

ARBOREAL SPACING PATTERNS OF THE LARGE PENCIL-TAILED TREE MOUSE, *CHIROPDOMYS MAJOR* (MURIDAE), IN A RAINFOREST IN SABAH, MALAYSIA

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Abstract. Spacing patterns and demography of the arboreal large pencil-tailed tree mouse, *Chiropodomys major* Thomas, 1893, was examined by live trapping in the subcanopy of a primary rainforest in Sabah, Malaysia over five months. Traps were placed on the ground and in the canopy at an average height of 13.5 m, where tree crowns are well interconnected. *C. major*, which was mainly active in the canopy, was by far the most frequently trapped species in this habitat layer. Home range areas were calculated as 90 % core convex polygons for 18 individuals, for which ≥ 5 recaptures (mean of 13) were obtained. Home range size varied between sexes, with males generally having larger home ranges ($2971 \pm 1104 \text{ m}^2$) than females ($1580 \pm 780 \text{ m}^2$). Home range areas of both sexes overlapped with those of conspecifics and with individuals of the opposite sex, suggesting that individuals do not maintain exclusive ranges. *C. major* used nearly the entire examined arboreal habitat space, but analysis of microhabitat preferences revealed that the activity of this arboreal rodent was positively associated with an increase in tree connections and the presence of lianas and gaps. Accepted 16 June 2003.

Key words: home range estimate, microhabitat use, persistence, rodents, tropical rainforest canopy.

INTRODUCTION

Many rodent species have proved valuable as models for studies of spacing patterns. Basically, observed space-use and the resulting mating systems have been examined by evaluating resource availability and spacing of the opposite sex (e.g., Ims 1988, Ostfeld 1990). While some species appear to maintain territories exclusive of conspecifics (e.g., Ims 1988, Lambin & Krebs 1991), other species show considerable intrasexual overlap in the utilised space (e.g., Ims 1988, Adler *et al.* 1997). However, most studies were conducted on terrestrial species in relatively species-poor communities in temperate regions, whereas only a few studies dealt with home ranges of tropical rat species in species-rich communities (e.g., Sanderson & Sanderson 1964, Adler *et al.* 1997, Sommer 1997, Lindsey *et al.* 1999). Even less is known about arboreal species (Kays & Allison 2001), for which studies on spacing patterns and mating systems are confined to a few larger species such as primates (e.g., Sterck *et al.* 1997, Di Bitetti

2001, Eberle & Kappeler 2002), squirrels (Wauters & Dhondt 1990, Saiful *et al.* 2001), kinkajous (Procyonidae) (Julien-Laferrriere 1993, Kays & Gittleman 2001), or marsupials (e.g., Soderquist 1995, Lindenmayer 1997, McCarthy & Lindenmayer 1998). However, trapping in the true canopy of tropical forests has shown that small mammals, particularly murids, are abundant dwellers of the canopy, living in diverse communities (Malcolm 1995, Zubaid & Ariffin 1997, Malcolm & Ray 2000).

Species foraging in the canopy clearly have to face differing environmental conditions compared with those confined to the ground, as the canopy is a more variable habitat both in terms of its three-dimensional complexity and structural heterogeneity as well as its more pronounced climatic fluctuations (e.g., Emmons 1995). Particularly the outstanding diversity of many of the evergreen, perhumid lowland rainforests, where several hundred tree species per hectare occur, with a considerable variety in growth forms and fruiting patterns (Newberry *et al.* 1992), should lead to a highly variable resource distribution both in space and time.

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The high floristic heterogeneity, and the resulting resource dispersion was found to influence the distribution and population demography of terrestrial spiny rats, *Proechimys*, in the Neotropics (Adler 1994, 2000). Resource abundance and its distribution was also reported as a major determinant of spacing patterns of some larger arboreal mammals (e.g., Lurz *et al.* 2000, Di Bitetti 2001, Kays & Gittleman 2001). Furthermore, locomotion in the canopy for non-volant and non-gliding species is necessarily confined to suitable pathways, which are prone to considerable changes due to the growth and breaking of branches. Thus the characteristics of tropical forest canopies, with their unique patterns of food abundance and variability in food availability, should be of major importance for the spacing of arboreal mammals, especially those relying on plant resources. Present knowledge of resource use and spacing patterns of arboreal mammals, particularly for small mammals, is very limited. As only a few species have been studied thoroughly, there is still a fundamental need for more data on arboreal spacing patterns in order to gain a less fragmented picture and to evaluate the impact of canopy features on foraging activity and social organization of these species.

In this paper, we describe observations on spacing patterns of the large pencil-tailed tree mouse, *Chiropodomys major* Thomas, 1893, an arboreal nocturnal species endemic to Borneo. These investigations were part of a study comparing the diversity and space use of arboreal and terrestrial small mammals (Wells *et al.*, accepted), in which *C. major* was the most frequently trapped species. There is little information on this genus of tree mouse, which consists of six known species (Musser 1979, Jenkins & Hill 1982, Wu & Deng 1984). All these mice occur in South-East Asian forest sites and are assumed to be mainly arboreal. Their feet are relatively short and broad, characterized by a semi-opposable hallux with a flat nail, an adaptation typical for a canopy dweller. Most information has been gathered on *C. gliroides* Blyth, 1856, a species found in various forest types throughout Indochina and the Sunda Shelf region (possessing the most extensive geographic range within the genus), which is mostly associated with bamboo stands. Females of this species are polyestrous. They have estrous periods of one day at intervals of only seven days and breed throughout the year, at least in Peninsular Malaysia (see Nowak 1991). However, very little is known of the biology of *C. major*, which is recorded only from a few localities in the

northern part of Borneo (Musser 1979, Payne *et al.* 1985).

The aim of the present study was to assess the use of space by *C. major* in the subcanopy layer of a primary rainforest, investigating home ranges and microhabitat utilization of this species. Although the data represent a period of only half a year, our paper gives a first insight into the spacing of a little-known arboreal species.

STUDY AREA

Fieldwork was conducted in the primary lowland rainforest of Kinabalu National Park (754 km²) in Sabah (Malaysia) in the north of Borneo. The majority of vegetation in Kinabalu National Park consists either of tropical montane rainforest (37%) or lowland rainforest (35%) (Kitayama 1992). The number of mammal species was estimated as about 100 (Lim & Muul 1978), nearly half of all species recorded for Borneo. Three species of tree mouse are known to occur on Borneo (*Chiropodomys major*, *C. gliroides*, *C. muroides*; Payne *et al.* 1985), as well as two species of the similar and probably closely related mice *Haeromys* sp. (see Musser & Newcomb 1983). The dipterocarp forest is characterized by its emergent trees (mainly Dipterocarpaceae and the legume *Koompassia*), rising up to heights of 50–70 m, well above the actual interconnected, multi-layered, and light-screening canopy that occurs at heights of between 10 and 40 m. The heterogeneous canopy structure is a result of the vast floral diversity of the Bornean rainforest: up to three hundred tree species can be found on a single hectare (Kitayama 1992, Newberry *et al.* 1992).

The study area was located in the lowland rainforest at an elevation of between 800 and 900 m near the village of Poring Hot Spring. This site comprised a basically undisturbed primary forest, though the area at large is not completely unaffected by anthropogenic disturbances. Poaching as well as touristic activities on a public canopy walkway system have affected the diversity of wildlife adversely. Probably these influences do not affect small species such as *C. major*, though unknown secondary effects such as predator-prey interactions cannot be excluded.

MATERIALS AND METHODS

Trapping design. Trapping was conducted within two sampling grids separated by a distance of approximately 200 m (and by a ravine). As our fieldwork also

intended to compare small mammal assemblages on the ground and in the canopy, capture activity included both arboreal and ground traps. In each area 31 grid points were established. Grid points were separated by 20 m, but the distribution of points differed in the two areas due to topographic constraints. Grid 1 sampled approximately 0.80 ha, comprising 6 rows with 4, 4, 5, 6, 6, and 6 trap stations, respectively. Grid 2 comprised 8 rows with 5, 4, 5, 4, 4, 3, 3, and 3 trap stations, covering roughly 0.78 ha. At each grid point we placed one arboreal trap at a height between 6 m and 25 m (mean 13.5 m) and one ground trap. Trees were climbed initially using slings as 'foot belts', and after establishing a hoist line, conventional single rope climbing equipment was used. This method benefits from the little equipment required, a flexible choice of trees for trapping, and little damage or alteration to the canopy structure or tree bark.

We used locally produced wire mesh live-traps (28 cm × 14 cm × 14 cm, and some larger traps measuring 35 cm × 14 cm × 14 cm), equipped with a roof made from plastic sheet for protection from rain. Arboreal traps were fixed with wire on horizontal branches near trunks. Traps were baited with ripe bananas, checked every morning, and rebaited immediately after captures or after four days. Total trapping effort was 6445 trap-nights during 7 trapping sessions, each lasting for 16 consecutive days. Trapping sessions were conducted alternately in the two areas, with a break of approximately 20 days between trapping sessions in a single area.

Fieldwork was conducted from April to August 2001 during a dry period at this rainforest site. Though rainfall usually increases in Kinabalu Park from May to July (Kitayama 1992), the entire trapping period was characterized by a similar pattern of low rainfall (Wells 2002).

For each trap station, we estimated ten vegetation parameters. Tree sizes and their distribution were evaluated by a simple 'thumb relascope' method: a 2-cm-broad plastic block was held at a constant distance from the left eye by the stretched right arm. The number of trees visible (with a diameter at breast height, DBH, > 10 cm) when extending the plastic piece while focusing it was used as a score. Further, the DBH of the tree with the arboreal trap and the distances to the five nearest trees (DBH ≥ 10 cm) were measured. We assessed the understory foliage density using a 'profile board' technique (see Malcolm and Ray 2000): the visibility of a 2-m plastic pole with

alternating red and yellow 10-cm segments placed near ground traps was scored from 2 and 5 m distances in six different directions determined with a compass (60° angles, starting from North). The number of segments covered by foliage was used as a score for understory density and summed for both distances. We also scored the proximity and sizes of logs near the ground traps on a scale from 3 to 0 (3: one log > 20 m long and/or numerous small logs (< 20 m) less than 0.5 m away from the trap; 2: logs of that size at a distance d of $0.5 < d < 5$ m away from the trap; 1: small logs at $d = 0.5 < d < 5$ m; 0: no log at $d < 5$ m). Close to the arboreal trap, the extent of branch connections of the tree to its neighbors was censused, with a score range from 3 (≥ 5 branches interconnected) to 0 (no branch contact to neighboring trees). Crown density in the vicinity of about 10 m around the arboreal trap was visually evaluated and scored on a scale from 3 to 0 (3: ≥ 80% of the surrounding area covered by foliage; 2: 60–80%; 1: 30–60%; 0: < 30% covered) both for the foliage above and below the trap. The bark of the trap tree was scored to evaluate the roughness on a scale from 3 (rough) to 0 (nearly smooth). We also recorded the presence/absence of extended gaps (gap of at least 10 m diameter with the crown of the trap station tree partially exposed to the open space) and the presence/absence of lianas in trap trees.

Handling of animals and data collection. Captured animals were anesthetized with diethyl ether before marking and measuring, and released near the station of capture immediately following data collection. We marked individuals with a subcutaneously placed transponder (Trovan, AEG), which allowed permanent and reliable identification and was relatively painless for the animal, leading to no obvious restriction of locomotion and behavior after release. All individuals were weighed and lengths of total body (front of nose to base of tail), tail, hind foot (excluding the nail), and anal-genital distance measured. Animals with scrotal testes or visible mammae were classified as adults, whereas all other individuals with no visible sex organs but non-juvenile pelage were classified as immatures.

A spool-and-line device was tested on four individuals of *Chiropodomys major* for locating nests, using quilting spools ('cocoon bobbins'; Danfield Ltd., Moss Industrial Estate, U.K.), which weighed approximately 1.7 g and contained 180 m of nylon thread. Spools were placed in a piece of shrinking tube (normally used in electric engineering) with the thread

able to trail easily from inside the spool. Spools were applied to the back of anesthetized animals with glue (cyanoacrylate), and the end of the thread was tied to vegetation. Threads were followed the next day.

Data analysis. Home range analysis was performed by calculating the 90 % core convex polygon centered on the arithmetic mean based on individuals with five or more captures, with the computer package *TRACKER 1.1* (Camponotus AB & Radio Location Systems AB 1994). Individual home ranges were calculated for captures over the entire study, which was justified because of the relatively sedentary behavior of individuals for which sufficient captures were obtained (see results). Persistence rates were calculated as the number of trapping sessions between first and last capture of an individual. Further, we developed a habitat profile by comparing the cumulative means of habitat variables for traps where individuals were captured with the means of all trap locations, which represented the overall sampled habitat. To reduce any bias arising from philopatric behavior or trap affinity, individuals were considered only once for a single trap station. All statistical analyses were performed using STATISTICA 6.0 (Statsoft 2001).

RESULTS

Demography and home ranges. With 275 captures of 40 individuals, *Chiropodomys major* was by far the most frequently trapped species in the canopy. The same trapping effort on the ground resulted in captures of only two individuals of *C. major*. Other small mammal species trapped in the canopy (numbers of captures in parenthesis, total: 101) were the murids *Niviventer cremoriventer* (52), *Lenothrix canus* (15), *Leopoldamys sabanus* (1); the sciurids *Sundasciurus hippurus* (2), *S. brookei* (2), *Callosciurus notatus* (1), *Hylomyscus spadiceus* (1); the tupaiids *Tupaia minor* (24), *Prilocercus lowii* (1); and the lorises *Nycticebus coucang* (2). In area 1, we trapped 22 individuals of *C. major* (9 males, 7 females, 3 immatures, 3 unidentified) 174 times, and there were 101 captures of 18 individuals (7 males, 7 females, 3 immatures, 1 unidentified) in area 2. Adult males weighed on average 41.4 ± 5.4 g ($n = 16$), while females weighed 38.4 ± 4.4 g ($n = 14$) with no significant differences between the sexes. However, males appeared to be slightly larger in head-body measurement (males: $HB = 106.7 \pm 3.6$ mm ($n = 12$), females: $HB = 99.6 \pm 2.4$ mm ($n = 7$); Mann-Whitney U-test, $U = 16.5$, $p < 0.05$).

No individual was trapped at both trapping sites, and maximum observed distance traveled was 113 m by a male. On two occasions, we trapped two individuals (an adult female with an immature, and the same female with an adult male) in a single trap.

The persistence rates of individuals were significantly biased by age (Mann-Whitney U-test, $U = 42$, $p < 0.05$): the average persistence rate P_r of adults ($P_r = 2.88$ trapping sessions, $n = 16$) was higher than that of immatures ($P_r = 1.33$, $n = 6$).

Single individuals were caught up to 11 times within a trapping session (mean 4.3 ± 2.8). All individuals with more than five captures in total persisted for an average of $P_r = 4.22 \pm 1.83$ trapping sessions, significantly longer than the mean in the study area (Mann-Whitney U-test, $U = 40.5$, $p < 0.01$). We thus assumed that these individuals were resident and temporally coinciding in their presence, and calculated their home range areas from data of the entire study. Home range analysis included 18 individuals (7 males, 10 females, 1 immature, Fig. 1) with a total of 234 captures (mean 13 ± 6.2). The mean home range size for males varied from 1600 m^2 to 4600 m^2 (mean $2971 \pm 1104 \text{ m}^2$) and was significantly larger than that for females (t -test, $t = -3.06$, $p < 0.01$), which varied from 200 m^2 to 2600 m^2 (mean $1580 \pm 780 \text{ m}^2$). There was no correlation between home range size and the number of captures (Spearman, $r = 0.23$, $p = \text{n.s.}$, 5–27 captures per individual). On average, home range overlap of conspecifics was significantly larger in males than in females (male: 2.3 ± 0.5 individuals, female: 1.0 ± 0.7 , Mann-Whitney U-test, $U = 5.0$, $Z = -2.93$, $p < 0.01$). Comparing intersexual overlap, we found that a male's home range overlapped on average those of 3.4 ± 1.3 females, while a female's home range overlapped those of 2.5 ± 1.0 males.

Trap and microhabitat use. *Chiropodomys major* was trapped in 56 out of 62 arboreal traps, thus was distributed throughout the sampled habitat space. However, comparing the habitat profile of *C. major* with the entire sampled habitat space revealed a significant impact of the presence of gaps and lianas on the trap success of trap stations. *C. major* was most frequently trapped at stations in the proximity of gaps (Mann-Whitney U-test, $U = 522.5$, $Z = -4.77$, $p < 0.01$) and in traps on trees with lianas present (Mann-Whitney U-test, $U = 170.0$, $Z = -4.22$, $p < 0.01$). None of the parametric habitat parameters showed any significant differences between the estimated habitat profile of

C. major and the overall available habitat (t-test, $p > 0.6$, n.s. for all variables). There was no correlation between trap height and number of captured individuals or captures. The spool-and-line device was not the right size for normal behavior of *C. major*, as most individuals recognized the presence of the spool after recovering from anesthesia and tried to remove it. However, individuals with an attached spool were still able to climb, and four (of eight) threads were followed successfully. One individual nested in a tree hollow approximately four meters above the ground. Another

individual had to move over the ground to reach its den inside the stump of a dead tree (approximately five meters above the ground), as there was no connection between the stump and the canopy. Two others descended into holes in the ground near tree roots and a log respectively.

DISCUSSION

Chiropodomys major was an abundant species in the subcanopy layer of the studied primary rainforest sites,

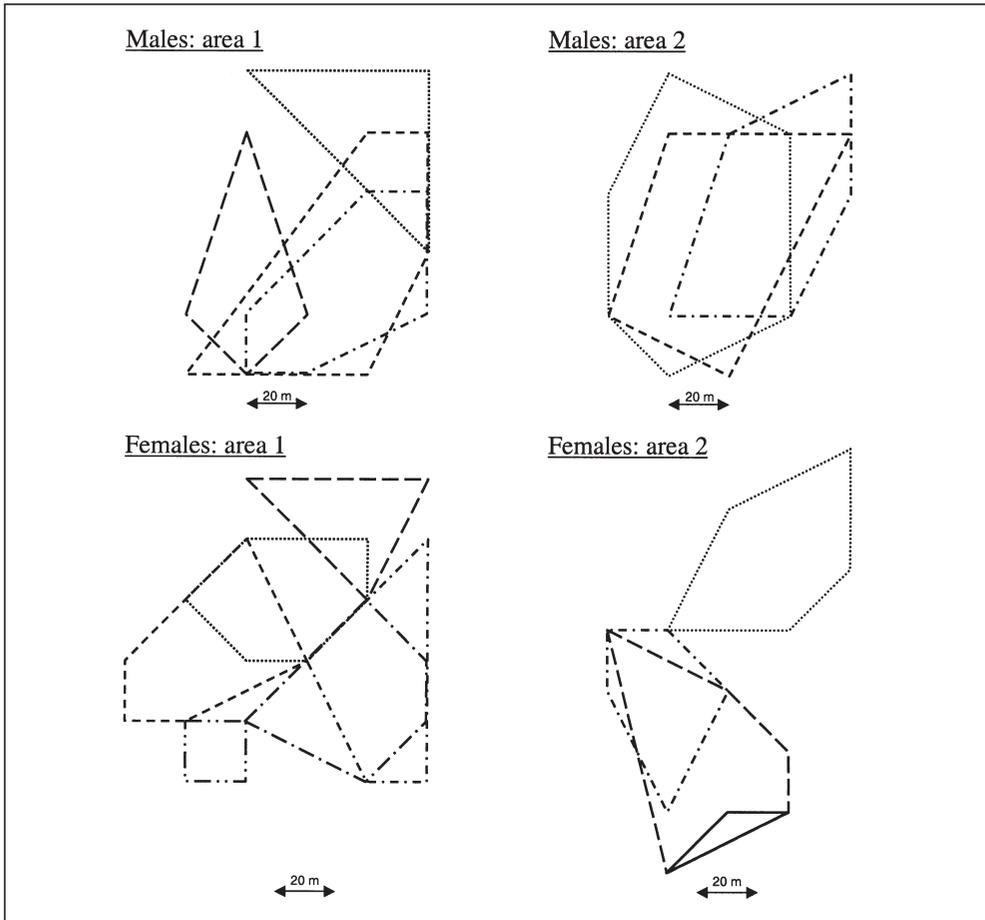


FIG. 1. 90 % core convex polygons representing home range areas utilized over the entire sampling period for all adult males and females. In area 1 we mapped four home ranges of males and six of females, in area 2 three home ranges of males and four of females.

using nearly the entire sampled habitat space. The relatively frequent captures and recaptures gave some insight into the spacing patterns and range use of this species, although it has to be considered that observations were limited to a single layer of the subcanopy in a rather complex three-dimensional habitat (see Risch & Brady 1996), and also by the spatial and temporal limitations of observations intrinsic to the live-trapping design. Of course, these point estimates of the presence of different individuals have to be evaluated carefully, and a more accurate concept of an individual's activity and its home range would necessitate the use of radio telemetry or other advanced techniques (Jones & Sherman 1983). However, a number of studies using both telemetry and trapping data on terrestrial species revealed similar patterns of space use when a sufficient number of captures was obtained over a short time (Jones & Sherman 1983, Lambin & Krebs 1991, Quin *et al.* 1992). Some authors suggest that live trapping is even a conservative approach, as movements of individuals appear to be more restricted when the spatial data are collected through trapping (Price *et al.* 1994, Szacki 1999). The home ranges presented here might be underestimates of the total sizes, as the sampling areas were not large enough to encompass complete home ranges of all individuals, and several ranges were along the edges of the grid area. Yet our data clearly show that ranges are overlapping and territories are not maintained. As our study is based on a mean of 13 observations per individual, and because we found no correlation between capture frequency and calculated territory size, we assume that our trapping data give an initial insight into the spatial activity patterns of individuals within the studied population of *C. major* during the sampled season. Home range estimates from the present data were mostly obtained for adult individuals (17 out of 18), while immature individuals seemed to remain for much shorter periods in the study area. Both sexes revealed considerable overlap with other individuals of both sexes, arguing against the defense of exclusive ranges. However, our data are based on a half-year study period during a dry period, and changing resource availability during the course of a year might lead to some shifts in home range use between seasons. For example, an arboreal trapping survey of 234 trap nights in the same area in December 2002 (beginning of the rainy season, more than one year after this study) included no captures of *C. major*, most probably due to differences in resource availability (K. Wells, unpublished). A lack of exclusive ranges was

also reported for the Neotropical spiny rat *Proechimys*, for which Adler *et al.* (1997) suggested that food resources in the rainforest environment might be too scattered and unpredictable for efficient establishment of exclusive territories. This might also be the case for *C. major*, as this species also relied on plant resources, with most of its foraging activity in the heterogeneous canopy. There is a lack of knowledge of the vertical spacing of individuals, but the application of the spool-and-line device revealed that at least some nesting or hiding places are located near the ground, indicating that individuals frequently travel in the vertical dimension and even down to the ground. A presumably agile movement behavior of *C. major* in the canopy is also confirmed by the microhabitat utilization, as nearly the entire sampled habitat space was used. Though *C. major* preferred trapping points with an increased number of tree connections by branches and lianas, it was observed to drop down to lower foliage layers when there were no suitable branches to walk on (this drop-and-go strategy was also used for escape), a behavior that was not observed for larger rats such as *N. cremoriventer* or *L. canus* (pers. obs. K. Wells). Apparently, tree mice are the smallest non-volant mammalian species in the canopy (see Payne *et al.* 1985), a feature that should promote an agile movement on branches and vertical trunks.

The observed spacing patterns suggest that each adult can be expected to encounter several other individuals of both sexes in its foraging area. The locations of polygons showed no association between certain pairs of males and females, and the overlap patterns, with each individual overlapping with several others of the opposite sex, make a promiscuous mating system possible. Females revealed less overlap with individuals of the same sex than males. Assuming that female spacing is driven by the relatively high energy expenditure of reproduction and need for a sufficient resource supply (e.g., Emlen & Ohring 1977, Ostfeld 1985), competition for primary food resources might be reduced by avoiding too much female intrasexual overlap. However, it is not clear whether this concept – basically derived from temperate species – is accurate for a species residing in a tropical rainforest canopy. Too little is known about resource distribution and also about the expenses of locomotion in this habitat, and the ultimate reasons for any consensual overlap may range from tolerance due to a scattered and unpredictable resource dispersion up to an inefficiency of habitat defense due to the complex canopy structure. Furthermore, we need much more species-

specific data on taxonomic, morphological, and physiological adaptations or constraints to properly evaluate spacing patterns and social organization of arboreal species. Since sympatric species in diverse small mammal communities in rainforests show a differing extent of arboreal activity and resource utilization along the vertical axis of the canopy habitat (e.g., Mauffrey & Catzeflis 2003), and also differ in their abundance patterns (Malcolm 1995), intensive comparisons of different species and sites would be of much value for a better understanding of arboreal adaptations and species distributions.

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