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ORIGINAL ARTICLE

Sleeping site selection by golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian flooded forests

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Abstract In Amazonian seasonally flooded forest (igapó), golden-backed uacaris, *Cacajao melanocephalus ouakary*, show high selectivity for sleeping trees. Of 89 tree species in igapó, only 16 were used for sleeping (18%). *Hydrochorea marginata* (Fabaceae) and *Ormosia paraensis* (Fabaceae) were used most frequently (41% of records) despite being uncommon (Ivlev electivity ratios were 0.76, and 0.84, respectively), though the third most commonly used species (11%), *Amanoa oblongifolia* (Euphorbiaceae), was selected at near parity. All three species have broad, open canopies with large horizontal limbs and uncluttered interiors. Compared with random trees, sleeping trees had above average diameter at breast height (DBH) and height, lacked lianas and wasp nests, and were more frequently within 5 m of open water. Uacaris generally slept one adult per tree or widely separated in the same canopy and on the outer third of the branch. These behaviours are interpreted as maximising detection of both aerial and arboreal predators.

Keywords *Cacajao melanocephalus ouakary* · Igapó · Sleeping site · Predation

Introduction

Sleeping trees are significant features of primate ecology (Anderson 1998, 2000). Primates can, after all, spend up to 15 h a day in them. Their distribution can have strong influences on ranging patterns and/or foraging decisions (e.g. van Roosmalen 1985 for *Ateles p. paniscus*; Day and Elwood 1999 for *Saguinus midas*; Spironello 2001 for *Cebus apella*), as well as being a key defence against nocturnally active predators (Chapman 1989 for *A. geoffroyi*; Di Bitelli et al. 2000 for *C. apella*). Sleeping-site choice is thus likely to be multifactorial (Anderson 2000). Primates are often highly selective of their sleeping sites, sometimes choosing very specific tree species that are presumed to maximise predator protection, comfort and social contact (e.g. Heymann 1995 for *Saguinus mystax* and *Saguinus fuscicollis*; Radespiel et al. 1999 for *Microcebus murinus*; Spironello 2001 for *C. paella*; Li et al. 2010 for *Rhinopithecus bieti*; Sousa-Alves et al. 2011 for *Callicebus coimbrai*; Wang et al. 2011 for *Trachypithecus francoisi*; Zhang et al. 2011 for *Rhinopithecus roxellanae*), minimise the distance to the first feeding tree of the following morning (von Hippel 1998) and have a low probability of branch loss under windy conditions (Di Bitetti et al. 2000). For primates living in temperate climes, avoiding climatic stress can also be an important consideration in sleeping-site choice (Anderson 2000; Li et al. 2010; Xiang et al. 2010; Zhang et al. 2011). For species in limestone areas, access to water may also be key (Wang et al. 2011 for *T. francoisi*).

Sleeping-group size may also be influenced by ecology, and disease risk may be affected by group size, for example, malaria infection increases with sleeping group size (Davies et al. 1991; Nunn and Heymann 2005). Blackwater river areas, such as those inhabited by *Cacajao melanocephalus ouakary*, have low densities of malaria-vectoring mosquitoes (Goulding et al. 1988), and uacaris that live on them have low levels of infection (Deane 1992).

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There are only three previous extended studies of uacari ecology (Ayres 1986; Boubli 1997; Bowler 2007), and none furnish data on nocturnal sleeping sites. Although field reports have mentioned briefly the nature of *Cacajao* sleeping sites, there has been no detailed analysis comparable with those undertaken, for example, by Chapman (1989) and Mittermeier (1988) of *Ateles* species sleeping sites. Defler (2004) recorded *C. m. ouakary* sleeping in both flooded and unflooded forests. In the former habitat, *C. m. ouakary* slept on the ends of large strong branches in leafless canopy, up to 15 m above the floodwaters. In the latter habitat, they used trees 25–30 m tall and with a leafed canopy. For *C. c. ucayalii,* Aquino (1998) reported six to seven sleeping animals per tree, at sites mostly in the crowns from 17 to 32 m tall, dispersed across an area up to 2 ha.

Here we report on the characteristics of trees used by *C. m. ouakary* as sleeping sites in the igapó forests of central Brazilian Amazonia, test hypotheses concerning the choice of sites and consider the effects of sleeping-site selection on uacari daily movements. This is the first detailed analysis of sleeping-site choice in a pitheciine species and the first to explore the series of factors potentially involved in sleeping-site selection in a Neotropical flooded forest. It also considers how associated social behaviour might influence sleeping-site choice. The Latin name for the golden-backed uacari follows Hershkovitz (1987), as the precise appellation is currently disputed (vide Boubli et al. 2008; Ferrari et al., 2010).

In particular, we investigate the following predictions:

1. Uacaris are selecting the species of tree used for sleeping, i.e. species used as sleeping trees will not simply occur in the same frequency as they occur in the habitat.
2. Uacaris are selecting their sleeping trees for their physical characteristics, and thus sleeping trees will not simply be a random selection. We predict that the physical characteristics involved will include physical tree size and features related to predator avoidance (proximity to open water, presence of lianas, touching canopies, a canopy that exceeds that of the general uppermost level of the forest, i.e. an emergent tree)
3. Uacaris are selecting trees for features relating to comfort. We therefore predict that sleeping trees will have lower numbers of such features as ant, bee and wasp nests than trees chosen at random.
4. Uacaris are selecting sleeping locations based on branch size or part of the canopy. These locations may reflect a compromise between the risk of nocturnal arboreal and aerial predators. We therefore predict that uacaris will sleep at locations midway between trunk and canopy edge and at sites that maximise the possibility of early detection of aerial and arboreal predators.
5. As noted above, primate sleeping group size has been related to the local risk of malaria. However, blackwater rivers are low risk environments for malaria, and we therefore predict that *C. m. ouakary* will either be clumped in small groups or occur in large widely dispersed groups within the canopy of a sleeping tree.
6. Features of the *C. m. ouakary* time budget indicate it is very time limited (Barnett 2010; Bezerra et al. 2010). Therefore, we predict that uacaris will use time to forage at the expense of resting time and will be active in food-related activities until visual acuity is compromised by sundown, and that they will also begin to forage very soon after sunrise.
7. Based on studies of *Colobus gсветовое*

9 months (generally February to October). The rainy season extends from November to July, with very little rain falling between August and October (Ferreira 1997). Igapó rarely extends more than 200 m from the bank and is a tree community in which flood tolerance structures species composition into longitudinal bands (Parolin et al. 2004). Canopy heights may reach 30 m, which may only be 15 m above water level at peak inundation.

Field protocol

Primate field data were collected over 211 days from 15 months between October 2006 and April 2008. During this time, observation of uacari sleeping trees was achieved on 15 evenings (Table 1). Data were collected from uacaris using three areas of igapó, each separated by water and used by a different group of uacaris. Two of the areas were approximately 2 km long and an average of 200 m wide (approximately 40 ha each); the third was a 78-ha island. Botanical composition was quantified using eight 0.25 ha quadrats within which all plants with a diameter at breast height (DBH) = 25 cm were counted and identified using Gentry (1993), Ribeiro et al. (1999) and specialist floras in the *Flora Neotropica* series (e.g. Mori and Prance 1990 for the zygomorphic Lecythidaceae). Data to determine the characteristics involved in sleeping-tree selection (Table 1) were collected whenever uacaris were observed sleeping in trees or entering them to search for sleeping sites. When foraging or moving, uacaris generally spend <5 min in one canopy area, restricting activities to the outermost third of the canopy.

Preretirement behaviour and group size of the uacaris was recorded ad libitum, as was their post-waking behaviour in the morning before sunset and 45 min after sunrise. Group sizes were recorded for all uacaris that were visible to observers when studying sleeping trees. Because of the relative openness of the igapó habitat, animals up to 250 m away could be seen. Following Symington (1990), a group was operationally defined as two or more animals moving in unison and separated by <25 m. Uacaris have fission–fusion sociality (Bowler and Bodmer 2009), so if several such entities were seen moving in the same approximate direction, then the smaller groups were considered to be subgroups of the larger whole. Between February 2007 and January 2008, data were compiled for a total of 43 uacari sleeping trees. The distribution of observations per month is given in Table 2. Distance measurements >4 m were made with a laser rangefinder (Yardage Pro 450, Bushnell, Overland Park, KS, USA: accurate to 1 m). For primates with sleeping trees in unflooded forests, presence of faeces and seeds under their canopies makes it possible, even in the absence of direct observations, to assess repeated site usage (Chapman 1988a). This is not possible in flooded forest, as currents wash away such debris. Consequently, sites were only recorded upon direct contact, which may have led to underestimation of repeated site use.

Prediction 1 was tested by calculating Ivlev electivity index (Ivlev 1961) for sleeping trees. The Ivlev electivity index compares the relative frequency of species in a sample of used items, with their relative frequency in the habitat in which the animal was using them. Ivelv's electivity index ranges from 1 to +1, with species used by the animal at parity to their relative frequency in the habitat having an Ivlev electivity index of 0. Those in which the frequencies in the used item sample exceed those for the habitat sample are being positively selected and have positive value, and species used at less than parity will have a negative value. Here we compared the frequency of species in the sleeping-tree sample with those in the sample of 1,412 trees present in five 0.25 igapó habitat botanical plots. To test prediction 2 and investigate whether uacaris were selecting larger trees, DBH was measured from trees randomly selected from the igapó quadrat data set ($N = 39$, to match the number of sleeping trees for which DBH was measured). Based on the assumption of uniform transspecies allometric scaling, DBH is widely used as a proxy for canopy size and overall tree height (King 1995). To test whether sleeping-tree location differed from a random sample of trees (a component of prediction 2), we compared distances from the water's edge for the 35 individual sleeping trees for which this data had been recorded with those 119 individual feeding trees where distance to water's edge had been documented. To test prediction 3 (and one component of prediction 2), the cumulative

Table 1 Number of evenings per month when uacaris were encountered in sleeping trees and the number of trees on which data was collected

	Wetter					Drier			
	Dec 2007	Jan 2008	Feb 2007	Mar 2007	Apr 2007	May 2007	Jun 2007	Aug 2007	Sep 2007
No. evenings retiring uacaris encountered	0	1	2	4	3	2	1	1	1
No. sleeping trees recorded	0	3	7	10	9	6	3	4	1
No. trees per evening	0	3	4, 3	2, 5, 2, 1	4, 2, 3	3, 3	3	4	1

Table 2 Data collected for each sleeping tree

Species identity
Diameter at breast height (DBH) (to nearest cm)
Maximum canopy altitude (measured to top of visible canopy)
Maximum canopy diameter
Tree an emergent? (if so, by how much)
Canopy contiguous with that of neighbouring trees
Distance to river (if tree in igapó)
Distance to igapó (if tree in terra firme)
Distance to nearest feeding tree (from the same day's feeding records)
Number of sleeping uacaris
The location of sleeping uacaris in the canopy and distances between them
Tree dead or alive
Presence of lianas
Presence of ant, bee or wasp nests

Table 3 Data collected for each tree during liana survey

Lianas present/absent
If present—density extent (very high, covering >50% of branches; high, covering 25–30% branches; low, 10–24% of branches; sparse, <10% of branch area
Number of lianas—if possible to distinguish
Aerial or terrestrial contact: if any reaching ground or not

frequencies of sleeping trees with ant, bee or wasp nests and those with lianas were compared against those counted on 100 randomly selected trees with DBH $= 100$ cm (Tables 2, 3). Prediction 4 was tested by allocating to one of six site categories the location within the tree at which each individual uacari was observed to sleep (within one body length of main trunk; crotch of large vertical branch; crotch of large horizontal branch; on large horizontal branch, middle third; on large horizontal branch, outer third; at branch–twig interface). To test prediction 5, the number and dispersion of primates observed sleeping was recorded. Infants were not counted separately, as their behaviours were not independent of those of their mothers. To test prediction 6, it was necessary to correct for the fact that sunset does not (even in the tropics) occur at exactly the same time each day. Accordingly, the chronometric times at which individual uacaris had been recorded entering a sleeping tree to settle were recalculated as minutes before sunset on the day of observation, using http://www.usno.navy.mil/USNO/astronomicalapplications/data-services/rs-one-year-world (Table 4). To test prediction 7, we recorded the distance between the final evening feeding tree and the sleeping site and the distance between that sleeping site and the first morning feeding tree of the next day ($N = 7$).

Table 4 Uacari entry times into sleeping trees

Minutes before sunset	No. of records
26–30	1
21–25	9
16–20	13
11–15	24
6–10	5
0–5	0

To test prediction 8, that *C. m. ouakary* foraging groups come together at night, we compared (Mann–Whitney *U* test) the size of all groups observed within 250 m of sleeping trees for 45 min before sunset with those observed within the same space 45 min after sunrise. To test prediction 9 (characteristics of sleeping sites will vary seasonally), we compared the mean DBH (chi-squared), rank order of species used as sleeping trees (Spearman's rank correlation: species with fewer than three records excluded), and mean distance from the water (chi-squared) for two periods of the year. The number of observations and number of evenings on which sleeping-tree data were collected were not of equal frequency across the months (Table 1). To provide sufficiently large samples for statistical analysis, these were made by grouping the records into wetter months (December–April: mean monthly rainfall >275 mm, range 240–325) and the drier months (May–November: mean monthly rainfall 100 mm, range 30–190: Ferreira 1997). Records for these two periods are given in Table 5.

Results

All 43 documented sleeping trees were in igapó and were recorded in 15 sites over 15 nights. Complete numerical data sets were obtained for 39 trees. A total of 62 adult or subadult uacaris were observed in sleeping trees (as uacaris could not be individually recognised, some individuals may have been sampled more than once). Uacaris slept in 16 types of tree (14 identified to species). All were living trees. The time at which uacaris entered the sleeping tree was recorded for 52 individuals, all of which were seen entering trees to sleep within 30 min before sunset. The earliest entrance was 28 min before sunset, the latest 5 min before (Table 4). Of the 43 sleeping trees, only six (14%) were within 200 m of a tree previously used for sleeping. Uacaris were never recorded re-using sleeping trees. Sleeping uacaris rarely used adjacent trees (three records). Mean distance between the two sleeping trees used by uacaris on the same night was collected for 18 pairs of trees. The mean distance between them was greater than

Table 5 Summary of statistical tests on sleeping-tree data collected in different seasons

	Wetter season	Drier season	Statistical test	Test result
DBH (cm)	Mean = 120.2	Mean = 125.2	Mann–Whitney *U* Test	$U = 188.5$
	SD = 39.78	SD = 31.1		$z = 0.581$
	$N = 26$	$N = 13$		$p = 0.561$ (2-tailed)
Rank of species used (number of trees)	1 (9), 2 (3), 3 (2), 4 (2), 5 (2), 6 (1)	1 (4), 3 (3), 4 (2), 2 (2), 5 (1), 6 (1)	Spearman's rank correlation	z test = −1.149 $p = 0.25$
Distance to open water (m)	Mean = 20.6	Mean = 16.9	Mann–Whitney *U* test	$U = 182.0$
	SD = 11.28	SD = 15.6		$Z = 1.331$
	$N = 13$	$N = 23$		$p = 0.561$ (2-tailed)

DBH diameter at breast height, *SD* standard deviation

the mean distance between each of the 36 trees and the ten trees closest to them (mean between sleeping trees 81.4 m, range 17–215 m; mean between sleeping trees and nearest ten neighbours 5.7 m, range 0.5–18.3). This is statistically significant (Mann–Whitney *U* test, $z = 5.79$, $U = 656.0$, $p < 0.001$, 2-tailed). In consequence, the area encompassed by a sleeping group of uacaris could be substantial and, on two occasions it was estimated that five uacaris were dispersed over an area of some 1,000 m^2. Uacaris, therefore, slept at very low densities. Uacaris did not vocalise from the recorded sleeping trees, and though it was not quantified, calling rates were noted to drop markedly as dusk approached. Uacaris began calling as soon as it was fully light, but, unlike other primates at Jaú, were not observed to sunbathe or groom extensively on waking. Results are given below aligned with the seven predictions and two additional tests outlined above.

Prediction 1: selection of species

Of the five species of which more than two individuals were recorded (Table 6), two were selected almost in proportion to the environmental frequency *Amanoa longifolia*, Ivlev electivity index 0.06, and *Eleoluma glabrescens*, 0.05), and three were highly selected with values >0.7 (*Ormosia paraensis, Hydrochorea marginata; Hevea spruceana*). Nearly all tree species have positive values, with the only negative values being for trees that were recorded as sleeping trees only once (Table 6). This suggests that uacaris positively select (at least some) sleeping-tree species.

Prediction 2: selection of physical characteristics of trees

Sleeping-tree mean DBH was 121.9 cm [standard deviation (SD) 37.6, range 63–210, $N = 39$], whereas mean DBH for 39 randomly selected trees was 52.9 cm (SD 22.8, range 25–110). The trees selected as sleeping sites therefore had a significantly larger DBH than those in the random sample (Mann–Whitney *U* test, $z = 7$, $U = 1461.5$, $P < 0.001$, 2-tailed). Trees exceeding the mean selected size for sleeping trees are uncommon in igapó; in this study they constituted only 3.5% trees in a 0.25-ha igapó forest sample covering interior and forest edge ($N = 30/867$ trees). In the flooded forest, these can be furnished by the permanent forest edge at the forest–river interface, or more ephemeral sites such as clearings created by large tree falls: both have extensive areas of adjacent canopy absence. Such areas could, at least, limit the directions for predator attack. Of the 19 sleeping trees within 5 m of a water–forest edge, 14 were emergents. Of the total 43 sleeping trees, 31 were emergents. The emergents used as sleeping sites had a canopy that was, on average, 3.75 m above the surrounding canopy (SD 1.8, range 1–8). The mean distance of the feeding trees from the water's edge was 84.3 m (SD 79.4, range 0–400 m), and that of the sleeping trees was 18.3 m (SD 15.8, range 0–50 m). This is significantly different (Mann–Whitney *U* test; $z = 6$, $U = 3487.0$, $p < 0.001$).

To test whether sleeping trees were more concentrated at the forest margin simply because more large trees were present there, DBH of the 39 largest trees in the quadrats along the igapó forest edge was compared with the largest 39 trees from a study quadrat within the igapó forest. Though the interior quadrat sample had slightly larger mean DBH (128.6 cm, SD 24.2, $N = 39$) than those from the flooded forest edge (125.5 cm, SD 23.9, $N = 39$), the differences were not significant (Mann–Whitney *U* test: $z = 1$, $U = 846$, $p > 0.05$, 2-tailed test). The number of large (>90 cm DBH) trees in two 0.25-ha plots (combined) in the igapó interior was compared with those in the 0.25-ha forest plot at the igapó margin. There were 115 (13.9%, $N = 829$) such trees in the former and 51 (10.8%,

Table 6 Sleeping trees: species, frequency and selection ratios

Sleeping-tree species	No. records	Percent of sleeping-tree sample (A)	No. in igapó quadrats	Percent of igapó quadrats (B)	Ivlev electivity index	Selection ratio A/*B*
Hydrochorea marginata (Fabaceae)	13	30.2	59	4.1	0.762	7.42
Amanoa oblongifolia (Euphorbiaceae)	5	11.6	150	10.3	0.058	1.12
Ormosia paraensis, (Fabaceae)	5	11.6	14	1.0	0.847	12.08
Eleoluma glabrescens (Sapotaceae)	3	7.0	92	6.3	0.048	1.10
Hevea spruceana (Euphorbiaceae)	3	7.0	15	1.0	0.743	6.7
Sclerolobium hypoleuca (Fabaceae)	3	7.0	41	2.8	0.424	3.16
Ocotea sp. (Lauraceae)	2	4.6	4	0.3	0.890	17.18
Pouteria gomphifolia (Sapotaceae)	1	2.3	7	0.5	0.657	4.8
Swartzia acuminata (Fabaceae)	1	2.3	1	0.1	0.950	38.66
Poutera elagans (Sapotaceae)	1	2.3	147	10.1	−0.627	4.36
Acosmium nitidum (Fabaceae)	1	2.3	13	0.9	0.445	2.6
Eschweilera tenuifolia (Lecythidaceae)	1	2.3	137	9.4	−0.605	0.24
Aldina laevicarpa (Fabaceae)	1	2.3	2	0.1	0.886	16.57
Homalium guianense or *H. racemosum* (Flacourtiaceae)	1	2.3	21	1.4	0.234	1.44
Unknown (but the two not conspecific)	2	4.6	–	–	–	–

A tree used by multiple uacaris is counted once

$N = 472$) in the latter. The difference was not significant ($\chi^2 = 0.028$ with $df = 1$, $p > 0.05$).

In addition to being larger than average, and more likely to be close to a water–forest margin, sleeping trees were less likely to have lianas when compared with a random sample of 100 large (=100 cm DBH) trees in igapó, ($N = 39$, 39% of random sample vs. $N = 3$, 7% of sleeping trees: $\chi^2 = 9.1$ with $df = 1$, $p < 0.01$). Sleeping trees were also less likely than average to possess a canopy touching that of another tree, whereas 86% ($N = 86$) of random trees had canopies that touched other trees, this occurred in only 16% of sleeping trees ($N = 7$: $\chi^2 = 19.419$ with $df = 1$, $p < 0.0001$). Therefore, uacaris are choosing trees that are larger, closer the to water's edge and lack lianas and contiguous canopy. The null hypothesis is rejected and active choice is supported.

Prediction 3: features relating to comfort

Uacaris were significantly ($\chi^2 = 3.87$ with $df = 1$, $p < 0.05$) less likely than average to use trees that had wasp or ant nests: these occurred on nine of the 100 random sample large trees but in none of the sleeping trees. Thus, uacaris appear to use potential comfort as a criterion in sleeping-tree selection. Unlike other primates (e.g. Fan and Jiang 2008: *Nomascus concolor jingdongensis*; Li et al. 2010: *Rhinopithecus bieti*; Phoonjampa et al. 2010: *Hylobates pileatus*), uacaris were never observed to rest on top of epiphytic plants.

Table 7 Where uacaris slept in the tree

Location	No. of records	Percent total records
By main trunk (within 1 body length)	5	8.3
In crotch of large vertical branch	3	5
In crotch of large horizontal branch	18	30
On large horizontal branch (middle third)	5	8.3
On large horizontal branch (outer third)	16	26.7
At branch–twig interface	13	21.7
Total	60[a]	100

[a] Data for two individuals has been lost

Predictions 4 and 5: dispersion and group size in canopy

Nearly half of sleeping records (48.3%, $N = 29$) came from the outer third of the branches (Table 7). There were no records of uacaris sleeping within the terminal branching sector of the canopy, and very few records close to the trunk. The distribution is not equal across all locations ($\chi^2 = 20.80$, $df = 5$, $p = 0.0009$), and the null hypothesis is rejected. Over 40% of records were of uacaris sleeping singly in trees, a highly dispersed situation (Table 8). The remainder were separated by 0.5–6 body lengths (30–360 cm), with nine (35%) of the multiple occupancies involving branch sharing. Our prediction is not confirmed: uacaris neither clump nor occur in

Table 8 Number of sleeping uacaris per tree and their dispersion patterns

No. of sleeping individuals	Records % (N)	Mean interindividual distance in body lengths and range	Mean interindividual distance in M^a (cm)	No. records with individuals on same branch (L) II different branch (ES) (R)
1	40.3 (25)	–	–	–
2	11.3 (7)	2.1 (0–6)	83	2/5
3	6.4 (4)	3 (1–5)	120	4/8
4	1.6 (1)	4.5 (4–6)	180	2/2
5	1.6 (1)	0.5 (0–0.5)	20	5/0
Adult female and infant	3.2 (2)	–	–	–

[a] Mean adult body length = 40 cm (Hershkovitz 1987)

large dispersed groups within a canopy. For some primates, females with young may choose different sleeping trees with different characteristics than those chosen by other group members (Anderson 1998, 2000). However, the sample of female uacaris with young (two of 62 sightings, 3.2%), is too small for statistical analysis. The failure to record more females in this category may indicate that, as with other primate species (Anderson 1998, 2000), female uacaris with young may be choosing more concealed sleeping sites.

Prediction 6: retiring times

As predicted, uacaris appeared to feed for as long as possible. Latency from last feeding bout to entry into a sleeping tree was short. Though the latency was quantified on only 11 occasions, the values (mean 32 s, SD 7.6) are low. This may have been because the last feeding tree of the day was often close to the tree the uacari slept in (60% within 20 m, 33% within 10 m, $N = 15$). Entry time into sleeping trees was recorded on 52 occasions [42 of the 62 individuals for which sleeping position was recorded (Table 7), plus ten additional uacaris, the determination of whose sleeping sites was prevented by thick vegetation]. Uacaris were only once seen in the sleeping trees earlier than 25 min before sunset, and individuals were occasionally recorded feeding within 20 min of sunset (nine records). The majority (71.1%, $N = 37$) of records of uacaris entering sleeping trees were obtained between 11 and 20 min before sunset (Table 4), though the small number of records between 10 min and sunset could partly have been due to viewing conditions. Mean time of entering sleeping tree was 15.8 min before sunset (SD 4.6, $N = 52$). Uacaris were active as soon as there was light to see by, with individuals being observed on 23 occasions to move quickly out of the sleeping tree and begin, in all cases, to feed in <60 s after leaving the sleeping tree. No uacari was seen in a sleeping tree >7 min after sunrise.

Prediction 7: food proximity as a sleeping-tree determinator

The distance from sleeping tree to first morning feeding tree (mean 12.14 m, SD 9.11 m, $N = 7$) was less than the distance from final evening feeding tree to sleeping site (mean 18.2 m, SD 10.8 m, $N = 15$), but the result was not significant (Mann–Whitney U test, $Z = 67.5$, $p = 0.305$, $N = 22$). This rejects the null hypothesis and provides no evidence that uacari sleeping trees are chosen for their proximity to feeding trees. Although all of the 14 tree species serving as uacari dormitories also furnished food (either fruits, seeds, leaves or flowers), we only observed two instances of uacaris feeding in a tree in which they had just slept (*Eschweilera tenuifolia* and *E. glabrescens*).

Prediction 8: foraging groups fuse at night

Sizes of uacari groups observed within 250 m of sleeping trees during the 45 min before sunset were significantly larger than those encountered within 250 m of sleeping trees during the 45 min after sunrise (Mann–Whitney U test, $U = 91.5$, $z = 2.75$, $p < 0.01$, two-tailed: evening groups, mean 18.3, SD 13.1, range 3–40; morning groups, mean 4.4, SD 1.8, range 2–7). This is interpreted as confirmation of sightings of small uacari bands joining to form bigger groups in the hour before dark.

Prediction 9: effects of seasonality

The rank correlation test was conducted on 32 trees (20 from wetter months, 12 from drier months, six species in both). Results show that data collected in the two seasons were statistically indistinguishable (Table 5).

Discussion

Results indicate that at Jaú, *C. m. ouakary* come together at night. How these accumulations of uacaris are coordinated remains to be determined. However, similar events have been observed for *Pithecia monachus*, where several otherwise separate family groups will come together to sleep in the same tree at night (Moynihan 1976). In Colombia, Defler (2004) reported both igapó and terra firme sleeping sites for *C. m. ouakary*. However, at Jaú, we were unable to track uacaris to their sleeping sites during November–January, when they were in terra firme. So, though multiple factors are likely to influence sleeping-site choice (Anderson 1998, 2000), we can only examine those operating when uacaris were active in igapó. Below, we cast these factors in terms of three principal influences: food proximity, parasitic infection avoidance, and predation risk reduction. We also consider those behaviours that, once the sleeping structure has been chosen, further reduce the risks of predation and parasitism.

Breakfast in bed? Food proximity and sleeping-tree choice

Perhaps because of the late feeding (see prediction 6), the last feeding tree of the day was often close to the sleeping tree. This may indicate that uacaris are adopting a strategy of within-forest movement that brings them, near sunset, into contact with a pair of sleeping and feeding trees in close proximity, permitting one final feeding bout before retiring. Such strongly determined forms of movement have been recorded for other primates (e.g. Normand and Boesch 2009 for *Pan troglodytes*), and a thorough mapping of trees within a group's home range will permit the determination of their presence in uacaris.

Von Hippel (1998) proposed a resource-based hypothesis for primate sleeping-tree choice in which trees are chosen either because they are close to trees that can be fed in next morning or because they can be both slept and fed in. The current study did not find first morning feeding trees to be closer to sleeping trees than the last feeding tree of the previous evening. Additionally, *H. marginata*, the tree most frequently slept in, was a minor diet item, and uacaris fed only twice in the tree in which they had slept. We conclude that immediate proximity to food is not a prime consideration in uacari sleeping-tree choice.

Avoidance of parasites

Several studies (e.g. van Roosmalen 1985 for *A. paniscus*; Chapman 1988a, b for *Alouatta paliata* and *A. geoffroyi*; Di Bitetti et al. 2000 for *C. apella*) have recorded multiple individuals sleeping simultaneously in the same tree, each on its own branch. Numbers involved generally varied in direct relation to the size of the occupied crown. This was not the case with adult or adolescent *C. m. ouakary* in our study, as they mostly slept alone (65.5% of records). In the 14 records when multiple adults were in the same canopy, they were, with one exception when five individuals clustered together, widely spaced and occupying different branches. The significance of such solitary and dispersed sleeping remains to be researched, but it may reflect a balance between avoiding two night-time dangers: predators and disease-vectoring haematophagous insects. On whitewater rivers, the overpowering prevalence of biting insects means that sleeping primates cluster for protection. Blackwater rivers, such as the Jaú, are noted for low mosquito populations (Goulding et al. 1988). So, freed from the need to cluster to minimise the chance of being bitten, sleeping uacaris may well disperse either to cryptically minimise being discovered by predators or to maximise the change of individual escape. Though this does agree with the position of Davies et al. (1991), who reported a positive relationship between primate sleeping group size and rate of malaria infection, it also supports Nunn and Heymann (2005), who pointed out that the situation is more complex than mere numbers and that quantifying group spread and classifying spatial arrangements (e.g. clustered vs. dispersed sleepers) may also be key. Here, in a situation of low malarial risk, individuals form both very small groups and are widely dispersed, one extreme of the continuum posited by Nunn and Heymann (2005).

Avoidance of predators

Likely nature of C. m. ouakary predators

If sleeping trees function as defensive redoubts, their height and architecture and dispersion of the primates within them might logically be expected to reflect the predator types most likely to attack. Mammals (including other primates), birds and snakes all predate Neotropical primates (Ferrari 2009; Sousa-Alves et al. 2011). Five primate-eating felids occur at Jaú (jaguar *Panthera onca*, jaguarondi *Puma yagouaroundi*, margay *Felis weidii,* ocelot *Leopardus pardalis,* puma *P. concolor*: Calleia et al. 2008), as do tayra (*Eira barbara*: Mustelidae), and large snakes such as Boa constrictor (both known primate predators: Bezerra et al. 2009; Ferrari et al. 2004). However, flooded igapó is not a predator-rich environment (Gudger 1946; Wallace et al. 1998; Haugaasen and Peres 2007). Jaguar, for example, rarely enter it, as their main prey base (terrestrial medium-sized mammals: Seymour 1989; De Oliveira 2002) are absent or at lower densities than in adjacent terra firme (Bodmer 1990; Haugaasen and Peres 2005). Yet *C. m. ouakary* sleeping sites appear to maximise nocturnal predator avoidance. The tayra, and tree hunting felids such as margays, are too small to take any but the youngest uacaris (Emmons 1987; Calleia et al. 2009). However, as adult primates show strong offspring defense against smaller nocturnal mammalian carnivores (Shahuano Tello et al. 2002; Broom et al. 2004; Harris 2007), predation risk from these species as a potential structuring factor in sleeping-tree choice in uacaris (and other primates) should not be neglected.

Though diurnal raptors attack uacaris (Barnett et al. 2011), such attacks most frequently occur in full daylight (Touchton et al. 2002) and so are unlikely to influence sleeping-site choice. Attacks by owls, however, may be a factor; the two largest Neotropical owls (crested owl, *Lophostrix cristata* and great horned owl, *Bubo virginianus*) inhabit lowland rainforest. Though owls are known predators of Old World primates (Isbell 1994; Hart 2007), evidence for their predation on Neotropical species is sparse; Wright (1989) reported *B. virginianus* preying upon *Aotus*, and Rehg (2006) listed *L. cristata* among potential predators of three tamarin species. *Lophostrix cristata* has been recorded at Jaú (Borges et al. 2001), and could be capable of taking a small (or juvenile) primate, but as one of the world's least well-known owls (Barros and Cintra 2009), its feeding ecology is completely unstudied. *Bubo virginianus*, however, regularly takes prey exceeding 3 kg (Zimmerman et al. 1996). Accordingly, the possibility cannot be discounted that the threat of owl predation may contribute to structuring uacari sleeping-tree choice.

Location in determining selection of sleeping trees

Trees in which uacaris slept were significantly more often within 5 m the interface between igapó and open water than the random tree sample. Matsuda et al. (2010) reported *Nasalis larvatus* in Bornean riverine forests choose similarly and considered this maximised protection against terrestrial and arboreal predators, which must approach from landwards, enhancing primate opportunity to perceive and avoid them. However, in the flooded forest habitats of *Nasalis* and *Cacajao*, dropping into the water to escape nocturnal arboreal predators may not be a secure option; though both are competent swimmers (Matsuda et al. 2008, *Nasalis*; Barnett, unpublished data, *Cacajao*), the presence in both habitats of large Crocodilia (*Crocodylus porosus* for *N. larvatus*, *Caiman crocodilus* and *Melanosuchus niger* for *Cacajao*) would be a disincentive. All are primarily nocturnal carnivores (Stuebing and Sah 1996 for *C. porosus*; Marioni et al. 2008 for *C. crocodilus*, *M. niger*). Direct predation of primates by Crocodilia has yet to be observed in the Neotropics, but crocodile predation has been reported on primates in Borneo (Galdikas and Yeager 1984 on *Macaca fascicularis,* and Galdikas 1985 on *N. larvatus*), and Boonratana (2000) recorded avoidance behaviour of *N. larvatus* towards *C. porosus*. In Africa, crocodiles are often listed as potential primate predators (e.g. Collins 1984; Condit and Smith 1994), and supportive evidence appears in an unpublished video of a young *Papio* escaping a crocodile attack at an African waterhole: http://mais.uol.com.br/view/e8h4xmy8lnu8/macaco-x-crocodilo04026AC8996366?types=A.

Tree-canopy structure in determining selection of sleeping trees

Three species, *H. marginata, O. paraensis* and *H. spruceana*, had an electivity index that suggested active selection by uacaris. All have broad open canopies, clean wide horizontal limbs, and a branching pattern that furnishes an uncluttered interior. This form appears attractive to a variety of Neotropical primates (e.g. Mittermeier 1988 for *Ateles;* Di Bitetti et al. 2000 for *Cebus*; Sousa-Alves et al. 2011 for *C. coimbrai*) Uacaris selected either large or emergent trees, a preference commonly recorded for primates (e.g. *Papio*, Hamilton 1982; *Cebus*, Di Bitetti et al. 2000, Wahungu 2008; *Propithecus*, Wright 1998; *Rhinopithecus*, Zhang et al. 2011: see; Anderson 1998, 2000 for reviews). Their use is generally considered both a predator avoidance strategy and a means of gaining maximum warning of a predator's impending arrival (Wright 1998; Anderson 2000). In addition, trees selected by *C. m. ouakary* tend to lack lianas, ant and wasp nests, are close to open water and have crowns not touching those of neighbouring trees. All but nest avoidance could most parsimoniously be interpreted as being associated with trees offering the highest protection against nocturnal arboreal mammalian predators. Additionally, the absence of social hymenoptera nests from uacari sleeping trees may be due to other factors: for many ants and wasp species, nest-site location criteria appear highly specific (e.g. Cruz et al. 2006; Diniz and Kitayama 1994; Djieto-Lordon and Dejean 1999) and may simply be overlapping minimally with those employed by uacaris, giving an false impression of linked events.

Though we cannot discount the possibility that uacaris changed position within the canopy after dark, the majority of *C. m. ouakary* were observed to, at least begin, sleeping in the outer third of large horizontal branches, or at branch–twig interface. This could represent a compromise between avoiding attacks by arboreal and aerial predators. *N. concolor* also displays such a preference, which potentially provides (by vibration) an early-warning system against approaching predators (Fan and Jiang 2008). *Semnopithecus entellus* and *T. johnii* langurs sleep alone on horizontal branches away from the main trunk, possibly to aid detection of heavier arboreal predators such as leopards (Ramakrishnan and Coss 2001). As found in our study, *P. diadema* arranges resting sites to interpose voluminous foliage between themselves and potential aerial predators

(Wright 1998). Also as found in our study, *N. concolor* and *H. pileatus* avoid trees with lianas when choosing sleeping sites (Fan and Jiang 2008; Phoonjampa et al. 2010). The authors of this research believed this impeded predator access and lianas can certainly play an important role in felid attempts at primate predation (Calleia et al. 2009).

Whereas our study found a preference for sleeping trees with canopies not touching those of neighbouring trees, other studies found exactly the opposite (Fan and Jiang 2008; Matsuda et al. 2010; Phoonjampa et al. 2010) and proposed contiguous canopies provide easy nocturnal escape routes. Locomotion form may explain the differences: Fan and Jiang (2008) and Phoonjampa et al. (2010) studied nonleaping brachiating hylobatids, Matsuda et al. (2010) studied the heavy-bodied *N. larvatus*, which does not leap far. In contrast, uacaris, like other pitheciines, are great leapers (Walker 1996), with single saltations commonly exceeding 5 m (Barnett unpublished data). The substantial between-canopy gaps separating sleeping trees from their neighbours may permit uacaris to exploit these locomotor advantages. In addition, gaps could force potential predators to leap, invoking the vibratory warning hypothesis of Fan and Jiang (2008).

Retiring time

Many primates stop feeding and enter sleeping trees up to 160 min before dusk (*H. lar*, Reichard 1998; *N. concolor*, Fan and Jiang 2008; *N. larvatus*, Matsuda et al. 2010; *C. coimbrai*, Sousa-Alves et al. 2011), with primates entering sleeping trees not synchronously but over an extended period. Fan and Jiang (2008) believe this may conceal sleeping sites from potential predators. However, *C. m. ouakary*, like *C. c. ucayalii* (Swanson-Ward and Chism 2003), continues feeding almost until sunset. This may be a consequence of a highly time-limited foraging strategy to which much, including social interactions and grooming, appears to have been sacrificed (Barnett 2010; Bezerra et al. 2010). Entering close to sunset may also conceal sleeping sites.

Calls at sleeping sites

A. geoffroyi subgroups appear to coordinate sleeping activities with contact calls (Chapman 1988a, b). At Jaú, uacaris at sleeping trees were notably quiet, uttering very few of their otherwise near-incessant twitter and chock calls (Barnett 2010). No contact calls were heard. Similar quietude is widely recorded (Dawson 1979 for *S. geoffroyi*; Bowler 2007 for *C. c. ucayalii*; Fan and Jiang 2008 for *N. concolor*; Zhon et al. 2009 for *T. francoisi*), and may conceal sleeping sites from predators (Fan and Jiang 2008).

Repeat usage and choice of sleeping sites

Though uacaris were not recorded using sleeping trees more than once, broad temporal gaps between re-use are known to be extensive in certain species (Smith et al. 2007). It is possible that, like *A. geoffroyi* (Chapman 1988a, b), *C. m. ouakary* may sequentially use a series of very widely spaced trees, returning to individual trees after several days absence, whenever they forage again in an area. The exacting nature of the uacaris' choice criteria for sleeping trees, plus their rarely sleeping more than three to a tree, makes this more probable. Subgroups rejoin at night, so a group of 15–40 sleeping individuals would require several trees. Chapman (1988a, 1988b) reported *A. geoffroyi* subgroups also tended to fuse prior to entering sleeping sites. Heymann (1995) considered not using the same tree on sequential nights to be a predator avoidance strategy. But, for uacaris, at least, it may be a consequence of their foraging strategy and the fact that the very specific suite of characters uacaris appear to favour for their sleeping trees is probably rarely met at a day's end, even within a range as extensive as that of a *C. m. ouakary* troop.

In this study, we have shown that uacaris display behaviours that can be attributed to crypsis and enhanced predator detection. In addition, they are highly selective of the architecture, location and characteristics (absence of lianas and touching canopy) of their sleeping trees. Appropriate trees are not common and, as noted by Anderson (1998, 2000) for primates in general, disposition of such trees could, therefore, be of extreme importance in structuring *C. m. ouakary* foraging and general patterns of forest use. As noted by Moraes and Chiarello (2005, p. 842) for another Neotropical arboreal mammal, the woolly mouse opossum (*Micoureus demerarae*): "We sometimes tend to overestimate the importance of food sources for the survival of individuals in a particular forest site, not considering that other types of resources such as shelters or sleeping sites might be equally important". We believe this is also true for primates, and consequently, studies of sleeping trees should be a high priority for future uacari research.

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