Sleeping site selection in two Asian viverrids: effects of predation risk, resource access and habitat characteristics

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Abstract. Factors related to sleeping site selection in terrestrial and semi-arboreal mammals vary depending on the environmental conditions they live in and the suite of species they interact with. These factors include proximity to food resources and availability of suitable sites that offer protection from severe weather and from risk of predation. We explored habitat characteristics which may influence sleeping site selection of masked palm civets (*Paguma larvata*) and binturongs (*Arctictis binturong*) and assessed whether selection was related to food resources and/or reduction of predation risk. Most of the sleeping sites were in trees close to canopy level (*c.* 19–24 m). A majority of the sites consisted of tangled structures created by vines, leaves and/or woody climbers and moderate to high levels of canopy cover which typically concealed sleeping animals from below and above. However, selection of sleeping sites did not appear to be related to density of fruiting stems within the sites, probably because fruits may have been available in similar quantities across home ranges. Although sleeping site selection varied among individuals, selection appeared to reflect choices for habitat characteristics at both sleeping trees and sleeping sites to enhance concealment. While enhanced concealment may have multiple benefits, we postulate that it is mostly likely intended to reduce predation risk.

Key words. binturong; masked palm civet; sleeping site; Southeast Asia; Thailand

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INTRODUCTION

Animals often face complex trade-offs between access to food (Joshi et al., 1995; Emsens et al., 2013; Gess et al., 2013), access to mates (Cant et al., 2002), minimising physiological stress (Zielinski et al., 2004; Lesmeister et al., 2008), territorial defense (Endries & Adler, 2005; Espirito-Santo et al., 2007), and minimising risk from predation (Lesmeister et al., 2008; Emsens et al., 2013). Understanding the decision-making criteria animals use to balance these demands is invaluable to the understanding of animal ecology.

Sleeping is one of the most dangerous stages in an animal's life (Lima et al., 2005) particularly because animals must consider potential threats from predators when selecting a sleeping site. Several strategies have been suggested by which mammals may avoid predation while sleeping: seeking sites with high canopy cover (Lesmeister et al., 2008; Nakashima et al., 2013), choosing tall trees to avoid ground predators (Joshi et al., 1995), choosing trees with no woody climbers to inhibit predators climbing up (Phoonjampa et al., 2010), or, in contrast, choosing trees with liana/woody climbers which create a complex tangled structure which may reduce visibility to predators (Joshi et al., 1995; Mudappa, 2006; Su Su & Sale, 2007; Nakashima et al., 2013), and regularly changing sleeping sites to avoid odor building-up which could potentially attract predators (Day & Elwood, 1999; Phoonjampa et al., 2010). Placement of sleeping sites may also relate to maintaining access to food. Some species place their sleeping sites close to a prior feeding site in order to regain quick access and reduce time and energy costs of travel during subsequent days such as observed in common palm civets *Paradoxurus hermaphroditus* (Joshi et al., 1995). Minimising physiological stress is another consideration for animals in choosing sleeping sites (Zielinski et al., 2004; Lesmeister et al., 2008), however we did not address this issue in this paper.

Studies that integrate several aspects of sleeping site selection have focused primarily on primates (e.g., Day & Elwood; 1999; Phoojampa et al., 2010; Albert et al., 2011) and are rare among other taxa, particularly small mammalian carnivores (Rabinowitz, 1991; Colon, 2002; Jennings et al., 2006, 2010a, 2010b). In this paper we investigate the sleeping site selection by two small carnivore species, binturong *Arctictis binturong* (Raffles, 1821) and masked palm civet *Paguma larvata* (Smith, 1827). We investigate selection at two spatial scales; (a) at sleeping trees—trees where animals chose for sleeping, and (b) within sleeping sites—a defined area surrounding sleeping trees (see below). Following the resource access hypothesis (Joshi et al., 1995) we predict there would be a positive relationship between sleeping sites of these frugivorous civets and fruit availability if sleeping sites were selected based on access to food resources. We

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Table 1. Variables measured at sleeping sites and available sites at two spatial scales: (a) at sleeping trees and (b) within sleeping sites within a 20 m radius centered at sleeping trees, of three masked palm civets (*Paguma larvata*) and two binturongs (*Arctictis binturong*) in Thung Yai Naresuan Wildlife Sanctuary – West, Thailand between 2010/2011 and 2011/12. Short variable names used throughout the paper are in square brackets. §These variables are not measured at available sites.

Predictor Variable	Description
(a) At sleeping tree	
Height of first branch (m) [1st branch]	Height of first branch of the sleeping tree (m)
Size of sleeping tree (cm)	Diameter at breast height (DBH) of sleeping tree (cm)
Height of sleeping tree (m)	Height of the trees (m) animals used for sleeping
Height of sleeping position (m) [position height] §	Height of sleeping position in the sleeping trees (m)
Position [position] §	Descriptive; whether animals choose the end of a branch or close to main trunk
(b) Within sleeping site (20 m radius)	
Forest type [forest]	Classification of forest types where sleeping sites located. Forest types include dry dipterocarp forest (DDF), mixed deciduous (MDF), semi- evergreen (SEF), and gallery evergreen (GEF) forests.
Abundance of trees [abundance of trees]	Number of small (DBH 10–40 cm) trees and large (DBH ≥ 40 cm) trees within plots
Tallest tree (m)	Height of the tallest tree in a plot (m)
Percent tangled structure [% tangle]	Tangled structure, defined as the percentage of structure created by lianas, vines, or woody climbers, estimated within 4 sections of the sample plot, with each subsection representing 25%. However, if the sleeping site contained no tangled structure, it was assigned '0%'.
Percent canopy cover [% canopy]	Canopy cover, defined as the percentage of ground covered by the horizontal projection of tree crowns, estimated within 4 sections of the plot, categorised as 1 (≤ 25%), 2 (26–50%), 3 (51–75%), or 4 (> 75%)
Canopy connectivity [connectivity]	Determined by connection among trees via branching and/or woody climbers; if trees are more isolated with no touching branches or connected by woody climbers, it is defined as "low", otherwise "high"
Density of fruiting stem [fruit stems]	Density of trees (DBH ≥ 10 cm) and woody climbers bearing fruits within 20 m radius of sample plots, calculated as the number of stems per hectare (stems ha^{-1})

then investigated the predation risk hypothesis (Joshi et al., 1995; Mudappa, 2006; Su Su & Sale, 2007; Lesmeister et al., 2008; Nakashima et al., 2013), for which we predicted sleeping site characteristics, as well as their sleeping position within it, reflect the selection of characteristics that inhibit detection by predators. At sleeping trees animals may (1) choose the tallest and largest sleeping trees, and (2) trees with high first branches. At sleeping sites, animals may choose (3) sites with high canopy cover which provide cover from above, (4) sites with high canopy connectivity which can facilitate movement among trees without descending to ground, and (5) sites with a high percentage of tangled structures which also provide cover from above and below and act as a supporting structure. Due to limited information on even description on sleeping sites of these semi-arboreal civets, we further explore the placement of sleeping sites within home ranges in relation to forest types and whether sleeping sites tend to be located near the center of home ranges, in peripheral areas, or are randomly placed. We also describe the pattern of reuse of sleeping sites. All variables are detailed in Table 1.

Study animals. Binturongs (weight 6–20 kg) are partially diurnal but peak activity periods occur at night (Grassman et al., 2005). Masked palm civets (3–6 kg) are mainly nocturnal with occasional day-time activity (Rabinowitz, 1991; Grassman, 1997; Zhou et al., 2014). Both species spend the majority of their time in trees but also descend to ground, especially binturongs, which are heavier and must descend to the ground to move from one tree to another (Than Zaw et al., 2008), whereas masked palm civets can leap between trees (W. Chutipong, pers. obs.). Although there have been studies on ranging behavior (Rabinowitz, 1991; Grassman, 1998; Austin, 2002; Grassman et al., 2005; Zhou et al., 2014), existing information is limited regarding sleeping site selection in these two viverrids. Rabinowitz (1991) briefly described sleeping sites of a female masked palm civet in western Thailand. Wang & Fuller (2001) provided descriptions of the sleeping sites of five masked palm civets in southeast China. For binturong, there has been no systematic study of sleeping site selection. This species is listed as Vulnerable due to habitat loss, hunting and the pet trade (Widmann et al., 2008) and information on sleeping
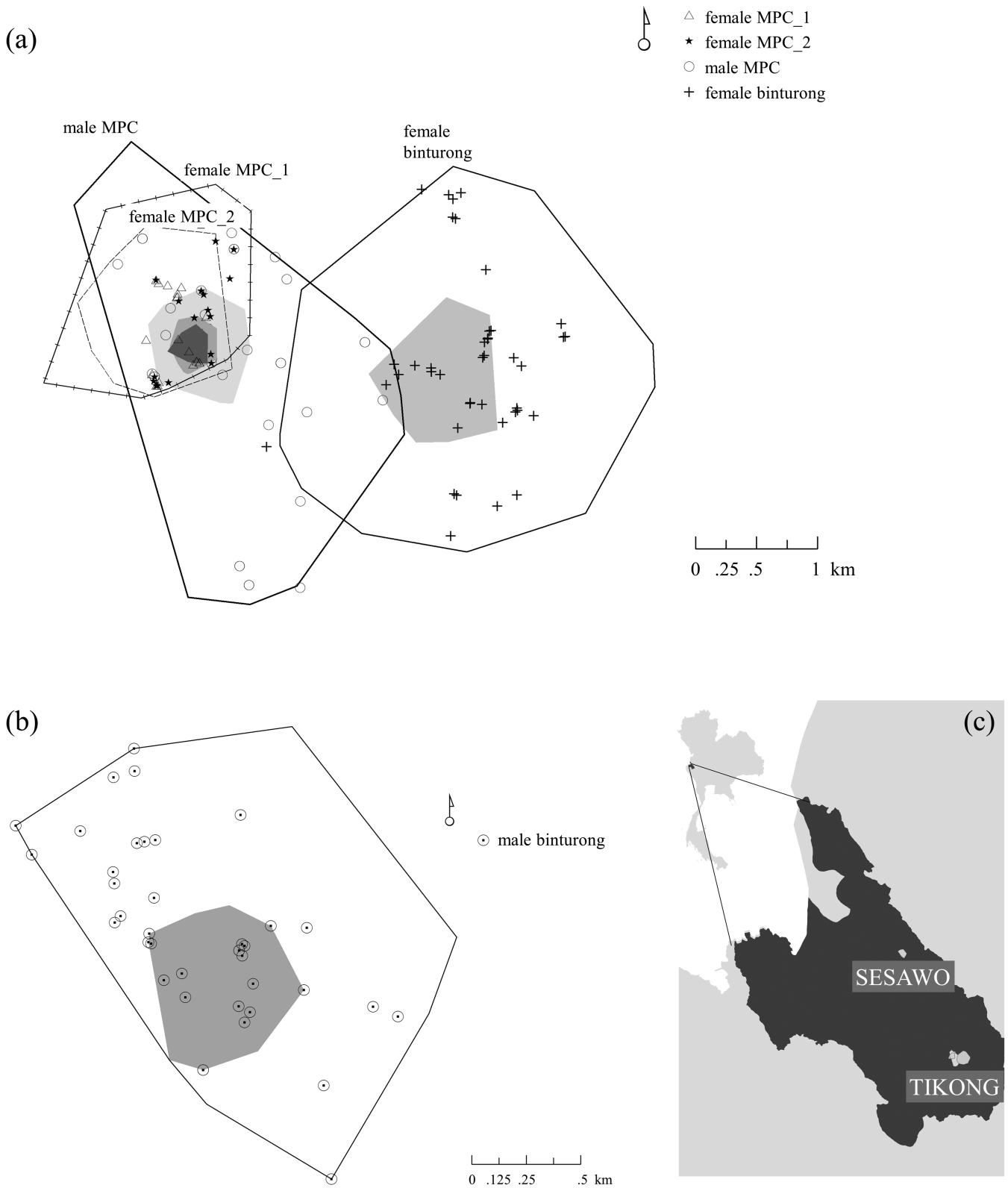
Fig. 1. Home ranges, core areas and sleeping sites of binturongs (*Arctictis binturong*) and masked palm civets (*Paguma larvata*). Home ranges (minimum convex polygon [MCP] 95%) and core areas (MCP 50%) with sleeping sites overlaid of (a) three masked palm civets and a female binturong at Tikong, (b) a male binturong at Sesawo, and (c) location of study sites (Sesawo and Tikong) within the study area (Thung Yai Naresuan Wildlife Sanctuary – West). Different gray shades within home ranges represent core areas of each animal.

site selection may contribute to a better understanding of factors that affect this species.

METHODS

Study site. We conducted the study in Thung Yai Naresuan Wildlife Sanctuary – western Thailand (15° 00'–15° 23' N, 98° 30'–99° 05' E). Three distinct seasons are found in the study area: cool dry (November–February), hot dry (March–May), and rainy (May–October). Mean annual temperature is 28°C (Thai Meteorological Department, 2005). The sanctuary is characterised by rugged mountainous terrain with elevations ranging from 250 m up to 1,811 m. Major habitat types include mixed deciduous (45%), seasonal dry evergreen (28%), hill evergreen (15%), secondary growth (4%), and a combination of grassland and dry dipterocarp (5%) (Nakhasathien & Stewart-Cox, 1990). We established two study sites, Tikong—covered by dry evergreen forest with interspersed small patches of dry dipterocarp and mixed deciduous forest, and Sesawo—covered by dry dipterocarp and mixed deciduous forest with large patches of grasslands and gallery evergreen forest along the many streams that bisect the area. Dry evergreen forest is tall, with a closed canopy at 25–40 m formed predominantly by evergreen tree species (Webb, 2007). Mixed deciduous forest is dominated by deciduous tree species, and tree density and plant species richness is lower than in evergreen forest (van de Bult, 2003; Webb et al., 2011). Dry dipterocarp forest is characterised by a very open canopy and is dominated by dipterocarp species (Dipterocarpaceae) with thick grassy ground cover sustained by annual fires (Webb et al., 2013). Further details of forest structure and site characteristics can be found elsewhere (van de Bult, 2003; Webb, 2007; Webb et al., 2011, 2013).

Animal capture, telemetry and home range estimate. We live-trapped small mammalian carnivores at Tikong and Sesawo in two phases; (1) between December 2010 and April 2011 and (2) December 2011 and January 2012, using 20 mesh traps (50 × 50 × 120 cm) baited with fresh chicken meat and live chickens caged in a different compartment. Captured small carnivores were immobilised with Zoletil (Vibrac Laboratories, Inc., Carros, France) at 3.5 mg kg^{-1}. We fitted two binturongs and three masked palm civets with Telonics MOD-125 VHF Transmitters (Telonics, Inc., Mesa, AZ, USA) which weighed 53 g, less than 5% of the animals' body weight. Transmitters were set-up with activity modes (active versus inactive indicated by different beep tones per minute) determined by animal movements. We radio-located all animals twice a day: once in morning (0600–0800 hours) and again in evening (1800–2000 hours). We radio-located animals on foot using a handheld, 3-element folding Yagi antenna attached to a digital ATS receiver (model R410, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) and manual Telonics receivers (model TR-4, Telonics, Inc., Mesa, AZ, USA) by triangulation from 2–3 stations. Because of rugged terrain, sometimes signals were lost, therefore we moved stations to find locations (mostly hilltops or ridges) where signals could be received clearly. However, we maintained > 500 m distance between stations. We used only radio-locations that were at least 10 hours apart to estimate

home ranges of all animals (Swihart & Slade, 1985). We defined a home range as an area traversed by and familiar to an individual, where animal conducts its day-to-day activities (Burt, 1943; Powell, 2000). Home ranges were estimated using 95% minimum convex polygons (MCP) and core areas were estimated using 50% MCP (Powell, 2012).

Locating sleeping trees and sites. We located animals at sleeping trees during the day, 2–3 times a week. Searches were initiated using bi-angulation. Once in the general vicinity, we intensively searched with binoculars, guided by the strength of the radio signal with antennae detached (which spans a radius of approximately 20 m).

Sleeping sites of radio-collared animals were assigned as 'used' locations, and were compared with randomly sampled 'available' locations within the home range of each animal (i.e., Design 3 following Thomas & Taylor, 1990). The design allows us to make inferences about factors influencing selection of sleeping trees (trees where animals sleep) and selection of sleeping sites (the surrounding habitat conditions) within home ranges of each animal (third order of selection; Johnson, 1980).

We ensured that the sites where we located animals during the day were their actual sleeping sites based on the following criteria. First, based on routine radio locations of all animals twice per day and during data collection for sleeping site description, we verified that the animals never left their sleeping site during the daytime, i.e., the animals used their sleeping site for sleeping. Second, in all cases where we could observe the animal, the animal appeared to be sleeping, with eyes closed and head tucked in. Third, at sleeping sites we sometimes observed animals waking up due to being disturbed by us, but they never left the sites.

Quantifying structure of sleeping trees and sleeping sites. At each sleeping tree, we set-up a circular plot with a 20 m radius centered at the tree. In cases where we failed to locate the animals directly due to poor visibility caused by dense vegetation, we assigned the center of the plot where the strongest signal from receiver was heard. We estimated height of the first branch of sleeping trees. In all cases when we directly observed the animals, we estimated height of the position where animals were sleeping. We also categorised sleeping locations in sleeping trees as (a) above mean canopy height (above canopy), (b) at the same level of canopy height (canopy), or (c) below mean canopy height (sub-canopy). We also recorded details of the position where animals slept (close to main trunk or mid or end of a branch).

At each sleeping site we identified the forest type and counted the number of small (diameter at breast height (DBH) 10–40 cm) and large (DBH ≥ 40 cm) trees. We visually estimated percent canopy cover, defined as the percentage of ground covered by the horizontal projection of tree crowns, within four sections of the plot and categorised as either 1 (≤ 25%), 2 (26–50%), 3 (51–75%), or 4 (> 75%). We also estimated the percent of tangled vegetation structure—structure created by lianas and/or woody climbers which could support an

animal's body while sleeping, at the same time obscuring detection from the ground—in a similar manner as that of percent canopy cover (Table 1). However, if the sleeping site contained no tangled structure, it was assigned '0%'. We estimated canopy connectivity, defined as the extent that branches and canopies of trees were close enough (nearly touching) to facilitate animal movements to adjacent trees, as follows. If canopies of trees within a plot were isolated from each other we defined connectivity as 'low', otherwise 'high' (Pliosungnoen et al., 2010). These qualitative assessments were made by three observers, who were all trained together.

Fruit resources. Masked palm civets and binturongs eat a wide variety of fruit from both trees and lianas (e.g., Rabinowitz, 1991; Grassman, 1998; Kitamura et al., 2002; Zhou et al., 2008). We counted all trees (DBH $\geq$10 cm) and woody climbers bearing fleshy fruits within each plot to estimate density of fruiting stems ha^{-1}. This was used as an indicator of fruit abundance.

Available sites. We randomly generated available points (n = 40) within home ranges of each animal using ArcGIS 9.2 (Esri, CA, USA). We assumed these were locations available to animals. We located these points using a hand-held GPS (Garmin GPSMAP 60CSx), assigned the nearest tree at the center of the point with DBH > 20 cm as a potential sleeping tree (based on observed sleeping trees, which had mean minimum DBH of 25 cm) and measured the same variables as that of used sleeping sites within 20 m radius plots as above with the exception of the actual sleeping positions (see Table 1).

Data analysis. We tested the difference between variables measured within sleeping sites and those from available sites, using randomisation (permutation) tests with Monte Carlo resampling (9,999 replicates). Specifically we tested whether the observed differences between groups was greater than we would expect by chance (Manly, 1997 in Quinn & Keough, 2005).

We examined the spatial arrangement of sleeping sites within the home ranges to test whether the animals tended to locate their sleeping sites close to the home range periphery or nearer to a core area. We counted numbers of sleeping sites falling into the core area (MCP 50%) and the periphery (area subtracted from the core area, calculated as MCP 95%−MCP 50%). We specified equal probabilities for both parts of home ranges (i.e., probability that a sleeping site would be either in the core area or the periphery is 0.5) and tested using Pearson's chi-square tests for population probabilities based on Monte Carlo simulations with 10,000 iterations. We qualitatively examined patterns of reuse and characteristics of reuse sleeping trees. Because we did not follow animals on consecutive days, we could not determine the distance the animals moved from a previous sleeping site to the next and also we could not be certain as to the number of consecutive days animals remained at the same sleeping sites. Because all animals reused their sleeping sites, to maintain independence, each sleeping site was included only once in all analyses. All analyses were conducted in

R 3.1.1 (R Core Team, 2014) with package 'coin' (Hothorn et al., 2008) for randomisation tests. The P-value of the randomisation test is based on the proportion of possible data re-arrangements (e.g., between two groups) that are equal to, or more extreme than, the one observed in the samples (Quinn & Keough, 2005).

RESULTS

From 1,304 live-trap nights we captured 13 masked palm civets (five adult males, two immature males, six adult females), and two binturongs (a male and a female), We radio-tagged a female binturong (adult; 11.5 kg) and three masked palm civets (all adults; two females [3.4 kg and 5.2 kg] and a male [6.2 kg]) at Tikong and a male binturong (adult; 6 kg) at Sesawo. Activity signals indicated that animals were always at their sleeping trees when we started radio-locating them in the morning (0600–0800 hours).

Home range size. Because animals were captured at different dates and therefore length of study was different and not all animals could be located on each sampling occasion, different numbers of radio-locations were used to calculate home range sizes. The home range size of the female binturong was 6.9 km^2 and entirely within evergreen forest, (153 radio-locations from a period of 10 months) with a core area of 0.87 km^2 (Fig. 1). The male binturong's home range was 2.4 km^2 (67 radio-locations from 5 months), 88% of which was in evergreen forest (including gallery evergreen) and 12% in dry dipterocarp forest; his core area (0.38 km^2) was entirely in evergreen. Female masked palm civets (MPC_1 and MPC_2) had home ranges of 2.2 km^2 and 1.3 km^2 whereas the male's was 5.9 km^2. The masked palm civets had core areas of 0.14 km^2, 0.07 km^2, and 0.59 km^2, respectively. These three animals were each tracked for 6 months with 189, 74 and 142 radio-locations used, respectively. Habitat composition of the masked palm civet home ranges was a combination of mixed deciduous (53%, 47%, and 23%) and evergreen forest (47%, 53%, and 77%, respectively, for the two females and the male).

Sleeping tree and sleeping site structure. We observed 41 sleeping sites for the female binturong, 37 sites for the male binturong, 18 sites for female civet MPC_1, 26 sites for female civet MPC_2, and 29 sites for the male masked palm civet. Nearly all sleeping trees (> 99%, n = 151) of all animals were in live trees; a single sleeping site, of the male masked palm civet, was at ground level in a rock crevice. Direct observations of animals at sleeping trees were made at 94 out of 151 total sleeping sites (64%). These observations indicated that the sleeping height of animals was usually close to the canopy level (61% of observations) except a female masked palm civet (MPC_1) which used sub-canopy (46%) more than other strata (Fig. 2). Overall, 58% of the animals' sleeping positions had thick cover created by leaves above and/or tangled structure below. Both binturongs and all masked palm civets slept on branches a few meters away from the main trunk, although sometimes further away (> 5 m) from main trunk.

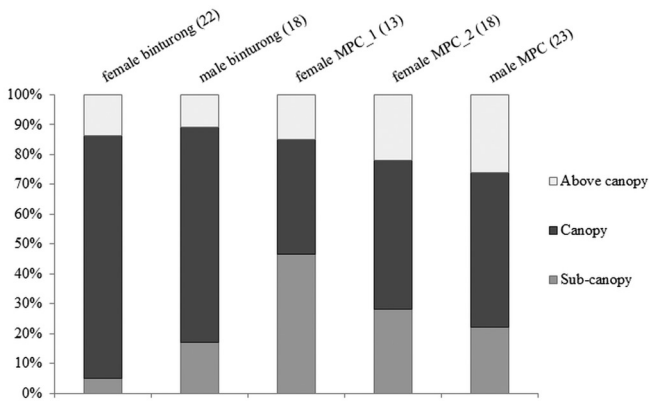On average, height of sleeping trees of all animals was over

Fig. 2. Use of vertical strata for sleeping sites. Percentage use of different vertical strata of sleeping sites by five radio-collared viverrids (two binturongs *Arctictis binturong* and three masked palm civets *Paguma larvata*). Strata are: Above canopy, Canopy, and Sub-canopy. Numbers in parenthesis represent number of sleeping sites where animals were directly observed, excluding reused sites.
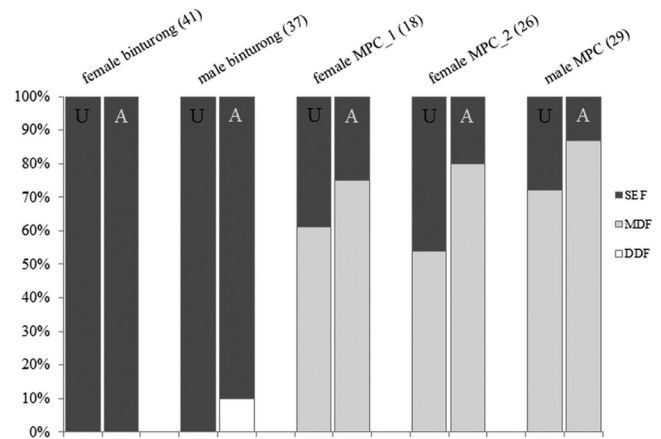

Fig. 3. Use of sleeping sites within different forest types. Percentage of different forest types used (denoted as U) for sleeping sites versus forest types available (A) for two binturongs (*Arctictis binturong*) and three masked palm civets (*Paguma larvata*). Forest types are: semi-evergreen forest (SEF), mixed deciduous forest (MDF), and dry dipterocarp forest (DDF). Numbers in parenthesis after individual animals represent the number of sleeping sites used in the analysis, excluding reused sites.

25 m, with a first branch height over 11 m (Table 2). For female MPC_1 the sleeping trees were significantly shorter than those available (Wilcoxon Rank Sum Test: Z = 2.063, P = 0.04), but those of male MPC were taller (Z = −2.516, P = 0.012) with also higher first branches (Z = −2.862, P = 0.004) (Table 2). For the other three animals, heights of sleeping trees were not different from availability. Although sleeping trees of all animals were relatively large (DBH > 50 cm), only in the female MPC_1 and the male masked palm civet were sleeping trees larger than available (Z = −3.261, P = 0.001 and Z = −2.535, P = 0.009, respectively; Table 2). Height of sleeping position and height of sleeping tree were positively correlated in all masked palm civets (Spearman Correlation Test: Z > 2.6, P < 0.008) but not binturongs (Z < 0.39, P > 0.7). Similarly, for all masked palm civets height of sleeping trees were positively correlated with the tallest trees in the plots (Z > 2.6, P < 0.005) but, again, not for binturongs (Z < 1.39, P > 0.11).

In relation to forest type, both binturongs' sleeping sites were exclusively in evergreen forest. The male binturong never had sleeping sites in mixed deciduous and dry dipterocarp forest although these drier forests accounted for 12% of its home range (Pearson's χ^2 Test: χ^2 = 3.805, P = 0.115; Table 2, Fig. 3). In contrast, most of the masked palm civets' sleeping sites were in mixed deciduous forest (61%, 54%, and 72% for MPC_1, MPC_2, and male MPC, respectively). However, in the case of MPC_2 the use of sleeping sites in this dry forest (MDF) was lower than the availability (80%) (χ^2 = 3.805, P = 0.036) (Table 2, Fig. 3).

No animals chose sleeping sites with higher abundances of small trees (P-values > 0.15; Table 2). On average abundance of small trees ranged from 15.9 trees per plot in MPC_1 to 25.6 trees per plot in the male binturong (Table 2). On the other hand, abundance of large trees was higher in sleeping sites than in available plots for the female binturong (34%) and the male MPC (23%) (Z = −3.403, P < 0.001 and Z = −2.079, P = 0.042, respectively; Table 2).

Sleeping sites of all animals were partially or entirely covered

by tangled vegetation. There was no clear relationship between sleeping sites and percentage of tangled structures, and selection by animals seemed to vary in different directions and degree. For example, sleeping sites of the female binturong had significantly lower percentage of tangled vegetation structure (25%) than that available (100%) (χ^2 = 4.463, P = 0.038; Table 2), whereas MPC_1's sleeping sites had more tangled structure than available (75% vs 0%; χ^2 = 5.024, P = 0.030), as well as MPC_2 (50% vs 25%; χ^2 = 6.988, P = 0.011) (Table 2). The male binturong tended to use sites with a high percentage (100%) of tangled structure (χ^2 = 3.530, P = 0.063), but the male MPC chose sites with tangled structure in proportion to availability (25%; χ^2 = 0.333, P = 0.632) (Table 2). Three animals tended to have sleeping sites with a higher percentage of canopy cover relative to what was available, particularly the female binturong (76–100%; χ^2 = 17.309, P < 0.001), male binturong (76–100%; χ^2 = 5.203, P = 0.026), and MPC_1 (51–75%; χ^2 = 4.52, P = 0.039), with the exception of MPC_2 (26–50%; χ^2 = 0.086, P = 0.873) and the male masked palm civet (51–75%; χ^2 = 0.006, P = 1.0) (Table 2). Canopy connectivity within sleeping sites was generally as high as available (range 83%–89% vs 73%–98%, for use and available sites, respectively), reflecting a background availability of high connectivity within each animal's home range (all animals, P-values > 0.1; Table 2).

Characteristics of reuse sleeping trees and sleeping sites. All animals reused their sleeping sites to some degree, but as noted above we were unable to assess the exact interval of reuse. The cumulative number of unique sleeping sites in relation to the total number observed (Fig. 4) indicated that both binturongs rarely reused their former sleeping sites (2% and 8% for female and male binturongs, respectively). In contrast, masked palm civets reused former sleeping sites more frequently (17%, 31% and 28% for MPC_1, MPC_2, and male MPC, respectively). For each masked palm civet,

Table 2. Comparisons of sleeping site characteristics between (a) used and (b) available sites of two binturongs (*Arctictis binturong*) and three masked palm civets (MPC; *Paguma larvata*). Number of independent sleeping sites used in analyses shown in parenthesis. The mode is presented for categorical and ordinal variables: position of sleeping (Above canopy, Canopy, and Sub-canopy), forest type (three levels; Dry Dipterocarp Forest [DDF], Mixed Deciduous Forest [MDF], Semi-evergreen Forest [SEF]), percentage of tangled structures (5 levels: 0%, 25%, 50%, 75%, 100%), percent canopy cover (four levels: 1–25%, 26–50%, 51–75%, 76–100%), and connectivity (high/low). The mean and standard deviation (in parenthesis) are presented for continuous variables: first branch height (m), size of sleeping tree (DBH in cm), height of sleeping tree (m), height of sleeping position (m), abundance of trees with DBH ≥10 cm and ≥40 cm, and density (stems per ha) of fruiting stems (trees and woody climbers or vines). For variables measured at sleeping sites those in bold are statistically significant (alpha = 0.05) based on permutation tests. No tests were performed for height of sleeping position and position where animals sleep (NA; not applicable). For female binturong, there are two forest types (DDF and SEF – the latter includes gallery evergreen). †For female binturong, there is only one forest type (SEF). ‡for male binturong.

	Female Binturong†		Male Binturong‡		Female MPC_1		Female MPC_2		Male MPC	
	Used (41)	Available	Used (37)	Available	Used (18)	Available	Used (26)	Available	Used (29)	Available
Sleeping trees										
1st branch height (m)	11.5 (4.4)	10.7 (5.3)	13.0 (5.1)	13.1 (6.7)	11.8 (7.9)	14.0 (9.0)	14.8 (7.4)	12.7 (9.4)	**14.1 (5.4)**	9.6 (6.3)
DBH of sleeping tree (cm)	55.4 (29.9)	42.0 (21.1)	51.3 (17.5)	62.1 (4.8)	**71.7 (45.6)**	45.0 (21.6)	57.8 (19.4)	49.8 (21.3)	**60.7 (29.4)**	45.7 (22.1)
Height of sleeping tree (m)	25.2 (5.9)	24.7 (7.0)	25.5 (7.4)	26.8 (8.2)	**26.3 (9.3)**	31.2 (9.3)	28.7 (8.2)	31.7 (11.3)	**30.3 (7.2)**	25.9 (8.2)
Height of sleeping position (m)	23.4 (3.8)	NA	20.9 (6.8)	NA	19.3 (10.2)	NA	23.3 (6.7)	NA	24.2 (7.7)	NA
Position of sleeping	Canopy	NA	Canopy	NA	Sub-canopy	NA	Canopy	NA	Canopy	NA
Sleeping sites										
Forest type	SEF	SEF	SEF	SEF	MDF	MDF	MDF	MDF	MDF	MDF
Tallest tree (m)	33.1 (4.6)	32.8 (6.3)	34.1 (7.4)	33.1 (7.3)	32.1 (9.0)	42.7 (10.7)	33.2 (7.8)	43.0 (9.3)	34.8 (6.3)	38.8 (7.5)
Abundance of tree (≥10–40 cm DBH)	22.2 (6.7)	23.1 (8.1)	25.6 (9.6)	24.4 (7.1)	15.9 (7.2)	15.4 (6.2)	17.2 (7.2)	14.5 (4.8)	16.2 (7.4)	16.6 (10.6)
Abundance of tree (>40 cm DBH)	**4.4 (2.2)**	2.9 (1.4)	3.9 (2.4)	4.2 (2.4)	3.5 (1.9)	2.8 (2.0)	3.3 (1.4)	2.8 (1.6)	**4.0 (2.0)**	3.1 (2.2)
% Tangled structure	**25%**	100%	100%	25%	**75%**	0%	**50%**	25%	25%	25%
% Canopy cover	**76–100%**	26–50%	**76–100%**	51–75%	**51–75%**	26–50%	26–50%	51–75%	51–75%	26–50%
Connectivity	high (85%)	high (98%)	high (89%)	high (80%)	high (83%)	high (73%)	high (88%)	high (75%)	high (86%)	high (88%)
Fruit stem density (stems/ha)	3.3 (4.9)	2.8 (1.8)	3.2 (2.6)	3.9 (2.2)	3.0 (1.7)	3.0 (2.0)	2.9 (1.9)	2.7 (1.8)	3.1 (1.9)	3.6 (2.7)

Table 3. Frequency of use between core and peripheral areas. Expected and observed frequency of sleeping sites of two binturongs (*Arctictis binturong*) and three masked palm civets (MPC; *Paguma larvata*) between core (minimum convex polygon [MCP] 50%) and periphery (MCP 95% – 50%) of the home range. Pearson's chi-square tests were used to test the null hypothesis that sleeping sites were distributed equally in both parts of the home ranges. P-values derived from Monte Carlo simulation (10,000 iterations). P-values in bold indicate significantly more sleeping sites in the periphery, at alpha level = 0.05.

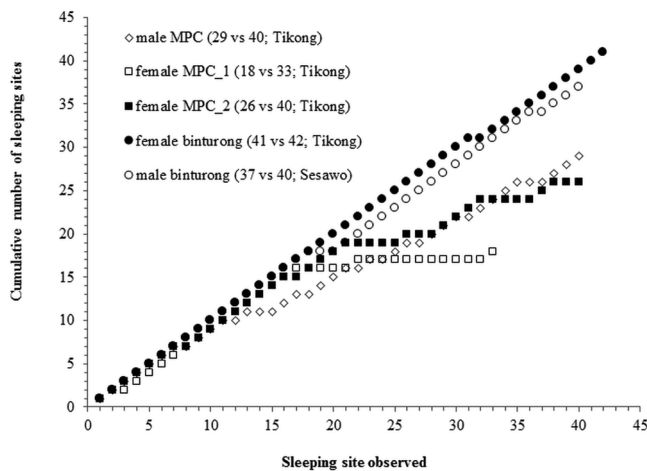|	Observed Core Use	Expected Core Use	Observed Periphery Use	Expected Periphery Use	Chi-square	P-values
Female binturong	17	20.5	24	20.5	1.195	0.349
Male binturong	17	18.5	20	18.5	0.243	0.738
Female MPC_1	4	9	14	9	5.556	**0.030**
Female MPC_2	11	13	15	13	0.615	0.558
Male MPC	11	14.5	18	14.5	1.690	0.263

Fig. 4. Use and reuse of sleeping sites. Cumulative number of unique sleeping sites in relation to the total number of sites observed for two binturongs (*Arctictis binturong*) and three masked palm civets (*Paguma larvata*). Numbers of unique sleeping sites (sites that are not re-used) versus total sleeping sites observed and study areas are indicated in parenthesis.

only two sites were reused more than twice. All reused sleeping sites of the male binturong were in evergreen forest but those of masked palm civets (MPC_1, MPC_2, and MPC male, respectively) were both in evergreen (one, two, and four sites) and deciduous forest (two, six, and five sites). On average, reused sleeping sites of masked palm civets tended to have a lower percentage of tangled structure (25% and 50%) while that of the two binturongs had a higher percentage (75% and 100%). Reused sleeping trees of all animals were relatively large (mean DBH 56.7 cm, range 48–75 cm) with a mean height of 25 m (range 19–30 m) with relatively high first branches (13 m, range 8–16 m). In one special case, a lactating female masked palm civet (MPC_1) repeatedly reused two cavities (2.3 m and 4.5 m above ground) for six and 11 days consecutively while rearing its three offspring. There was also one event where a sleeping site of the male masked palm civet was used by a female masked palm civet (MPC_2).

Location of sleeping sites in the home range. Four animals placed their sleeping sites equally in both the core and periphery of their home ranges (female binturong, χ^2 = 1.195, P = 0.349; male binturong, χ^2 = 0.243, P = 0.738;

female MPC_2, χ^2 = 0.615, P = 0.558; and male MPC, χ^2 = 1.690, P = 0.263; Table 3). In contrast, 78% of female MPC_1's sleeping sites was in the periphery (χ^2 = 5.556, P = 0.030; Table 3).

Fruit resources. Overall, densities of fruiting stems at sleeping sites and available sites were similar (range 2.9 to 3.3 stems ha^{-1} and 2.7 to 3.9 stems ha^{-1}, respectively) for all animals (Wilcoxon Rank Sum Test: P-values ranged from 0.124 in the male binturong to 0.833 in the male masked palm civet; Table 2), indicating that sleeping sites and the remaining area within home ranges were similar in quality in terms of fruit availability at the time of these surveys. Animals rarely chose fruit bearing trees as sleeping trees. For female binturong, only two sleeping trees (5%) were bearing fruits, five trees (14%) for the male Binturong, two trees (11%) for the female masked palm civet (MPC_2), only one sleeping tree (3%) of the male masked palm civet bore fruits while all sleeping trees were fruitless in the case of the female masked palm civet (MPC_1).

DISCUSSION

We explored factors affecting sleeping site selection in two Asian viverrids by considering habitat characteristics at two spatial scales, sleeping sites and sleeping trees. Because there are few studies of sleeping site selection for masked palm civets (but see Rabinowitz 1991, Wang & Fuller, 2001) and none for binturongs, in this discussion we make comparisons with other similar species that have been more extensively studied, such as brown palm civet *Paradoxurus jerdoni* (Mudappa, 2006) and common palm civets (Rabinowitz, 1991; Joshi et al., 1995; Su Su & Sale, 2007; Nakashima et al., 2013).

Access to food resources. Placement of sleeping sites may be related to an animal's desire to maintain access to food in order to regain quick access and reduce time and energy costs of travel during consecutive days (Joshi et al., 1995; Phoonjampa et al., 2010). However, we did not find evidence that the study animals chose sleeping sites with regards to access to fruiting stems. We observed that the density of fruiting stems in the vicinity of sleeping trees (mean 3.1 ± SD 0.2 stems ha^{-1}) was similar to that available elsewhere in each animal's home range (3.2 ± 0.5 stems ha^{-1}) (Table

2). This suggested that one sleeping site was as good as another with respect to fruit availability. Fruit resources were apparently widespread and distributed at rather even densities within home ranges, which perhaps obviated the need for animals to choose sleeping sites in relation to available fruit. Other studies have found a similar pattern. For common palm civets in Borneo, temporal variation in fruit availability affected the temporal and spatial use of habitat within home ranges, but selection of sleeping sites was consistently determined not by fruit availability but rather the availability of suitable structures particularly dense tangled vegetation (Nakashima et al., 2013). Thus, sleeping site selection of civets, at least in this study, appeared to be constrained by other factors that may reflect the suitability of the sites for serving other purposes than gaining quick access to food resources.

Characteristics of sleeping trees and sleeping sites that might minimise predation risk. All animals exclusively selected large live trees as their sleeping trees. Sleeping trees tended to be tall (> 25 m) (but not the tallest trees in the sites) and large (DBH > 50 cm) with high first branches (c. 11 m). Moreover, there were positive relationships between heights of sleeping trees and heights of tallest trees in the plots as well as heights of sleeping positions and height of sleeping trees in all masked palm civets but not binturongs. Altogether, these results indicate that the civets were more likely to choose relatively taller trees for sleeping sites when available—characteristic that might reflect an effort to minimise predation risk as we predicted.

Selection of large live trees appears to be common in other palm civets. For example, 70% of brown palm civets' day beds in India were large trees (mean DBH c. 32–95 cm) with < 1% in dead trees (Mudappa, 2006), and similarly 82% of common palm civets and masked palm civets beds in Thailand were in large live trees (mean DBH c. 63 cm; Rabinowitz, 1991). Rabinowitz (1991) also reported the height of sleeping positions of palm civets at approximately 17 m in trees which was similar to our findings (c. 19–24 m). Even when faced with limited availability of large and tall trees, common palm civets in a small secondary mixed deciduous forest of Myanmar usually selected the tallest available trees (> 12 m tall) as sleeping sites (57% of n = 279 sites observed; Su Su & Sale, 2007).

Sleeping high in trees might be preferable when there are many predators roaming on the ground. There are four cat species—tigers *Panthera tigris*, leopards *P. pardus*, clouded leopards *Neofelis nebulosa* and Asiatic golden cats *Catopuma temminckii*—and dholes *Cuon alpinus* co-occurring in our study areas with these civets (Chutipong et al., 2014). Other studies have established that, although viverrids are not the primary food source of these larger predators, they are eaten occasionally (Rabinowitz et al., 1987; Rabinowitz, 1989; Joshi et al., 1995; Grassman, 1999; Phetdee, 2000; Kamler et al., 2012; Lam et al., 2014). Pythons, which occur at our study site, are also predators of arboreal civets (Shine et al., 1998). The threat of predation, not just its actual frequency, is sufficient to induce strong behavioral responses in potential

prey (Preisser et al., 2005; Creel & Christianson, 2007; Ritchie & Johnson, 2009; Vanak et al., 2013).

These predators likely represent real threats to civets. Tigers and dholes are terrestrial, while leopards and clouded leopards are active both on ground and in trees and often capture arboreal prey (Lekagul & McNeely, 1977; Borries & Koenig, 2014). These predators are active both during day (when civets sleep) and night (when civets are active) (Lynam et al., 2013). In addition, the felids use not just olfactory but also visual cues in locating prey (Lekagul & McNeely, 1977; Emsens et al., 2014), making cover such as tangled structure potentially important for civets in choosing sleeping sites. The terrestrial activities of these predators probably also makes ground-based sleeping sites particularly dangerous for these civets. The presence of diverse potential predators is probably taken into account by potential prey when selecting their sleeping sites because sleeping can leave animals particularly vulnerable to predators (Lima et al., 2005).

However, there are situations when civets did not sleep in trees. When there were no suitable trees common palm civets were reported to rest on the ground with dense vegetation cover or in tangled shrubs 2–3 m above the ground (Su Su & Sale, 2007; Nakashima et al., 2013). Or even when there were suitable trees around, Wang & Fuller (2001) reported the exclusive ground (burrow) sleeping of masked palm civets in South China. It is most likely that the ground sleeping sites were safe from potential predators in such study areas where nearly all potential predators were absent (see Wang & Fuller, 2001; Su Su & Sale, 2007; Nakashima et al., 2013). Altogether, the evidence suggests that civets tend to choose sleeping in trees rather than on ground when trees particularly large and tall are available. Ground-based sleeping, however, is not unusual when there was little risk from predation. Wang & Fuller (2001) found that sleeping sites of five radio collared masked palm civets in southeastern China (n = 124) were exclusively located in abandoned porcupine burrows underground, even though there did not seem to be a lack of large suitable tree in these animals' home ranges to serve as sleeping sites. We suspect that this could be due to the lack of potential predators in their study system caused by the long-term and extensive harvest for the wildlife trade (Lau et al., 2010). In addition, the burrows might be small enough to prevent access to predators (e.g., Emsens et al., 2014). Furthermore, the lower temperatures of the sites in China (mean temperature 16°C versus 28°C for this study), may have compelled these civets to choose underground burrows to maintain body temperature, as in many temperate animals (e.g., fishers: Zielinski et al., 2004; Eastern spotted skunks: Lesmeister et al., 2008). Nakashima et al. (2013) also reported the use of ground-based sleeping sites of common palm civets c. 26% (n = 51) of the time. This may also indicate that predation risk in their study system (eastern Borneo) was probably minimal as suggested by the low densities of Sunda clouded leopard *Neofelis diardi*, the largest predator in the study area (Brodie & Giordano, 2012; Wilting et al., 2012).

Four of five animals selected sites with canopy cover > 50%, and three of five selected sites with significantly higher cover than was available in their home ranges. No animals slept in sites with low canopy cover (< 25%). Thus, there seemed to be a tendency for animals to select high cover areas for their sleeping sites. High canopy cover might be related to aspects of concealment additional to tangled structure. Other studies have reported contrasting patterns. For example, sleeping sites of brown palm civets tended to have low percent canopy cover (Mudappa, 2006). The cause of this apparent difference in selection pattern with our study is unclear; both sites appear to have a similar suite of potential predators (e.g., Mudappa, 2006). Selection of canopy cover might also relate to factors which we did not measure such as temperature, which possibly varies for each micro-habitat point chosen for sleeping.

We did not observe differences in canopy connectivity between sleeping sites and available sites of our study animals probably because they both have high canopy connectivity which may reflect background availability within the home ranges of the animals. However, brown palm civets were reported to select sites with greater canopy connectivity around sleeping trees (Mudappa, 2006). This canopy connectivity was believed to facilitate movement, including escape from predators, of civets in trees helping them avoid descending to the ground (Mudappa, 2006). This difference may be due to differences in forest structure between the two studies, such that overall canopy connectivity in our study areas was relatively high throughout most of the home ranges studied.

All sleeping sites of our study animals consisted of tangled structures (i.e., vegetative cover) in varying degrees. This variation was also reported in other civets. Dense cover created by tangled structure which can hide an animals' body completely, either on the ground or in trees, was an important component of rest sites of common palm civets from Borneo (Nakashima et al., 2013). Similar structures were also selected by the same species in Nepal (Joshi et al., 1995) and brown palm civets in India, although in lower proportion (Mudappa, 2006). Tangled structure can both reduce visibility and provide cover from predators (Joshi et al., 1995; Zielinski et al., 2004; Lesmeister et al., 2008; Emsens et al., 2013; Nakashima et al., 2013) and enhance thermoregulation (Zielinski et al., 2004; Lesmeister et al., 2008). Although varied, tangled structure appeared to be an important component of sleeping site selection of these civets.

Enhancing thermoregulation. Although we did not test this idea herein, animals might choose sleeping sites with high vegetation cover and/or canopy cover to prevent body heat loss and regulate body temperatures while sleeping (Zielinski et al., 2004; Lesmeister et al., 2008). In temperate forests where temperatures can vary widely between seasons, animals choose sleeping sites with structure that may prevent heat loss including sites with extensive canopy cover (Zielinski et al., 2004; Lesmeister et al., 2008). Although we did not measure temperature, temperatures are notably higher (mean 28° C) and relatively constant throughout the year in our

area compared to more temperate locations, thus the selection of high percentages of canopy cover for limiting heat loss may be less important.

Reuse of sleeping sites. All animals reused some sleeping sites, particularly the masked palm civets. Even though animals reused sleeping sites, they did not do so regularly and only two sleeping sites were reused more than twice by the masked palm civets over a 6-month study period. All reused trees were relatively large with a high first branch. The reuse of sleeping sites by civets has been linked to a limitation of suitable trees in the animals' home ranges, as has been documented in common palm civets (Joshi et al., 1995; Su Su & Sale, 2007; Nakashima et al., 2013) and brown palm civets (Mudappa, 2006). Reuse of sleeping sites was more pronounced in the lactating female MPC_1, which was raising young and reused two sleeping sites (tree cavities) for a lengthy period of time; the availability of trees with suitable cavities could be important for reproduction in this species. The lengthy reuse observed in this lactating female is common in other reproductive female mammals (e.g., Zielinski et al., 2004). Carnivores often stay at the same den site for relatively long periods of time when rearing young, e.g., Small-toothed ferret badger *Melogale moschata* (Wang & Fuller, 2003) and bears (Lunn et al., 2004; Ciarniello et al., 2005).

Reuse of sleeping sites might also be related to feeding habits of palm civets. Common palm civets repeatedly used the same sleeping trees when they foraged in the same area (or the same fruiting trees; Joshi et al., 1995). This repeated feeding on the same fruiting trees seems to be a common pattern in palm civets and perhaps binturongs. Masked palm civets repeatedly visited and fed on the same fruiting trees, but stopped visiting when biomass of the fruits dropped below c. 4.5 kg tree^{-1} (Zhou et al., 2008). We could not determine whether our animals repeated use of the former sleeping sites to gain a quick access to previous feeding trees/resources because we did not follow animals every day from tree to tree. To test this prediction, future research should follow animals on a daily basis and quantify the amount of fruits at feeding trees while at the same time monitoring the selection of sleeping sites. In addition, this could be extended to a comparison of reuse of sleeping sites between seasons of low and high fruit abundance when reuse could be predicted to be more often when resources are limited and clumped in distribution (e.g., Joshi et al., 1995; Nakashima et al., 2013).

Locations of sleeping sites within home ranges. There was no clear pattern of sleeping site placement; with the exception of a female masked palm civet (MPC_1), sleeping sites of all animals were not clumped with respect to core or periphery of home ranges, but rather distributed relatively equally between these portions of the home range. Previous ranging studies of binturongs and masked palm civets reported that both females and probably males of each species have large parts of their home ranges overlapping, indicating a lack of territoriality (Grassman et al., 2005; Zhou et al., 2014). This was also observed in our study with the two female masked palm civets' home ranges almost entirely

overlapping (Fig. 1). The lack of territoriality might explain the random placement of sleeping sites within home ranges at least for these masked palm civets.

Potential impacts of human disturbance. Our study was conducted in the interior of a large intact protected area which receives relatively extensive patrolling and was relatively far from human settlements (the closest one being c. > 30 km). Moreover, there were few incidences of hunting in the area, and hunting cases observed or reported to us targeted different species such as deer and gaur, not small animals such as civets. Although, these civets were probably hunted for subsistence, this mainly occurs near agricultural fields in the vicinity of villages (Steinmetz et al., 2006). Therefore, we are confident that the behavior of our studied animals reflects their natural behavior in the absence of human hunting.

Conclusions. The viverrids in our study tended to choose sleeping sites with extensive canopy cover and slept high up in large trees, when they were available, with structural components that enhanced concealment such as tangled vegetation. We hypothesise that this selection reflects a response to predation risk. This could be more directly tested by studying sleeping site selection in relatively predator-free communities compared with communities with abundant predators. We did not find an effect of fruit availability on sleeping site selection for either species, both of which are primarily frugivorous. We hypothesise that this was due to widespread availability of fruits within their home ranges, but also perhaps because of the primacy of concealment against predation risk as the civets' predominant concern in choosing sleeping sites. Currently there are still few studies on sleeping site selection in tropical civets. As an animal's choice of a sleeping site is probably one of the most important determinants of its survival, much more experimental work and systematic observations of sleeping site selection are needed (Lima et al., 2005).

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