

BEHAVIORAL MONOGAMY AND FRUIT AVAILABILITY IN THE LARGE TREESHREW (*TUPAIA TANA*) IN SABAH, MALAYSIA

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Behavioral monogamy in mammals varies from male–female pairs that spend most of their time in close spatial contact (associated pair-living) to pairs that occupy exclusive territories but travel, forage, and sleep alone (dispersed pair-living). We present radiotelemetry data on 46 adult large treeshrews (*Tupaia tana*) from 2 populations in Sabah, Malaysia, that indicate that this species forms dispersed pairs across a range of ecological conditions. Dispersed pair-living was the primary behavioral mating system in primary forest during a major fruit masting event, in nonmasting primary forest, and in selectively logged forest with significantly higher fruitfall than in primary forest. Territories of behavioral partners were spatially concordant, but both male and female territories typically overlapped the boundaries of 1–3 extra-pair territories. Comparison between masting and nonmasting forests indicated that females exhibited better body condition during masting, whereas males exhibited larger home-range areas and longer daily movements. Both males and females exhibited better body condition in selectively logged versus primary forests, but ranging patterns were not significantly different between these habitats. We argue that intraspecific foraging competition is the most likely explanation for the evolution of dispersed pair-living in *T. tana*.

Key words: Borneo, Danum Valley, dispersed pair-living, fruit abundance, large treeshrew, Malaysia, monogamy, Sabah, social organization, *Tupaia tana*

Monogamous mating systems occur in only 5% of mammalian species overall (Clutton-Brock 1989; Kleiman 1977), but are much more prevalent among the Euarchonta (dermopterans, treeshrews, and primates), canids, rodents, and some nocturnal taxa, such as dwarf lemurs (Fietz 1999) and bats (McCracken and Wilkinson 2000). Characterizing monogamy has been aided by recent molecular genetic studies that have failed to confirm exclusive mating in behaviorally monogamous species (e.g., Fietz et al. 2000; Goossens et al. 1998; Schülke et al. 2004; Spencer et al. 1998). These results underscore the need to understand the ecological and social factors promoting

behavioral monogamy, or pair-living, as a phenomenon distinguished from genetic monogamy in mammals (Reichard 2003).

Early hypotheses for the evolution of behavioral monogamy stressed the importance of biparental care to reproductive success (Clutton-Brock 1989; e.g., California mouse [*Peromyscus californicus*]—Gubernick et al. 1993; obligate, or type I, monogamy—Kleiman 1977; American beavers [*Castor canadensis*]—Sun 2003; Djungarian hamster [*Phodopus campbelli*]—Wynne-Edwards 1987). However, biparental care evolved secondarily in most pair-living mammalian lineages (Komers and Brotherton 1997), and these hypotheses cannot explain behavioral monogamy in mammals without substantial paternal care. Ecological scenarios argue that high spatial dispersion of females promotes pair-living by preventing males from monopolizing more than 1 female (Emlen and Oring 1977; e.g., golden-rumped sengi [*Rhynchocyon chrysopygus*]—FitzGibbon 1997), or that intensive mate guarding strategies

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arise when home ranges of females are small, exclusive, and defensible (e.g., Kirk's dik-dik [*Madoqua kirkii*]—Brotherton and Komers 2003). A 3rd group of behavioral hypotheses predicts that males gain enhanced fitness from pair-living by providing services that increase survival of females or reproduction. These services may include protection from predation (Kleiman and Malcolm 1981; trail maintenance in rufous sengis [*Elephantulus rufescens*]—Rathbun 1979; van Schaik and Dunbar 1990), protection from infanticide (Kappeler and van Schaik 2002; especially in primates—van Schaik and Kappeler 2003) and other forms of male aggression (Smuts and Smuts 1993), or foraging competition (Wittenberger and Tilson 1980).

A single ecological factor is unlikely to explain behavioral monogamy in mammals, because pair-living may vary from pairs that remain cohesive in space and time (associated pairs) on a common territory (*Peromyscus* spp.—Ribble 2003), to pairs that may share a territory but travel, forage, and sleep alone (e.g., Cape porcupines [*Hystrix africae australis*]—Corbet and Van Aarde 1996; maned wolves [*Chrysocyon brachyurus*]—Dietz 1984; Zanzibar galago [*Galago zanzibaricus*]—Harcourt and Nash 1986; golden-rumped and rufous sengis—Rathbun 1979; bushveld sengi [*Elephantulus intufi*]—Rathbun and Rathbun 2006). This behavioral mating system also is prevalent among nocturnal prosimians, and thus dispersed pairs may represent the ancestral primate condition (Müller and Thalmann 2000). Dispersed pair-living in a few of these species has been described in detail (fat-tailed dwarf lemur [*Cheirogaleus medius*]—Fietz 1999; fork-marked lemur [*Phaner furcifer*]—Schülke and Kappeler 2003), and may have evolved because of fitness gains to females from reduced competition for scarce, patchily distributed food resources (Schülke and Ostner 2005).

In this study, we examine behavioral monogamy in the large treeshrew, *Tupaia tana* (Mammalia, Scandentia), in Sabah, Malaysia. Male–female pairs in *T. tana* and a few other tupaiids have been reported to live on joint territories, but also to exhibit sex-specific territorial defense, forage solitarily, and never share sleeping sites (*T. gracilis*, *T. longipes*, and *T. tana* in Borneo—Emmons 2000; previously described as “solitary ranging pairs” in *T. glis* in Singapore—Kawamichi and Kawamichi 1979). Here we present the most detailed study of behavioral monogamy in treeshrews to date, using radiotelemetry data from 22 adult *T. tana* in lowland primary rain forest in Sabah, Malaysia (northeastern Borneo). We also use spatial data collected from 17 adults during a fruit-masting episode and 7 adults in selectively logged forest to investigate the influence of short- and long-term increases in fruit abundance on behavioral monogamy, respectively.

We examine the predictions that increased fruit abundance is associated with superior body condition; smaller, less exclusive home ranges of females due to a relaxation of territoriality by females; and greater day-range lengths in males and overlap with multiple home ranges of females. These predictions are derived from the hypotheses that territory size of females is linked to resource abundance, and that the ability of males to control individual females depends on the defendability of home ranges of females. If females reduce their home ranges during

periods of high resource abundance, then some males should be able to defend more than 1 female (i.e., one may observe a switch from a strictly behaviorally monogamous population to a situation where some males exhibit polygyny). Alternatively, if increased resource abundance results in less intense territoriality by females and larger home ranges of females, then males may not exhibit the predicted spatial overlap with multiple females. After examining these predictions, we evaluate alternative evolutionary hypotheses for behavioral monogamy in this species.

MATERIALS AND METHODS

Study sites.—We studied large treeshrews in primary lowland rain forest in Sabah, Malaysia, from August to December 2002–2004. This study also includes a reanalysis of radiotelemetry locations collected by Emmons (2000) during a major fruit-masting event from September to December 1990, and after the mast from March to September 1991. Both studies were conducted in forest that is part of the Danum Valley Conservation Area (Danum, 4°58'N, 117°48'E). Danum represents the largest lowland rain forest in Borneo likely to remain undisturbed indefinitely (438 km²), and is nested within a much larger timber concession that comprises nearly 13% of the entire land area of Sabah (Marsh and Greer 1992). Most of the concession surrounding Danum was selectively logged in the 1980s and then left to recover without subsequent disturbance.

Climate and phenology at Danum do not follow strongly predictable patterns, but September through January tends to have the highest recorded rainfall and fruit abundance (Walsh and Newbery 1999). Community-wide synchronous reproduction of trees in the family Dipterocarpaceae, known as mast fruiting, occurs every 5–13 years in Borneo (Curran and Leighton 2000; Janzen 1974) and is often accompanied by enhanced production of soft, fleshy fruits by nondipterocarp species responding to the same phenological cues. Emmons (2000) observed that the reproductive output of large treeshrews was 2–3 times higher than normal during the 1990 fruit mast in Sabah, presumably due to increased resources for reproduction.

We also studied large treeshrews in selectively logged forest from September to December 2003–2004 within the Malua Forest Reserve (Malua, 5°5'N, 117°38'E), approximately 53 km from the primary forest site. Malua was logged in the early 1980s and has yet to recover the multiple closed canopies (typically 10 m and 20–30 m in height) and tall emergent trees (up to 70 m) that characterize lowland dipterocarp rain forests (Whitmore 1984). Selective logging may increase fruit abundance if surviving trees and subsequent pioneers exhibit increased reproductive activity due to greater solar input (Johns 1988). Previous studies in peninsular Malaysia and Borneo have recorded either higher (Chivers 1972; Hussin 1994; Laidlaw 1994) or no overall differences (Heydon and Bulloh 1997) in fruit production after selective logging.

Study species.—The large treeshrew is a small (200- to 250-g), diurnal frugivore–insectivore that inhabits the lowland rain forests of Borneo and Sumatra. Male–female pairs of this

species defend approximately concordant territorial boundaries (Emmons 2000), and several aspects of their biology indicate that large treeshrews may respond behaviorally to variation in fruit abundance. Female *T. tana* have a litter size of 2, and typically give birth 1–3 times per year. However, they exhibit postpartum estrus and are capable of reproducing 9 times annually in captivity if fed fruit ad libitum (Emmons 2000). Females also exhibit a unique, energetically costly maternal care system, whereby females deposit their young in a secluded nest that they subsequently visit only once every 48 h for intense bouts of nursing (Emmons and Biun 1991; Martin 1966). Both male and female *T. tana* are extremely active and spend almost their entire activity period foraging. Although primarily insectivorous, individual *T. tana* will concentrate their foraging activity around fruiting trees when available, suggesting that fruit is a favored resource that influences reproduction (Emmons 2000).

Data collection.—The same trapping transects and similar general methodology were used in 2002–2004 as Emmons (2000) employed at Danum in 1990–1991. Large treeshrews were trapped at each site with locally made wire-mesh traps placed every 25 m along two 500-m transects in 1990–1991, and 3 transects in 2003–2004. In 2004 we placed 2 additional 500-m transects at the logged site to increase captures. We conducted trapping sessions every 3–4 weeks during the study period, and habituated animals by prebaiting open traps for 2 days before each session. Traps were baited and set at 0600 h with slices of a local variety of banana (local name: *pisang emas*) previously established as optimal for capturing tupaiids (Bernard 2003), and checked twice daily at 1030 h and 1500 h. Captured animals were transferred to cloth bags, weighed, and sedated with a ketamine hydrochloride injection (10-mg/kg dose). Treeshrews were marked with ear tags and tail hair clipping in 1990–1991. During the 2002–2004 study period, we measured hind-foot length, collected hair samples and ear clips for genetic analyses, and injected animals with a subdermal passive integrated transponder (Biomark, Inc., Boise, Idaho) for permanent identification. We noted lactation and checked for the presence of embryos through palpation of abdomens of females.

If adults were in good condition, then we fitted them with radiocollars manufactured by Wildlife Materials Inc. (Murphysboro, Illinois; 1990–1991, 2002, model SOM-2190, ~4.5–5.0 g) or Holohil Systems Ltd., Carp Ontario, Canada; 2003–2004, model PD-2C, ~4.0 g). Juveniles were identified by their small size (mass < 180 g, based on growth curve in Emmons [2000]) and the presence of milk teeth or newly erupted unworn adult teeth, and were not collared unless trapped later as adults. To avoid confounding effects of age, we excluded juveniles that were radiotracked in the same study period as their birth from analyses of space use in adult *T. tana*. Radiocollared treeshrews were followed throughout their entire activity period (0600 h until nesting at 1530–1800 h) on foot by an observer with a radioreceiver for 3 consecutive days to estimate home-range sizes and day-range lengths. We tracked 1 focal individual at a time instead of a behavioral pair because male–female partners could not always be trapped and collared

at the same time. However, several times during a tracking day we checked the radiosignals from other collared individuals for proximity to the focal individual's signal, and noted visual sightings of any other treeshrews nearby.

Compass bearings in the direction of the animal's radiosignal were taken every 20 min from 3 different marked sites. Emmons (2000) established that home-range areas of *T. tana* no longer increased after collecting more than 3 days of location points. Simple linear regression of 95% kernel home-range area (ha; see below for calculation) on the number of locations recorded per individual indicated that our estimates of home-range size in 2002–2004 also did not increase with these additional tracking points ($y = 4.45 \pm 0.002x$; $n = 46$, $P = 0.85$, $R^2 = 0.001$). Nevertheless, 3 weeks or more after the original 3-day tracking period we followed most collared individuals for 1 or 2 additional days. All animals that were located during the additional tracking days remained on the same ranges recorded during the initial 3-day session. This study includes a total of 1,562 h of radiotelemetry observations on 46 adult *T. tana* in masting forest in 1990 ($n = 8$ adults, 322.5 h), postmasting forest in 1991 ($n = 9$, 312.9 h), primary forest in 2002–2004 ($n = 21$, 679.9 h), and selectively logged forest in 2003–2004 ($n = 8$, 247.1 h). We also radiotracked 10 subadult *T. tana* for a total of 328 h during the 2002–2004 study periods. All animal handling procedures conformed to guidelines of the American Society of Mammalogists (Gannon et al. 2007), and were approved by the University of Maryland's Institutional Animal Care and Use Committee.

In 2003 and 2004 we used fruit traps to compare fruitfall between the primary and logged sites. Only fruit that has fallen to the ground is available to large treeshrews (Chapman and Wrangham 1994). We constructed each trap from a 1-m² section of plastic netting suspended 60 cm above the ground by 4 polyvinyl chloride pipes. The traps were then installed every 50 m along the trapping transects ($n = 41$ fruitfall traps at each site). We collected the contents of each trap weekly and sorted soft, fleshy fruits from other materials. We recorded the number of fruits and total wet weight in grams for each trap, and then dried the fruits in an 80°C oven before recording the dry weight (g). Fruitfall is not reported for 2004 because the fruit traps in logged forest were repeatedly destroyed by elephants.

Radiotelemetry and spatial analyses.—We triangulated radiotelemetry bearings and calculated error polygons for each individual tracked from 2002–2004 using Locate II (Nams 2000), and then imported the location points and error ellipses into ArcView GIS 3.3 (ESRI 2002). Location points for treeshrews tracked by Emmons (2000) in 1990–1991 were digitized from hand-drawn maps using Windig 2.5 (Lovv 1996), imported into ArcView, and then analyzed using the methods described below. For each individual, we calculated 95% minimum convex polygon home ranges (5% of outlying observations excluded using harmonic mean method), 95% kernel home ranges (fixed kernel; smoothing parameter chosen using least squares cross validation), and minimum day-range length using the Animal Movement extension (Hooge et al. 1999) in ArcView. We calculated minimum convex polygon home ranges for comparison with studies on other taxa, but

kernel home ranges were used for statistical analyses because kernel methods are very robust to autocorrelation and do not constrain the geometry of territorial boundaries as severely as do minimum convex polygons (Kernohan et al. 2001). We measured minimum day-range length as the cumulative distance between sequential locations recorded for an individual in a single day.

From the maps of adult territories for each site and study period, we designated pairs of *T. tana* when at least 50% of a female's territory was contained within the territory of a single male. Spatial concordance between male–female pairs was quantified as the percentage overlap between their 95% kernel home ranges using the “Clip by shape” function of the Home Range extension (Rodgers and Carr 1998) in ArcView. The number of opposite-sex extra-pair ranges overlapping each individual's 95% kernel home range, and the percentage overlap with both same- and opposite-sex extra-pair individuals, were calculated for each study period.

Statistical analyses.—To avoid influences of fruit masting and selective logging, we examined sexual dimorphism in body mass, 95% kernel home-range size, and mean day-range length using only data from individuals captured in primary forest from 2002–2004. We tested for differences between the sexes using 2-sample *t*-tests assuming unequal variances. To examine overall fruit production and phenology in primary versus logged forests, we calculated mean dry weight of fruit (g/trap) gathered weekly from fruitfall traps and tested for an overall difference between sites using a matched pairs *t*-test. We compared the relative condition of treeshrews in different ecological conditions by using the residuals of a least-squares regression of body mass (g) on hind-foot size (mm). Residual body mass was used to examine differences in mass due to factors other than overall skeletal size. Body mass values for females known to be pregnant were excluded from these analyses.

To examine pair-living in relation to short-term increases in fruit abundance, we compared body condition, home-range area, mean day-range length, and number of overlapping extra-pair territories between individuals in primary forest during the 1990 masting, primary forest after masting in 1991, and primary forest from 2002 to 2004. The postmasting forest in 1991 was considered separately because population turnover through either death or displacement of former residents led to a new group of individuals on the study site after the mast (Emmons 2000). We compared the same variables between treeshrews in primary forest from 2002 to 2004 and selectively logged forest from 2003 to 2004 to examine pair-living in relation to long-term changes in fruit abundance. In both cases we tested for significant differences in the variable of interest using a 2-way analysis of variance (ANOVA) for unequal sample sizes with sex, forest category, and the interaction between sex and forest category as model effects. We excluded the interaction between sex and forest category when it did not contribute to the overall significance of the model. We used 10,000 replicates of randomized, mixed-model factorial ANOVA (Manly 1991) with sex, forest category, and the interaction term as model effects to examine differences in percent territorial overlap with behavioral partners and both same- and opposite-sex extra-pair

individuals. The Satterthwaite correction for unbalanced designs was used to calculate the correct degrees of freedom for unequal sample sizes between our study sites (Searle 1987). We used randomization techniques because these overlap percentages were measured for male–female dyads and thus are not independent observations.

To examine whether pair-living in *T. tana* can be explained by the dispersion of females, we calculated 2 indices of territorial defendability for males during all 4 study periods. These 2 measures, *D* (Mitani and Rodman 1979) and *M* (Lowen and Dunbar 1994), are based on the relationship between day-range length and territory size in territorial and nonterritorial primate species. We calculated *D* using the formula $d/(4A/\pi)^{0.5}$ in Mitani and Rodman (1979), where *d* is the average day-range length and *A* is home-range area. We calculated *M* using the formula $M = N (sv/d^2)$ in Lowen and Dunbar (1994), where *s* is the mean intruder detection distance, *v* is the day-range length, and $d = (4A/\pi)^{0.5}$, as defined above. To examine the influence of variable intruder detection distances, we calculated *M* assuming *s* equaled 50 m and 10 m for male *T. tana*. We used the PROC MIXED procedure in SAS 8.02 (SAS Institute Inc. 2001) for the randomization tests, and JMP 5.0 (SAS Institute Inc. 2003) for all other statistical analyses.

RESULTS

Space use and ranging patterns of large treeshrews.—Individuals in primary forest from 2002–2004 did not exhibit significant sexual dimorphism in body mass (Table 1; *n* = 7 females and 12 males, *t* = 0.41, *P* = 0.69), territory size (*n* = 9 females and 13 males, *t* = –1.29, *P* = 0.21), or mean daily distances traveled (*n* = 9 females and 13 males, *t* = –0.16, *P* = 0.88). Home-range analyses indicated that male–female pairs of large treeshrews occupied joint areas in all habitats examined in this study (Figs. 1 and 2). The location of individuals' home ranges did not change within study periods, but only 2 adults survived for 2 entire study periods (F14 in primary forest and M35 in selectively logged forest in 2003–2004). Two males disappeared within the 1st month of the 2003 study period in primary forest (M14 and M20) and were quickly replaced by new males that occupied similar home ranges (M28 and M29, respectively).

The percentage of individuals' 95% kernel home range that overlapped with their partner was highly variable across sites, averaging from 36% to 62% for males and 62% to 72% for females (Table 1). Overlap with opposite-sex extra-pair individuals was common for both males and females, but averaged only 7–20% of home-range area (Figs. 1 and 2; Table 1). No home ranges of males overlapped more than 50% of 2 separate home ranges of females. Mean home-range area varied from 3.4 to 4.2 ha for females and 4.0 to 6.9 ha for males, and individuals traveled more than 1 km per day within their home ranges regardless of sex or study period (Table 1).

Direct sightings of radiocollared treeshrews in the 2002–2004 study periods were rare (*n* = 20), but all sightings were of solitary individuals. Signal monitoring of all treeshrews on the site throughout the day indicated that partners occasionally

TABLE 1.—Body mass, space use, and ranging patterns of large treeshrews. Means \pm SE of body mass; 95% kernel home-range area; day-range lengths; number of opposite-sex, extra-pair overlapping territories; percent of territory overlapping behavioral partner's territory; and percent of territory overlapping both same- and opposite-sex extra-pair territories are presented for male and female *Tupaia tana* during different study periods.

Variable	Study period							
	Masting 1990		Postmasting 1991		Primary 2002–2004		Logged 2003–2004	
	Male	Female	Male	Female	Male	Female	Male	Female
Body mass (g)	231 \pm 9.2	252 \pm 12.1	228 \pm 9.0	202 \pm 6.6	213 \pm 4.9	215 \pm 3.5	223 \pm 5.1	227 \pm 2.9
Territory size (ha)	6.9 \pm 1.5	3.4 \pm 0.7	4.0 \pm 0.1	3.5 \pm 0.3	5.5 \pm 0.9	4.1 \pm 0.7	5.0 \pm 1.4	4.2 \pm 1.5
Day-range length (km)	1.8 \pm 0.1	1.2 \pm 0.9	1.2 \pm 0.07	1.1 \pm 0.1	1.5 \pm 0.1	1.5 \pm 0.2	1.6 \pm 0.3	1.4 \pm 0.1
No. extra-pair overlaps	1.5 \pm 0.5	1.2 \pm 0.4	1.0 \pm 0	1.3 \pm 0.5	0.8 \pm 0.2	1.2 \pm 0.3	0.13 \pm 0.13	0.3 \pm 0.18
% Partner overlap	0.36 \pm 0.21	0.7 \pm 0.15	0.62 \pm 0.03	0.72 \pm 0.05	0.47 \pm 0.05	0.7 \pm 0.1	0.49 \pm 0.04	0.62 \pm 0.02
% Extra-pair overlap	0.07 \pm 0.02	0.11 \pm 0.05	0.14 \pm 0.05	0.1 \pm 0.05	0.11 \pm 0.04	0.2 \pm 0.06	0.05 \pm 0.05	0.21 \pm 0.21
% Same-sex overlap	0.12 \pm 0.04	0.12 \pm 0.07	0.11 \pm 0.02	0.12 \pm 0.06	0.04 \pm 0.02	0.06 \pm 0.02	0.02 \pm 0.02	0.03 \pm 0.02

spent more than 1 tracking interval (≥ 20 min) in close proximity ($n = 7$). In 1 case, partners spent 2 entire days together (F14–M19 pair in 2003). Other cases of proximity ($n = 3$) involved a radiocollared subadult and adult on the same territory. During the 2004 study period in primary forest, we observed an adult (M40) male and subadult (m37) male on adjacent territories engaging in chasing and calling at the common boundary of their respective territories. Three subsequent tracking days indicated that m37 did not enter the area of dispute again (Fig. 1). Subadults were either spatially associated with an adult pair, or used relatively small, exclusive ranges (Fig. 1).

We suspected 2 instances of predation in 2004 when we recovered the damaged, hair-covered radiocollar of a subadult female in 2004 (f23), and a subadult male's (m37) radiocollar buried under 6 inches of leaf litter and soil. One radiocollared adult male (M19) in 2003 was eaten by a mangrove snake (*Boiga dendrophila*—Munshi-South 2005). A *T. tana* followed by Emmons (2000) also was eaten by a predator.

Space use and ranging patterns in relation to fruit abundance.—First, we examined differences between treeshrews in masting and nonmasting primary forest. In accordance with our predictions for periods of high fruit abundance, males in primary forest exhibited significantly larger home ranges and longer day-range lengths than females, and day-ranges of males were significantly longer during the masting period (Table 2; Fig. 1). However, males did not gain greater access to extra-pair females despite greater day-range lengths. Body condition varied widely among the masting, postmasting, and nonmasting study periods in primary forest (Table 1), but body condition of females was superior during the masting period (Fig. 3). The significant interaction between sex and forest type reflected higher values for body condition of females during the masting period than body condition of females in nonmasting years (Fig. 3; Table 2). The proportion of variation in body condition and day-range length explained by our models exceeded 0.30, but R^2 equaled only 0.15 for territory size.

The temporal pattern of fruitfall in the logged and primary forest sites was similar during the study period in 2003, but the weekly mean dry weight of fruit per trap was consistently

greater in logged forest (Fig. 4; weekly mean fruit per trap in primary forest = 0.09 ± 0.07 g, logged forest = 0.54 ± 0.08 g, $t = 4.16$, $P = 0.006$). As predicted if body condition is related to fruit biomass, body condition values for both males and females were significantly higher in logged forest than in primary forest (Table 3). Of the spatial and behavioral factors compared between primary and logged forest in the 2002–2004 study periods, only the number of extra-pair overlapping ranges was significantly different between primary and logged forests (Table 3). The mean number of overlapping extra-pair territories was nearly 3 times fewer in logged forest than in primary forest for both sexes (Tables 1 and 3), but the proportion of variation explained by this model was only 0.18. In contrast to our predictions, females did not have smaller home ranges, and males did not range more, in logged forest despite higher fruit abundance.

Defendability indices.—We calculated 2 indices of territorial defendability that measure the ability of an animal to monitor the boundaries of its home range. The Mitani–Rodman index (D) measures how often an average male could travel the length of his home range given the size of the area and the male's daily movements. D -values calculated for male *T. tana* during each study period were substantially higher than the cutoff value calculated for territorial versus nonterritorial primates (Table 4; $D \geq 0.98$ for territorial primates—Mitani and Rodman 1979). Values ranged from 5.32 for the 1991 postmasting period to 6.34 for selectively logged forest in 2003–2004. The Lowen–Dunbar index of defendability (M) also is based on the relationship between day-range lengths and home-range area, but indicates how often the male can actually detect intruders at the boundaries of his range. Assuming a mean intruder detection distance of 50 m or 10 m for male *T. tana*, we calculated M -values that also greatly exceeded the cutoff for territorial primates (Table 4; $M \geq 0.08$ for territorial primates—Lowen and Dunbar 1994). The latter conservative detection distance assumption resulted in M -values ranging from 0.2 in masting forest to 0.25 in selectively logged forest.

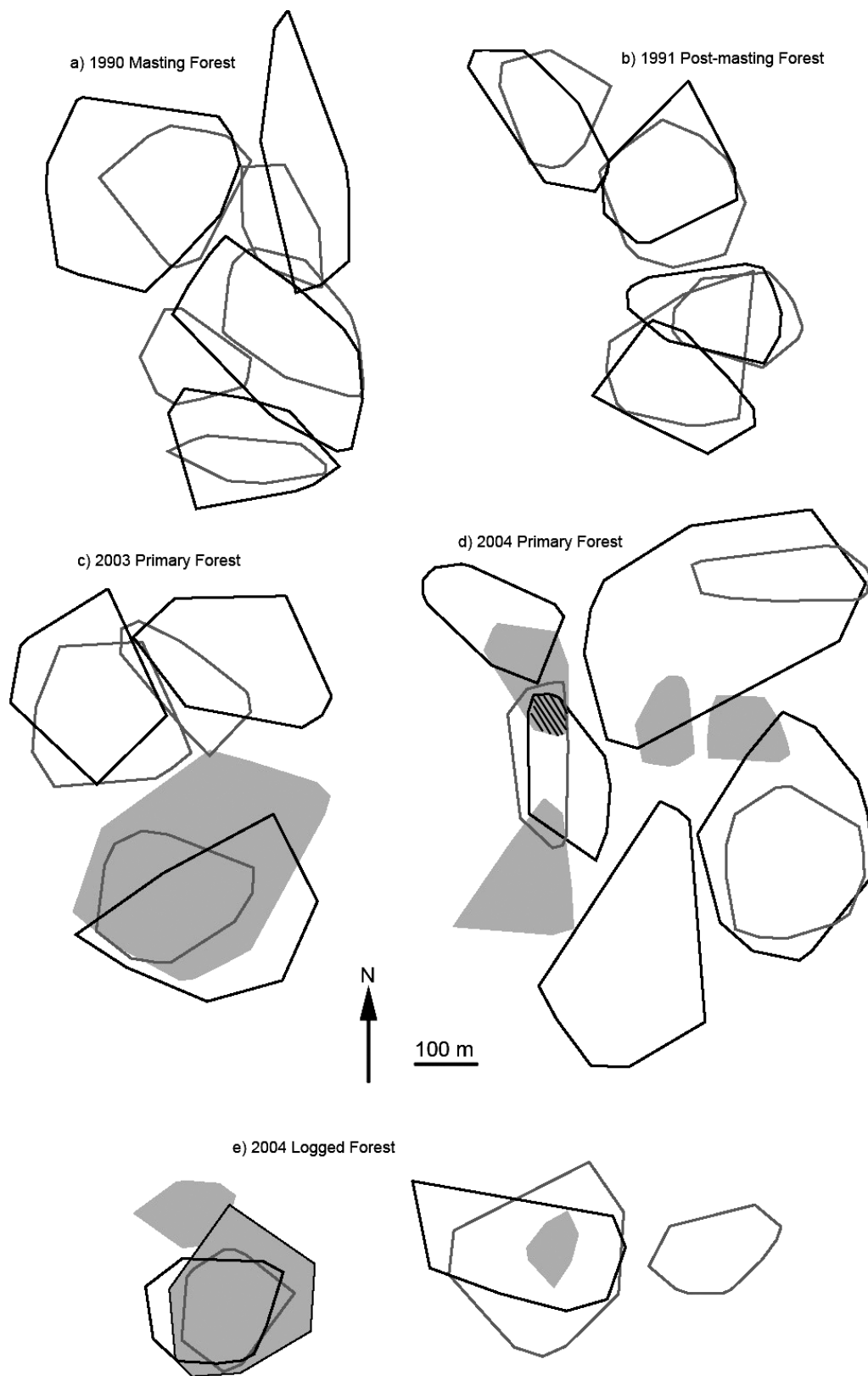


FIG. 1.—Ninety-five percent minimum convex polygon home ranges of behavioral pairs in a) masting forest in 1990, b) postmasting forest in 1991, c) primary forest in 2003, d) primary forest in 2004, and e) selectively logged forest in 2004. Black outlines represent home ranges of males, gray outlines represent home ranges of females, and solid gray polygons represent home ranges of subadults. The hatched area in d) represents an area of territorial conflict between an adult and subadult male.

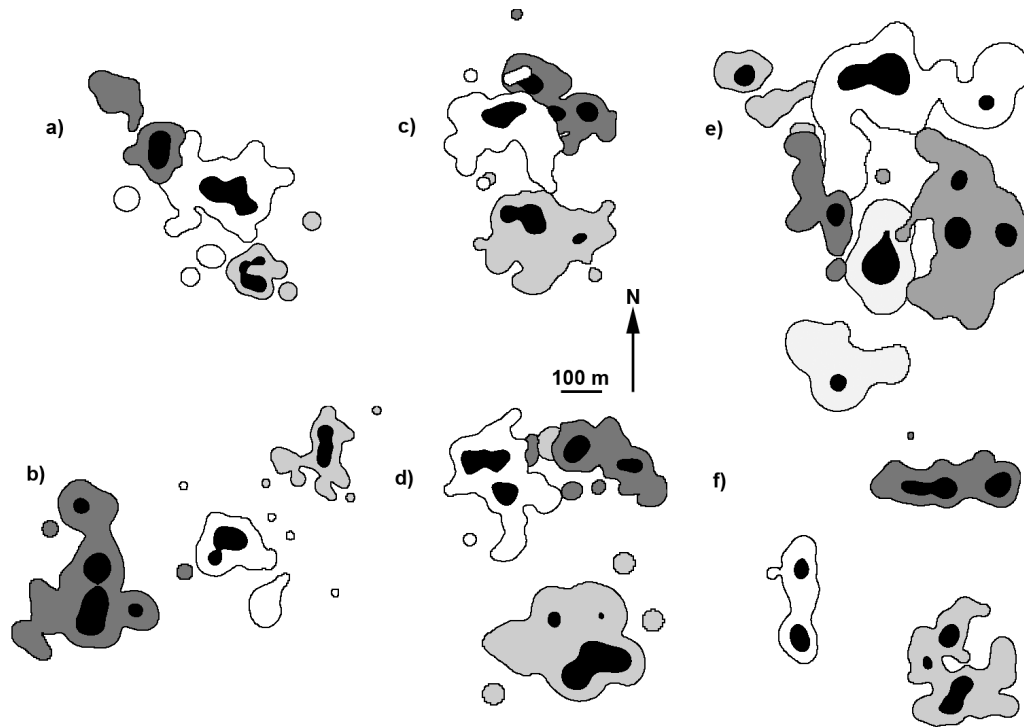


FIG. 2.—Examples of kernel home ranges calculated for *Tupaia tana*. Kernel home ranges are shown of a) males and b) females in primary forest in 2002, c) males and d) females in primary forest in 2003, and e) males and f) females in primary forest in 2004. Black areas represent 50% kernel ranges and lighter areas represent 95% kernel ranges.

DISCUSSION

Behavioral mating system of large treeshrews.—Male-female pairs of large treeshrews occupied joint, spatially associated home ranges (Figs. 1 and 2). A significantly higher percentage of the home range of the female partner was typically contained within the home range of the male, but no males were associated with home ranges of 2 females despite this sex difference in spatial cohesion. Most individual home ranges slightly overlapped the spatial boundaries of opposite- and same-sex ranges, but individuals were much less spatially associated with extra-pair individuals than with their partner. Formation of 2-adult groups does not necessarily imply pair-bonding (primates, Fuentes 2002), belying the need to distinguish between associated and dispersed pairs sensu van Schaik and Kappeler (2003). Because of the elusive nature and nearly constant activity of *T. tana*, it was impossible to assess quantitatively affiliative behaviors indicative of pair-bonding, such as patterns of proximity or reciprocity between pair members (Fuentes 2002). However, all direct observations were of solitary individuals, and radiocollared treeshrews were rarely in proximity to other individuals. Emmons (2000) also predominantly observed solitary *T. tana*. These results indicate that *T. tana* forms dispersed pairs, and exhibits less spatial and behavioral cohesion than dispersed pairs in nocturnal prosimians (Fietz 1999; Schülke and Kappeler 2003).

Behavioral monogamy and fruit abundance.—Comparison of males and females during masting and nonmasting periods indicated that males exhibited substantially larger territories,

longer day ranges, and less territorial overlap with their behavioral partners during the masting period (Fig. 1). Only body condition of females increased in response to the masting (Fig. 3), and some females gave birth to 3 litters in succession (Emmons 2000). During similar time spans in nonmasting primary forest in 2002–2004, females gave birth to 0 or 1 litter,

TABLE 2.—Differences in body condition and space use between large treeshrews in masting and nonmasting primary forest. Forest types (FTs) include masting (year 1990), postmasting (1991), and nonmasting (2002–2004). The degrees of freedom (*df.*) and *F*-values resulting from ANOVAs with sex and forest type as main effects are reported, as well as the *R*²-value associated with the entire model. Day-range length was log_e-transformed to improve normality. *P*-values for the 2%-overlap variables were computed by comparing the *F*-statistic to a distribution of *F*-statistics computed from 10,000 randomizations of the data. Tests with *P*-values equal to or below a significance level of 0.05 are marked * for $P \leq 0.05$ and *** for $P \leq 0.001$. NS = not significant.

Factor	<i>df.</i>	Sex	Forest (FT)	Sex × FT	Model <i>R</i> ²
Body condition	5, 30	3.21*	0.31	4.33*	0.35
Territory size	3, 35	4.71*	0.65	NS	0.15
Day-range length	3, 35	4.50*	3.79*	NS	0.31
No. extra-pair individuals overlapping	3, 33	0.28	0.47	NS	0.04
% Within-pair overlap	3, 23	12.96***	1.73	NS	0.42
% Opposite-sex extra-pair overlap	3, 33	0.77	0.41	NS	0.04
% Same-sex extra-pair overlap	3, 33	0.18	2.71	NS	0.15

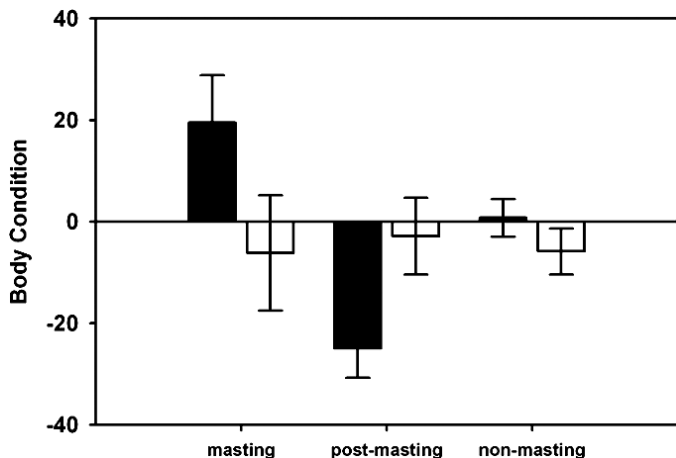


FIG. 3.—Mean body condition (residuals from regression of mass on hind-foot length) during masting and nonmasting periods at the primary forest site. Black and white bars are for data on females and males, respectively. Error bars represent ± 1 SE of the mean body condition.

with only 1 female reproducing twice in succession (J. Munshi-South, in litt.). Females may have used the extra resources provided by fruit masting for increased reproduction, whereas males may not have exhibited substantial weight gain because they used the extra resources for increased daily movements. However, males did not gain greater overall access to female territories during the masting period despite increased ranging. These results suggest that mast fruiting in Borneo increases reproductive output of female treeshrews, but does not substantially change the behavioral mating system of *T. tana*.

We recorded consistently higher fruitfall and better treeshrew body condition in logged forest than in primary forest, but did not find the predicted differences in space use or ranging behavior between the primary and logged sites. We cannot definitively rule out other explanations for superior body condition, but this result in conjunction with the pattern found during the mast fruiting implicates fruit abundance as an

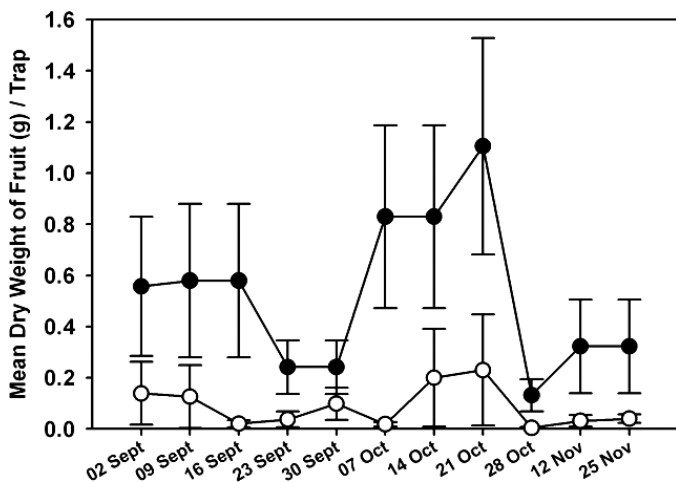


FIG. 4.—Mean dry weight of fruit collected per trap at the primary (white circles) and logged forest site (black circles) in 2003. Error bars represent ± 1 SE of the mean.

TABLE 3.—Differences in body condition and space use between large treeshrews in primary (years 2002–2004) and logged (2003–2004) forest. The degrees of freedom (*df.*) and *F*-values resulting from ANOVAs with sex and forest type as main effects are reported, as well as the *R*²-value associated with the entire model. The interaction term between sex and forest type was not significant for any model and thus was not included. Day-range length was log_e-transformed to improve normality. *P*-values for the 2%-overlap variables were computed by comparing the *F*-statistic to a distribution of *F*-statistics computed from 10,000 randomizations of the data. Tests with *P*-values equal to or below a significance level of 0.05 are marked * for $P \leq 0.05$ or ** for $P \leq 0.01$.

Factor	<i>df.</i>	Sex	Forest type	Model <i>R</i> ²
Body condition	2, 21	1.3	4.69*	0.23
Territory size	2, 26	1.55	0.03	0.06
Day-range length	2, 26	0.24	<0.01	0.01
No. extra-pair individuals overlapping	2, 26	0.95	4.92*	0.18
% Within-pair overlap	2, 12	11.24**	0.06	0.48
% Opposite-sex extra-pair overlap	2, 26	1.46	0.04	0.05
% Same-sex extra-pair overlap	2, 24	0.33	0.78	0.04

important causal factor. The availability of invertebrate prey could have been greater in the selectively logged forest, but previous studies found lower abundance of litter invertebrates (Burghouts et al. 1992), and fewer species of moths (Willott 1999) and termites (Eggleton et al. 1999), in logged forest than in the primary forest at Danum. It is unclear why home ranges of females were not smaller in logged forest, but the population density of competitors may have been lower despite greater fruit abundance and better body condition. Logging in southeast Asia often results in a greater frequency of large tree-fall gaps than in primary forest (Grieser Johns 1997; Whitmore 1984), and the spatial pattern of treeshrews in logged forest indicated that pairs occupied islands of suitable habitat that were separated by gaps of unoccupied, suboptimal habitat (Fig. 1). Individuals occasionally entered and moved across tree-fall gaps but did not engage in any sustained activity within them (J. Munshi-South, in litt.). Alternatively, females may simply invest less in territorial behavior when resource abundance increases rather than defending smaller territories. Under this scenario females may even use larger home ranges

TABLE 4.—Ranging data and defendability indices for male *Tupaia tana* during 4 different study periods. Territorial primate species generally exceed values of *D* > 0.98, and *M* > 0.08. See text for details of calculations.

Study period	<i>A</i> (km ²)	<i>d</i> (km)	<i>D</i>	<i>M</i> (<i>s</i> = 0.05 km)	<i>M</i> (<i>s</i> = 0.01 km)
Masting 1990	0.069	1.8	6.07	1.02	0.2
Postmasting 1991	0.04	1.2	5.32	1.18	0.24
Primary 2002–2004	0.055	1.5	5.67	1.07	0.21
Logged 2003–2004	0.05	1.6	6.34	1.26	0.25

when resource abundance is high because female territoriality is relaxed. We also may not have sampled adults on the logged site that were using tree-fall gaps as home ranges.

Evolution of behavioral monogamy in large treeshrews.—Several hypotheses have been proposed for the evolution of behavioral monogamy in mammals, but no single hypothesis has been robustly supported in mammals. Recent reviews of pair-living in primates found support for contrasting sets of explanations: in 1 case, energetic constraints, predation reduction, and mate guarding (Fuentes 2002), and in the other, infanticide reduction and predation reduction through nest-guarding (van Schaik and Kappeler 2003). Below we discuss the relative support for different evolutionary hypotheses for pair-living in *T. tana*.

Does female dispersion explain pair-living in large treeshrews?—Emlen and Oring (1977) predicted that pair-living will occur when females are so widely dispersed that males cannot monopolize more than 1 reproductive female. For example, when male golden-rumped sengis defend 2 female territories, they experience increased activity levels, weight loss, and increased rates of intrusion by neighboring males (FitzGibbon 1997). To examine male defendability of multiple home ranges of females in *T. tana*, we used day-range length and home-range size of males to calculate 2 indices of territorial defendability. The 1st index, *D*, is successful at predicting territorial defense in primate species using only the ratio of day-range length to home-range diameter. We calculated *D*-values for large treeshrews that were more than 5 times higher than the cutoff value for primates, indicating that male *T. tana* can routinely cross their territories multiple times in 1 day. The *D* index does not account for the length of the territorial boundary that must be defended, so we also calculated a 2nd index of defendability, *M*, that describes the collision rate per unit boundary length (Lowen and Dunbar 1994). Assuming the lowest *M*-value we calculated for *T. tana*, males exceed the defendability threshold for primates only if they attempt to defend home ranges of more than 3 females. Thus, spatial dispersion of females alone does not explain pair-living in *T. tana*, unless space use of male treeshrews is substantially different from space use of territorial primates. However, if energy intake is reduced for male treeshrews traveling over very large areas, then these defendability indices will not provide an accurate measure of the relationship between daily range lengths and home-range sizes.

Do male large treeshrews provide services to females?—Several hypotheses for behavioral monogamy propose that pair-living evolved because male partners provide services that enhance the survival and reproduction of their female partners. Many of these hypotheses are unlikely to apply to *T. tana* because absentee maternal care and dispersed pair-living limit male–female and parent–offspring interactions. For example, direct paternal care cannot explain pair-living in large treeshrews because only females visit young in the nest, and care of treeshrew pups by males has not been recorded in the field or laboratory (Emmons 2000), even in species with substantial pair-bonding (Martin 1968).

Prevention of infanticide appears to be associated with the evolution of pair-living in primates, because males typically protect infants in species that form permanent pairs and carry their young (van Schaik and Kappeler 1997, 2003). However, absentee maternal care, female reproductive physiology, and solitary foraging lead us to reject the infanticide prevention hypothesis for *T. tana*. Extra-pair males are unlikely to know the location of offspring cached in nests visited only briefly by female *T. tana*. In contrast to adults, large treeshrew young in the nest are nearly odorless and motionless (Emmons 2000). Long lactation periods in relation to gestation make infanticide a successful strategy for males in some mammals (van Schaik 2000), but female *T. tana* become receptive to mating almost immediately after giving birth if sufficient food is available (Emmons 2000).

Solitary foraging in *T. tana* also reduces the potential for defense by males against predation or sexual harassment. Except in 1 instance of a pair that spent nearly 2 entire days together, females in this study were not recorded in close proximity to other individuals. However, we recorded 1 instance of predation by a snake (Munshi-South 2005) and suspected predation in a few other cases. Diurnal predators such as yellow-throated martens (*Martes flavigula*) and raptors were often observed on the study site, and both male and female *T. tana* sometimes gave alarm calls upon detecting a human observer (Emmons 2000; J. Munshi-South, in litt.). Quantitative assessments of proximity between behavioral partners and male vigilance behaviors are needed before predator defense or protection from harassment by males can be ruled out as explanations for pair-living in *T. tana*. Arboreal treeshrew species, particularly the pygmy treeshrew (*Tupaia minor*) and pentail (*Ptilocercus lowii*), form more cohesive pairs that travel together and exhibit substantial antipredator behavior (i.e., frequent alarm and contact calls—Emmons 2000). Protection from predation was likely an important historical force in promoting behavioral monogamy in the Scandentia, but the evolution of dispersed pair-living in large treeshrews may be related to a decreased prevalence of antipredator behavior in *T. tana*.

Variations on the protection from harassment by males or predation hypotheses predict that males provide indirect protection by maintaining escape routes or shelter sites (Kleiman and Malcolm 1981). For example, males of 2 sengi species, *R. chrysopygus* and *E. rufescens*, maintain multiple nests or extensive trail systems that are used by females for resting and traveling, respectively (Rathbun 1979). However, female *T. tana* nest separately from males in hollow logs or trees that have not been obviously manipulated (Emmons 2000). Large treeshrews avoid open areas and may concentrate their foraging along stream banks or fruit trees (Emmons 2000; J. Munshi-South, in litt.), but no evidence of trail maintenance has been observed for any treeshrew species (Emmons 2000; Kawamichi and Kawamichi 1979; Martin 1968).

The final hypothesis in this group proposes that males provide defense against conspecific foraging competition. One version predicts that females pair with a male based on the quality of the feeding territory guarded by that male (Fuentes

2002; Thalmann 2001), whereas another proposes that female–female avoidance due to foraging competition leads to territoriality, and that males defend a single female’s territory against other males to limit the number of foraging individuals in the same area (intersexual feeding competition hypothesis—Schülke 2005). This 2-step scenario has received support from comparative studies of behavioral monogamy in nocturnal prosimians (Müller and Thalmann 2000; van Schaik and Kappeler 2003) and other mammals (Komers and Brotherton 1997). Several aspects of space use and reproduction by large treeshrews suggest that females benefit from reduced foraging competition. Both male and female *T. tana* spend most of their time foraging, resulting in our observations of relatively long daily movements compared to home-range areas (e.g., high territorial defendability indices—Lowen and Dunbar 1994). Reduced reproductive output in the wild compared to captivity, intense bouts of nursing only once every 48 h while lactating, concentrated foraging activity at fruiting trees, and improved body condition of females and reproduction when fallen fruit is abundant indicate that energy limits reproduction in female *T. tana* (this study; Emmons 2000). If females choose male partners based on their feeding territories, some high-quality territories of males should support 2 or more females (variable pairs in van Schaik and Kappeler [2003]). The largest home ranges of males in this study (> 10 ha) did not support 2 females, even when fruit was abundant. Our observation that males typically defend larger territories than females provides additional support for sex-specific territoriality in *T. tana*.

Does mate guarding by males explain pair-living?—The mate-guarding hypothesis proposes that pair-living evolved because males benefit from monopolizing a single female. Pair-living in mammals is associated with small, exclusive home ranges of females, and may represent a risk-aversion strategy that guarantees mating with a single female while reducing aggressive encounters with other males (Komers and Brotherton 1997). In this scenario, males may continually monitor their female partner (klipspringer [*Oreotragus oreotragus*]—Roberts and Dunbar 2000; gibbons [*Hylobates*]—van Schaik and Dunbar 1990), or infidelity results in costly aggressive conflicts (dik diks—Brotherton and Rhodes 1996), or both.

Multiple authors have argued that mate guarding by males may be responsible for behavioral monogamy in sengis (FitzGibbon 1997; Rathbun and Rathbun 2006), because home ranges of males that are larger than home ranges of females facilitate short-term polygyny when neighboring females are widowed. Additionally, cryptic, short estrus in these species may favor the evolution of mate guarding by facilitating reproductive monopolization by the guarding male. Large treeshrews share the characteristics of larger home ranges of males and cryptic, short estrus with sengis (Emmons 2000; Martin 1968), but mate guarding seems unlikely to explain pair-living in large treeshrews or other species that forage solitarily and exhibit low spatial cohesion (Schülke and Ostner 2005) unless guarding is intensified while females are receptive (golden lion tamarins [*Leontopithecus rosalia*]—Baker et al. 1993; maned wolves—Dietz 1984). Given that pairs occupy

home ranges of 5–10 ha and forage solitarily, receptive females can likely engage in sexual liaisons with neighboring males when their partner is not present. Emmons (2000) observed males making short-term forays into neighboring territories, presumably to seek extra-pair mates. Quantitative data on mate-guarding behavior, such as over-marking of female scent marks by males or pair cohesion during receptive periods, will generally be difficult to collect for dispersed pairs of *T. tana*. However, the high rates of extra-pair paternity in *T. tana* revealed by genetic parentage analyses (Munshi-South 2006) indicate that intensive mate guarding, if it occurs, may not be very successful at assuring paternity in large treeshrews.

In conclusion, large treeshrews form monogamous pairs across a range of ecological conditions, but partners generally travel, forage, and sleep alone. Male *T. tana* are spatially associated with 1 female on a joint feeding territory, but generally exhibit larger territories than females and may seek extra-pair mating by extending their territorial boundaries beyond the home range of their partner. Female treeshrews also typically overlap 1–3 extra-pair males at the margins of their territory. Reproductive biology and space use indicate that direct male care, infanticide prevention, and dispersion of females are not primary explanations for pair-living in large treeshrews. Intraspecific foraging competition may have driven the evolution of pair-living in *T. tana*, but experimental manipulations of resource abundance are needed to confirm the importance of foraging competition.

ACKNOWLEDGMENTS

We are very grateful to the Economic Planning Unit of Malaysia and the Danum Valley Management Committee for permission to work in protected areas in Sabah; the Royal Society Southeast Asian Rainforest Research Programme and G. Reynolds for substantial logistical support; the American Society of Mammalogists, the University of Maryland Center for Biodiversity and Biology of Small Populations Research Training Grant, the Cleveland Zoological Society, Sigma Xi, the Animal Behavior Society, and the Explorers Club for research funds; J. A. Jensen, K. Johnius, A. Leong, T. Misiewicz, R. E. Sham, P. Ulok, and the staff of the Sabah Biodiversity Experiment for excellent field assistance; and J. Dietz, D. Kleiman, G. Rathbun, G. Wilkinson, and 2 anonymous reviewers for constructive comments on the manuscript.

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Submitted 27 August 2006. Accepted 31 March 2007.

Associate Editor was Jane M. Waterman.