

Sleeping Site Selection by White-faced Capuchins (Cebus capucinus) in the Area de Conservación Guanacaste, Costa Rica

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Abstract: Several hypotheses for sleeping site selection have been proposed in response to the wide range of slumber patterns exhibited by primate species. We examined the “predation-avoidance”, “comfort”, and “security” sleeping site selection hypotheses for white-faced capuchin monkeys (*Cebus capucinus*) in the Santa Rosa sector of the Area de Conservación Guanacaste, Costa Rica. From February through April 2008 we recorded the plant species, height, diameter at breast height (DBH), canopy cover, lowermost branch height, subcanopy height, and phenology of sleeping trees selected by three habituated groups. White-faced capuchins preferentially selected sleeping trees of tall, emergent height, with DBH > 65 centimeters, and a low percentage of canopy cover. The girth of their sleeping trees was wider and the canopy cover was less than predicted from other primate studies. Emergent height, wide girth and sparse canopy cover are all hypothesized to reduce predation risk. Our findings suggest that white-faced capuchins employ a predation-avoidance strategy in their selection of sleeping trees, while also taking into account the comfort and security of their sleeping sites. By increasing our knowledge of the characteristics of preferred sleeping sites we can improve our overall understanding of the needs and interdependence of white-faced capuchins and their environment.

Key Words: capuchin monkeys, comfort, predation, primate, security, sleeping tree

INTRODUCTION

It is generally agreed that the sites primates use for sleeping are not chosen randomly, however it has been difficult to conclusively determine the factors involved in sleeping site selection (e.g., Anderson 1998, Di Bitetti et al. 2000). We tested three hypotheses regarding sleeping site selection in white-faced capuchin monkeys (*Cebus capucinus*) at the Santa Rosa sector (hereafter Santa Rosa) of the Area de Conservación Guanacaste (ACG), Costa Rica: 1) the predation-avoidance hypothesis, 2) the comfort hypothesis and 3) the security hypothesis. The predation-avoidance hypothesis proposes that primates use specific trees, sites and behaviors that help them to minimize harm through predation (e.g., Anderson 1998; Di Bitetti et al. 2000; Reichard 1998). The comfort hypothesis proposes primates will sleep more often with other group members in the forks of exposed branches of living trees to enhance comfort (e.g. Anderson and McGrew 1984; Di Bitetti et al. 2000), while the security hypothesis proposes that primates will sleep more often in trees with many, forked branches to enhance security against falling (e.g., Di Bitetti et al. 2000; von Hippel 1998).

Accordingly, we investigated the following research questions: What are the structural characteristics of sleeping trees selected by white-faced capuchins? Do white-faced capuchins select certain tree species or genera more often than others as sleeping trees? Finally, do capuchin sleeping tree selection patterns meet the predictions of the hypothesized predation-avoidance, comfort and/or security strategies? The hypotheses and predictions associated with these three strategies (only some of which are mutually exclusive) are listed in Table 1.

Table 1. Hypotheses and the associated predictions investigated in sleeping tree selection by white-faced capuchins at Santa Rosa, Costa Rica.

Hypothesis	Associated Predictions	Prediction Supported by this Study?	Overall Support?
Predation-avoidance	White-faced capuchins will follow a predation-avoidance strategy by selecting trees with the following characteristics: a. Tall, emergent height (> 25m) b. Bottommost branch height > 18m c. Subcanopy height > 20m d. DBH > 65cm e. Canopy cover < 75% And: f. Low densities of mature fruits and flowers. g. Avoidance of same sleeping site used on consecutive nights. h. Presence of defensive properties (e.g., spines: <i>Hura crepitans</i>) on branches or trunk.	a. Moderate b. No c. No d. Yes e. Yes f. Moderate g. Moderate; two of three groups support prediction h. Moderate; one of three groups support prediction	Moderate
Comfort	White-faced capuchins will follow a comfort strategy by selecting trees with the following characteristics: a. Tall, emergent height (> 25m) b. DBH > 65cm c. Many forked, wide branches to curl up with other capuchins (e.g., added warmth and/or social partners). d. Lack of defensive properties on branches or trunk.	a. Moderate b. Yes c. Yes d. Moderate; two of three groups support prediction	Moderate
Security	White-faced capuchins will follow a comfort strategy by selecting trees with the following characteristics: a. Tall, emergent height (> 25m) b. DBH > 65cm c. Canopy cover < 75% d. Many forked, wide branches to provide space and a stable platform for security against falling	a. Moderate b. Yes c. Yes d. Yes	Moderate

Sources for a) height predictions: Cui et al. (2006), Day and Elwood (1999), Di Bitetti et al. (2000), Liu and Zhao (2004), Reichard (1998), von Hippel (1998); b) bottommost branch height predictions: Day and Elwood (1999), Liu and Zhao (2004); c) subcanopy height predictions: Day and Elwood (1999), Zhang (1995); d) DBH predictions: Brownlow et al. (2001), Chapman (1989), Cui et al. (2006), Day and Elwood (1999), Di Bitetti et al. (2000), Hankerson et al. (2007), Liu and Zhao (2004), Rasoloharijaona et al. (2007); and e) canopy cover predictions: Brownlow et al. (2001), Di Bitetti et al. (2000).

We predicted that capuchins would use sleeping trees of tall, emergent height and large diameter both to deter predators, and also for greater comfort and security. If white-faced capuchins implement a comfort strategy in their sleeping site selection, then tree branches should be wide enough to curl up with other individuals in the forks of branches for greater comfort. We also predicted that capuchins would use trees with wide, forked branches for greater security. Tall trees of wide girth could also increase the security of sleeping individuals, as larger trees may be less likely to shed branches in windy weather and storms, or may reduce the chance of individuals falling and incurring injuries during the night (Di Bitetti et al. 2000).

Capuchin monkeys at various sites in Costa Rica have been observed to exhibit anti-predator responses to many predator species [e.g., pumas (*Felis concolor*), ocelots (*F. pardali*) and tayras (*Eira barbara*)] (Rose et al. 2003). Costa Rican carnivores exhibit increased arboreality (Janzen and Wilson 1983), however, tall trees with high bottommost branches and large girth may be more difficult for terrestrial predators to climb (Di Bitetti et al. 2000, Liu and Zhao 2004). Most Costa Rican carnivores have been observed to forage on ripe-fruit, although they retain specialized traits for carnivory (Janzen and Wilson 1983). Seed species found in the dung of the carnivores include *Ficus* spp., *Genipa americana*, and *Manilkara zapota* (Janzen and Wilson 1983); these species are also important components of the capuchin diet and may impact ranging and sleeping patterns. In addition, jaguars (*Felis onca*) and pumas, two obligate carnivores found at Santa Rosa, are both nocturnal and known to prey on monkeys (Koford 1983). We predicted that white-faced capuchins should avoid sleeping in fruiting trees in order to minimize exposure to the multiple nocturnal and/or semi-frugivorous carnivore species found at Santa Rosa.

Plant species may have evolved protective spines to deter predation or damage by larger mammals, however there is still un-certainty as to the actual adaptive significance of this trait (Grubb 2003, Hallwachs 1983). Defensive properties on the bark of trees could deter capuchins and/or large predator species (e.g., pumas) from climbing, foraging or resting within them. We predicted that if capuchins avoid trees with obvious defensive properties on their bark they could be implementing a comfort strategy in sleeping tree selection. However, if they prefer trees with these defensive characteristics they could be employing a predation-avoidance strategy in their selection of sleeping trees. It is not necessary for sleeping trees to have all of the characteristics mentioned above in order to provide white-faced capuchins with some comfort or some additional protection from predators.

METHODOLOGY

Study Site

Santa Rosa consists of 108 square kilometers of semi-deciduous tropical dry forest, and forms part of the ACG, a major conservation project in tropical forest restoration in Guanacaste Province, Costa Rica (Fedigan and Jack 2001). Almost all of the annual rainfall occurs from mid-May to mid-December, creating distinct seasonality. All data collection took place during the dry season, when only patches of semi-evergreen and riparian vegetation retain their leaves.

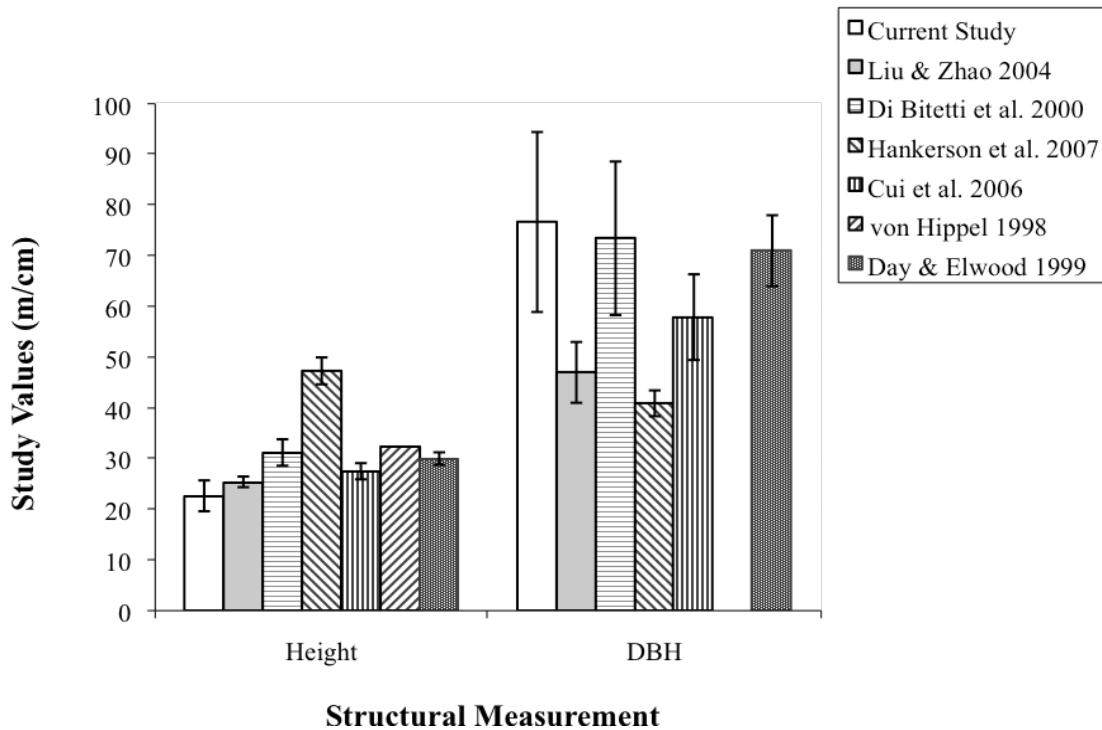
Data Collection and Analysis

From February through April 2008 we followed three habituated study groups (LV, CP, and GN) and recorded 113 exact sleeping trees (identified as to species and location) over 53 nights (LV: 12; CP: 19; GN: 22 nights). We measured the following characteristics of sleep trees: species, height, diameter at breast height (DBH), canopy cover, lowermost branch height, subcanopy height, and phenology. To identify the species of sleeping trees we consulted local ecologists and a taxonomic key (Enquist and Sullivan 2001). We used a clinometer and standard measuring tape to calculate tree, subcanopy, and bottom-most branch heights at each location (Williams et al. 1994). We measured the percentage of crown projection of each sleeping tree using an internal crosshair sighting tube and 20 sample points per tree (Jennings et al. 1999). Crown projection refers to the proportion of total observations where sky is obscured by vegetation (Johansson 1985). We defined low canopy cover as ≤ 75 percent crown projection and high canopy cover as > 75 percent crown projection (Hankerson et al. 2007). We collected basic phenology data for the sleeping trees on the day after use according to the following scale for maturity and density of leaves, fruit and flowers: 0 (none), 1 (1-25 percent), 2 (26-50 percent), 3 (51-75 percent), and 4 (76-100 percent). We measured DBH at 1.3 meters from the ground (Husch et al. 2003). To avoid problems with inter-observer reliability in data collection, one observer (TDH) recorded all measurements. We performed all statistical analyses using R (2.6.1, R Foundation).

RESULTS

The mean total height of the sleeping trees across our study groups was 23.47 ± 6.45 meters, which is significantly lower than the average height of sleeping trees selected by other primate species at other sites (Figure 1) ($\mu > 25$ meters: Cui et al. 2006; Day and Elwood 1999; Di Bitetti et al. 2000; Liu and Zhao 2004; Reichard 1998; von Hippel 1998) (one-sided single sample t-test, $t = -2.304$, $df = 112$, $P = 0.0073$).

Figure 1. A comparison of height (m) and DBH (cm) of sleeping trees (mean \pm sd) used by white-faced capuchins at Santa Rosa to the following primate species: *Rhinopithecus bieti* (Liu and Zhao 2004), *Cebus apella nigrinus* (Di Bitetti et al. 2000), *Leontopithecus rosalia* (Hankerson et al. 2007), *R. bieti* (Cui et al. 2006), *Colobus guereza* (von Hippel 1998), *Saguinus midas midas* (Day and Elwood 1999). Error bars indicate standard deviation of structural measurements.



The mean DBH of the sleeping trees was 76.7 ± 36.2 centimeters, which is significantly larger than the average DBH of trees recorded in previous studies of primate sleeping trees (Figure 1) ($\mu = 65$ centimeters: Brownlow et al. 2001; Chapman 1989; Cui et al. 2006; Day and Elwood 1999; Di Bitetti et al. 2000; Hankerson et al. 2007; Liu and Zhao 2004; Rasoloharijaona et al. 2007) (one-sided single sample t-test, $t = 4.464$ $df = 112$, $P < 0.0001$). We also compared the mean DBH of sleeping trees to the mean DBH of all trees measured along transects placed in the home ranges of our study groups. Based on data from 142 2 x 100 meter transects (Melin and Parr, unpubl. data), the mean DBH of 12,077 trees in the home ranges of our study groups was 5.3 centimeters (range: 0-192.8 centimeters; median= 2.8 centimeters). Due to the over-representation of small saplings, we used the following subsets of transect data to conduct our statistical analyses: DBH greater than 50 percent, 75 percent, 90 percent, 95 percent, and 99 percent of all transect trees. We present here only comparisons to the largest DBH category (> 99 percent; median = 51.0 centimeters, mean = 56.6 centimeters, range: 41.00 - 192.8 centimeters), because this is the most conservative comparison. The mean DBH of the sleeping trees in this study are significantly larger than the

largest category of the trees recorded on transects (one-sided single sample t-test, $t = 4.531$, $df = 63$, $P < 0.0001$) This indicates that the capuchins are selecting trees of very large girth for sleeping.

The mean canopy cover for all sleeping trees used during the study period was low (54.9 percent crown projection). The mean height of the lowermost branches of sleeping trees in this study was 5.44 ± 2.54 meters, which is significantly lower than the average lowest branch heights of trees used by other primate species ($\mu > 18$ meters: Day and Elwood 1999, Liu and Zhao 2004) (one-sided single sample t-test, $t = -52.618$, $df = 112$, $P < 0.0001$). The mean height of the subcanopies of sleeping trees in this study was 11.03 ± 3.69 meters, which is significantly lower than the average subcanopy heights published for other primate species ($\mu > 20$ meters: Day and Elwood 1999, Zhang 1995) (one-sided single sample t-test, $t = -24.889$, $df = 112$, $P < 0.0001$). Although we did not have access to height data from surrounding trees for comparison, Guimarães et al. (2009) have demonstrated a positive correlation between DBH and height using polynomial and logistic models.

The capuchins slept in trees containing fruit on 20.4 percent of total sleeping trees (23 of 113 sleeping trees used). The three fruiting species used as sleeping trees were *Sciadodendron excelsum* ($n = 1$), *Enterolobium cyclocarpum* ($n = 15$), and *Bursera simaruba* ($n = 7$). The fruits from these species are normal constituents of *C. capucinus* diet (Fragaszy et al. 2004). CP group selected trees on three nights that were directly adjacent to fruiting *Ficus morazaniana* and *F. cotinifolia* on which they had been foraging. CP group also used the same sleeping trees on repeated nights, representing 5.2 percent of total nights observed.

A total of 20 different species of sleeping trees were used across all three groups during the study period (Table 2). Our study groups preferentially selected *E. cyclocarpum* ($n=22$) and *Hymenaea courbaril* ($n=16$) as sleeping trees (50 percent more often than each other sleep tree species). *E. cyclocarpum* exhibited a low percentage of canopy cover (57.2 percent) and a low density of mature leaves during the study period, whereas *H. courbaril* exhibited high canopy cover (76.4 percent) and a greater density of mature leaves. Based on 142 2 x 100 meter transects in the home ranges of our study groups (Melin and Parr, unpubl. data), *E. cyclocarpum* and *H. courbaril* account for 0.46 percent and 1.83 percent respectively of trees with a DBH > 24 centimeters (our minimum recorded sleeping tree DBH). Thus, these two species were selected significantly more often than expected based on their availability in our study groups' home ranges (chi-square goodness of fit test, $\chi^2 = 484.98$, $df = 1$, $P < 0.05$).

DISCUSSION

Although all three of the study groups chose trees that were shorter than the predicted height (based on the average tree heights chosen as sleeping trees by other primate species), selected trees were still visibly emergent relative to other trees in the surrounding Santa Rosa forest. *E. cyclocarpum* and *H. courbaril* typically attain large, emergent size with branches of substantial girth (Enquist and Sullivan 2001), which could account for the preferential selection of these species as sleeping trees. The lower mean height of sleeping trees in our park compared to other sites may result from the forest's young age and its ongoing regeneration since the founding of Santa Rosa in 1972 (Fedigan and Jack 2001). According to Meyfroidt and Lambin (2008), if surrounding secondary forest is composed of trees of small girth and height, then even relatively tall, emergent trees in that forest will be shorter than those found in primary forests. A lower average tree height across Santa Rosa as compared to other sites where primate sleeping trees have been documented would also explain why we found the lowermost branch and sub-canopy heights of the sleeping trees to be relatively low compared to older forests.

Table 2. A comparison of the percentage of nights spent in different tree species by three groups of white-faced capuchins in Santa Rosa, February-April 2008. Parentheses contain the number of exact sleeping tree locations observed for each group during the study period.

Tree Species	CP (n=44)	GN (n=41)	LV (n=28)	Total (N=113)
<i>Astronium graveolens</i>	-	-	0.7	1.8
<i>Ateleia herberth-smithii</i>	-	-	3.6	0.9
<i>Bombacopsis quinata</i>	-	12.2	-	4.4
<i>Bursera simaruba</i>	15.9	7.3	3.6	9.6
<i>Calycophyllum candidissimum</i>	2.3	12.2	7.1	7.1
<i>Cedrela odorata</i>	-	2.4	7.1	2.7
<i>Enterolobium cyclocarpu</i>	22.7	26.8	3.6	19.5
<i>Ficus cotinifolia</i>	-	4.9	-	5.3
<i>Ficus morazaniana</i>	-	14.6	-	5.3
<i>Guazuma ulmifolia</i>	-	2.4	-	0.9
<i>Hymenaea courbaril</i>	25.0	-	17.9	14.2
<i>Licanea arborea</i>	13.6	2.4	3.6	7.1
<i>Lonchocarpus minimiflor</i>	-	-	14.3	3.5
<i>Lysolima divaricatum</i>	4.5	-	-	1.8
<i>Maclura tinctoria</i>	2.3	2.4	14.3	5.3
<i>Manilkara chicle</i>	11.4	9.8	-	8.0
<i>Samanea samon</i>	-	-	3.6	0.9
<i>Sciadodendron excelsum</i>	2.3	-	-	0.9
<i>Spondias radlkoferi</i>	-	-	14.3	3.5
<i>Tabebuia rosea</i>	-	2.4	-	0.9

Primates using the predation-avoidance strategy select specific sites and behaviors that aid them in avoiding harm through predation (e.g., Anderson 1998, Reichard 1998). All three of the study groups were observed close to mammalian predators, and numerous snake and raptor species. Based on these observations, we assume that white-faced capuchins at Santa Rosa are under considerable predation pressure. Characteristics of sleeping trees selected by white-faced capuchins in this study show moderate support for use of a predation-avoidance strategy (Table 1). This hypothesis proposes that tall, emergent trees with high subcanopy and bottommost branch heights and large girth (i.e., higher DBH) decrease tree accessibility to terrestrial predators, and a lower percentage of canopy cover (< 75 percent) facilitates increased ability to detect predators, but also increases visibility to predators. The mean canopy cover for all sleeping trees was low, and the mean DBH was significantly higher than predicted based on other

primate studies. The maturity and density of fruits on sleeping trees also could affect a primates' proximity to predators that have frugivorous/carnivorous diets (e.g., tayra: Asensio and Gómez-Marín 2002). These nocturnal predators might forage in the same or nearby trees during the capuchins' inactive period. All three of the study groups slept in both fruiting and non-fruiting *E. cyclocarpum* and *B. simaruba*. Therefore, capuchins do not appear to avoid sleeping in fruiting trees, as we would predict from the predation-avoidance strategy. The predation-avoidance hypothesis also predicts that primates will avoid sleeping sites used on the previous night as strategies to minimize predation (Di Bitetti et al. 2000) and two of our three study groups (LV and GN) met this prediction. Furthermore, even in the third group (CP), repeated use of sleeping trees on consecutive nights was low (only 5.2 percent of total nights observed).

Variation in the emergence of leaves could account for the variation in canopy cover for the sleeping trees that capuchins selected. *H. courbaril* differs from many other tree species in Santa Rosa by producing foliage during the dry season (Janzen 1983). Increased vigilance in exposed positions (e.g., bare branches) has been observed in other capuchin species (van Schaik and van Noordwijk 1989), so these capuchins may be selecting *H. courbaril* as sleeping trees during the dry season to facilitate concealment from predators. Further investigation into the site selection, leaf phenology and canopy cover of sleeping trees during other seasons at Santa Rosa would allow analysis of a crypsis advantage versus the predator detection advantage predicted in this study.

The comfort and security hypotheses propose that larger-bodied primates will sleep more often in close proximity with other group members for comfort, and on the forks of exposed branches of living trees for security against falling (Di Bitetti et al. 2000; Reichard 1998; von Hippel 1998). Although detailed behavioral observations after arrival at the sleeping site were not possible due to poor lighting conditions, it was possible for us to observe the capuchins curling up on the forks of branches alone and with other individuals. The finding that our study animals selected trees with above average DBH (> 65 centimeters) compared to the girth predicted from other primate studies coupled with their use of wide branch forks for curling up with other individuals provides evidence that white-faced capuchins do employ the comfort and security strategies. However, GN group sometimes (12.2 percent of sleeping trees used) selected trees with obvious defensive properties on their branches and trunks; in particular, they selected spiny *B. quinata* as sleeping trees at two different sites. This contradicts one prediction of the comfort hypothesis and suggests predator avoidance may be more important than comfort for GN group.

In sum, the white-faced capuchins at Santa Rosa preferentially select sleeping trees of tall, emergent height, with DBH > 65 centimeters, and a low percentage of canopy cover. Our study suggests that white-faced capuchins do implement a predation-avoidance strategy, but they also take into account comfort and security in their selection of sleeping trees. Di Bitetti et al. (2000) found that tufted capuchin monkeys at Iguazú National Park and capuchins in other populations also follow a predation-avoidance pattern in the selection of their sleeping trees. Comfort and security were found to be an additional factor in the selection of sleeping trees for the Iguazú National Park study. However, these hypotheses were not tested in the other capuchin studies of sleeping tree selection (e.g., Zhang 1995; Valenta et al. 2009). Predictions from these three hypotheses are not mutually exclusive, and animals may employ more than one strategy. Our results provide a first step from which to investigate additional hypotheses and their associated predictions. Measures of sleeping tree crown and branch diameters as well as locations of individuals within trees would help us to better understand sleeping positions. Ecological measurements of surrounding forest characteristics would also provide more definitive answers concerning the strategies involved in sleeping tree selection. A comprehensive knowledge of the structural characteristics of sleeping sites should help to explicate other phenomena related to sleeping trees, such as the effects of nocturnal seed dispersal by monkeys on forest regeneration (Valenta et al. 2009). There is also a potential to use primate behavioral research to investigate models of hominid activity patterns, as a supplement to archaeological findings (e.g., Sept 1992). Studies such as ours broaden understanding of the substrate use and needs of this monkey

species and its overall interdependence with the environment, and thus have the potential to promote the conservation of tropical ecosystems as a whole.—

NOTE

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