the home range size between the two sexes. As reported for other frugivorous bat species (Morrison 1978a, August 1981, McCracken & Bradbury 1981, Fleming 1988, Handley & Morrison 1991) individuals leave their day roosts soon after sunset in order to fly to foraging areas where they feed for varying periods. Individuals of *P. jagori* showed a high fidelity to foraging areas, e.g., female 709 visited its first foraging area immediately after sunset for at least seven days. Moreover, some bats moved between their other foraging areas in quick succession, probably to increase dietary diversity since most foraging areas differed by offering different food resources. The predictability of foraging movements (as in *Syconycteris australis*, Winkelmann et al. 2000) together with the constancy of resource availability (nearly all of the bats included a particular *Ficus* species (Moraceae) in their diet, the individuals of which were fruiting continuously throughout the year) indicate some kind of "trap-lining" behavior in *P. jagori* in the short term. The small sizes of foraging areas and a preferential direction of the home range strengthen this indication. "Trap-lining" minimizes travel distances and energy cost (Kunz 1982).

Heideman & Heaney's (1989) prediction that small species in rainforest should display relatively short foraging distances of the order of 0.1 to 1.0 km in any one night (in contrast to small bat species foraging over much longer distances in, e.g., dry forest, Morrison 1978b) agrees largely with our results. Rainforest and late successional stages are believed to provide a higher density of food resources than do other habitat types (Winkelmann et al. 2000).

The present study has come up with a number of differences between the sexes falling short of statistical significance. Published conclusions of "no difference" without an inclusion of a statistical power analysis are common (e.g., Winkelmann et al. 2000). We are aware of our small sample sizes. However, the observed differences in the variables between the

two sexes are so small that they are not expected to be of great importance, in biological terms, even if the sample size were increased enormously. Cohen (1969) provides help in calculating the power of statistical tests. In our case, power = 0.05 at P = 0.05 relates to effect size d = 0.13. Note that if we assume that the differences between the two sexes reported above are negligible, we would need sample sizes that are so large that the associated "proof" of the null hypothesis is probably most often impossible (Milinski 1997). Using Cohen's (1969) desired power convention of 0.80, our sample size needed would be n = 931 at P = 0.05 for each sample.

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