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# Multiple Ecological Factors Influence the Location of Proboscis Monkey (*Nasalis larvatus*) Sleeping Sites in West Kalimantan, Indonesia

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**Abstract** Multiple ecological factors have been hypothesized to influence primate sleeping site selection. Testing multiple hypotheses about sleeping site selection permits examination of the relative strength of distinct ecological factors and expands our ability to understand how selection pressures influence primate sleeping behavior. Here we examine how avoidance of biting insects, thermoregulation, foraging efficiency, tree stability, and interspecific competition influence selection of sleeping sites by proboscis monkeys (*Nasalis larvatus*) in Indonesian Borneo. We collected data on relative insect abundance, temperature, rainfall, food availability, group size, sleeping site location, and presence of other primates for 12 mo. Using formal model comparison and information criteria, we analyzed the relative importance of these ecological factors in determining one aspect of sleeping site location: distance from the river. Our models supported the avoidance of biting insects and the foraging efficiency hypotheses. Proboscis monkeys slept further inland on nights when the abundance of sandflies was high along the river, and when less food was available along the river. Many studies suggest that primates select sleeping trees and locations to reduce predation risk; our study indicates that additional factors may also be important in determining sleeping site selection.

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## Introduction

Primates select sleeping sites in response to various ecological factors and their choices are assumed to enhance fitness by reducing the risk of predation, limiting opportunities for disease transmission, or regulating body temperatures (Anderson 2000). Many factors can influence sleeping site selection, such as the distribution of food (Albert *et al*. 2011; Chapman *et al*. 1989; Smith *et al*. 2007), temperature (Cui *et al*. 2006; Lutermann *et al*. 2010), elevation (Cui *et al*. 2006; Koops *et al*. 2012), the width (Matsuda *et al*. 2010; Yeager 1993) or water level of adjacent rivers (Matsuda *et al*. 2008, 2010), avoidance of parasite larvae (Hausfater and Meade 1982), presence of insects (Whitten 1982), or the chemical composition of sleeping tree leaves to reduce exposure to parasitic arthropods (Samson *et al*. 2013).

Various hypotheses related to sleeping site selection have received empirical support. Primates are particularly vulnerable to predation risk during sleep and there is much evidence supporting sleeping-related behaviors and sleeping site selection as antipredator tactics (Anderson and McGrew 1984; Barnett *et al*. 2012; Cheyne *et al*. 2012; Matsuda *et al*. 2008; Phoonjampa *et al*. 2010; Xiang *et al*. 2011). Primates may also reduce the risk of disease transmission by selecting sleeping sites with fewer biting insects or avoiding exposure to parasites found in primate feces under sleeping sites. For instance, chimpanzees (*Pan troglodytes*) at the Toro Semliki Wildlife Reserve, Uganda, preferred to sleep in trees of *Cynometra alexandri*, which seems to have repellant properties against arthropods, including mosquitoes (Samson *et al*. 2013), while chimpanzees living in the Ugandan highlands slept in areas with lower densities of anopheline mosquitoes, which carry malaria (Krief *et al*. 2012). Sleeping group size and characteristics of sleeping sites, i.e., sleeping in tree holes and vine tangles, were associated with lower prevalence of malaria in 16 Neotropical primate genera (Nunn and Heymann 2005). Besides avoiding transmission by insects, primates also avoid diseases carried in feces. Yellow baboons (*Papio cynocephalus*) alternate their sleeping sites to avoid exposure to intestinal nematodes, while bonnet macaques (*Macaca radiata*) reduce the accumulation of fecal materials under sleeping trees by sleeping in branches that overhang rivers (Ramakrishnan and Coss 2001).

The influence of weather on sleeping site selection varies among primate species. Black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) selected sleeping trees in wind shadows and with access to sunlight (Xiang *et al*. 2011), while long-tailed macaques (*Macaca fascicularis*) may sleep near the river in areas with higher levels of humidity to reduce energy loss while sleeping (van Schaik *et al*. 1996). Chimpanzees living in the Republic of Guinea seemed to use a humidity avoidance strategy in nest building, sleeping in nests higher in the trees during nights with high humidity, and also sleeping at higher altitudes in wet seasons (Koops *et al*. 2012). Grey mouse lemurs (*Microcebus murinus*) slept in nests during the wet season but in tree holes during dry seasons and when young were present (Lutermann *et al*. 2010).

Besides predation, disease, and thermoregulation, other factors might influence primate sleeping site locations. For example, spider monkeys' choices of sleeping locations are influenced by the distance from feeding sites (Chapman *et al.* 1989), macaques (*Macaca leonina* and *M. fascicularis*) are influenced by distance from human settlements (Albert *et al.* 2011; Brotcorne *et al.* 2014), and other primates have an affinity for sleeping near key geographic features, such as cliffs for baboons (*Papio* spp.: Hamilton 1982) or rivers for some Southeast Asian primates (Matsuda *et al.* 2011).

Proboscis monkeys (*Nasalis larvatus*) appear to exhibit strong preferences for sleeping along the edges of rivers, although they occasionally sleep further inland (Bennett and Sebastian 1988; Matsuda *et al.* 2008, 2009, 2010; Sebastian 2000; Yeager 1991). This heavy reliance on a small, localized part of their full range for sleeping sites suggests that they are sensitive to ecological factors, presenting an interesting test case to examine how ecological factors influence the distance monkeys sleep from the river's edge. Results of detailed field studies have produced various hypotheses regarding the ecological underpinnings of sleeping site selection in proboscis monkeys. For example, sleeping sites have been hypothesized to be selected to increase escape routes from predators (Matsuda *et al.* 2008), to increase visibility (Matsuda *et al.* 2011), or to provide potential opportunities for group reunification and feeding (Salter *et al.* 1985), although patterns appear to differ among sites and over time (Bernard *et al.* 2011; Feilen and Marshall 2014; Matsuda *et al.* 2008; Thiry *et al.* 2016). Examining simultaneously the effects of multiple ecological factors may help elucidate observed variation among sites and enhance our understanding of the relative strengths of ecological factors in determining sleeping site selection in proboscis monkeys.

Our previous work demonstrated that proboscis monkeys at Sungai Tolak, West Kalimantan, Indonesia show strong preferences for certain aspects of sleeping tree structure; specifically, they disproportionately sleep in trees that are large, have few canopy connections to neighboring trees, and are located close to the river (Feilen and Marshall 2014). Here we examine whether ecological aspects may also play an important role in determining the location of sleeping sites. Specifically, we examine how insect (sandflies and mosquitoes) densities, temperature, rainfall, food availability, river level, and presence of other primates influenced small-scale variation in the distances that proboscis monkeys slept from the river's edge. We test five non-mutually exclusive hypotheses concerning sleeping site selection that involve avoidance of biting insects, thermoregulation on colder nights, improving foraging efficiency, seeking trees with greater stability, and reducing interspecific competition (Table I).

## Methods

### Study Site and Subjects

We gathered data at Sungai Tolak (1°27′59″S, 110°4′54″E), West Kalimantan, Indonesia from August 3, 2011 to November 30, 2011 and from April 4, 2012 to October 20, 2012. Although West Kalimantan does not experience a predictable seasonal cycle, our study included both dry and wet months. The site encompasses three forest types (mangrove, riverine, and peat swamp forest) that grow along 30 km of the Tolak River (map available in Feilen and Marshall 2014). The width of the Tolak River varies from 15 m to 60 m. Forest types change as distance from the mouth of the river increases,

**Table I** Hypotheses, predictions, and models of how ecological factors influenced the distance proboscis monkeys slept from the river at Sungai Tolak, Indonesia from April 2011 to October 2012

| Hypotheses and predictions | Factors in model |
|---|---|
| H1. Proboscis monkeys selected locations of sleeping sites to avoid insects. | |
| i. Monkeys slept at distances with low relative abundances of biting insects. | Mosquitoes + sandflies |
| ii. Monkeys slept at distances with low relative abundances of sandflies. | Sandflies |
| iii. Monkeys slept at distances with low relative abundances of mosquitoes. | Mosquitoes |
| H2. Monkeys selected locations of sleeping sites to facilitate thermoregulation. | |
| i. On cool nights, monkeys slept farther inland. | Temperature |
| ii. On cool, wet nights, monkeys slept farther inland. | Temperature + rainfall |
| iii. On wet nights, monkeys slept farther inland. | Rainfall |
| H3. Monkeys selected sleeping sites to maintain proximity to food sources. | |
| i. Monkeys slept closer to the river when there was more total food available near the river. | Fruits + flowers + leaves |
| ii. Monkeys slept closer to the river when there were more new leaves available near the river. | Leaves |
| iii. Monkeys slept closer to the river when there were more fruits available near the river. | Fruits |
| iv. Monkeys slept closer to the river when there were more flowers available near the river. | Flowers |
| H4. Monkeys selected stable trees to avoid trees that might fall. | |
| i. Monkeys slept farther inland when river levels were high. | Max river level |
| ii. Monkeys slept farther inland when the river exhibited large fluctuations of water levels. | Δ River level |
| iii. Monkeys slept farther inland when there were many individuals in a tree. | Group size |
| H5. Monkeys selected sleeping sites to avoid competition with other primate species. | |
| i. Monkeys slept farther inland in the presence of other primate groups. | Primates |

with mangrove forest found along the river near its mouth, and peat swamp forest found farthest upstream. Riverine forest is a transitional forest type located between the mangrove and peat swamp forests (Feilen and Marshall 2014).

We collected data on a population of proboscis monkeys at Sungai Tolak that consisted of *ca.* 20 groups of monkeys ranging in size from 2 to 35 individuals, totaling roughly 500 individuals. Proboscis monkeys form groups with one male and multiple females. The individual groups then aggregate to form a hierarchical social structure called a band. At our site, bands were comprised of two to six groups. Groups and bands had overlapping home ranges and were not territorial. Although we did not estimate home range size at our site, proboscis monkeys elsewhere had home range sizes of 130 ha (Yeager 1989) to 900 ha (Bennett and Sebastian 1988). Owing to the physical layout of forest types at Sungai Tolak, groups found in the mangrove forest spent their time primarily in the mangrove forest, while groups in the peat swamp forest were restricted primarily to peat swamp forests (Feilen 2014). As the riverine forest is a transitional forest, groups that lived in this forest type often traveled between forest types. The density of proboscis monkeys varied slightly between forest types, with the highest density found in the peat swamp (*ca.* 0.49 groups/km) and the lowest density found in the riverine forest (*ca.* 0.31 groups/km). At the time of data collection, all monkey groups were semihabituated, allowing us to approach within 15–20 m of the group by boat, but not allowing us to approach on foot.

## Sleeping Site Data Collection

We searched for sleeping sites 18 days per month along three equally sized sections of the Tolak River from 15:30 to 18:30 h using a small boat with an outboard motor. To prevent time of day from influencing our search efforts, we began searches at 15:30 h either at the mouth of the river or 18 km upstream (at our forest camp). Searches from the mouth of the river focused on the mangrove forest, while searches started at our forest camp focused on either the riverine section (downstream from our camp) or the peat swamp forest (upstream from our camp). We searched each forest type for 3–4 days before rotating to a different forest type. Although proboscis monkeys slept inland (further than 50 m from the river—the distance at which detection of proboscis monkeys declined sharply in all forest types) *ca.* 10% of the time, we focused on sleeping sites along the river as these comprised the majority of sleeping sites and we could collect comprehensive data on sleep trees ≤50 m from the river.

We measured the distance of each sleeping tree from the river's edge and the GPS location of the sleeping trees (GPS location marked from the boat located on the river, perpendicular to the midpoint of all sleeping trees used by one group of monkeys,) with a Garmin GPS 60CSx. We recorded other characteristics of sleeping trees, such as genus and physical characteristics, for a different study. Although proboscis monkeys preferred large sleeping trees at Sungai Tolak (Feilen and Marshall 2014), the availability of trees at this site meant that even the large trees had branches fairly close to the trunk and branches rarely extended over the river.

## Insects

We estimated the abundance of sandflies (likely the genus *Sergentomyia*: Ceratopogonidae) and mosquitoes (*Aedes* and *Anopheles*: Culicidae) on the river at dusk (17:00–18:30 h) using four categories: absent, low, moderate, and high. Although the presence of insects may have fluctuated throughout the night, insect abundance at the time proboscis monkeys were selecting sleeping sites was the most relevant measure for testing our hypotheses. Based on the work by Freeland (1977), who measured the abundance of biting insects at sleeping sites by counting the number of bites on his own body, we measured the relative abundance of insects on the river using our experience of the insects. We categorized sandflies and mosquitoes as absent if we did not see, hear, or feel the insects on the observation boat. If we could hear or see the insects, but were not bitten by them, we categorized levels as low. If we could hear or see the mosquitoes or sandflies and also feel them biting us, we classified the level of abundance as moderate. We categorized insect abundance as high when the insects were biting and they became extremely bothersome, causing us to cover all exposed skin and use mosquito repellent (we did not use mosquito repellent until biting was at high levels so as not to affect the results). Although the insect taxa that were attracted to human observers may have been slightly different than the insects that were attracted to monkeys, available literature on the behavior of Bornean mosquitoes and sandflies indicates a substantial degree of host overlap. For example, *Anopheles latens* (the mosquito that spreads *Plasmodium knowlesi*—simian malaria) is attracted to monkeys in the canopy as well as people walking at ground level near forests at dusk (Vythilingam *et al.* 2006), and many sandflies are generalists, attracted equally to humans and mammals (Lassen *et al.* 2012; Tiwananthagorn *et al.* 2012). Although insect abundance may have been higher in the boat than in other areas because of the presence of three of the same human observers in the boat for all days of data collection, we assume that the insect abundance we recorded on the river in our boat tied to the river bank correlated positively with that to which the monkeys were subjected at the river's edge.

### Weather

From the boat positioned near the sleeping sites, we recorded the temperature using a Taylor Indoor Outdoor Digital Thermometer and Digital Hygrometer. We also collected daily minimum and maximum temperature using a Taylor Minimum and Maximum Thermometer and daily rainfall using an All-Weather Rain Gauge at our research camp, located on the edge of the river in the middle of the study site. Rainfall patterns across our site were fairly consistent; therefore, we assumed that one measure of rainfall would accurately describe the rain patterns at all sleeping sites. We attempted to collect data on the humidity and temperature at various distances from the river as part of a pilot study, but our instruments were not precise enough to detect any differences at ground level at 05:30 h. Other studies (Matsuda *et al.* 2011; van Schaik *et al.* 1996) have directly assessed the variation in temperature and humidity with distance from the river and found very little variation (tenths of a degree).

### Food Availability

We monitored food availability in 10 nested botanical plots (25 m × 20 m) located at the river's edge in mangrove, riverine, and peat swamp forest. We placed all plots using a stratified random design (Feilen 2014). An experienced, well-trained Indonesian field assistant identified trees to genus level. As part of a study on feeding ecology (Feilen 2014), we monitored each of the 680 tagged trees (representing 37 families and 70 genera) monthly for the presence of new leaves, buds, flowers, and fruits. Species accumulation curves indicated that our plots captured most of the tree diversity at the site. Fruits were classified as immature (still small), mature (fruit was full size, flesh was still tough), and ripe (fruit pulp had softened and changed color). As we did not have a complete list of all taxa fed on by proboscis monkeys at this site, we based food availability measures on all trees in the plots, rather than focusing on foods know to be eaten by proboscis monkeys.

### River Level

As the Tolak River flows into the nearby South China Sea, the level of the river is influenced by tidal patterns as well as by rainfall, causing both daily and seasonal fluctuations in river level. We recorded the level of the river at the river's edge at two locations: the Tolak dock near the mouth of the river and at our research camp, 18 km upriver from the Tolak dock. We measured river depths four times each day at 05:00–05:30 h, 10:00–12:00 h, 15:30–16:30 h, and 18:45–19:15 h. We determined the daily maximum and minimum height of the river from the recorded values and calculated the change in water level per day (the difference between the maximum and minimum).

### Other Primates

The site has seven species of primates in addition to the proboscis monkeys: pig-tailed macaques (*Macaca nemestrina*), long-tailed macaques, red leaf monkeys (*Presbytis rubicunda*), silvered langurs (*Trachypithecus cristatus*), Bornean orangutans (*Pongo pygmaeus*), and western tarsiers (*Tarsius bancanus*). We recorded the presence of all other diurnal primate species sleeping ≤40 m from the river's edge and ≤100 m upriver or downriver of the proboscis monkeys' sleeping trees each night. We did not collect data on tarsiers, as they were rare and nocturnal.

### Statistical Analysis

We used R statistical software, version 3.02 (R Development Core Team 2013) for all analyses. We calculated means, standard deviations, and proportions for each of the predictors. We used ANOVA and chi-squared goodness of fit tests to compare values across forest types. To assess food availability, we calculated the density of trees with new leaves, flowers, and fruits per month in each forest type.

#### *Imputation*

In April 2012, we began gathering data on two more variables (insect densities and river height) in addition to our initial 15 ecological variables. As excluding the data collected from August 2011 to December 2011 due to missing values for the two additional variables would have greatly reduced our data set and introduced potential biases, we imputed missing values for the two additional variables for August 2011 to December 2011 from our data set (Nakagawa and Freckleton 2011). Imputation is a statistical process that uses the available data to probabilistically predict a value for the missing data fields. We imputed data using the "mice" package (van Buuren and Groothuis-Oudshoorn 2011) in R, which made five different data sets with different imputed values for each missing value. We ran models on the five imputed data sets within the "mice" package, which allowed error values of the imputed data to be propagated throughout the analysis. To check that imputed data sets did not skew the result of our study, we also ran models on only complete cases, i.e., using data only from April to October 2012; imputed values did not change the ranking of models.

#### *Model Selection*

To determine how each ecological factor influenced the location of sleeping trees, we fit generalized linear models using a Poisson distribution. We included only one measurement of temperature per day owing to the collinearity of our measurements. We compared 29 models (14 predictors listed in Table I, 14 additional models that included the 14 predictors with an interaction term of forest type, and 1 model with forest type alone), based on our five hypotheses (Table I). We determined the AICc of each model and selected the model with the lowest AICc value. We also calculated ΔAICc and model weights (Burnham and Anderson 2002).

### Ethical Note

This research complied with rules and regulations of the Institutional Animal Care Committee at the University of California, Davis and the laws of the Republic of Indonesia and the United States of America.

## Results

### Distance from the River

Proboscis monkeys slept in 391 trees ≤50 m of the river during 131 nights of data collection. Proboscis monkeys slept inland (beyond 50 m) on 15 additional nights. Although sampling effort in each forest type was equal, 25% of 391 sleeping trees were in the mangrove forest, 22% in riverine forest, and 52% in peat swamp forest. Proboscis monkeys were more likely to form bands in the peat swamp forest (55% of observations of bands occurred in peat swamp forest), hence, slept in more trees in this forest type. Proboscis monkeys generally slept near the river's edge (mean distance from river = 7 ± SD 7 m, range: 0–40 m; Fig. 1a). The mean and maximum distance from the river's edge differed among forest types. On average, proboscis monkeys slept twice as far inland in the mangrove forest (mean distance from river = 12 ± SD 7.7 m; Fig. 1b) than in riverine (mean distance from river = 6 ± SD 5.0 m; Fig. 1c) and peat swamp forests (mean distance from river = 6 ± SD 5.9 m; ANOVA: $F = 35.9$, df = 2, $P < 0.001$; Tukey's HSD: peat–mangrove = –6.3, $P < 0.001$; riverine–mangrove = –6.0, $P < 0.001$, riverine–peat = 0.3, $P = 0.9$; Fig. 1d).

### Insects

Relative insect abundance varied from night to night. Of the 75 nights on which we collected data, we classified 53% as absent, 13% as low, 19% as moderate, and 15% as high for sandfly abundance ($\chi^2 = 26.4$, df = 6, $P < 0.01$). For mosquitoes, we classified 67% of nights as absent, 19% as low, 13% as moderate, and 1% as high ($\chi^2 = 72.3$, df = 3, $P < 0.01$). Relative levels of insects varied among forest types. Few nights had high sandfly abundance (15%) but those that did occurred mainly in the mangrove forest (83% and secondarily in the riverine forest 17%). In contrast, sandfly abundance was absent on 77% of nights in peat swamp forest. Sandfly abundance appears to be negatively associated with mosquito activity, with all nights having high mosquito levels occurring in the peat swamp forest where sandflies were largely absent, and nights with high sandfly abundance having absent mosquito levels. Overall, however, mosquitoes were absent during most nights in each forest type: 57% of nights in mangrove forest, 67% in riverine, and 73% in peat swamp forest.

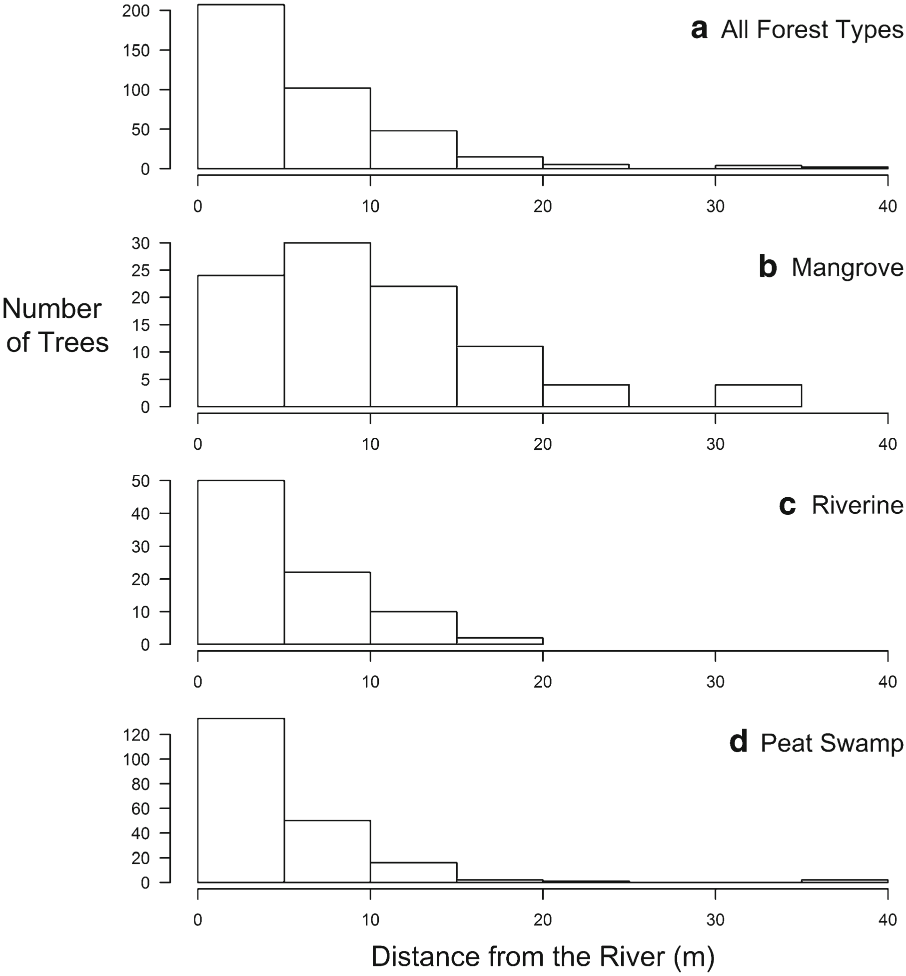

**Fig. 1** Histogram of distances proboscis monkeys slept from the river in all forest types (**a**), mangrove forest (**b**), riverine forest (**c**), and peat swamp forest (**d**) at Sungai Tolak, West Kalimantan from April 2011 to November and April 2012 to October 2012.

## Weather

Daily rainfall varied from 0 to 72.5 mm (mean daily rainfall = 4.4 ± SD 12.1 mm) (Fig. 2a). Temperatures at the site ranged from 21° to 37°C, mean maximum temperature was 32 ± SD 2.0°C (Fig. 2b), and the mean minimum temperature was 24 ± SD 1.2°C (Fig. 2c). Temperatures at sleeping sites ranged from 27°C to 33°C (mean temperature = 30 ± SD 1.3°C).

## Food Availability

Food availability along the river varied by forest type and month (Fig. 3). New leaves were the most abundant food sources in all forest types and all months.

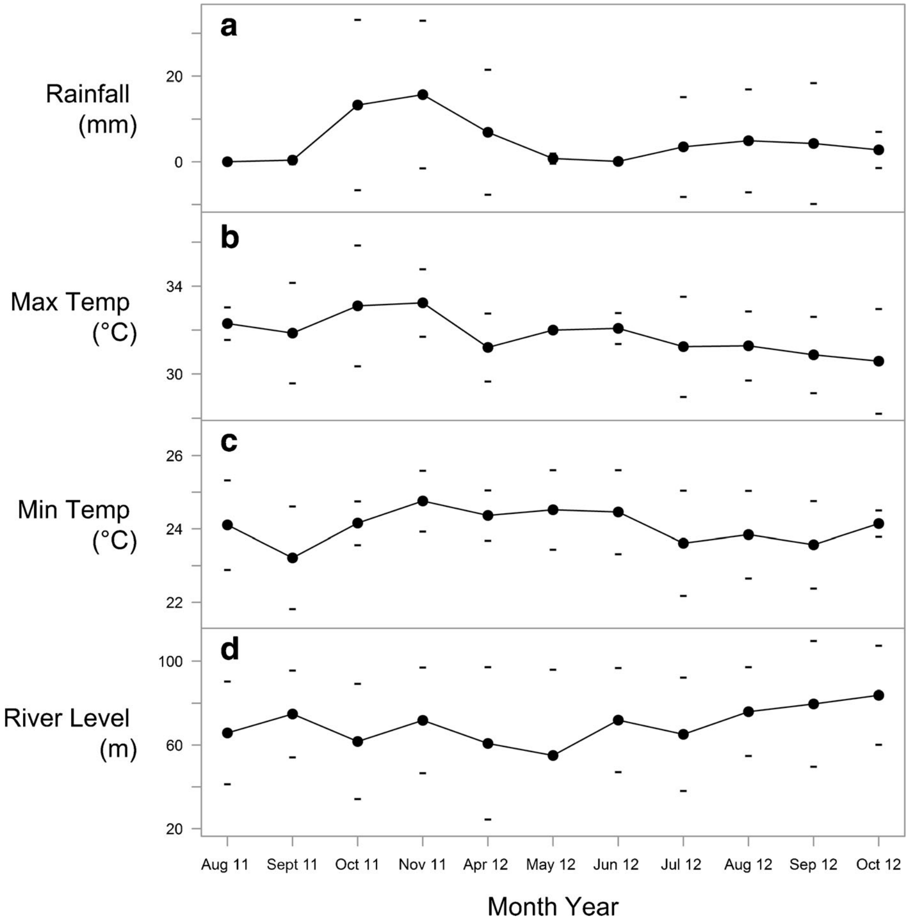

**Fig. 2** Monthly rainfall (**a**), maximum temperature (**b**), minimum temperature (**c**), and difference in river level (**d**) experienced by proboscis monkeys from April 2011 to November 2011 and April 2012 to October 2012 at Sungai Tolak, West Kalimantan, Indonesia. Circles are monthly means and dashes are standard deviations.

## River Level

River levels varied considerably among days and seasons. The minimum river level was 0 cm, i.e., the river had receded from the location at which river height was measured, and the highest recorded level was 145 cm. Daily maximum river levels ranged from 30 to 145 cm (mean maximum height = 87 ± SD 23 cm). The daily difference in river level ranged from 0 to 120 centimeters (mean = 72 ± SD 29.5 cm; Fig. 2d).

## Primates

Of the seven species of primates at our site, proboscis monkeys slept in proximity only to long-tailed macaques and silvered langurs. Of 391 sleeping trees, 17% of the sleeping trees had a group of long-tailed macaques within 100 m, whereas 4% of sleeping trees had silvered langurs within 100 m proximity. Generally, proboscis monkeys slept without another primate species group within 100 m (79%).

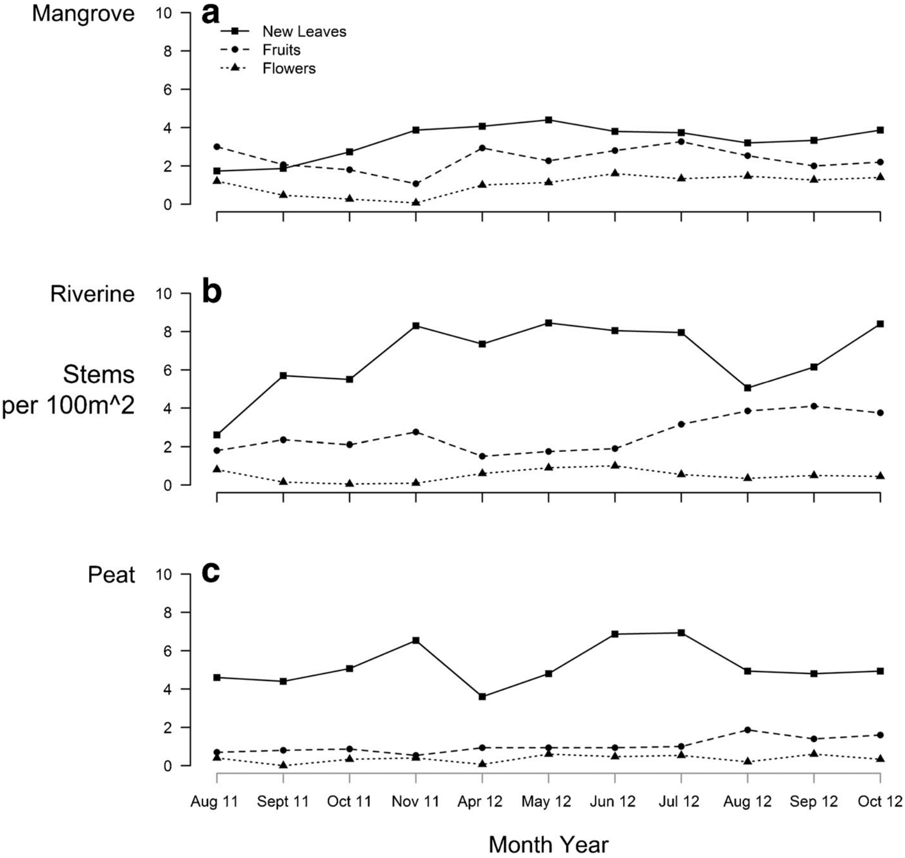

**Fig. 3** Food availability for proboscis monkeys (measured by stems per 100 m$^2$ with new leaves, flowers, and unripe and mature fruits) along the river of mangrove forest (**a**), riverine forest (**b**), and peat swamp forest (**c**) at Sungai Tolak, Indonesia April 2011 to November 2011 and April 2012 to October 2012.

## Model Selection

Of the 29 models that we fit, the model with the lowest AICc value and 87.6% of model weight contained main effects of density of mosquitoes and sandflies and an interaction with forest type (Table II). The model with main effects for availability of new leaves, fruits, and flowers and an interaction with forest type was the second best model ($\Delta$AIC = 4; weight =12.3%). According to the best fit model, forest type was an important predictor of distance from the river: mangrove ($\beta = 2.64$, SE = 0.08), riverine ($\beta = -0.87$, SE = 0.09), and peat swamp ($\beta = -0.83$, SE = 0.10) (Table III), with monkeys sleeping further inland in the mangrove forest (Fig. 4a, b) compared to riverine (Fig. 4c, d) and peat swamp forest (Fig. 4e, f). As sandfly levels increased, the model predicted that the monkeys would sleep further inland. Although the abundance of mosquitoes was in the top model, it was a relatively weak predictor of how far the monkeys slept from the river, as it had large standard errors relative to β coefficient estimate.

**Table II** The top four models with degrees of freedom (df), log likelihoods, AICc values, ΔAICc, and model weights for the distance proboscis monkeys slept from the river's edge at Sungai Tolak Indonesia from April 2011 to November 2011 and April 2012 to October 2012

| Model components | df | Log likelihood | AICc | ΔAICc | Model weights |
|---|---|---|---|---|---|
| (Mosquitoes + Sandflies) * Forest Type | 21 | –1564 | 3176 | 0 | 87.6% |
| (Leaves + Flowers + Fruits) * Forest Type | 12 | –1578 | 3180 | 4 | 12.3% |
| Sandflies * Forest Type | 12 | –1588 | 3207 | 31 | 0.0 |
| Rain * Forest Type | 6 | –1596 | 3208 | 32 | 0.0 |

+ indicates main effects; * indicates interaction between predictors.

## Discussion

We found that proboscis monkeys generally slept along the river. Although our study did not specifically test why proboscis monkeys return to the river's edge to sleep rather

**Table III** Beta coefficient estimates, standard errors, and *P* values of predictors in the model with the lowest AIC values: (Mosquitoes + Sandflies) * Forest Type predicting the distance proboscis monkeys slept from the river's edge at Sungai Tolak, West Kalimantan in 2011 and 2012.

| Predictors | β coefficient estimate | Standard error | *t* value | df | Pr(>\|t\|) | Sig. |
|---|---|---|---|---|---|---|
| (Intercept) | 2.64 | 0.08 | 31.66 | 13.23 | $7.3e^{-14}$ | **** |
| Mosquito low | –0.10 | 0.15 | –0.68 | 7.06 | 0.52 | |
| Mosquito moderate | –0.21 | 0.16 | –1.33 | 13.17 | 0.21 | |
| Mosquito high | –0.36 | 0.25 | –1.44 | 6.63 | 0.19 | |
| Sandfly low | 0.09 | 0.19 | 0.50 | 6.22 | 0.64 | |
| Sandfly moderate | –0.31 | 0.13 | –2.42 | 13.70 | 0.03 | * |
| Sandfly high | –0.21 | 0.17 | –1.23 | 7.41 | 0.26 | |
| Riverine | –0.87 | 0.09 | –9.26 | 16.33 | $6.7e^{-8}$ | *** |
| Peat swamp | –0.83 | 0.10 | –8.19 | 64.18 | $1.4e^{-11}$ | *** |
| Mosquito low: riverine | –0.02 | 0.22 | –0.08 | 7.16 | 0.94 | |
| Mosquito moderate: riverine | 0.23 | 0.37 | 0.63 | 5.89 | 0.56 | |
| Mosquito high: riverine | 0.03 | 0.24 | 0.13 | 19.13 | 0.90 | |
| Mosquito low: peat swamp | –0.15 | 0.24 | –0.60 | 13.61 | 0.56 | |
| Mosquito moderate: peat swamp | –0.34 | 0.20 | –1.65 | 88.53 | 0.10 | |
| Mosquito high: peat swamp | 0.25 | 0.26 | 0.97 | 15.47 | 0.35 | |
| Sandfly low: riverine | –0.43 | 0.43 | –1.01 | 4.84 | 0.36 | |
| Sandfly moderate: riverine | 0.29 | 0.30 | 0.96 | 6.44 | 0.37 | |
| Sandfly high: riverine | 0.36 | 0.26 | 1.40 | 32.82 | 0.17 | |
| Sandfly low: peat swamp | –0.43 | 0.54 | –0.80 | 6.29 | 0.45 | |
| Sandfly moderate: peat swamp | 0.49 | 0.15 | 3.36 | 326.11 | $8.7e^{-4}$ | *** |
| Sandfly high: peat swamp | 0.98 | 0.32 | 3.07 | 7.83 | 0.02 | * |

Sig = Significance:* < 0.05, ** < 0.01, *** < 0.001.

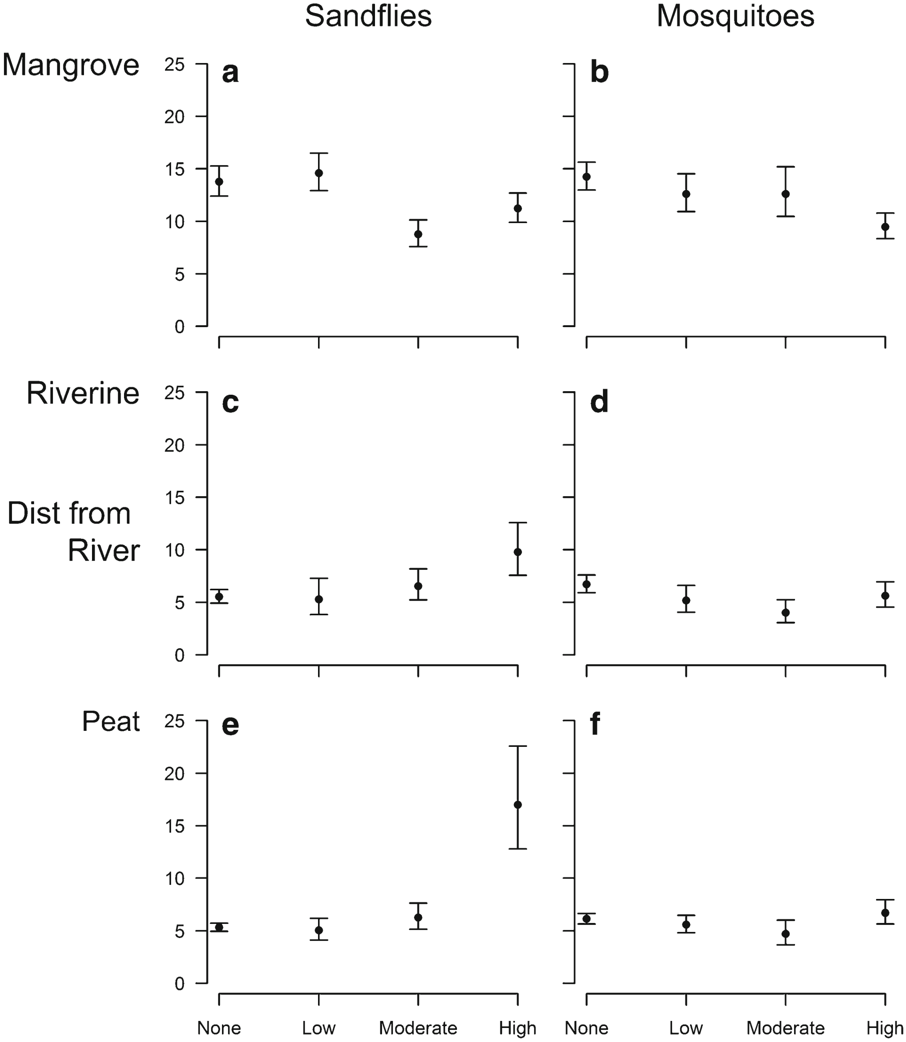

**Fig. 4** Predicted distances proboscis monkeys slept (with lower and upper 95% confidence limits) from the river's edge as a function of forest type, sandfly, and mosquito abundance at Sungai Tolak, Indonesia from April 2011 to November 2011 and April 2012 to October 2012.

than sleeping farther inland, we found that ecological factors influenced the distance that proboscis monkeys slept from the river's edge. The best predictors of the distance the proboscis monkeys slept from the river were the relative levels of mosquitoes and sandflies; the forest type; and the availability of fruits, flowers, and leaves. Regardless of the abundance of sandflies present during a night, proboscis monkeys slept farther from the river's edge in mangrove forests than in riverine and peat swamp forests. During nights with moderate to high abundance of sandflies, proboscis monkeys slept farther inland in riverine forests. Rainfall, temperature, changes in river level, group size, and presence of other primate species were less important in determining the distance the proboscis monkeys slept from the river's edge.

Our study design had limitations that prevent a full understanding of how ecological factors influenced the distance proboscis monkeys slept from the river's edge. We measured two ecological factors, i.e., temperature, insect density, from our boat at dusk, rather than monitoring these factors throughout the night at the sleeping sites of the monkeys. Thus, these measures are only approximations of what monkeys experienced at their sleeping sites during the night. To understand further why proboscis monkeys select sleeping site locations near the river, the ecological factors recorded in this study should be monitored throughout the forest and not just at the forest edge. In addition, we collected insect density on a relative scale rather than an absolute count of the presence of insects. As the insects were measured on the boat with humans, our measurement of insects may have been influenced by the presence of the human observers and may or may not reflect insect abundance at the sleeping tree. It seems reasonable, however, to assume that the insect levels experienced in the two locations were positively correlated and therefore to infer that insect levels were important to sleeping site selection. Alternatively, insect levels at the river's edge might be correlated with some other, unmeasured ecological factor of importance to proboscis monkeys; this interpretation is plausible but a less parsimonious explanation of our results. The importance of insects in sleeping site selection certainly requires direct examination through, for instance, use of $CO_2$- or light-emitting traps, to permit a more accurate measurement of insect densities and identification of insects at higher levels of taxonomic resolution. We also suggest investigation of variation of all ecological factors in various forest types, at various distances from the river, and in trees with distinct characteristics. Gathering these data in conjunction with measuring sleeping site selection would provide a more complete understating of how ecological factors influence sleeping site selection in proboscis monkeys and other species of primates.

In spite of its limitations, our study supports the hypothesis that proboscis monkeys select sleeping tree locations to avoid insects, as the model with the lowest AICc score included the predictors of mosquito abundance, sandfly abundance, and forest type and had 87.6% of the model weight. Although both mosquito and sandfly abundances were predictors in the best model, the abundance of sandflies influenced the proboscis monkeys more than the abundance of mosquitoes. Similarly, we found high sandfly abundance most often in mangroves, the forest type closest to the coast. In mangrove forests, areas with high sandfly abundance, proboscis monkeys selected sleeping trees as far inland as in the other forest types. The general ecology of sandflies in West Kalimantan is poorly understood, but in India, high numbers of sandflies are found in coastal areas (Ozbel *et al.* 2011). Anecdotally, we found that when sandfly abundance was high on the river, we could walk 5–10 m inland to avoid them, suggesting that even small differences in the distance from the river might have important effects on the extent to which the monkeys were affected by sandflies. Although abundance of mosquitoes was present in the best model, it did not have a strong effect on the distance proboscis monkeys slept from the river's edge in most forest types. This could be because mosquito abundance was low along the river. Also, as mosquitoes are often drawn to animals, sleeping farther inland might have only provided a slight benefit to proboscis monkeys seeking to avoid mosquitoes. Proboscis monkeys might use other strategies to avoid mosquitoes, such as changing group size and distribution, or selecting sleeping trees with characteristics that provide some protection against mosquitoes, such as relatively tall trees (Feilen and Marshall 2014).

Insects can influence primates on both a proximate and ultimate level. At a proximate level, primates may avoid insects at sleeping sites to reduce their exposure to bites. Gibbons

(*Hylobates klossii*) select sleeping trees without a type of epiphytes (*Myrmecodia tuberosa*: Rubiaceae) that has a symbiotic relationship with biting ants (Whitten 1982). Howlers (*Alouatta palliata*) spend a substantial amount of time swatting at flies and mosquitoes, which could impose a significant energetic cost (Dudley and Milton 1990). To date, it has yet to be determined whether sandflies in Indonesia transmit any diseases, but much like the biting ants and flying insects that cause howlers to swat at insects, the mere presence of biting insects might bother monkeys enough to influence sleeping site selection. Like sandflies, mosquitoes could pose a proximate cost of causing an irritating bite or annoyance from sound. Many mosquitoes in Southeast Asia are known to transmit diseases. One locally occurring species of mosquito, *Anopheles latens* is the vector for *Plasmodium knowlesi* (Simian malaria), while *Aedes albopctus* carries sylvatic dengue (Vasilakis *et al.* 2011). Selection of sleeping sites to avoid malaria has been reported in 16 Neotropical primate genera (Nunn and Heymann 2005) and chimpanzees (Krief *et al.* 2012).

Weather did not strongly influence the distance proboscis monkeys slept from the river's edge at our site. Like the proboscis monkeys, ursine colobus monkeys (*Colobus vellerosus*) seemed not to be influenced by weather, as they did not huddle with other monkeys, sleep at lower elevations, or select trees with less exposure to the elements on cooler nights (Teichroeb *et al.* 2012). As noted previously, further studies need to examine the role of temperature within the tree and at various heights.

We found that spatial variation in the availability of food sources might also influence sleeping site selection in proboscis monkeys, although we are cautious in the interpretation of these data. We measured the stem densities of foods in plots along the rivers (0–25 m). This scale of data collection does not permit differentiation among sleeping site locations ≤25 m from the river. Our results likely indicate a general tendency of proboscis monkeys to sleep near food sources but are not sufficiently precise to ascertain whether the location of foods influences the specific distance monkeys slept from the river's edge. Some primates appear to use sleeping site locations to increase foraging efficiency (Albert *et al.* 2011; Chapman *et al.* 1989), but other studies of proboscis monkeys have found varying support for food availability influencing proboscis monkey grouping behavior or sleeping site selection. At Tanjung Puting National Park, there was no relationship between the availability of foods and banding behavior of proboscis monkeys (Yeager 1993) and at the Menanggul River, Sabah, Malaysia, food availability did not seem to influence the location of sleeping sites, whereas at the Kinabatangan River, Sabah, Malaysia proboscis monkeys were more likely to select sleeping trees with higher abundances of leaves and fruit than surrounding trees.

Unlike other studies of proboscis monkeys (Matsuda *et al.* 2010; Yeager 1993), we did not find a significant relationship between the distance the proboscis monkeys slept from the river and the height of the river. At the Menanggul River, Sabah proboscis monkeys slept much farther inland when river levels were high and the forest was flooded (Matsuda *et al.* 2010). There are several possible explanations for why our results differ from those from the Menanggul River. First, the changes in river levels were much more substantial at the Menanggul River than at our site, as they recorded a maximum change in river levels of 425 cm, while we recorded a maximum change of only 120 cm. Also, at the Menanggul River site, the entire range of the proboscis monkeys was inundated for a month, while at our site, the forest was flooded only for a few hours in a few months.

Competition for sleeping sites with other primate species did not seem to influence the distance that proboscis monkeys slept from the river. Although we did not find any evidence of competition for sleeping sites, we observed long-tailed macaques supplanting proboscis monkeys from their sleeping sites on multiple occasions. Proboscis monkeys, long-tailed macaques, and silvered langurs regularly returned to the river's edge to sleep, but we rarely observed pig-tailed macaques, red leaf monkeys, or Bornean orangutans doing so. This pattern is similar to that seen at other sites with similar species composition (Matsuda *et al.* 2011). If other primate species experience similar selective pressures to proboscis monkeys on sleeping site selection, one could predict that they should use similar strategies. However, owing to factors such as metabolic rate, group size, and body size, similar ecological factors might be experienced differently by various species. Although long-tailed macaques and the proboscis monkeys both returned to the river's edge to sleep, macaques huddled together (*pers. obs.* KLF), while most proboscis monkeys slept separately, suggesting that they might be more sensitive to changes in temperature. As orangutans sleep in nests (Prasetyo *et al.* 2009), they likely also have distinct strategies for sleeping site selection.

For many years, the sleeping site literature has focused primarily on the selection of sleeping trees as an antipredator strategy (Anderson 2000). Although we are unable to compare the relative strength of insect densities, weather conditions, and food availability to that of predation risk (as our numbers of observations of predators were extremely low, none of which were near sleeping sites), our study demonstrates that these other factors may also importantly influence sleeping site selection. This highlights the importance of considering multiple ecological factors when analyzing sleeping site selection.

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**Compliance with Ethical Standards**

**Conflict of Interest** The authors have no conflict of interest or competing financial interests to declare.

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