

Home range and activity of the Indian giant flying squirrel (*Petaurista philippensis*) in Taiwan: influence of diet, temperature, and rainfall

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Abstract Knowledge on home range and activity patterns, along with their responses to environmental fluctuations, is important for the understanding of wildlife ecology and conservation, but related studies on giant flying squirrel species (genus *Petaurista*) are still limited. We radio-tracked five Indian giant flying squirrels (*Petaurista philippensis*) in subtropical Taiwan to assess their home range and activity patterns, as well as their behavioral strategy to cope with fluctuations in food quality. Specifically, we assessed the travelling and resting times of *P. philippensis* in relation to its energy requirements during periods of low food quality in winter. The influence of temperature and rainfall was also investigated. A total of five individuals were radio-tracked for 1–6 months. The home ranges of four individuals averaged 2.8 ± 2.0 ha (\pm SD), based on the 95 % kernel method. Mean home ranges of two adult males (4.4 ± 1.3 ha) were larger than a female (1.8) and sub-adult male (0.8). *P. philippensis* was found to be more active around dusk and dawn and less active at midnight. Daily ranging distance and activities were negatively associated with proportion of mature leaves in diet of the only female that we tracked. Rainfall had negative effects on activities of the males, while temperature had no significant influence. The current study suggested an energy conservative strategy of *P. philippensis*. Home ranges of *P. philippensis* are smaller than those of smaller flying squirrel species (genus

Glaucomys and *Pteromys* spp.), which may be related to the differences in food habits and gliding efficiency.

Keywords Activity · Food quality · Foraging strategy · Home range · *Petaurista philippensis*

Introduction

Home range is the area within which an animal travels across to fulfill daily needs, including food gathering, mating, and caring for the young (Burt 1943). Due to its adaptive significance, an understanding of home range size, shape, and pattern of utilization has important implications for wildlife ecology. This includes a species' feeding strategy, population density, or social systems (Schoener 1981; Harris et al. 1990). Understanding a species' home range may also be valuable for its future management and conservation (Rodrigues and Monteiro-Filho 2000; Foerster and Vaughan 2002). Despite this, understanding wildlife ecology and behavior from home ranges alone is limited and must incorporate information on species' activity patterns (Corp et al. 1997). When constrained by energy and time, an animal may allocate activities in accordance with their relative adaptive significance (Smith 1977; Hill et al. 2003). Activity patterns may therefore reveal factors that confine behavior the most (Benedix 1994). For example, the nocturnal behavior of martens (*Martes americana*) during the winter suggested the importance of avoidance of diurnal predators and synchronization with nocturnal prey in comparison with minimization of energy expenditure during the night (Drew and Bissonette 1997).

An animal's home range and activity pattern are not static and will vary due to environmental changes, including climate and food availability (Cotton and Parker 2000; Rodrigues and Monteiro-Filho 2000; Rezende and Bozinovic 2001). As a

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result, animals may employ different strategies to cope with these environmental fluctuations. For instance, seasonal variation in food availability could determine diet, which could in turn influence home ranges and activities of mammalian herbivores (Clutton-Brock 1977; Dasilva 1992; Rodrigues and Monteiro-Filho 2000; Masi et al. 2009). During food shortage, herbivores may subsist on mature leaves (Kuo and Lee 2003; Mendiratta et al. 2009) that are typically less nutritious than other plant parts (e.g. fruits, flowers, or young leaves) due to their high cellulose content (Garber 1987). To compensate for a lower energy intake rate, some herbivores spent more time searching and foraging, while others traveled less and rested more to conserve energy (Clutton-Brock 1977). For example, chimpanzees (*Pan troglodytes verus*) and François' langurs (*Trachypithecus francoisi*) increased feeding time when higher-quality food was scarce (Doran 1997; Zhou et al. 2007), while gray langurs (*Presbytis entellus*) ranged more during periods of food shortage (Curtin 1982). Alternatively, Siamang (*Hylobates syndactylus*) and lar (*H. lar*) gibbons traveled less due to food scarcity (Raemaekers 1980), while western black-and-white colobus (*Colobus polykomos*) rested more when feeding on mature leaves (Dasilva 1992). The latter example suggests that in some cases a lower energy intake does not enable an accompanied searching cost.

Indian giant flying squirrels (*Petaurista philippensis*) are distributed from west India to southeastern China and Malay Peninsula (Nowak 1999). In Taiwan, this nocturnal and solitary species lives primarily in broadleaf forests below 2200 m in elevation and nests mainly in tree cavities (Lee et al. 1986). Weighing 1260 g for males and 1334 g for females (Lee et al. 1993), *P. philippensis* prefers fruits, buds, and young leaves, but can subsist on mature leaves in winter when the preferred plant parts are not available (Kuo and Lee 2003).

Until now, the only home ranges and activity pattern data available for *P. philippensis* were quantified by direct observation (Lin et al. 1988). However, tracking *P. philippensis* was difficult or unlikely when individuals moved to certain habitats, as noted by Lin et al. (1988), suggesting that home range may be underestimated using this method. The only radio-tracking study on a giant flying squirrel species (*P. leucogenys*) lasted for only 2–7 days (Baba et al. 1982), in contrast to extensive radio-tracking studies on other smaller (< 200 g, Nowak 1999), boreal, or temperate flying squirrel species, including the Southern flying squirrel (*Glaucomys volans*, Bendel and Gates 1987; Fridell and Litvaitis 1991), the Northern flying squirrel (*G. sabrinus*, Witt 1992; Hough and Dieter 2009), and the Siberian flying squirrel (*Pteromys volans*, Hanski et al. 2000).

In this current study, we assessed home range size, daily ranging distance, and activities of five *P. philippensis* in subtropical Taiwan. We also evaluated the behavioral responses of this species to fluctuations in food quality,

temperature, and rainfall. We assessed whether *P. philippensis* traveled or rested more to meet their energy requirements when they subsisted on low-quality food resources during winter. While difficulties of trapping this species limited our sample size to five *P. philippensis*, this study provides the first insights into space utilization, activity budget, and foraging strategy of *P. philippensis* and other giant flying squirrel species.

Materials and methods

Study site

The study site is located in the Fushan Experimental Forest Station (24° 46'N; 121° 34'E) in northeastern Taiwan. The site sits at 600–800 m above sea level and is covered with primary and secondary forests dominated by Lauraceae and Fagaceae (Kuo and Lee 2003). Average monthly temperature ranged from 12.1 to 24.4 °C between July 1997 and December 1998. Monthly rainfall varied from 66.5 to 1082.5 mm (Y. J. Hsia, personal communication).

Capture of *P. philippensis*

At dusk we placed a fishing net at the entrance of nesting sites and hit tree trunks to force *P. philippensis* into the net. Once captured, individuals were weighed and anesthetized with Zoletil 50 (Virbac, Carros, France) through intramuscular injection using a syringe (0.3 ml/kg). Gender and reproductive status were recorded, as well as body weight (kilogram), length of head and body, tail (both in centimeter), ear, and hind foot (both in millimeter). Only *P. philippensis* ≥ 1 kg were fitted with radio transmitters (about 30 g, AVM Instrument Company, Colfax, CA; Telonics, Mesa, AZ) so that the transmitter weighs < 3 % body weight. *P. philippensis* were not released until fully recovered from anesthetization, and data were not recorded until 1 week later to allow for habituation. All procedures fulfilled Taiwan wildlife protection legislative requirements.

Home range and daily ranging distance

From October 1997 to November 1998, *P. philippensis* were radio-tracked for a minimum of four nights each month using receivers and RA-2A Yagi (Telonics). Tracking was conducted from 1700 to 0600 hours when individuals were mostly active outside of their nests. Due to the dense vegetation in the study area, we could not sometimes observe *P. philippensis* or approach the trees where individuals were observed, rendering direct positioning with GPS unlikely. Locations of *P. philippensis* were therefore determined with two researchers taking bearings simultaneously at GPS-

positioned locations. Individuals were approached as close as possible, typically within 60 m. Angles of triangulation were kept between 45 and 135° to reduce inaccuracy (White and Garrott 1990).

To assess possible telemetry error, a radio collar placed 3-m high was positioned where tagged *P. philippensis* were frequently observed. The bearings were then determined by researchers unaware of where the radio collar was placed. Blind tests were processed at four locations and assessed five times per site. The resulting bias averaged 6.8 ± 2.6 m (\pm SD). Given the small bias, we believe that the estimation of home range size in this study should be reliable.

Several methods have been used for the estimation of home range size using telemetry data, including minimum convex polygon (MCP), harmonic mean estimator, fractal estimator, kernel method, etc. (Powell 2000). Each method has shortcomings, but kernel method was generally favored over other methods due to its being less sensitive to extreme observations and not influenced by the size and position of superimposed grids (Powell 2000). We thus calculated home ranges as 95 % fixed kernel method with least-squares cross validation bandwidth selection; however, home range size with 100 % MCP was also reported to facilitate comparisons with related studies (Baba et al. 1982; Lin et al. 1988). Core area was estimated with 50 % kernel. To minimize spatial auto-correlation of observations that would under-estimate home range size (Harris et al. 1990), a *P. philippensis* was tracked every 30 min in the early stage of the study to determine the minimum time interval for spatial auto-correlation to be negligible. Following the method suggested by Swihart and Slade (1985), it was determined that a minimum of 2-h interval was required. Individuals were thus tracked hourly to more accurately calculate daily ranging distance, defined as the sum of distance between successive hourly fixes (including the nesting sites), while only fixes at 2-h interval were used to estimate home range size.

Stability of home range size was evaluated by plotting increment of home range size (with both 95 % kernel method and 100 % MCP) against sequential addition of fixes to see if it reached asymptote (Harris et al. 1990). Space utilization was compared using four parameters following Spencer and Barrett (1984): spread (distances among fixes), skewness (degree of deviation between arithmetic and harmonic mean center), kurtosis (intensity of activity at harmonic mean center), and relative dispersion (dispersion of fixes against the activity center). Home range size, home range stability, and space utilization were assessed using the software Ranges7 (Anatrack Ltd., Wareham, UK).

Activity patterns

With a motion-sensitive instrument that can transmit one of two different pulse rates depending on whether the radio-

transmitter is parallel to horizontal, we could tell whether *P. philippensis* was active or not. However, specific behavioral categories, such as forage or travel, cannot be distinguished based on the pulse rates. Activity pattern was thus represented only by being active or not. From 1700 to 0600 hours, we recorded the hourly activity of *P. philippensis*. For a preliminary test, we continuously recorded activities of one individual for three consecutive nights, and hourly activities were then tallied. We then determined the maximum time interval for a similar hourly activity as continuous recording, and the following method was applied. At the beginning of every 6 min, we checked activity of *P. philippensis* for 5 s. Thus, there were ten records for the percentage of hourly activity. For example, if *P. philippensis* was active in three of ten records, percentage of activity in that hour would be 30 %. We also calculated the total daily activities by summing the percentage of hourly activity between 1700 and 0600 hours.

Data sources of diet and abiotic factors

Sunset and sunrise time was obtained from the Central Weather Bureau in Taipei. Temperature and rainfall were accessed from a meteorological station < 1 km of our study site. Daily mean temperature (degree Celsius) and total rainfall (millimeter) were tallied from 1700 to 0600 hours. Proportion of mature leaves in diet was a negative indicator of food quality (Kawamichi 1997) and was derived from our parallel study on food habits of *P. philippensis* (Kuo and Lee 2003). We used monthly proportion of mature leaves in diets across all *P. philippensis* to represent daily proportion in that month because radio-tracking and diet observation were not carried out at the same night.

Statistical analyses

Differences in daily ranging distance among *P. philippensis* were assessed with ANOVA if the data were normally distributed and had equal variance. When significant results were found, Tukey's tests would be followed to test for pairwise difference. We instead used a non-parametric Kruskal–Wallis test when both assumptions could not be fulfilled, and if required, followed by pair-wise Mann–Whitney *U* test after Bonferroni adjustment to correct for inflated type I error. Temporal association between leaving nest and sunset, and returning nest and sunrise was respectively tested with Pearson correlation if normality could be confirmed. Otherwise, non-parametric Spearman rank correlation would be applied.

The relationship between daily ranging distance and activities to temperature, rainfall, and proportion of mature leaves in diet was determined using multiple linear regression analysis. Each *P. philippensis* was analyzed separately to reveal

possible individual variation. Variance inflation factor (VIF) measures the degree of multicollinearity among explanatory variables, and a high VIF suggests that the estimation of regression coefficient and the significance level may be biased. Explanatory variables with a $VIF > 10$ were excluded from further analyses (Kutner et al. 2005). Normality of residuals was assessed with Shapiro–Wilk test, while heteroscedasticity was determined by inspecting plots of residuals against dependent and each explanatory variable. Data were log-transformed if both assumptions were not fulfilled. Data have been standardized to have a mean ± 1 standard deviation (SD).

Results

The difficulty of capturing *P. philippensis* has limited our radio-tracking to five individuals, including three adult males (AM1, AM3, and AM4), one adult female (AF1), and one sub-adult male (SM2) (Table 1). AM1 and SM2 could not be located after 1 month. The other three individuals were tracked until transmitters lost power (3–6 months).

Home range sizes

Between October 1997 and November 1998, *P. philippensis* were radio-tracked for a total of 71 nights, with 397 fixes determined (excluding nests). Depending on the length of time tracked (1–6 months, 6–33 nights), 28–139 fixes were recorded for each individual (Table 1). Except for AM1, home ranges of four individuals reached asymptote with both 95 % kernel method and 100 % MCP (Fig. S1).

AM1 was thus excluded from subsequent home range analysis.

The home range of four individuals, estimated with 95 % kernel method, averaged 2.8 ± 2.0 ha (\pm SD). The home range of two adult males (4.4 ± 1.3 ha) was larger than that of the adult female (1.8 ha) and the sub-adult male (0.8 ha) (Table 1). Home range estimated with 100 % MCP averaged 2.8 ± 1.7 ha, with adult males (4.0 ± 1.3 ha) larger than the adult female (2.2 ha) and the sub-adult male (0.9 ha) (Table 1). Core area averaged 0.8 ± 0.6 ha with 50 % kernel method. Similarly, adult males had a larger core area than the adult female and the sub-adult male (Table 1).

Space utilization was assessed using four parameters. Spread, dispersion, skewness, and kurtosis were all higher in the two adult males than the adult female and the sub-adult male (Table 1).

Daily ranging distance

Due to short tracking periods, AM1 and SM2 were excluded from analyses. Daily ranging distance for the other three *P. philippensis* averaged 448.7 ± 193.0 m ($n=78$, range 108.0–1005.1 m). Ranging distance varied among these three individuals (ANOVA, $F=9.26$, $P<0.001$), with AF1 traveling much less (352.8 ± 164.2 m, $n=30$) than AM3 (570.3 ± 226.9 m, $n=19$) and AM4 (468.1 ± 145.2 m, $n=29$) (Tukey's test, $P<0.001$ and 0.05, respectively); however, there was no difference between the two adult males ($P>0.05$).

Daily ranging distance of AM3 was not correlated with temperature, rainfall, or proportion of mature leaves in diet (Table 2). AM4 ranged less with an increase in rainfall

Table 1 Home range, core area and space utilization of radio-tracked *Petaurista philippensis* between October 1997 and November 1998 in Taiwan

Individual	Gender	Tracking period	Tracking nights	Number of fixes	Home range size (ha)		Core area (ha)	Space utilization parameter			
					100 % MCP ^a	95 % Kernel		D ^b	S ^c	K ^d	S ^e
AM1	M	October 1997	6	28	/	/	/	/	/	/	/
SM2	M	November–December 1997	7	35	0.9	0.8	0.2	1.82	2.67	3.63	18.17
AM3	M	April–July 1998	19	75	3.1	3.4	0.8	2.15	4.13	4.14	42.07
AM4	M	June–November 1998	32	120	4.9	5.3	1.6	3.51	7.63	7.10	55.20
AF1	F	January–July 1998	33	139	2.2	1.8	0.4	2.07	1.87	4.11	26.86

The slash (/) indicates no estimation due to insufficient number of fixes

^a Minimum convex polygon

^b Dispersion: distance among fixes

^c Skewness: dispersion of fixes relative to activity center

^d Kurtosis: degree of deviation between arithmetic center and harmonic mean center

^e Spread: relative dominance of the peak of activity at harmonic mean center

Table 2 Statistical significance and coefficients of regression (*b*) of explanatory variables relating to daily ranging distance and activities of radio-tracked *Petauriata philippensis* in Taiwan

Individual	Variables	Temperature	Rainfall	Proportion of mature leaves
AM3	Ranging distance ^a	-51.60	-0.65	-18.79
	Activity ^b	13.19	-8.24**	4.24
AM4	Ranging distance	-7.43	-8.00*	-2.69
	Activity	-4.23	-3.44**	-0.56
AF1	Ranging distance	-10.36	-5.38	-2.47*
	Activity	0.80	-0.58	-2.06**

* $P<0.05$; ** $P<0.01$

^a Sum of distances between nests and serial hourly fixes from 1700 to 0600 hours

^b Sum of hourly activity from 1700 to 0600 hours

($b=-8.00$, $P<0.05$). AF1 moved less when this individual fed on more mature leaves ($b=-2.47$, $P<0.05$) (Table 2).

Activity pattern

Activities of five *P. philippensis* were recorded over 71 nights, with a total of 94 individual nights (we tracked more than one individual at some nights). We recorded a total of 12,220 activity data. *P. philippensis* left and returned to nests at sunset and sunrise, respectively ($r_s=0.91$ and 0.55, both $P<0.001$). Individuals left nests 17.0 ± 15.6 min ($n=94$) after sunset and returned to nests 45.3 ± 30.9 min before sunrise. An average of 10.6 ± 0.9 h (range 9.1–12.6 h) were spent outside of the nests, with the period of time increasing with the length of the night ($r_s=0.84$, $P<0.001$).

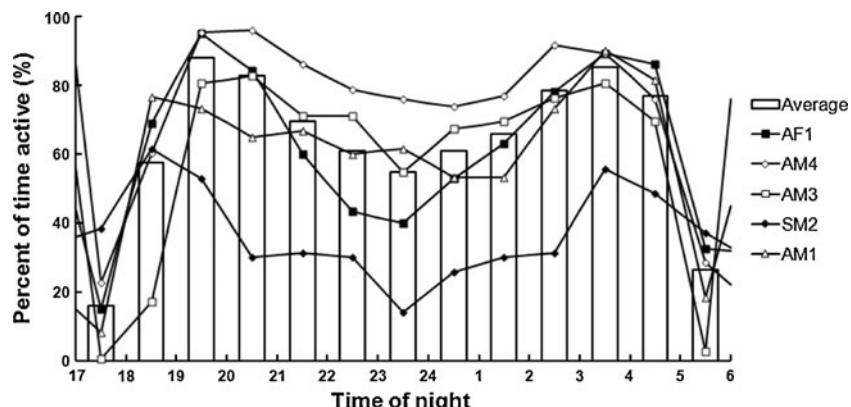
P. philippensis showed bimodal activity patterns, being more active around dusk and dawn and less active at midnight (Fig. 1). Activity patterns of *P. philippensis* varied with months (Fig. 2). For instance, AF1 was less active (hourly activity<50 %) at midnight from January to March, but was active almost the whole night from April to June

(Fig. 2a). Likewise, AM4 was mostly active from June to September, but became less active at midnight from October to November (Fig. 2b). AM3 was more active in June and July than in April and May (Fig. 2c).

Hourly activity between 1700 and 0600 hours of five *P. philippensis* averaged 63.3 ± 21.7 % ($n=94$). Total daily activities of AM3 were negatively affected by rainfall ($b=-8.24$, $P<0.01$), but was unrelated to temperature or proportion of mature leaves in diet (Table 2). AM4 was also less active with an increase in rainfall ($b=-3.44$, $P<0.01$), whereas AF1 was less active when it fed on more mature leaves ($b=-2.06$, $P<0.01$) (Table 2).

Discussion

Although the limited number of *P. philippensis* (up to five individuals) radio-tracked in this study suggests that results of the current study may not be conclusive, data collected so far suggests that *P. philippensis* prefer to rest more often when feeding on mature leaves during winter, rather than actively search further for higher-quality food resources. For example, the ranging distance and activity level of female AF1 was negatively associated with proportion of mature leaves in diet. Moreover, AF1 was mostly inactive at midnight from winter to early spring, but was active almost all night from spring to early summer. The change in ranging distance and activity pattern, nevertheless, could also be influenced by reproductive behavior. In early April 1998, we observed a clumsy juvenile around the nest of AF1. AF1 was later (early May) accompanied by a juvenile. Lactation is energy demanding (Gittleman and Thompson 1988) and often leads to an increase in feeding time (Munks and Green 1995). For example, lactating gelada baboons (*Theropithecus gelada*) spent 30 % more time feeding (Dunbar 1988), and red pandas (*Ailurus fulgens*) doubled duration of feeding bouts when suckling young (Gittleman 1988). The increase in ranging distance and activities may be related to the high energy requirement of this lactating female. The influence of diet and

Fig. 1 Activity pattern of five radio-tracked *Petauriata philippensis* between October 1997 and November 1998 in Taiwan

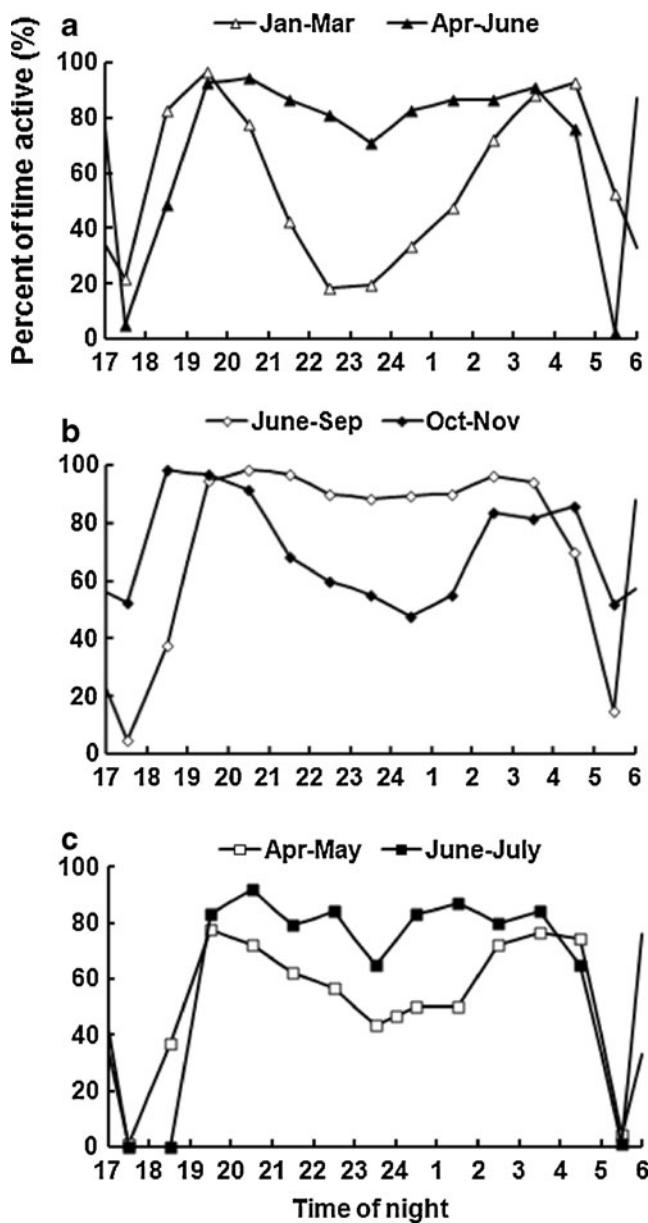


Fig. 2 Variation in activity pattern of three radio-tracked *Petaurista philippensis*—**a** AF1, **b** AM4, and **c** AM3—between January and November 1998 in Taiwan

reproduction, however, may not be mutually exclusive, and the change in ranges and activities is likely a synergistic effect of both factors. Further studies on both lactating and non-reproductive females could verify this hypothesis.

There were no significant effects of diet on movement and activities of adult males AM3 and AM4. We tracked both individuals when they did not feed much on mature leaves (spring to fall, Kuo and Lee 2003). Low variability in this factor may reduce the statistical power to detect any significant effect. Other than diet, home range size could also be affected by mating behavior. This is especially true for polygynous species, with males searching widely for

receptive females, leading to much larger home ranges of males than females, as exemplified in *P. volans* (Hanski et al. 2000). Mating system of *P. philippensis* is not known, but the much larger home ranges of the males than the females, as well as more spread and dispersion of locations in the males (Table 1), suggest a polygynous or promiscuous mating system similar to that of *P. volans* (Hanski et al. 2000). The influence of diet on ranges and activities of male *P. philippensis* could therefore be confounded by mating behavior, which could potentially occur year round except in February when active spermatogenesis does not happen (Lee et al. 1993).

Mammalian home range area typically increases with body size (McNab 1963), but it could be affected by diet (McNab 1963, 1978) or by gliding efficiency for gliding mammals (see below). Unexpectedly, radio-tracking studies on much smaller flying squirrel species (*Glaucomys* and *Pteromys* spp. < 200 g, Nowak 1999) revealed generally larger home ranges than *P. philippensis* of this study (averaged 2.8 ha with 100 % MCP; averaged 4.0 ha for adult males and 2.2 ha for the adult female) and giant flying squirrel studies elsewhere (Baba et al. 1982; Lin et al. 1988) although both of the other researches were conducted under unreliable method or limited time-frame and may not be representative. Home ranges of two female *P. philippensis* averaged 3.25 ha (100 % MCP) with direct observation for 3 months at a coniferous plantation in central Taiwan (Lin et al. 1988). The average home range of nine radio-tracked *P. leucogenys* was 2.30 ha (0.46–5.16 ha with 100 % MCP); however, each *P. leucogenys* was tracked for only 2–7 days (Baba et al. 1982). In contrast, the average home ranges of *G. volans* were 9.9 ha for males and 3.4 ha for females (95 % MCP, Fridell and Litvaitis 1991). *G. sabrinus* utilized an average of 11.2 ha for males and 6.9 ha for females (100 % MCP, Hough and Dieter 2009). Mean home ranges of female *P. volans* were 8.3 ha, and those of males were even as large as 59.9 ha (100 % MCP, Hanski et al. 2000). One plausible explanation for the violation of positive home range and body mass relationship is the difference in food habits. Folivores normally require smaller ranges than granivores due to the ubiquity of leaves (McNab 1978). *P. philippensis* are folivorous (Kuo and Lee 2003), whereas the patchy distribution of fruits, seeds, truffles, or mushrooms *G. volans* and *G. sabrinus* mainly feed on (Muul 1968; Maser et al. 1985; Thysell et al. 1997; Meyer et al. 2005) could lead to their similar or larger home ranges than *P. philippensis*. Lastly, body size could affect gliding efficiency (Scheibe and Robins 1998; Dial 2003), which may account for the difference in home range. Gliding conveys small gliders like *G. volans* energetic advantages; however, for large gliders like *P. petaurista*, gliding is more energetically efficient than quadrupedal locomotion only when the gliding distance is >100 m (Scheibe and Robins 1998).

Indeed, *P. leucogenys* leaped more often than glided (Stafford et al. 2003). Smaller flying squirrels, including *Glaucomys* and *Pteromys* spp., may be more inclined to glide than giant flying squirrels, thus having larger home ranges, although it could not be excluded that the ubiquity of leaves means less necessity for giant flying squirrels to glide as frequently as smaller flying squirrel species, which feed on more widely distributed fruits or seeds.

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