

Space use, habitat selection, and day-beds of the common palm civet (*Paradoxurus hermaphroditus*) in human-modified habitats in Sabah, Borneo

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Space use and habitat selection of mammals are determined by the distribution and availability of critical resources. Such information on space use and habitat selection is necessary for the conservation and management of wild populations. We revealed the determinants of habitat use for 12 common palm civets (*Paradoxurus hermaphroditus*) within a matrix of human-modified habitats in Sabah, Borneo. Although studies within natural forests have reported that space use of common palm civets is mainly determined by fruit availability, we hypothesized that space use in our study area might be affected by other factors because the habitat characteristics have been largely modified from those of natural habitats. Our results showed that, for both males and females, space use is largely affected by fruit availability. Specifically, the 95% minimum convex polygon home range was negatively affected by the presence of a fruit-rich oil palm plantation in the ranging area. In forest, civets increased home-range size during the fruiting season of specific pioneer plants; they visited the fruiting trees of those plants outside the ranging area of the nonfruiting season. However, availability of day-beds also influenced the ranging pattern of civets. During the day, civets used the oil palm plantation less frequently than expected from habitat availability and often retreated to adjacent forest or forest fragments. When resting in the plantation, they selected palm trees with dense mats of ferns and larger numbers of leaves, and often reused these trees. Our results indicate that fruit availability and suitable day-bed sites may be important for the survival of common palm civets in human-modified habitats and should be preserved or restored for civet conservation.

Key words: carnivores, forest logging, oil palm plantation, Paradoxurinae, radiotelemetry, Viverridae

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The common palm civet (*Paradoxurus hermaphroditus*) is a small carnivore (2–5 kg) that is widely distributed in South and Southeast Asia (Wozencraft 2005; Jennings and Veron 2009; see Patou et al. [2010] for current taxonomic status). Common palm civets live in a broad range of habitats, including primary and secondary forest, cultivated land, outskirts of villages, and urban areas (Yasuma and Andau 2000), although they may be negatively affected by forest logging (Heydon and Bulloh 1996). Common palm civets are mainly nocturnal and frugivorous (Joshi et al. 1995; Grassman 1998) and are important seed-dispersal agents (Nakashima et al. 2010a, 2010b); in human-modified habitats, this species may be one of the few frugivorous mammalian species that can disperse large seeds (Nakashima and Sukor 2010; Nakashima et al.

2010b). When fruit availability is low, common palm civets also consume small prey, such as insects, earthworms, mollusks, and small vertebrates (Joshi et al. 1995; Nakashima et al. 2010b). Despite their wide distribution and ecological importance, little is known about the natural history and ecology of common palm civets and no studies have been conducted on their space and rest-site use in human-modified habitats. In mixed dry deciduous forest in Nepal, Joshi et al. (1995) radiotracked 5 individuals and reported that space use was primarily affected by fluctuations in fruit availability. In a



mosaic of dry tropical forest in Thailand, Rabinowitz (1991) observed that 1 old male shifted his home-range center from dry deciduous dipterocarp forests to mixed deciduous forests during times of low fruit availability. Natural disturbances such as fire and floods also are likely to influence home-range sizes, activity centers, and activity patterns (Rabinowitz 1991). Grassman (1998) suggested that home-range size was affected by sex, body size, and habitat characteristics in seasonal evergreen forest in Thailand.

The common palm civet is considered a common species that can use disturbed habitats (Duckworth et al. 2008), but little is actually known about its conservation status and the impact of human-modified environments on wild populations. Although studies in natural forests have suggested that fruit availability is a major determinant of space use, a number of other factors also could affect space use and spatial organization in disturbed habitats. Given the large biotic and abiotic changes that may result from agricultural development, logging, and other human activities (Cannon et al. 1994; John 1997), we hypothesized that space use of common palm civets would be altered by these disturbances. To test our hypothesis and to identify resources that may be critical to their survival and reproduction, we radiotracked 12 common palm civets in a heavily logged forest and an adjacent oil palm (*Elaeis guineensis*) plantation in Sabah, Borneo.

MATERIALS AND METHODS

Study area.—Our study was conducted from August 2007 to September 2009 in Tabin Wildlife Reserve (hereafter called Tabin), eastern Sabah, Borneo (5°05'–5°22'N, 118°30'–118°55'E), Malaysia. Tabin covers an area of 122,539 ha and is almost exclusively surrounded by large agricultural areas that are planted with oil palm. Most of Tabin has been heavily logged, except for the Core Area (8,616 ha) located at the central part of Tabin, and 7 other smaller Virgin Jungle Reserves.

Our research was conducted in a forest on the western boundary of the reserve, and the adjacent oil palm plantation (Fig. 1). The forest was heavily logged at least twice in the 1980s (Mitchell 1994), and was dominated by pioneer species such as *Duabanga moluccana* (Lythraceae), *Neolamarckia (Anthocephalus) cadamba* (Rubiaceae), and *Macaranga bancana*, with a thick undergrowth dominated by tangles of climbers, giant herbaceous plants, and thorny creepers (Mitchell 1994). A small patch of “primary forest” remained in Virgin Jungle Reserve 83 (74 ha) around Mud Volcano. The oil palm plantation was about 25 years old and had a sparse understory of some shrubs, ferns, sedges, herbaceous plants, and grasses (Rajaratnam 2000; Rajaratnam et al. 2007). Within the plantation, small fragments (approximately 10 ha) of secondary forest remained. The topography of the study area was gently undulating, with the reserve at about 120 m above sea level.

Diet and fruit census.—We determined the diet of common palm civets by analyzing feces collected in 2-mm nylon mesh

bags along gravel roads in secondary forest. We identified species using molecular techniques or by the footprints surrounding the feces (Nakashima et al. 2010a, 2010b). We also collected feces from individuals captured in traps. We did not determine diets in the primary forest because this habitat was too small and thus it was impossible to discriminate whether fecal contents were from food consumed in the primary forest or the surrounding secondary forest. We also conducted a monthly fruit census within primary and secondary forests, using methods of Furuichi et al. (2000). We walked along forest trails to search for mature fleshy fruits that had fallen on the ground (termed “phenology” trails; total trail length was 1.7 km in primary forest and 6.8 km in secondary forest; Fig. 1). We counted the number of fruit clusters, which were defined as aggregations extending 1 m on each side of a transect that included fruit fallen from a single tree (Furuichi et al. 2000). When we encountered a large contiguous cluster of fruit from several trees of the same species, we divided the cluster by the number of fruiting trees. Thus, the number of clusters matched the number of fruiting plants that dropped fruit within the belt transect. We divided fruits into 4 categories: figs (*Ficus* spp.), *Leea aculeata*, *Endospermum diadenum*, and others. This grouping was selected because the first 3 fruit categories are the main diet of common palm civets (Nakashima et al. 2010b). We did not conduct a fallen-fruit census in the plantation because it was difficult to estimate fruit abundance on the same basis as that used in the forests. Instead, we counted the number of fruiting trees. However, it was clear that oil palm fruits were very abundant: in September 2010, 34.3% of 100 palm trees bore at least 1 cluster of fruit. Oil palm trees bore fruit year-round with little seasonal variation (Y. Nakashima, pers. obs.; Wood and Liao 1984).

Radiotracking.—We set 10 locally made wire-cage traps (approximately 80 × 40 × 40 cm) along the fallen-fruit trails and on the gravel road leading to the Core Area in August–September 2008. In addition, in January–April 2009, traps were set along the road to Tunku, which runs along the forest–plantation boundary (Fig. 1). Traps were baited with bananas, papayas, or cempedak (local fruits), and checked each morning. Trap locations were selected on the basis of the presence of animal trails and feces or any other signs of civet activity. Traps were placed on level, dry ground near a tree or other source of cover, and were staked to the ground. The trap floor was covered with a thin layer of humus and leaves to minimize detection of the spring mechanism by civets and to maintain substrate continuity (Colon 2002). Captured civets were immobilized with Zoletil (Vibrac Laboratories, Inc., Carros, France) at 3.5 mg/kg and examined to determine their health, sex, age, and reproductive status. Age was estimated from body size, tooth wear, and reproductive condition, with individuals being categorized as juvenile, subadult, adult, or old. Only adults were fitted with radiocollars (M2940B; Advanced Telemetry Systems, Inc., Isanti, Minnesota). Mean collar mass was about 60 g (2.1–3.5% of civet body weight). The animals were released once they were sufficiently

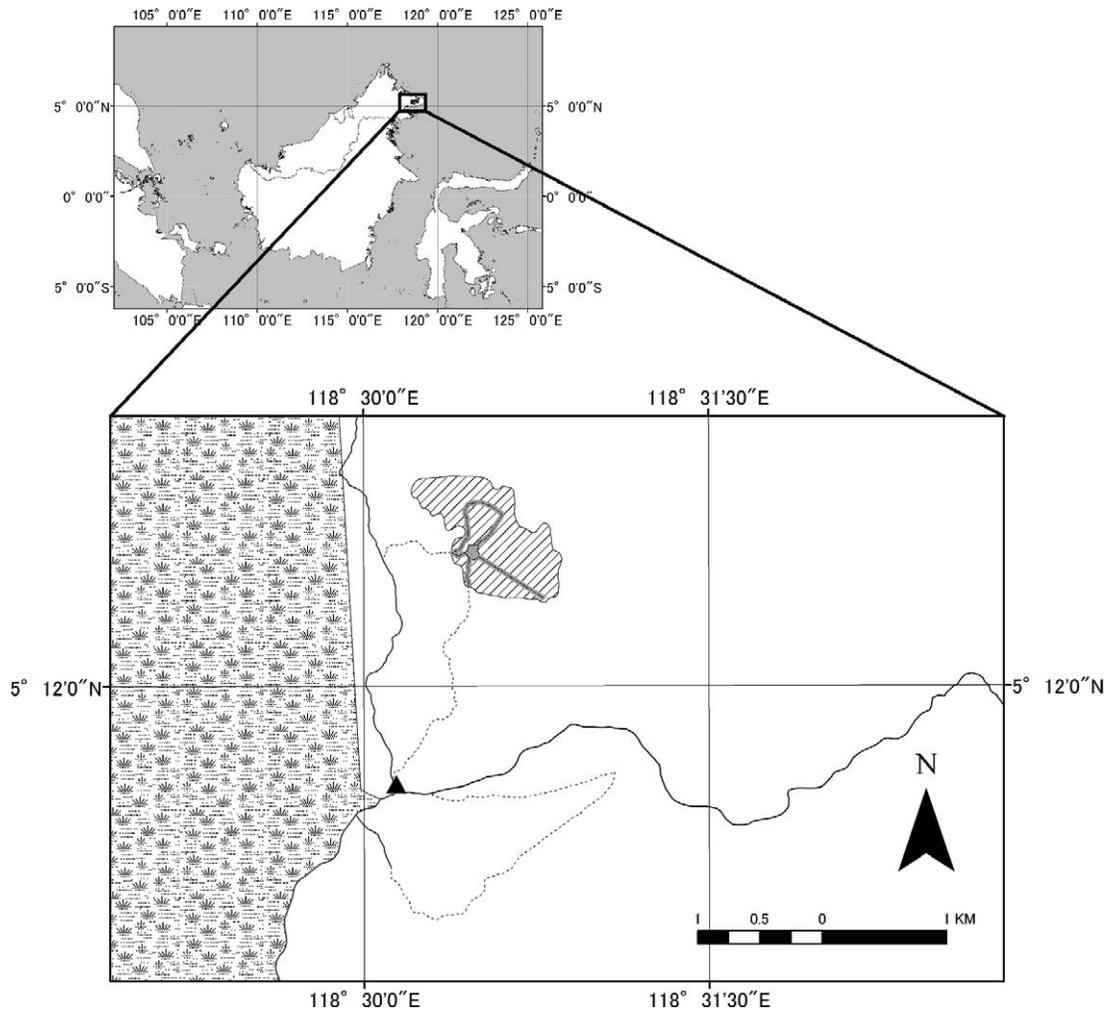


FIG. 1.—Map of the study area at Tabin Wildlife Reserve, Borneo, which shows the juxtaposition of primary and secondary forest habitats with the oil palm plantation and the locations where sampling was conducted.

recovered to assume a normal resting posture in the trap. All trapping and handling protocols conformed to guidelines sanctioned by the American Society of Mammalogists (Sikes et al. 2011). Except for 2 individuals (CPM2 and CPF3), radiocollars dropped off naturally or were removed when individuals were recaptured.

Individuals were radiotracked using receivers and handheld 3-element yagi antennas (ATS3EL; Advanced Telemetry Systems, Inc.). We triangulated bearings obtained by observers positioned at global positioning system-mapped stations. We obtained at least 3 bearings from marked positions for each tagged animal, using a sighting compass. Successive bearings were taken no more than 10 min apart to minimize location errors caused by movement. Radiocollared individuals were located a minimum of 5 times per week with an interval of > 12 h to ensure the statistical independence of successive locations (Harris et al. 1990). Tracked individuals were approached as close as possible to minimize distance errors. Tests on hidden transmitters (Kenward 2001) revealed a triangulation error of approximately 30 m at a distance of 300 m from the transmitter.

During the day, we attempted to locate day-beds of resting civets by homing (Mudappa 2001, 2006). However, it was impossible to systematically locate resting civets in the forests because dense mats of vines often covered trees. In the plantation, we identified the resting site by watching the animal emerge from the day-bed at dusk. Based on previous studies (Joshi et al. 1995; Mudappa 2006), we recorded 5 characteristics of each oil palm tree used for day-bed. For comparison, we also measured these variables at a tree that was randomly selected from the 8 neighboring oil palm trees (oil palm trees were planted in a reticular pattern). Tree heights were measured using a rangefinder (Nikon Forestry 550; Nikon, Inc., Tokyo, Japan). The number of visible leaves was defined as the number of those 50% of which could be seen in photographs taken at 10 m from the tree. The amount of fern was categorized as very dense (75–100% of tree face was covered with a dense mat of fern), dense (50–75%), sparse (25–50%), and less (0–25%). We used a single day-bed only once for a given individual in our analyses.

Data analysis.—We determined civet locations from triangulation bearings using LOAS (Ecological Software

Solution, Inc., Sacramento, California). We calculated home ranges using the 95% minimum convex polygon (MCP) method, with the Animal Movement Extension (Hooge and Eichenlaub 2000) of ArcView (ESRI 1999). These methods are commonly used, which enabled comparisons with other studies. "Total home ranges" were calculated using all locations. "Day home ranges" were calculated using locations recorded during the day (0700–1800 h), and "night home ranges" were calculated from night locations (1900–0600 h). Asymptotic curves of total home range were obtained with > 100 locations. Hence, we only calculated home ranges for individuals that were located > 100 times.

To identify factors that determine home-range size, we analyzed data using a generalized linear model, with a normal error distribution and identity link function. We incorporated body mass (W) raised to 0.94 power (Lindstedt et al. 1986), the sex of the individual (SEX), and presence or absence of plantation in home range (SITE) into the independent factors. Because day-bed sites are easy to find, it is simpler to call these locations and artificially increase the number of locations, which are different from locations taken when the animals are foraging. To avoid this bias, we used night home range as the response variable. To account for differences in sampling effort among individuals, we also incorporated the number of locations (n) into the models. In this analysis, we did not differentiate between locations in primary and secondary forest because our sample size was too small and we tracked civets mainly in the nonfruiting season of 2 highly preferred pioneer plants (*L. aculeata* and *E. diadenum*; see "Results"), when fruit availability in the 2 forests was expected to be similar. For individuals tracked both in the July–September fruiting season and nonfruiting season, we used the home-range size estimated from locations obtained only in the nonfruiting season. The significance of these effects was assessed by mean values of Wald tests.

To analyze habitat use and its seasonal difference, we used only independent locations (> 12 h apart) to avoid bias associated with autocorrelation (Swihart and Slade 1985). For individuals tracked both in the fruiting season and nonfruiting season, we tested seasonal differences in home-range size and space use (home-range shift). We calculated the difference in home-range size between 2 seasons and compared it to a null distribution (under the assumption of no seasonal difference in home-range size) obtained as follows. We randomly selected the same number of radiotracking locations as those obtained during the fruiting season and those during the nonfruiting season from total locations, and calculated the 95% MCP area difference between them. We repeated these procedures 1,000 times. We tested the presence or absence of home-range shift using similar procedures. We compared the proportion of home-range area overlapping between 2 seasons to a null distribution estimated by resampling. We performed this test on 95% MCP home range and 25% MCP home range (core area). For individuals inhabiting the primary or secondary forest, we tested whether space use was affected by fruit availability in each habitat. We compared the number of civet

radiotracking locations between fruiting and nonfruiting seasons of 2 highly preferred pioneer plants (see "Results") for each habitat (primary forest or secondary forest) using a chi-square test and residual analysis. In a subsequent analysis, we regarded the proportion of each habitat that was present in each animal's total home range as habitat availability, and we tested whether the animals used either forest more frequently than predicted by habitat availability using a chi-square goodness-of-fit test (White and Garrot 1990). We determined the area of primary forest according to the map drawn by Mitchell (1994). For the individuals inhabiting the forest-plantation boundary, we used chi-square tests to determine whether habitat use by civets was different between day and night on the basis of the number of locations in each habitat. We compared the number of daytime locations against habitat availability (the proportion of each habitat that was present in each animal's total home range) using a chi-square goodness-of-fit test to determine if one habitat was selected over the other.

To evaluate the preference for day-bed sites, we fit a generalized linear mixed model, with a binomial distribution and logit link function, using the lmer function of package lme4 (Bates and Sarkar 2008). We incorporated the civet individual (CIVET) into the model as a random effect. We gave an identity number (ID) to each sampling unit (a pair of day-bed tree and random tree, see above) and treated it as a random effect. We included 5 tree variables: tree height (HEIGHT), diameter at breast height (DBH), number of visible leaves (NLEAVES), percentage of fern coverage on the tree surface (FERN: 0 = less, 1 = sparse, 2 = dense, 3 = very dense), and presence or absence of mature fruits in the trees (FRUIT: 0 = absence, 1 = present). The significance of these effects was assessed by mean values of Wald tests. All statistical analyses were performed using R statistical environment (R Development Core Team 2008).

RESULTS

Diet and fruit availability.—Common palm civets were largely frugivorous in the secondary forests and the plantation (Fig. 2). Following fig and the other wild plant fruits (45.1% of feces), oil palm fruits (44.0%) were a major component of common palm civet diets in the plantation. Animals also were eaten (millipedes 16.5%, rodents 13.1%, and insects 2.1%).

Fruit species consumed by the civets in the secondary forest changed according to fruit availability (Fig. 2). Figs were constantly available throughout the study period, but 2 pioneer species, *L. aculeata* and *E. diadenum*, were abundant in the secondary forest from July to September (Fig. 2), and corresponding to the fruiting phenology of these 2 trees, civets changed fruit preference from figs to these pioneer plants (Fig. 2). Neither of these 2 tree species was present in the primary forest.

Home range.—We captured 15 adult individuals (7 males and 8 females). Sufficient data were collected to calculate total home ranges for 6 males and 6 females (Table 1). On average,

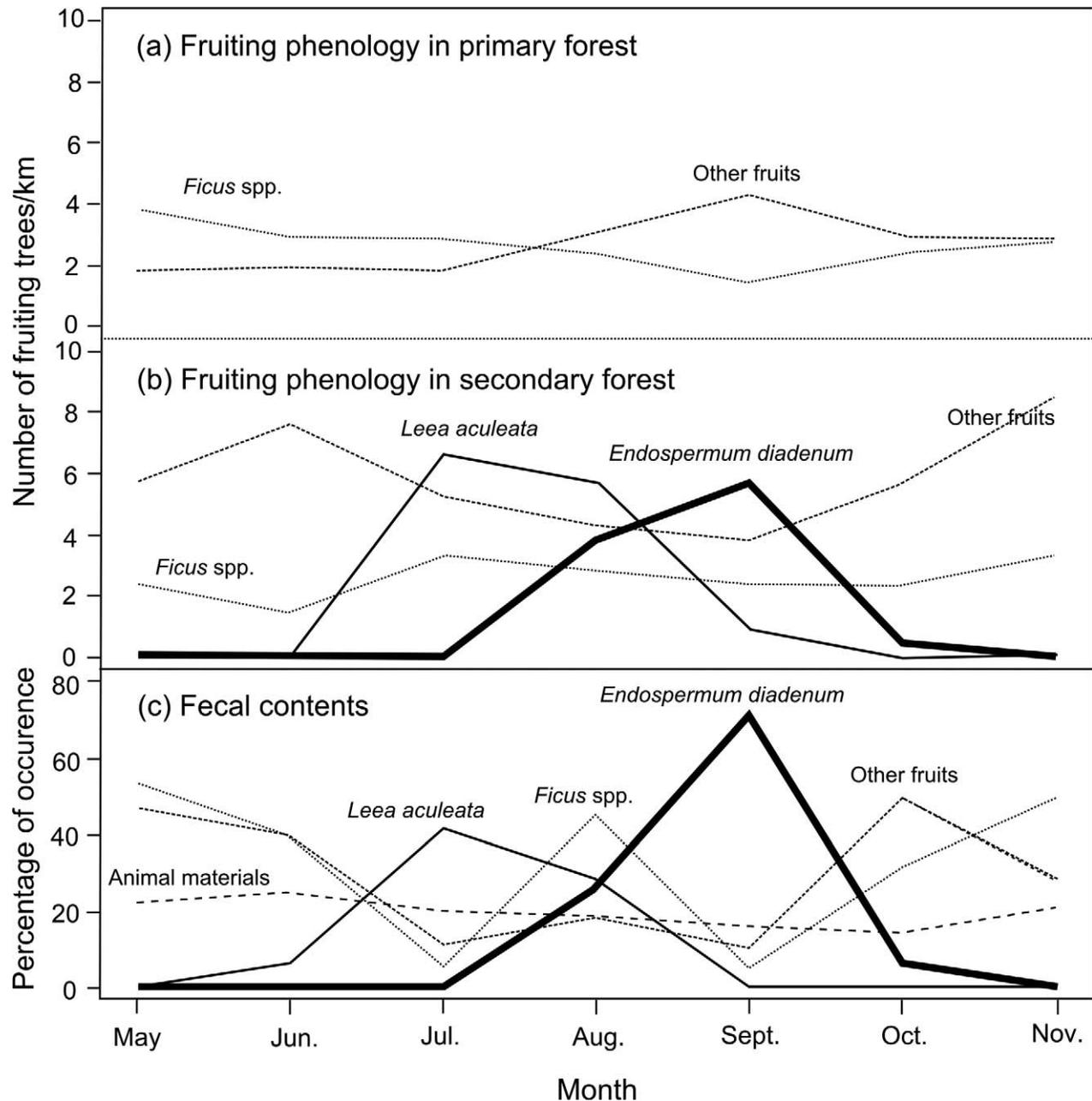


FIG. 2.—Fruiting phenology in a) primary forest and b) secondary forest, and c) the contents of common palm civet (*Paradoxurus hermaphroditus*) feces collected along Core Area road in Tabin Wildlife Reserve in 2008.

males ($\bar{X} \pm SD$; 2.2 ± 0.3 kg, $n = 6$) were slightly heavier than females (2.0 ± 0.3 kg, $n = 6$), but masses were not significantly different ($W = 28.0$, $P = 0.12$). Males had much larger total home ranges ($\bar{X} \pm SD$) than females (males: 95% MCP: 79.3 ± 66.4 ha; females: 95% MCP: 29.8 ± 18.9 ha), a difference that was statistically significant ($W = 34.0$, $P = 0.008$). Total home ranges (95% MCP) of 6 radiocollared individuals (3 males and 3 females) partly encompassed the oil palm plantation, whereas 3 others (1 male and 2 females) used both primary and secondary forest (Fig. 3; Table 1). Home ranges overlapped between and within sexes in both plantation and forest habitats (Fig. 3). We also regularly observed

uncollared individuals in the home ranges of these 12 radiotracked individuals.

Night home-range size (95% MCP) was positively related to body mass (coefficient $\pm SE = 160.24 \pm 35.96$, $t = 4.45$, $P = 0.003$) and negatively related to the presence of oil palm plantation (coefficient = -49.06 ± 22.12 , $t = -2.21$, $P = 0.062$). Effects of sex (coefficient = 16.01 ± 20.25 , $t = 0.79$, $P = 0.455$) and the number of locations (coefficient = -0.67 ± 0.52 , $t = -1.280$, $P = 0.241$) was not significant (overall model: $F = 8.842$, $P = 0.006$).

Habitat use.—We successfully tracked 3 individuals (M380, F420, and F543) throughout both the nonfruiting and July–

TABLE 1.—Home-range size (ha) of the common palm civet (*Paradoxurus hermaphroditus*) in the Tabin Wildlife Reserve, Sabah, Borneo. *n* is the number of independent locations. Asterisks (*) indicate that a plot of the number of fixes versus home-range size exhibited an asymptotic relationship. MCP = minimum convex polygon.

Identification	Sex	Date collared	Date signal lost	Mass (kg)	Site ^a	Day range (ha)		Night range (ha)		Total range (ha)		Locations in plantation (%) ^b	Day-beds located ^c
						<i>n</i>	95% MCP	<i>n</i>	95% MCP	<i>n</i>	95% MCP		
M525	M	17 January 2008	7 July 2008	1.8	F	81	35.8	61	41.4	142	43.1*	—	—
M380 ^d	M	22 January 2008	11 October 2008	2.6	F	75	121.1	87	177.1*	162	176.7*	—	—
M345	M	1 February 2008	19 July 2008	2.1	F	88	32.9*	103	42.1*	191	50.0*	—	—
CPM1	M	15 September 2007	19 April 2008	2.1	FO	53	11.1	55	20.4	108	19.7*	68 (62.5)	11
CPM2	M	17 September 2007	27 January 2008	2.7	FO	45	118.5*	57	134.9	102	145.0*	25 (24.5)	12
CPM3	M	19 September 2007	18 March 2008	2.2	FO	99	12.5	93	36.0*	192	40.9*	141 (73.4)	5
F543 ^d	F	15 January 2007	15 November 2008	1.8	F	177	25.8*	80	29.4	257	34.9*	—	—
F480	F	9 February 2008	10 July 2009	1.7	F	55	9.7	62	17.7	117	17.9*	—	—
F420 ^d	F	3 February 2008	9 October 2009	2.1	F	107	22.3*	94	F21.7*	201	26.5*	—	—
CPF1	F	15 September 2007	3 March 2008	2.1	FO	78	45.0	37	43.8	115	54.8*	106 (92.1)	12
CPF2	F	21 September 2007	15 April 2008	2.2	FO	76	22.2	35	25.2	111	33.2*	66 (59.5)	8
CPF3	F	25 September 2007	12 June 2008	1.7	FO	79	9.7*	52	9.2*	131	10.5*	101 (77.1)	28

^a Home range covering forest (F), plantation (O), and both (FO).

^b Day-beds were systematically searched for only in plantations.

^c Percentage of the total number in the plantation of all locations.

^d Individuals tracked throughout the fruiting season and nonfruiting season of the preferred pioneer plants.

September fruiting seasons of *L. aculeata* and *E. diadenum*. These animals consumed fruits of these pioneer trees located outside the ranging area of the nonfruiting season. Consequently, home-range sizes (95% MCP) significantly

increased in the fruiting season in all 3 individuals (M380: nonfruiting season versus fruiting season = 57.3 ha versus 195.0 ha, *P* < 0.001; F420: 19.9 ha versus 24.8 ha, *P* = 0.020; F543: 11.6 ha versus 30.1 ha, *P* = 0.011; Fig. 4). The home

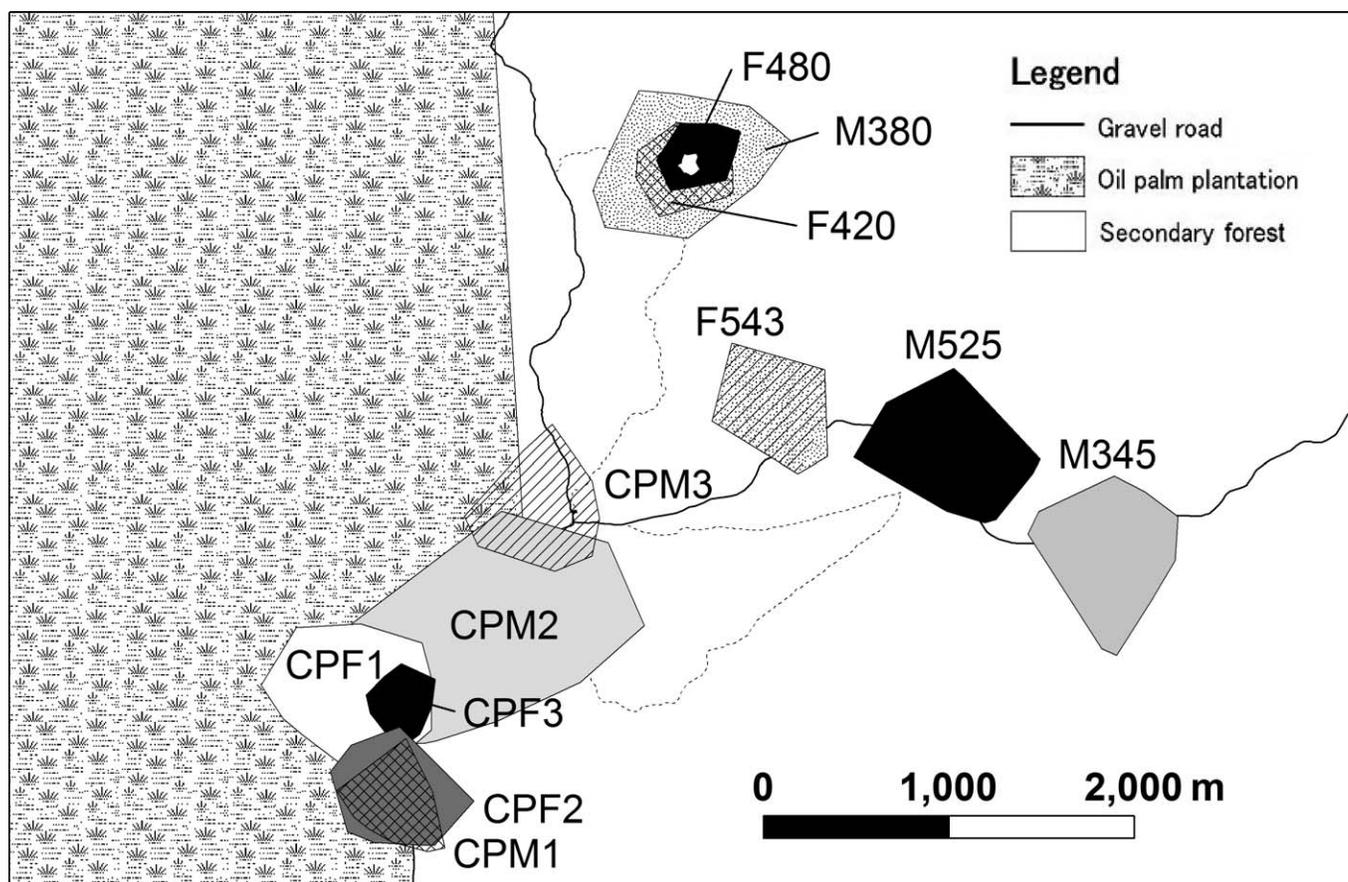


FIG. 3.—Total home ranges (95% minimum convex polygon) of adult common palm civets (*Paradoxurus hermaphroditus*) in the Tabin Wildlife Reserve and adjacent oil palm plantation, based on nocturnal and diurnal locations taken during the nonfruiting season.

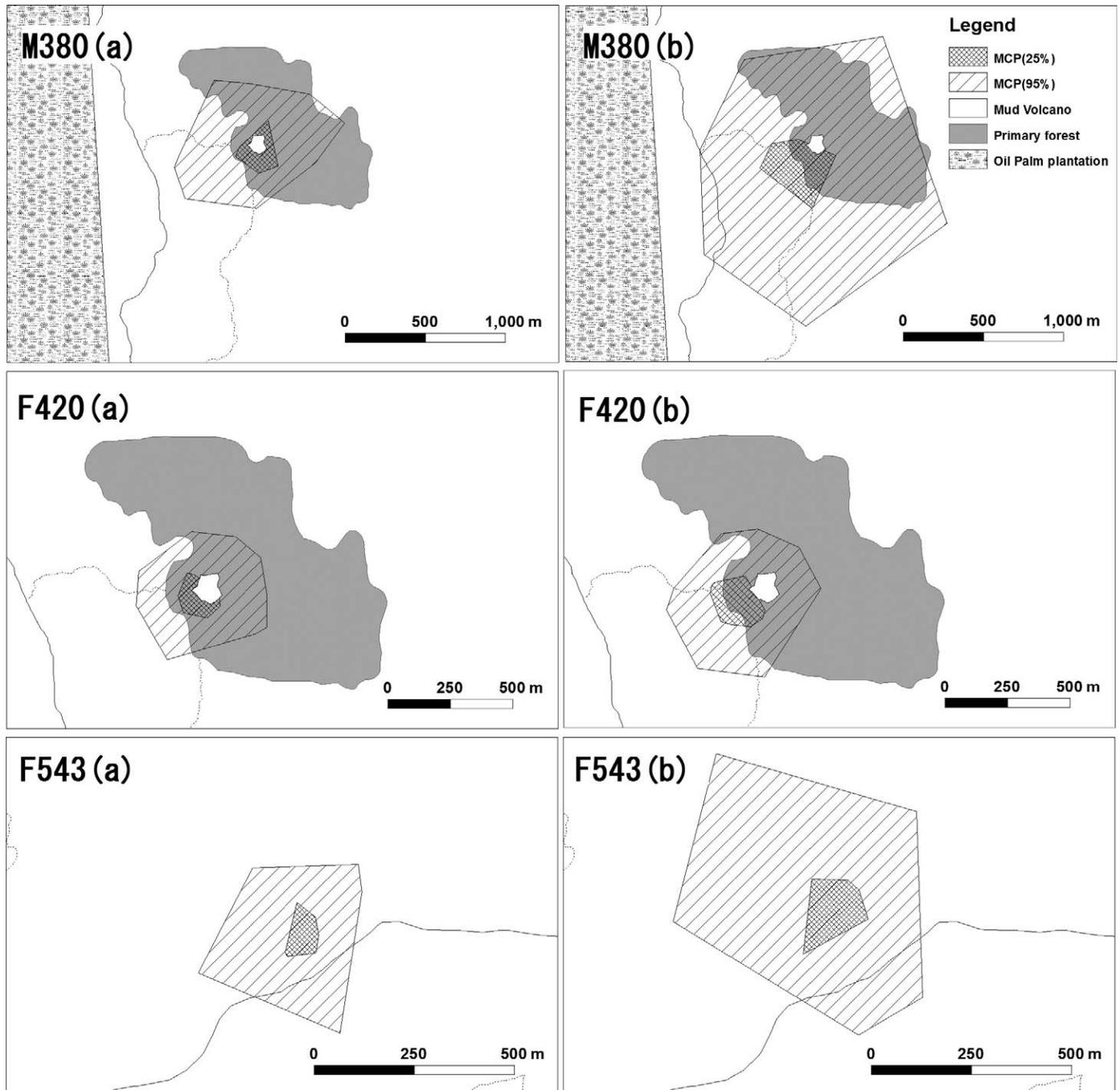


FIG. 4.—Home ranges (95% minimum convex polygon) and their core areas (25% minimum convex polygon) of common palm civets (*Paradoxurus hermaphroditus*) in a) the fruiting season and b) the nonfruiting season in Tabin Wildlife Reserve. The area outside of the primary forest was logged secondary forest (see Fig. 1). All 3 individuals significantly increased home-range size and shifted home-range area between the fruiting season and the nonfruiting season (see text).

ranges significantly shifted between the 2 seasons (M380: $P = 0.005$; F420: $P = 0.010$; F543: $P = 0.033$; Fig. 4). The core area of home ranges (25% MCP) also shifted between the seasons (M380: $P = 0.005$; F420: $P = 0.010$; F543: $P = 0.033$; Fig. 4). Two civets inhabiting the primary–secondary forest boundary (M380 and F420) used secondary forests more frequently in the fruiting season than in nonfruiting seasons (M380: $\chi^2_1 = 18.65$, $P < 0.001$; F420: $\chi^2_1 = 26.4$, $P < 0.001$). Their use of

secondary forest during the fruiting season did not differ significantly from that expected based on availability (M380: $\chi^2_1 = 1.12$, $P = 0.290$; F420: $\chi^2_1 = 0.70$, $P = 0.400$).

In the forest–plantation boundary, except for CPF3, significantly fewer daytime locations were obtained in the plantation than was expected from habitat availability (Table 2). Home ranges of only 2 individuals (CPF1 and CPM2) overlapped small fragments of secondary forest in the

TABLE 2.—Daytime habitat selection of the common palm civets that inhabit the secondary forest–plantation boundary of Tabin Wildlife Reserve, Borneo. += significantly selected, –= significantly avoided, NP = small forest fragments not present, NS = neither selected nor avoided. Small forest fragments in the plantation were present in home ranges of only 2 individuals (CPM2 and CPF1).

Identification	χ^2	<i>df.</i>	<i>P</i>	Forest	Plantation	Small forest fragments
CPM1	6.57	1	0.01	+	–	NP
CPM2	20.1	2	< 0.001	+	–	NS
CPM3	11.71	1	< 0.001	+	–	NP
CPF1	28.15	2	< 0.001	+	–	+
CPF2	42.41	1	< 0.001	+	–	NP
CPF3	0.13	1	0.717	NS	NS	NP

plantation, and only CPF1 selectively used the forest fragments. Four individuals (CPM1, CPM3, CPF1, and CPF2) used the plantation more frequently during the night than during the day ($P < 0.05$), although 2 others (CPM2 and CPF3) did not use the habitats differently between day and night ($P > 0.05$).

Day-bed use.—We located 51 different day-bed sites in plantation habitat. Civets rested in oil palm trees (74.5% of locations) or on the ground within dense vegetation (25.5%). Individual civets often rested in the same trees on different occasions: 24.2% of the sites were used 2 or more times. In particular, CPF3 used the same oil palm trees with a dense mat of ferns during a 2-month period. Oil palm trees that were used for day-beds had significantly more leaves (coefficient \pm SE = 0.011 ± 0.047 , $Z = 2.26$, $P = 0.024$) and a denser mat of ferns (coefficient = 0.720 ± 0.244 , $Z = 2.94$, $P = 0.003$) than random trees that were not known to be used (overall model: $\chi^2_1 = 28.9$, $P < 0.001$; Table 3). Although we did not systematically locate day-bed sites in the forest, we observed that civets rested in vine tangles, on the ground with dense herbaceous mat, or in tree hollows. One female (F543) and 1 male (M525) that inhabited a heavily disturbed area of logged secondary forest (Fig. 3) used the same tree hollows repeatedly.

DISCUSSION

Our results provide some of the 1st estimates of space use and habitat selection of the common palm civet in human-disturbed habitats. Total home-range sizes of civets in our study were much smaller than comparable estimates from Thailand, whereas our estimates seemed to be larger than those from Nepal: mean 100% MCP home-range size of 2 males was

1,060 ha in a mosaic of dry tropical forest in Thailand (Rabinowitz 1991), and that of 2 males and 1 female was 2,200 ha and 1,400 ha, respectively, in a dry evergreen forest in southern Thailand (Grassman 1998). In Nepal, the mean total 100% MCP home range was 14.1 ha (Joshi et al. 1995), although this estimate is not directly comparable to our estimates because of different sampling methods. These differences may be explained by the larger body sizes (often > 4 kg) of common palm civets in Thailand, or by differences in habitat productivity between the sites (Joshi et al. 1995; Grassman 1998).

In our study, common palm civets consumed fruits from early-successional trees in logged, secondary forest and from oil palms in the plantation. Temporal and spatial variation in fruit availability also affected space use within these human-modified habitats: home-range size was negatively affected by the presence of oil palm plantation within night home range, possibly because of the high fruit availability. In forest, 3 civets (1 male and 2 females) changed the space use during the fruiting season of specific pioneer plants: they visited the fruiting trees outside the ranging area of nonfruiting season. Along the primary–secondary forest boundary, 2 individuals used 2 pioneer fruiting tree species (*L. aculeata* and *E. diadenum*) more frequently in the fruiting season than in nonfruiting seasons. In Nepal, Joshi et al. (1995) found that home ranges of common palm civets were smaller during February and June, when the fruits of *Coffea benghalensis* and *Murraya koenigii* were abundant, and largest in March–May when ripe fruits were clumped and scarce on the landscape. Home ranges of civets overlapped significantly, especially when fruiting trees were at low densities or were clustered in distribution. Our findings therefore concur with those of studies from more natural settings that emphasize the importance of fruit availability and spatial distribution as determinants of space use of common palm civets.

Our results suggest that the availability of day-beds also influences use of plantation habitats by common palm civets. We found that dense cover was an important component of daytime rest sites in these areas: civets selected oil palm trees with thick leaves, dense ferns, and a thick mat of vegetation on the ground. Like those day-beds that we encountered in forest habitats, these substrates always completely concealed the animal. In Nepal, Joshi et al. (1995) reported that common palm civets rested in trees, choosing the tallest and largest tree in their immediate area at dawn. In addition, they rested more

TABLE 3.—Summary of generalized linear mixed model analysis ($n = 76$) for the determinants of day-bed selection by common palm civets (overall model: $\chi^2_1 = 28.9$, $P < 0.001$). The results of Wald tests on fixed effects are shown. Covariates are defined in the “Materials and Methods.”

Covariates	Estimate	<i>Z</i>	<i>P</i>
DBH	–0.01	–1.68	0.092
HEIGHT	–0.13	–0.80	0.421
NLEAVES	0.11	2.26	0.024
FERN	0.72	2.94	< 0.001
FRUIT	–0.59	–0.87	0.387

often in trees covered with dense vines than in trees without vines or holes, and trees with vines or holes were used for several consecutive days, whereas those lacking these features were not (Joshi et al. 1995). In India, Mudappa (2006) reported that brown palm civets (*Paradoxurus jerdoni*) most often used dreys of Indian giant squirrels (*Ratufa indica*), followed by trees with hollows and vine tangles. Although Mudappa (2006) argued that the height and size of trees are the primary criteria for day-bed choice, our findings suggest that common palm civets primarily select day-bed locations in plantations that can hide their body completely.

However, it is important to note that, in all but 1 case, civets were found less often in the plantation during the daytime than would be expected based on habitat availability, which suggests that suitable rest sites are limited within the plantation, and that civets often return to the forest to rest during the day. When civets did rest in the plantation, they used oil palm trees with specific characteristics that differed from the surrounding trees. They also often used the same trees repeatedly, as they did in the logged secondary forest. Collectively, these observations suggest that the availability of suitable day-bed sites may be limited in disturbed habitats.

Our results reveal that the availability and abundance of fruits and suitable day-bed sites are important factors that influence space use of common palm civets, and thus may be key resources in human-modified habitats. In terms of fruit availability, our results imply that the heavily logged forest in Tabin might provide suitable habitat for common palm civets. However, previous studies (e.g., Heydon and Bulloh 1997) have reported that the availability of figs and other fruits is often lower in logged forests, resulting in declines of many frugivorous mammals, including palm civets (Heydon and Bulloh 1997). In such areas, planting fleshy-fruited plants may enhance the habitat quality not only for common palm civets, but also for disturbance-vulnerable large frugivores, such as orangutans (*Pongo pygmaeus*—Ong 2010). Our results suggest that *E. diadenum* may be a good candidate for planting because it yields an extremely large crop and is consumed by various frugivores, including orangutans and small-toothed palm civets (*Arctogalidia trivirgata*—Y. Nakashima and M. Nakabayashi, pers. obs.).

It also may be important to increase abundance of suitable day-beds in heavily logged areas as well as in plantations. In the logged forest within the Tabin Wildlife Reserve, common palm civets sometimes rested in caves, tree hollows, and vine tangles. Although provision of nest boxes may not be a logistically or economically feasible option in rain-forest environments like those in this study, another possibility would be to promote the conservation value of vine tangles in logged forests. Lianas are regarded as pests that suppress the regeneration of commercial trees and increase the mortality of trees (Johns 1997); however, lianas also may provide day-bed sites, food for many animals, including civets (McConkey 2009; Nakashima et al. 2010b), and canopy-to-canopy access for arboreal animals (Emmons and Gentry 1983).

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