

RESEARCH ARTICLE

Sleeping Site Selection by Proboscis Monkeys (*Nasalis larvatus*) in West Kalimantan, IndonesiaKATIE L. FEILEN^{1*} AND ANDREW J. MARSHALL^{1,2,3}¹Department of Anthropology, University of California, Davis, CA²Animal Behavior Graduate Group, University of California, Davis, CA³Graduate Group in Ecology, University of California, Davis, CA

Primates spend at least half their lives sleeping; hence, sleeping site selection can have important effects on behavior and fitness. As proboscis monkeys (*Nasalis larvatus*) often sleep along rivers and form bands (aggregations of one male groups) at their sleeping sites, understanding sleeping site selection may shed light on two unusual aspects of this species' socioecology: their close association with rivers and their multilevel social organization. We studied sleeping site selection by proboscis monkeys for twelve months at Sungai Tolak, West Kalimantan, Indonesia to test two main hypotheses regarding the drivers of sleeping site selection: reduction of molestation by mosquitoes and anti-predator behavior. We identified to genus and collected data on the physical structure (diameter at breast height, relative height, branch structure, and leaf coverage) of sleeping trees and available trees in three forest types. We used resource selection function models to test specific predictions derived from our two hypotheses. The monkeys preferred to sleep in large trees with few canopy connections located along rivers. The selection of large emergent trees was consistent with both of our main hypotheses: decreased molestation by mosquitoes and reduced potential entry routes for terrestrial predators. Although we are only beginning to understand how sleeping sites might influence behavior, grouping, and potential survival of this species, our study has shown that proboscis monkeys (at Sungai Tolak) have a very strong preference for large trees located near the river. As these trees are often the first to be logged by local villagers, this may exacerbate the problems of forest loss for these endangered monkeys. *Am. J. Primatol.* 76:1127–1139, 2014. © 2014 Wiley Periodicals, Inc.

Key words: sleep; sleeping sites; anti-predator; grouping; mosquitoes

INTRODUCTION

Primates spend a substantial portion of their lives asleep; while sleeping, they are subject to many of the same selective pressures they face when active (e.g., predation, disease, thermoregulation). Therefore, sleeping site selection may have important fitness consequences. Identification of the factors influencing the selection of sleeping sites—and how these factors vary within and among species—can provide important insights into primate ecology and evolution. Sleeping site selection has received considerable attention in recent years [Barnett et al., 2012; Bernard et al., 2011; Gonzalez-Zamora et al., 2012; Matsuda et al., 2008, 2010b, 2011; Rasoloharijaona et al., 2008; Samson, 2012; Samson et al., 2013; Stanford & O'Malley, 2008; Teichroeb et al., 2012; Tsuji, 2011; Xiang et al., 2011].

Although much of the work on sleeping site selection has focused on anti-predator behaviors (pigtailed macaques (*Macaca leonina*) [Albert et al., 2011], Guinea baboons (*Papio papio*) [Anderson & McGrew, 1984], golden backed uacaris (*Cacajao*

melanocephalus) [Barnett et al., 2012]), empirical studies have suggested that primates may select sleeping sites for many additional reasons: protection against rain and temperature fluctuations (chimpanzees (*Pan troglodytes*) [Samson & Hunt, 2012], gorillas (*Gorilla gorilla*) [De Vere et al., 2011], Francois langurs (*Trachypithecus francoisi*) [Han & Hu, 2012]), reduction of disease transmission risk

Contract grant sponsor: US Fulbright Student Fellowship; contract grant sponsor: Boren Fellowship; contract grant sponsor: Davis Department of Anthropology, The University of California; contract grant sponsor: Primate Conservation, Inc.

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Received 11 December 2013; revised 7 April 2014; revision accepted 9 April 2014

DOI: 10.1002/ajp.22298

Published online 8 May 2014 in Wiley Online Library (wileyonlinelibrary.com).

(yellow baboons (*Papio cynocephalus*) [Hausfater & Meade, 1982]), and reduction of molestation by ants (gibbons (*Hylobates klossi*) [Whitten, 1982]). Although many recent studies have attempted to examine the role of factors other than predation, studies of sleeping site selection often suffer from the problem of equifinality (similar results caused by different underlying mechanisms). For example, selection of a tree near a river may be used as an anti-predator strategy (e.g., reducing entry routes for predators, promoting vigilance) but also may be used as a thermoregulatory or anti-parasite strategy. Researchers often highlight only one of the potential underlying explanations of the behavior, which may limit our understanding of the mechanisms influencing sleeping site selection in primates.

Proboscis monkeys have intriguing behaviors related to sleeping site selection, and therefore provide an interesting species in which to pursue this line of investigation. Proboscis monkeys regularly return to edges of rivers to sleep [Bennett & Sebastian, 1988; Matsuda et al., 2008, 2009, 2011; Yeager, 1991b], suggesting that they are selective in their sleeping sites and this selectivity provides potential advantages. Additionally, proboscis monkeys form bands (associations of one male groups) at their sleeping sites [Bennett & Sebastian, 1988; Yeager, 1991b], which might be related to limited availability of preferred places to sleep [Matsuda et al., 2010a]. In other species, such as hamadryas baboons (*Papio hamadryas*), the size of the secondary level of organization depends on the availability of sleeping sites [Kummer & Kurt, 1968; Swedell, 2006]; hamadryas baboons form larger aggregations of groups when sleeping sites are large but rare. Therefore, understanding the causal factors underlying sleeping site selection may shed light on the social structure of proboscis monkeys.

Although many researchers have concluded that proboscis monkeys select sleeping trees to reduce predation risk [Matsuda et al., 2008, 2011; Yeager, 1991a], these studies have documented various factors influencing sleeping site selection. For instance, proboscis monkeys living along the Menanggul River in Sabah, Malaysia preferentially slept in trees along rivers, which the authors interpreted as a tactic to increase detection of predators and decrease the number of potential entry routes for predators [Matsuda et al., 2011]. Along the Klias River in Sabah, although proboscis monkeys also slept along rivers, they selected trees with high levels of arboreal connectivity [Bernard et al., 2011]. As predation risk from terrestrial predators is assumed to be low at this site, the behavior was interpreted as a way of facilitating locomotion rather than increasing escape routes from potential predators. These studies imply that proboscis monkeys use various criteria for selection of sleeping trees at different sites, suggest-

ing that they might experience distinct selective pressures at different sites.

As proboscis monkeys live in areas with high densities of mosquitoes (Culicidae), the monkeys might also select sleeping trees that reduce molestation by these insects. In Neotropical primates, sleeping in closed sleeping sites (tree holes or dense tangles of vegetation) seems to reduce the prevalence of malaria [Nunn & Heymann, 2005]; proboscis monkeys might select trees with many leaves to gain similar benefits. In addition to possibly using areas with high leaf cover, proboscis monkeys might also select tall emergent trees as a strategy to avoid mosquitoes. A study from Uganda has demonstrated that *Anopheles* mosquitoes have lower densities in the emergent layers of trees than in the main canopy [Haddow & Ssenkubuge, 1965].

We examined a population of proboscis monkeys in West Kalimantan inhabiting three forest types to determine how forest structure and tree characteristics influence sleeping site selection. Our study had two main objectives. First, we sought to describe how the monkeys select sleeping sites (defined here as sleeping trees) based on their physical characteristics. Second, we tested several hypotheses about the adaptive function of sleeping site selection at our site using resource selection function modeling. Specifically, we tested the following, non-mutually exclusive hypotheses: H1. Proboscis monkeys select sleeping trees to reduce molestation by mosquitoes. H2. Proboscis monkeys select sleeping trees as an anti-predator strategy. The monkeys might use sleeping trees for various types of anti-predator strategies: increased detection of predators, increased concealment from predators, reduced potential entry routes for terrestrial and arboreal predators, increased potential escape routes, and dilution of predation risk by sleeping with many individuals. Predictions for each hypothesis are listed in Table I.

METHODS

Study Site and Subjects

We gathered data at Sungai Tolak (1°27'59"S, 110°4'54"E), located just outside Gunung Palung National Park, West Kalimantan, Indonesia. The site comprises land along both banks of the Tolak River beginning 500 m from the river's mouth at the South China Sea, and continuing upstream for 30 km. The width of the Tolak River ranges from 20 to 65 m. The site contains three forest types, mangrove, riverine, and peat swamp, which permitted assessment of the influences of different ecological factors and forest types on sleeping site selection (Fig. 1). Forest types at Sungai Tolak vary as a function of distance from the sea; mangrove forest occupies the mouth of the river, while peat swamp forest is located further upstream. Riverine forest is a transitional forest type between the mangrove and peat swamp forest. The

TABLE I. Hypotheses, Predictions, Model Framework, and AIC Values of Sleeping Site Selection by Proboscis Monkeys Based on Tree Characteristics

Hypotheses	Characteristics of sleeping trees							Model No.	Supported ^a	ΔAIC main effect ^b	Akaike weights ^c
	Predictions	DBH	Height	Branch Structure	Leaf Coverage	Canopy Connections					
H1. Protection against insects											
i. Proboscis monkeys select trees large enough to permit many individuals to sleep in one tree	+						1 ^f	Yes	20	0	
ii. Proboscis monkeys select large trees with many branches to permit more individuals to sleep in one tree	+			+			2 ^{i,f}	No	22	0	
iii. Proboscis monkeys select tall emergent trees			+			—	*3 ^{i,f}	Yes	101		
iv. Proboscis monkeys select large emergent trees	+					—	*4 ^{i,f}	Yes	0	0.11	
v. Proboscis monkeys select trees with high degree of leaf cover					+		*5 ^f	No	358	0	
vi. Proboscis monkeys select tall, leafy emergent trees			+		+	—	6 ^{i,f}	No	182	0	
H2. Anti-predator behavior											
H2.A Detection of predators											
i. Proboscis monkeys select tall trees			+				*7	Yes	185	0	
ii. Proboscis monkeys select trees with few leaves					—		*5 ^f	No	358	0	
iii. Proboscis monkeys select tall, bare trees			+		—		8 ^{i,f}	Yes	181	0	
H2.B Concealment from predators											
i. Proboscis monkeys select trees with high degree of leaf cover					+		*5 ^f	No	358	0	
H2.C Reduce entry from terrestrial and arboreal predators											
i. Proboscis monkeys select tall trees			+				*7	Yes	185	0	
ii. Proboscis monkeys select trees with few branches				—			9 ^f	Yes	332	0	
iii. Proboscis monkeys select trees with difficult entry points for terrestrial predators (tall with few branches)			+	—			10 ^{i,f}	Yes	26	0	
iv. Proboscis monkeys select large trees that are isolated	+					—	*4 ^{i,f}	Yes	0	0.11	
H2.D Increase escape routes from predators											
i. Proboscis monkeys selection trees with many escape routes (high number of canopy connects)						+	11 ^f	No	194	0	
H2.E Reduce predation risk											
i. Proboscis monkeys select trees large enough to permit many individuals to sleep in each tree	+						1 ^f	Yes	20	0	

The models that were used to test the prediction are indicated in the column titled, "Model No." Many of the models (hence the characteristics of sleeping trees) support multiple hypotheses (highlighted with asterisks). Positive signs and negative signs indicate the direction of the relationship predicted under each hypothesis. Bold text denotes the model with the lowest AIC value.

^aModels that supported predictions of multiple hypotheses. ⁱ signifies that an iteration of the model was run with an interaction between terms, while ^f signifies that an iteration of the model was run with an interaction with forest type. For example to test H1: ii we ran three models: a model with a main effect between DBH and branch structure, a model with an interaction between DBH and branch structure, and a model with the main effects of DBH and branch structure with an interaction of forest type with the other two variables.

^bPredictions that were generally supported signify that the trends and relationships of the characteristics are what we would expect if that prediction were true; however, although the trends were in the predicted direction, they were not supported under information criteria.

^c Δ AIC values are calculated in comparison to the best model, model 4, with AIC of 221.

^dAkaike weights were calculated using $\frac{\exp(-0.5\Delta\text{AIC})}{\sum_{j=1}^n \exp(-0.5\Delta\text{AIC}_j)}$.

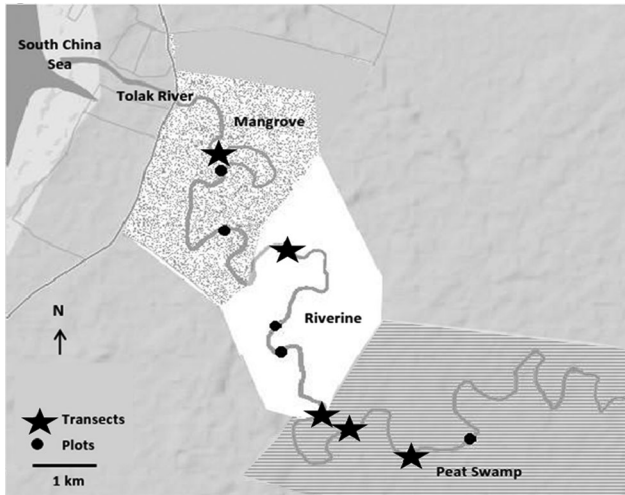


Fig. 1. Map of research area. Circles show locations of plots (located along the river's edge), while stars show the locations of line transects. Along each line transect, there were four plots beginning at the river's edge and spaced 100 m apart. Plots and transects alternated between the left and right side of the river. Forest types (mangrove (speckled), riverine (white), and peat swamp (striped)) changed as a function of distance from the South China Sea. Areas in medium gray indicate non-forested areas, which are either agricultural land or burned areas. Light gray next to the South China Sea indicates a tidal beach zone.

site lost approximately 10% of its forest cover during fires in 1997 and 2003, which has broken up the continuity of the forest along the river. The site experienced ongoing, small-scale selective logging during the time of data collection. Temperatures ranged from 21 to 39°C, the average minimum daily temperature was $25 \pm \text{SD } 1.3^\circ\text{C}$ and the average maximum daily temperature was $33 \pm \text{SD } 2.2^\circ\text{C}$. The site received 3,295 mm of rain from March 1, 2011 to February 29, 2012. Although there is no true seasonality in Borneo, there were general trends in weather patterns, with alternating seasons of relatively dry (February, May, August, and September) and wet months (March, April, June, and October).

Proboscis monkeys have many potential predators at Sungai Tolak which include reticulated pythons (*Python reticulatus*), sun bears (*Helarctos malayanus*), saltwater crocodiles (*Crocodylus porosus*), changeable hawk-eagles (*Nisaetus limnaeetus*), and crested serpent eagles (*Spilornis cheela*). It is possible that clouded leopards (*Neofelis nebulosa*) were also present although we have no definitive information regarding their presence or absence. Both clouded leopards and sun bears can be active at night [Ross et al., 2013; Te Wong et al., 2004] and may be threats to monkeys at their sleeping sites.

During the study period, approximately 20 groups of proboscis monkeys lived along the Tolak River (as inferred from 1,118 encounters with groups during behavioral study and line transect surveys over 22 months). Although we occasionally observed monkeys traveling alone, we encountered most in

one-male multi-female groups, with group sizes ranging from 2 to 35 members. A few groups included two resident males. One male groups joined to form bands containing two to seven groups. Ranges of groups overlapped substantially.

We established 16 vegetation plots (25 m \times 20 m) along a series of four transects that were placed using a stratified random design across the three forest types. We placed these four transects in a north to south orientation at 0, 125, 250, and 375 m from the river's edge. Using the same stratified random design, we placed six additional plots at the river's edge to increase our sampling of variation along the river. This design allowed us to detect differences in vegetation both among forest types and as a function of distance from the river's edge. Plots were 25 m long and centered lengthwise along the transects; we used a nested design to maximize the sampling area for larger trees while limiting the time spent sampling smaller trees [Marshall & Leighton, 2006; Marshall & Wich, 2013]. All trees within 5 m of the transect midline with a diameter at breast height (DBH) greater than 5 cm were tagged, measured, and identified to genus, while trees between 5 and 10 m from the transect midline were included only if DBH was greater than 10 cm. All tree identifications were made by an Indonesian field assistant with over 15 years of experience identifying trees in West Kalimantan. We identified trees to genus level rather than the species level because (1) performing analysis of tropical trees at the species level may skew results because of phylogenetic non-independence [Chazdon et al., 2003; Davies et al., 2013], (2) many trees have yet to be described at the species level due to the high level of botanical diversity on Borneo, and (3) we were unable to identify many plants to species because they did not flower or fruit during the observation period. We measured and identified 1,274 trees. We randomly selected 10% of the trees in each plot and gathered the same data on these trees as we did on sleeping trees (see below) to assess the availability of different characteristics in the forest. This subsample of 126 trees provided information on forest trees generally, and represented a manageable sampling effort given our study's focus on the monkeys themselves.

Sleeping Site Data Collection

We collected all data in accordance with the laws and regulations of Indonesia, the United States, the University of California-Davis, and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. We began habituating the monkeys in February 2011. By the beginning of data collection, the monkeys were semi-habituated to humans; we could approach monkey groups in our small boat to within 15 m without disturbing them or discernibly influencing

their behavior. We collected data on sleeping sites from August 3, 2011 to November 30, 2011 and from April 4, 2012 to October 20, 2012. On each evening of data collection (15:30–18:30), we searched for sleeping sites using a small boat with an outboard motor. We divided the river into four equal sections and searched for sleeping sites in each section for 4 days per month. By searching over 30 km of river, and recording group composition of roughly 20 groups, we captured the sleeping site selection behaviors of a population of proboscis monkeys rather than a particular group. We cancelled sampling on occasional nights because of inclement weather or nearby forest fires. On some nights of searching, we did not find monkeys in the pre-assigned search area, causing the number of sampling days to be slightly different than the number of search days. Although searching for sleeping sites along the river potentially biased our data since we only sampled sleeping sites along the river, it was the most accurate and efficient method to collect sleeping site data at Sungai Tolak. We verified that the monkeys generally slept along the rivers by searching for sleeping sites along our four transect routes early in the morning on 10 days per month. We did not find any proboscis monkeys sleeping inland along our transect routes.

When we encountered monkeys at sleep sites, we recorded the following characteristics for each sleeping tree: its location using a handheld GPS unit (Garmin Handheld GPS 60CSx), distance from the river, genus, structure of trunk and branches, number of canopy connections, leaf coverage, and relative height of the tree. We remained with the group until it became too dark to collect data and the monkeys ceased moving. The next morning, we returned to the sleeping tree to tag the tree and measure diameter at breast height (DBH, in cm). When proboscis monkeys used multiple trees in close proximity we collected data on each tree.

We characterized trees according to several features. First, we divided the structure of the trunk and branches into three categories: single-trunked, bifurcated, or multi-branched (Fig. 2). Single-trunked trees had stems lacking side branches below a point located three-fourths of the way up the trunk; trees with bifurcated trunks split into two main branches between half and three-fourths of the way along the tree trunk. Trees in which the trunk split to radial branches below the midpoint of the tree were multi-branched; typically they had many main branches.

Canopy connectedness described the crown of the sleeping tree in relation to the crowns of surrounding trees. Canopy connections were locations where primates could continuously travel from one tree to another, with branches of adjacent trees overlapping at least 10 cm with sleeping trees. We classified the number of connections using a score from 0 to 4. Zero represented an emergent tree (ones whose crowns did not touch another tree), while four represented the

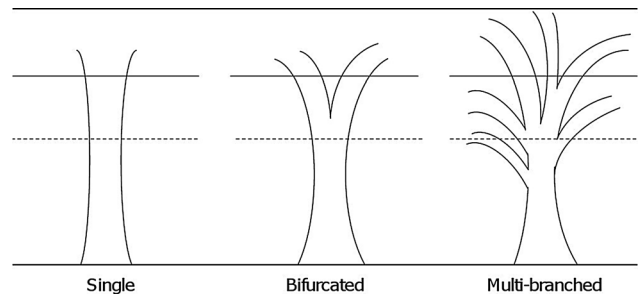


Fig. 2. Branch structural categories. Diagrams represent the characteristics of tree trunks used to classify sleeping trees. Trees were classified as having a single trunk, bifurcated trunk, or multi-branched trunk depending on the position and number of main branches along the trunk. The dashed line represents the midpoint of the tree (halfway between the ground and the top of the crown), while dotted lines indicate the location three-fourths of the way up the tree (tree crowns are not pictured). Most trees fell unambiguously into one of the three categories. For trees that had characteristics similar to two classes, we selected the category that more closely described the tree.

maximum number of canopy connections, a tree that had canopy connections on all four sides (the front, back, left, and right side of the tree from the perspective of the observer in the boat). Leaf coverage of the tree was defined in three broad categories: high (i.e., monkeys were completely concealed by leaves), moderate (i.e., monkeys were partially concealed by leaves), or low (i.e., the entire body of the monkey could be seen by the observer). Although at least some potential local predators (e.g., clouded leopards, *N. nebulosa*) probably use scent rather than visual cues, the method was designed to assess whether proboscis monkeys might be able to use visual concealment as an anti-predator strategy. Finally, the height of the sleeping tree was determined by visually comparing its height to all other trees located within a 200 m radius. The trees were divided into four height categories (quartiles) and each sleeping tree was assigned into the tallest (tallest 25% of trees within a 200 m radius), mid-tall (second quartile), mid-short (third quartile) and shortest (shortest 25% of trees) category. Although absolute heights of the trees could have also been measured, we chose this method because the different forest types (mangrove, riverine, and peat swamp) and even different areas within each forest type had different absolute canopy heights and it seems likely that relative height is more important than absolute height in determining sleeping site selection.

Data Analysis

We used R Statistical Software version 2.15.3 [R Core Development Team, 2013] for data analysis. We calculated summary statistics on characteristics (e.g., proportion of trees with each characteristic) for all sleeping trees (i.e., used trees) and our sample of 126 available trees. For DBH data, we calculated statistics on sleeping trees and all tagged trees in our

botanical plots (1,274 trees). For descriptive and summary statistics, we used only direct rather than imputed values (see below). We used mosaic plots to determine whether there was interrelatedness among categorical tree characteristics (e.g., to assess whether tall trees consistently had more canopy connections). As we detected no strong, consistent relationships among characteristics, we assumed independence for all analysis. We calculated genus-level diversity of available trees and sleeping trees with Shannon's Index of Diversity in the "vegan" package in R [Oksanen et al., 2013].

Data Imputation

Using only complete records of sleeping tree data is problematic as it reduces sample size and introduces potential bias by excluding some of the observations [Nakagawa & Freckleton, 2011]. Therefore, we used data imputation to impute missing values in our dataset. Fifty-two of our 518 trees had one or two missing values (of the six recorded variables) stemming from logistical difficulties, including the malfunction of data collection devices, forest fires, river closure, and storms that prevented us from returning to the sleeping trees to measure DBH from the previous night. Imputation is a statistical procedure that uses the available data to probabilistically predict a value for the missing data fields. Imputations were performed using the "mice" package [van Buuren & Groothuis-Oudshoorn, 2011] in R. The imputation produced five different data sets (the default setting of the program) with different imputed values for each missing value, which allows for comparison of results when different values are imputed into the data set. We ran models using each of the five imputed data sets through "mice," which permitted us to propagate the uncertainty about the missing values throughout the analysis. The "mice" program calculated coefficients and standard errors using all five data sets, but reported one combined coefficient and standard error per model. Reported AIC values for each model are mean values of AIC values from the five datasets.

Selectivity of Sleeping Trees

We used two methods to assess sleeping site preferences. To calculate the preference for particular tree genera, we calculated selection coefficients. We did not include terms for each genus in our resource selection function models because fitting such models with many dozens of factors is computationally prohibitive. We calculated genus-level selectivity by comparing the proportion of use of each genus to the availability of trees in our botanical plots ($N = 1,274$) [Savage, 1931] using the following formula:

$$S_i = \frac{U_i}{A_i}$$

where U_i is the number of sleeping trees of genus_{*i*} divided by total number of sleeping trees; A_i is the number of trees of genus_{*i*} in plots divided by total number of trees in plots.

Scores greater than one indicate positive selection of (i.e., preference for) the genus while scores less than one indicate avoidance.

To determine selectivity based on sleeping tree characteristics, we used a resource selection function [Manly et al., 2002] to compare the structure of sleeping trees to that of available trees in the 22 botanical plots. We devised 31 models that tested the predictions of our two hypotheses (Table I). Of the 31 models, 11 models tested predictions using main effects only (outlined in Table I), while 20 models tested the interactions between the parameters listed in Table I's characteristics, or the interaction between the main effects with forest type (i.e., model 2ⁱ tested the interaction between DBH and branch structure, and model 2^f included interactions of DBH and of branch structure with forest type). We included interactions of forest type with DBH, leaf coverage, canopy connection and branch structure to evaluate differences in sleeping tree selection across different forest types. We did not include a term for the interaction between forest type and height because our relative measure of height already controlled for differences in tree height among forest type; including an interaction would be redundant. We compared the fit of the models using Akaike Information Criterion (AIC). As we were trying to assess the support for several distinct hypotheses, we used a model selection approach rather than model averaging [Burnham & Anderson, 2002].

We fit a logistic regression model to calculate the resource selection function. Depending on the design of the observational study, on the types of variables included to predict resource use, and on the particular statistical methods used, it may or may not be possible to identify an intercept in a logistic regression model and therefore to predict absolute probabilities of use [Lele & Keim, 2006]. Two main features of our analysis prevented us from inferring absolute probabilities. First, some of the models included only categorical predictors; unlike models involving continuous predictors, models with categorical predictors do not produce intercepts. As it was important to use the same estimation method across all models, we therefore did not include intercepts in any of our models with identified intercepts. Second, because we used multiple imputed data sets, it was computationally prohibitive to combine multiple imputation inferences of absolute probabilities as implemented by Lele and Keim (2006). Because we were unable to calculate exact probabilities, and because relative probabilities were adequate to compare the predictions of our hypotheses, we calculated relative resource selection functions. By ignoring the intercept, we

calculated the relative odds of use compared to a baseline tree [Manly et al., 2002]. Our baseline tree was a hypothetical tree with DBH of 10 cm and multiple canopy connections. We selected this baseline tree as it is the most common type of tree at our study site.

RESULTS

General Characteristics of Sleeping Trees

Proboscis monkeys slept in 392 trees during 132 nights of data collection over 12 months and used 1–10 sleeping trees per night. They rarely used the same trees; of 392 recorded trees in our dataset, 87% were observed to be used only once during the sampling period. The monkeys generally slept in relatively large (mean DBH = $30.1 \pm \text{SD } 12.0$ cm, $N = 388$), tall (41%), emergent (51%) (Table II) trees that were located close to the river (mean distance = $7.2 \pm \text{SD } 6.8$ m, range 0–40 m). The mean sleeping tree size varied slightly between forest types (mean DBH in mangrove = $34.3 \pm \text{SD } 17.4$ cm, $N = 101$; mean DBH in riverine = $29.0 \pm \text{SD } 7.6$ cm, $N = 85$; mean DBH in peat = 29.0 ± 10.8 cm, $N = 206$, ANOVA: $F = 6.3$, $df = 2$, $P < 0.05$). This likely reflects the difference in available trees in each of these forest types (mean DBH for mangrove = $14.7 \pm \text{SD } 11.7$ cm, $N = 172$), compared to riverine (mean DBH = 11.6 ± 11.8 cm, $N = 512$), and peat swamp (mean DBH = $11.3 \pm \text{SD } 6.8$ cm, $N = 590$) (ANOVA: $F = 1.4$, $df = 2$, $P = 0.22$) (Fig. 3).

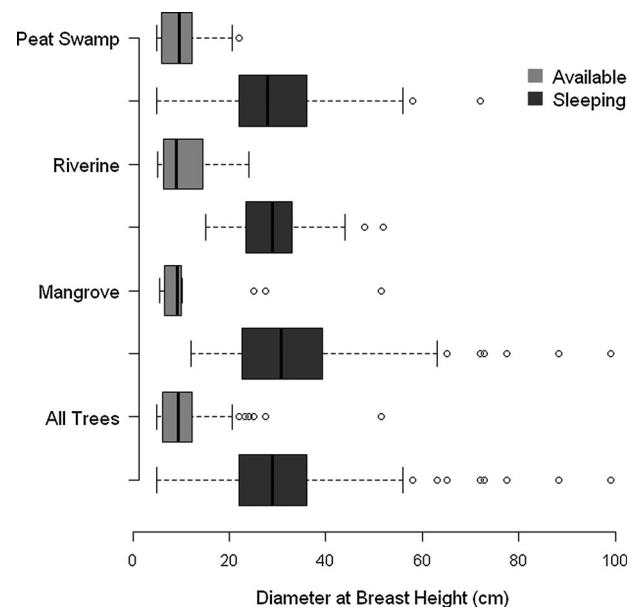


Fig. 3. DBH of available trees and sleeping trees by forest type. Size (DBH in cm) differed between available trees ($N = 1,274$ trees) and sleeping trees ($N = 392$) in each forest type: mangrove forest, riverine forest, and peat swamp forest. Boxplots show median and interquartile range, while circles indicate values outside of the interquartile range.

Although the monkeys slept in emergent trees (zero canopy connections) more often than trees with more canopy connections across all forest types, the percentages of used trees varied slightly between

TABLE II. Characteristics of Sleeping Trees ($N = 392$)* and Available Trees ($N = 126$) by Forest Type

	All sleeping trees	All available trees	Mangrove sleeping trees	Available mangrove trees	Riverine sleeping trees	Available riverine trees	Peat sleeping trees	Available peat trees
Branch structure								
Single	27% (107)	53% (67)	10% (10)	17% (3)	32% (27)	59% (16)	34% (70)	59% (48)
Bifurcated	33% (128)	18% (23)	12% (12)	28% (5)	49% (42)	33% (9)	36% (74)	11% (9)
Multi-branch	40% (154)	29% (36)	78% (77)	56% (10)	19% (16)	7% (2)	30% (61)	30% (24)
Canopy connections								
Zero	53% (199)	11% (14)	41% (39)	17% (3)	63% (53)	22% (6)	54% (107)	7% (5)
One	31% (118)	10% (12)	31% (30)	6% (1)	29% (24)	7% (2)	32% (64)	14% (9)
Two	12% (47)	24% (30)	22% (21)	22% (4)	7% (6)	15% (4)	10% (20)	27% (22)
Three	2% (9)	26% (33)	4% (4)	33% (6)	1% (1)	33% (9)	2% (4)	22% (18)
Four	2% (6)	29% (37)	2% (2)	22% (4)	0% (0)	22% (6)	2% (4)	33% (27)
Leaf coverage								
Low	39% (152)	35% (44)	35% (35)	28% (5)	40% (34)	48% (13)	41% (83)	32% (26)
Moderate	40% (156)	47% (59)	38% (38)	39% (7)	47% (40)	44% (12)	38% (78)	49% (40)
High	21% (80)	18% (23)	26% (26)	33% (6)	13% (11)	7% (2)	21% (43)	19% (15)
Relative height								
Short	1% (3)	17% (22)	0% (0)	11% (2)	0% (0)	15% (4)	2% (3)	20% (16)
Mid-short	14% (54)	59% (74)	4% (4)	67% (12)	16% (13)	44% (12)	18% (37)	62% (50)
Mid-tall	35% (133)	18% (23)	32% (31)	11% (2)	39% (33)	30% (8)	34% (69)	16% (13)
Tallest	50% (194)	6% (7)	64% (62)	11% (2)	45% (38)	11% (3)	46% (94)	2% (2)

Sleeping trees are trees that were slept in by proboscis monkeys while available trees are a randomly sampled subset of trees in our vegetative plots. Numbers in parentheses represent sample size in each category.

*Sums of trees in each category differ slightly as trees with missing values were not included in these calculations.

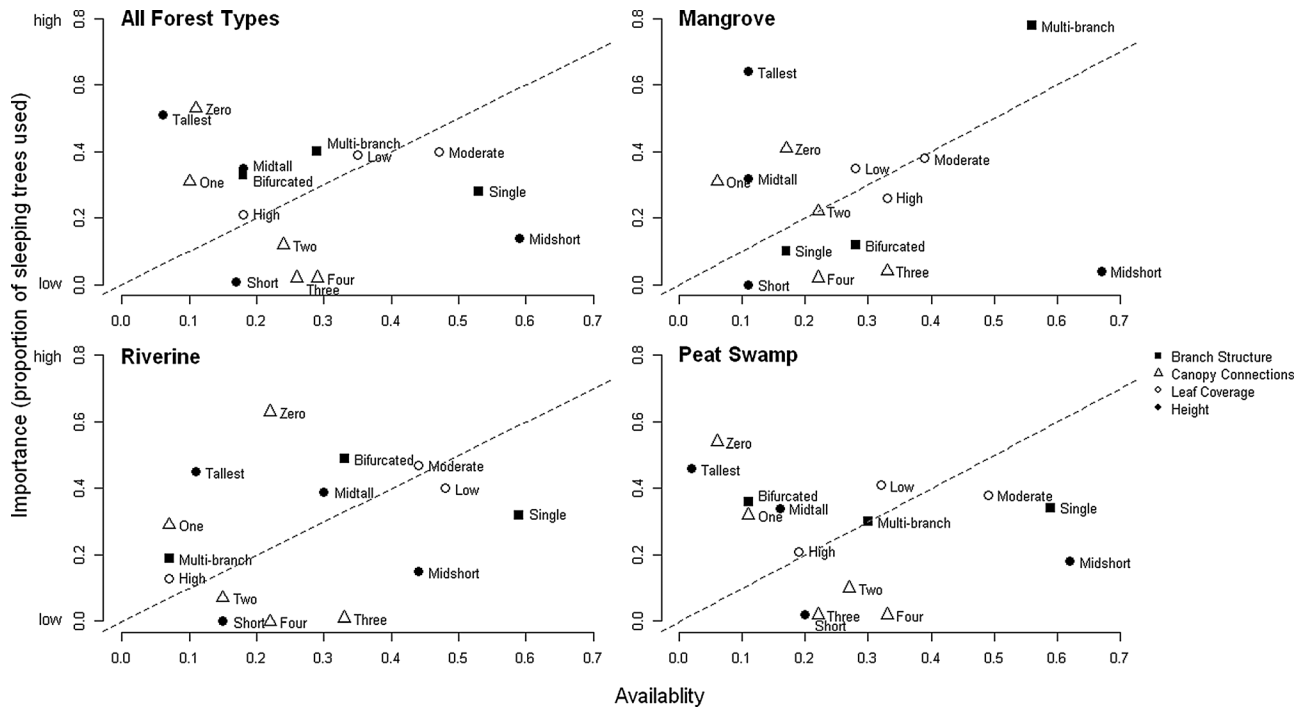


Fig. 4. Characteristics of sleeping trees: importance and availability by forest type. Proportion of sleeping trees with each characteristic are plotted in relation to their availability for all forest types combined, mangrove forests, riverine forest, and peat swamp forests. Tree characteristics (branch structure, canopy connections, leaf coverage, and relative height) plotted relatively high on the y-axis signify high proportion of use (high importance) while locations low on the y-axis signify low importance for sleeping trees. The dashed line indicates the 1:1 ratio of availability to use. Points located above the dashed line reflect characteristics that were preferred (selected disproportionately relative to their availability) while points located below the line represent characteristics of sleeping trees that were avoided. The levels for each sleeping tree characteristic are listed next to their plotted point: Branch structure (single, bifurcated, multi-branched), canopy connections (zero, one, two, three, four), leaf coverage (low, moderate, and high), relative height (tallest, midtall, midshort, and shortest).

different forest types (Table II). In mangrove forest, the monkeys slept in emergent trees (those with zero canopy connections) least often (41% of 99) compared to riverine forest areas (63% of 85) and peat swamp forests (54% of 205) (Fig. 4).

Proboscis monkeys also used tall trees more often than short ones; more than 80% of 392 sleeping trees were classified as tall trees or midtall trees. The importance of tall trees was slightly more pronounced in the mangrove forest compared to the other forest types, as 64% of sleeping trees were relatively taller (tallest trees) than the other trees in the area, compared to only 45% in riverine forest and 46% in peat swamp forests. The monkeys almost never slept in the shortest trees available (comprising 1% of sleeping trees).

Of all sleeping trees, the monkeys used 27% single-trunked trees, 33% trees with two main branches, and 40% trees with many branches. Trees with low leaf coverage (39%) and trees with moderate leaf coverage (40%) were almost equally represented. This trend was consistent across forest types except for riverine forest types, where they slept in slightly more trees that had low leaf coverage (40%) and moderate leaf coverage (47%) compared to trees with high leaf coverage (13%).

Selection of Genera

Importance (proportion of use) and preference (use compared to availability) varied substantially among tree genera (Table III). *Palaquium* (Sapotaceae) was the most important genus (39% of 392 sleeping trees) and was also preferred (selection coefficient = 3.5). *Excoecaria* (Euphorbiaceae) was the most preferred tree (selection coefficient = 16.3) but was relatively unimportant (1% of sleeping trees). *Syzygium* was important but not preferred (selection coefficient = 1.0). Of the 36 genera of sleeping trees, 25 of the genera were preferred trees (selected disproportionately to their availability). *Excoecaria* (Euphorbiaceae), *Pometia* (Sapindaceae) (selection coefficient = 13.0), and *Dialium* (selection coefficient = 12.2) had the highest selectivity coefficients (Table III).

As the availability of potential sleeping trees differed among forest types, we also analyzed data separately for each forest type. Selection of genera was different at the forest type level compared to all sleeping trees. Proboscis monkeys slept in 22 genera of trees in the mangrove forest, 9 genera of trees in the riverine forest, and 21 genera of trees in the peat swamp forest (Table IV).

TABLE III. Use, Availability, and Selectivity of Sleeping Trees by Genus

Genus	Family	Number of uses	Proportion of use (%)	Number of trees in plots	Proportion availability (%)	Selectivity coefficients ^a
<i>Palaquium</i>	Sapotaceae	152	38.9	143	11.2	3.5
<i>Syzygium</i>	Myrtaceae	52	13.3	179	14.1	1.0
<i>Bruguiera</i>	Rhizophoraceae	33	8.4	13	1.0	8.3
<i>Knema</i>	Myristicaceae	16	4.1	15	1.2	3.5
<i>Rhizophora</i>	Rhizophoraceae	16	4.1	20	1.6	2.6
<i>Dialium</i>	Fabaceae	15	3.8	4	0.3	12.2
<i>Heritiera</i>	Malvaceae	13	3.3	35	2.7	1.2
<i>Ficus</i>	Moraceae	8	2.1	4	0.3	6.5
<i>Vatica</i>	Dipterocarpaceae	8	2.1	59	4.6	0.4
<i>Elaeocarpus</i>	Elaeocarpaceae	6	1.5	16	1.3	1.2
<i>Ilex</i>	Aquifoliaceae	6	1.5	11	0.9	1.8
<i>Lophopetalum</i>	Celastraceae	6	1.5	4	0.3	4.9
<i>Excoecaria</i>	Euphorbiaceae	5	1.3	1	0.1	16.3
<i>Vitex</i>	Lamiaceae	5	1.3	2	0.2	8.2
<i>Aglaia</i>	Meliaceae	4	1.0	18	1.4	0.7
<i>Calophyllum</i>	Clusiaceae	4	1.0	11	0.9	1.2
<i>Nephelium</i>	Sapindaceae	4	1.0	4	0.3	3.3
<i>Peronema</i>	Verbenaceae	4	1.0	0	0.0	0.0
<i>Pometia</i>	Sapindaceae	4	1.0	1	0.1	13.0
<i>Shorea</i>	Dipterocarpaceae	4	1.0	27	2.1	0.5
<i>Macaranga</i>	Euphorbiaceae	3	0.8	0	0.0	0.0
<i>Pithecellobium</i>	Fabaceae	3	0.8	0	0.0	0.0
<i>Carallia</i>	Rhizophoraceae	2	0.5	0	0.0	0.0
<i>Dipterocarpus</i>	Dipterocarpaceae	2	0.5	3	0.2	2.2
<i>Durio</i>	Malvaceae	2	0.5	0	0.0	0.0
<i>Litsea</i>	Lauraceae	2	0.5	104	8.2	0.1
Maladi ^b	Unknown	2	0.5	0	0.0	0.0
<i>Parkia</i>	Fabaceae	2	0.5	12	0.9	0.5
<i>Xylocarpus</i>	Meliaceae	2	0.5	17	1.3	0.4
<i>Diospyros</i>	Ebennaceae	1	0.3	45	3.5	0.4
<i>Garcinia</i>	Clusiaceae	1	0.3	8	0.6	0.4
<i>Hydnocarpus</i>	Flacourtiaceae	1	0.3	0	0.0	0.0
<i>Lithocarpus</i>	Fagaceae	1	0.3	19	1.5	0.2
<i>Mezzettia</i>	Annonaceae	1	0.3	7	0.6	0.5

^aSelection coefficients were calculated by dividing the proportion of use by the proportion of availability. Numbers larger than 1 indicate use disproportional to availability (e.g., preference) while numbers less than 1 indicate avoidance of the trees.

^bMaladi is the local name for this taxon. We were unable to identify the tree to family or genus.

Proboscis monkeys used a more diverse assortment of trees in the mangrove forest (Shannon's index = 2.5) compared to riverine forest (Shannon's index = 1.3) and peat swamp forest (Shannon's index = 1.9) (Table IV). The diversity of sleeping trees used in each forest type differed from the overall diversity of trees in each forest type as the mangrove forest has the lowest overall tree diversity (Shannon's index = 2.7) and peat swamp has the highest overall tree diversity (Shannon's index = 3.5) (Fig. 5).

In the mangrove forest, the most important sleeping tree was *Bruguiera* (Rhizophoraceae). Although *Bruguiera* is a common mangrove species, it was selected disproportionately to its availability (selection coefficient = 3.5), indicating a preference for this genus. Other preferred mangrove sleeping trees included *Excoecaria*, *Peronema* (Verbenaceae), and *Rhizophora* (Rhizophoraceae). In riverine habitats, the monkeys utilized *Palaquium* for 67% of 205 recorded sleeping trees; this genus was also a

TABLE IV. Richness and Diversity (Shannon's Index) of Sleeping Trees and Available Trees by Forest Type

	All trees	Mangrove forest	Riverine forest	Peat swamp forest
Number of genera used	35	22	9	21
Diversity of used trees	2.4	2.5	1.3	1.9
Number of genera available	119	25	74	86
Diversity of trees available	3.7	2.7	2.6	3.5

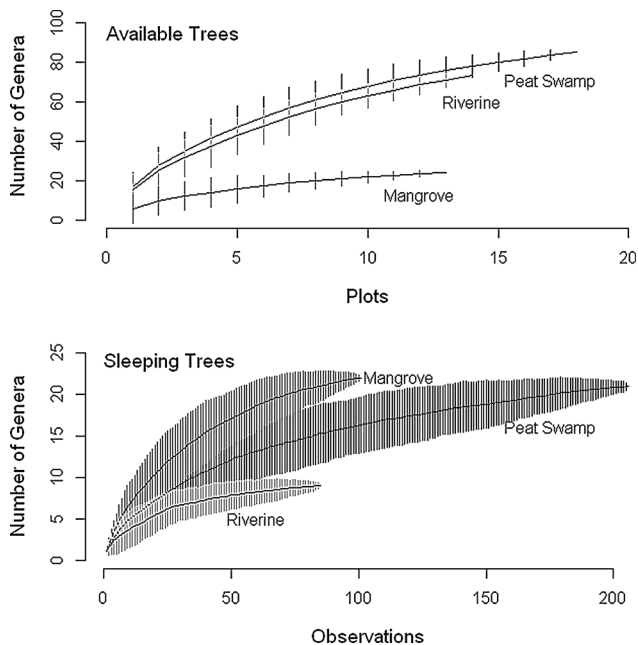


Fig. 5. Genus accumulation curves of available and sleeping trees by forest type. Graphs represent overall richness of tree genera for available trees and used sleeping trees by forest types. Forest types with higher curves represent more rich forests. For available trees (1,274 trees), genus accumulation curves were compared at the level of vegetative plot ($N=22$), for sleeping trees, the comparison was completed at the level of the sample ($N=392$).

preferred tree (selection coefficient = 5.7). The most preferred trees in riverine forest were *Dialium*; which only represented 7% of used sleeping trees (selection coefficient = 9.7) and *Pometia* which only represented 2% of used sleeping trees (selection coefficient = 6.5). The patterns in the peat swamp forest were similar to those in the riverine forest, with *Palaquium* being the most important tree (46%) and also a preferred tree (selection coefficient = 5.7). *Ficus* (selection coefficient = 14.3) and *Dialium* (Fabaceae, selection coefficient = 8.6) were two of the most preferred trees in the peat swamp forest although they account for only 2% and 5% of used sleeping trees, respectively.

Selection of Tree Characteristics

To determine which factors influenced selection of sleeping trees, we calculated resource selection functions using a model selection framework. The model most strongly supported by information criteria was Model 4^t (AIC = 217), which included sleeping tree size (DBH), canopy connections, and forest type as main effects, as well as interactions between forest type and the other two factors. Although this model had the lowest AIC, we present and interpret the version of model 4 excluding the interactions with forest type (the main effects only model, AIC = 221). In our judgment, sample sizes within the crossed factors (i.e., one canopy connec-

tion, mangrove) were not adequate for precise estimations of the interaction effects, which presented computational problems for model interpretations; however, it is important to note the potential biological importance of forest type on sleeping site selection. Models that included only leaf cover ($\Delta\text{AIC} = 358$), relative height ($\Delta\text{AIC} = 185$), branch structure ($\Delta\text{AIC} = 332$), and interactions of the factors had higher AIC scores, and therefore those tree characteristics were poorer predictors of sleeping tree use (Table I).

Model 4 (the model with the lowest AIC) indicates that the most important factor in determining the use of sleeping trees was the size of the tree, regardless of number of canopy connections (Fig. 6). The coefficient estimates of model 4 were logDBH 4.13 (SE = 0.52, $P < 0.05$), one canopy connection 0.77 (SE = 0.60), and multiple canopy connections -1.46 (SE = 0.44, $P < 0.05$). As described in the methods, the coefficient estimates were converted to the relative odds of use compared to our baseline tree (a tree of DBH 10, with multiple canopy connections). For a given number of canopy connections, the model implies a power-law relationship between the odds of use and DBH (in original units of cm): the odds of use are proportional to the DBH of the tree raised to the power of 4.14 (Fig. 6). Thus, a tree with a DBH = 25 and zero connections is about 200 times more likely to be used

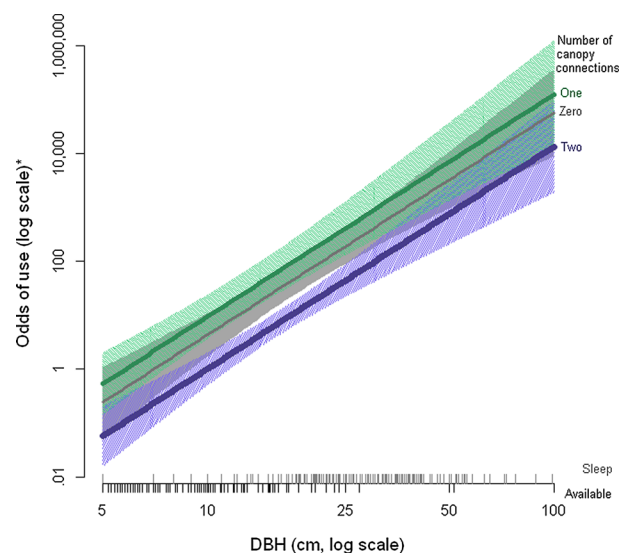


Fig. 6. Relative log odds of sleeping trees in best model: DBH and canopy structure. The log odds of use for trees with varying DBH and canopy connections are shown relative to an average tree (DBH 10 cm, multiple canopy connections). Confidence bands (95%) for the resource selection functions for each number of canopy connections are shown as shaded regions (the 95% confidence bands incorporate uncertainty from both the model and imputation). The considerable overlap of the bands indicates that canopy type plays a secondary predictive role, with DBH as the primary predictor. Tick marks above the x-axis represent DBH of sleeping trees in our study, while tick marks below the x-axis represent the available trees (represented by a random sampling of trees).

than a tree with a DBH = 10 and multiple canopy connections. The use of trees with different canopy structures was a more important factor in moderately sized trees compared to trees that were very small or very large. As the confidence intervals between zero canopy connections and one canopy connection overlap for all sizes of trees, we cannot distinguish between these two classes of canopy connections.

DISCUSSION

We found that proboscis monkeys were selective based both on the taxon and physical characteristics of sleeping trees. Large emergent and semi-emergent trees served as both important and preferred sleeping trees. Proboscis monkeys showed little preference for leaf structure or trunk structure. Although they used a wide variety of tree taxa as sleeping trees, proboscis monkeys showed a strong preference for certain genera. The characteristics that determined sleeping site selection by the monkeys at Sungai Tolak were fairly robust, as the trends of resource selection were very similar in different forest types despite differences in the availability of trees and distinct ecological characteristics.

By selecting large semi-emergent trees, proboscis monkeys might be choosing sleeping trees to protect themselves from predation. We found support for only one of the four proposed anti-predator strategies, namely that the height and isolation of trees could allow the monkeys to increase the detection of predators and competitors. Similarly, other studies have suggested that proboscis monkeys select sleeping sites along river's edges to increase detection of predators [Matsuda et al., 2011]. Golden black uacaris [Barnett et al., 2012], agile gibbons (*Hylobates albibarbis*) [Cheyne et al., 2012], and bonnet macaques (*Macaca radiata*) [Ramakrishnan and Coss, 2001] all prefer large emergent trees, which the authors of each study interpreted as a way to reduce predation risk.

We did not find evidence to support the hypothesis that proboscis monkeys select trees with many canopy connections to increase potential exit routes. Along the Klias River in Sabah, proboscis monkeys often slept in trees with many canopy connections [Bernard et al., 2011]. Although this behavior could be an anti-predator strategy, the authors suggest that there is little predation risk at Klias River, and therefore speculate that selecting trees with many canopy connections might increase locomotor, and potentially foraging efficiency. Differences in forest types among sites in Borneo could be hypothesized to account for these differences, although our results were consistent in all three forest types at Sungai Tolak. These differences indicate the importance of studying different populations of primates, as one population might have specific behaviors that cannot be generalized to other populations.

Our results indirectly supported the hypothesis that proboscis monkeys select tall emergent trees as a mechanism to reduce molestation by mosquitoes, and therefore potentially reduce disease risk. Although no study has yet to test how different structural characteristics of trees might influence the densities of biting mosquitoes, because the main malarial vector *Anopheles* has been reported to be a canopy specialist [Reid, 1968], it seems reasonable to hypothesize that proboscis monkeys would avoid sleeping in trees located in the main canopy. Various lines of evidence in other primates suggest that sleeping site selection and behaviors might reduce molestation by disease transmitting insects. Risk of malaria has been suggested to influence the sleeping group size in some South American primates [Davies et al., 1991; Nunn and Heymann, 2005], while preliminary studies suggest that chimpanzees (*P. troglodytes*) used tree species with natural mosquito repellent qualities for nests [Samson et al., 2013]. Chimpanzees also select sleeping site locations with fewer mosquitoes, potentially reducing the risk of malaria [Krief et al., 2012]. The importance of disease risk on sleeping site selection requires more attention and direct testing.

Our results suggest that sleeping group size might be important for proboscis monkeys, as larger sleeping trees may permit larger groups. Sleeping in larger groups could provide another strategy for proboscis monkeys to reduce their risk of predation [Busse, 1977; Hamilton, 1971] or molestation by disease-carrying insects [Freeland, 1977; Mooring and Hart, 1992]. There may be, however, advantages to having large stable groups that are unrelated to sleeping behaviors (e.g., between group feeding competition, social relationships), which would encourage proboscis monkeys to find sleeping trees that are large enough to fit their entire group. As proboscis monkeys tend to associate in bands at sleeping sites, sleeping tree size and distribution could be an important component in understanding grouping of proboscis monkeys, as the lack of a sufficient number of preferred trees in close proximity might discourage proboscis monkeys from forming bands.

As the selection of large, isolated trees supports two hypotheses, our results demonstrate the equifinality common to many studies of sleeping site selection. The same results, or physical manifestations of behavior, may be caused by distinct underlying mechanisms. One of the weaknesses of many sleeping site selection studies is that most conclusions are based on untested assumptions about the effects of hypothesized selective pressures. For example, although many studies have proposed that sleeping site selection is an anti-predator strategy, they are usually based on untested assumptions (e.g., regarding the effects of sleeping tree structure on predation risk) and therefore do not provide direct hypothesis tests. We fully acknowledge the same

limitation in our study, but also note that other (equally speculative) explanations, such as selecting sleep sites to avoid mosquitoes, may be equally probable. Therefore, the results of sleeping site studies, including ours, must be interpreted cautiously. We encourage other scientists that are investigating sleeping site selection in primates to test a variety of a priori hypotheses and to be aware of the equifinality of sleeping site selection studies. Primatologists can disentangle various hypotheses by examining simultaneously how different ecological factors (e.g., weather, water level, insect densities, food availability, and river width) influence sleeping site selection.

Our results have relevance for the conservation of this species. Proboscis monkeys are classified as endangered on the IUCN Red List due to habitat loss and hunting [Meijaard et al., 2008]. Although we are only beginning to understand how sleeping sites might influence behavior, grouping, and potential survival of this species, our study demonstrates that proboscis monkeys (at least at Sungai Tolak) have a very strong preference for large trees located near the river. Large trees located near the river's edge are often the first to be logged by local villagers, which may exacerbate the problems of forest loss for proboscis monkeys. If monkeys are selecting sleeping trees as a way to mitigate the risks of predators or diseases or both, the loss of preferred sleeping trees could further threaten their survival.

ACKNOWLEDGMENTS

The authors thank the Indonesian government, the State Ministry of Research and Technology (RISTEK), and the mayor of Sungai Tolak for giving us permission to conduct this research. All work conformed to research regulations at the University of California-Davis and laws of the Republic of Indonesia. We acknowledge the support and efforts of the Indonesian field assistants that worked on this project: Pak Ferman, Pak Iskandar, and Pak M. Ali. The authors thank Universitas Tanjungpura (UNTAN) and Flora and Fauna International-Indonesia for serving as our Indonesian counterparts for this project. Mark Grote provided invaluable assistance with statistical analysis. The authors thank Ikki Matsuda, one anonymous reviewer, and especially Marina Cords for thoughtful comments that improved the quality of this article.

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