

**Long term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*)  
and mustached tamarins (*S. mystax*)**

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**Abbreviated title: Sleeping site use in wild tamarins**

**Number of text pages: 28**

**Number of figures:**

**Number of tables:**

**Grant sponsorship:** Biotechnology and Biological Sciences Research Council,  
Deutsche Forschungsgemeinschaft and the University of Reading, UK.

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## **ABSTRACT**

Sleeping sites are an important aspect of an animal's ecology given the length of time that they spend in them. The sleep ecology of wild saddleback and mustached tamarins is examined using a long-term data set of observations of three mixed-species troops and more than 1,300 tamarin nights. Seasonal changes in photoperiod accounted for a significant amount of variation in entry and exit times to and from sleeping sites. Time of exit was more closely correlated with sunrise than time of entry was with sunset. Both species entered their sleeping sites when light levels were significantly higher than when they left them in the morning. Troops of both species used >80 individual sites, with the majority being used once. The pattern of reuse was similar for both species, with the exception of consecutive reuse; mustached tamarins never used the same site for more than two consecutive nights, but saddlebacks reused the same site for up to four consecutive nights. Mustached tamarins slept at significantly greater heights than saddleback tamarins. There were consistent interspecific differences in the types of sites used, with saddlebacks never using branches and mustached tamarins never using hollows. Neither the presence of infants, season nor rainfall affected the types or heights of sites chosen. Sleeping sites were located in the central area of exclusive use more often than expected, and their position with respect to fruiting trees indicated a strategy closer to that of a multiple central place forager than a central place forager for both species. These findings are discussed with reference to the ecology of these species, with particular reference to predation risk which is indicated as the major factor influencing the pattern of sleeping site use in these species.

The importance of sleeping sites as a potentially limiting resource for many primate species has been known for some time (see Anderson 1984; 1998 for reviews). Species for which their importance has been observed include both forest living species e.g. Central American spider monkeys (*Ateles geoffroyi*) (Carpenter, 1985), talapoin monkeys (*Miopithecus talapoin*) (Gautier-Hion, 1970) and golden lion tamarins (*Leontopithecus rosalia*) (Coimbra-Filho, 1978) and savannah and open grassland living species, e.g. baboons (*Papio* spp.) (Washburn and deVore, 1961; Patterson, 1973; Altmann, 1974; Hamilton *et al.*, 1976). Consequently sleeping sites may have been as important an aspect of the ecology of early hominids as they are today for anthropoid primates.

The choice of where to sleep on a given night and the pattern of reuse of sleeping sites may be affected by predation pressure, the distribution of food resources or the need to defend a home range. The relative influence of these factors on the Long term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*).

Further, Heymann (1995) outlined their importance to callitrichids, noting that in accordance with many other mammals (Meddis, 1983) they typically spend over half of their lives in them. With an active period of approximately 10 hours (Yoneda 1981; Ramirez, 1989; Buchanan-Smith, 1991; Smith, 1997), tamarins (*Saguinus* spp.) spend 14 hours in their sleeping site. Consequently, predation and other pressures, e.g. comfort, would be expected to have a significant influence on the choice of the location in which to spend such a relatively long period. This may be particularly true for callitrichids as not only do they face a wide range of predators (Moynihan, 1970; Terborgh 1983, Sussman and Kinzey, 1984, Peres, 1993) but many cats, mustelids, snakes and owls, are crepuscular or nocturnal.

Further, callitrichids reduce their body temperature and heart rate whilst sleeping (Hetherington, 1978; Thompson, 1988; Thompson, 1991; Schnell and Wood, 1993; Thompson *et al.*, 1994) and although this may be an important energy-saving mechanism

(Thompson *et al.*, 1994) many researchers have reported both wild and captive callitrichids to be “sluggish”, “inactive”, “torpid” or otherwise “difficult to arouse” at night (Moynihan, 1970; Hampton, 1973; Dawson, 1976; Coimbra-Filho, 1978; Petry *et al.*, 1986; Erkert, 1989; Thompson *et al.*, 1994). Such an inert state would greatly reduce the ability to detect and react to a predator. Hence, it may be important for callitrichids to sleep in sites that are as safe from predation as possible. There are three main ways in which an animal may minimize the threat of predation whilst in its sleeping sites; through the selection of sites with particular physical characteristics, behavior prior to entering a sleeping site, and the pattern with which sites are reused.

The choice of sleeping sites with particular physical characteristics may both reduce the probability of being detected and increase the probability of detecting a predator before it attacks. Whilst almost all of the types of sleeping site reported for callitrichids can be assigned to one of the 5 categories used by Heymann (1995), namely: palms, hollows, tangles, crotches or branches, there is no single type that is consistently common to either different species, or to the same species at different locations. For example, Heymann (1995) notes that whilst one subspecies of saddleback tamarins (*Saguinus fuscicollis weddelli*) uses ivy covered tree trunks and hollows of tall trees (Yoneda 1984b) another subspecies (*S. f. illigeri*) used crotches or proximal parts of branches (Soini 1987). In addition, whereas Soini’s main study group were not observed to use tree hollows, a smaller group was. Similar contradictory findings concerning use of holes have been reported for pygmy marmosets (*Cebuella pygmaea*) (Izawa 1979; Moynihan 1976; Soini 1988). If these differences between studies are due to factors specific to a particular habitat then it may be expected that groups of the same species occupying the same habitat would show similar preferences in their choice of sleeping sites.

Any behavioral adaptations which prevent the drawing of a predator’s attention to its prey’s sleeping sites would be advantageous (Caine, 1987). For example cryptic behavior prior to entering a sleeping site has been reported for a range of primate species from white-handed gibbons (*Hylobates lar*) (Reichard 1998) to several species of callitrichids (Heymann, 1995; Day and Elwood 1999). Rapid movement towards and reticence to enter sleeping sites or behavior analogous to an attempt to shake off a predator in the presence of

observers have also been repeatedly described for tamarins (Dawson, 1976; Neyman, 1978; Terborgh, 1983; Ramirez, 1989) illustrating their efforts to keep their sleeping sites unknown to predators. Further, anecdotal reports (Neyman, 1978; Dawson, 1979; Heymann, 1995) and empirical studies of captive (Caine 1984) and wild tamarins (Smith et al 2004) showing elevated levels of vigilance prior to entering sleeping sites are indicative of a high predation risk at this time.

The pattern with which individual sleeping sites are used may influence their detectability to predators. It has been suggested that species under high predation pressure, such as callitrichids, may be expected to change their sleeping sites more frequently (Goodall, 1962; Blaffer-Hrdy, 1977). Such a strategy would reduce the likelihood of a predator either associating a particular location with the sleeping site of its prey (Franklin 2004) or of developing a search image for a particular sleeping site (Sonerud 1985). Further, infrequent reuse of sleeping sites may minimize the build-up of odours which predators may cue to (Reichard 1998; Banks et al 2000; Franklin 2004). Indeed as Franklin (2004) notes birds using newer nest sites or nest boxes that had been moved have a higher breeding success (e.g. Sonerud 1985; 1989; Nilsson et al 1991). Alternatively reusing the same sleeping sites may allow more efficient detection of resident predators (Dow & Fredga 1983) and provide a better knowledge escape routes (Struhsaker 1967; Di Bitetti *et al* 2000). Behavior whilst entering, in, or leaving a sleeping site may influence the pattern of reuse. For example if a species behaves in a way which may draw the attention of a predator to the area, such as through calling from a sleeping site, then it may be expected to change sites more frequently than one which does not. This hypothesis lead Ramirez (1989) to suggest that tamarins which give contact calls to reform mixed-species associations may be expected to switch sleeping sites more frequently than those which do not. Following Norconk's (1990) finding that mustached tamarins called earlier than their associating saddlebacks it may be expected that they would be under greater pressure to either use more sleeping sites or to reuse them less frequently, although it should be noted that other workers (Heymann 1990; Peres 1991; Smith 1997) have reported both species to be equally likely to give the first call prior to reforming the association.

Predation may not be the only factor influencing the use of sleeping sites, body size, social organisation, the need for thermoregulation, protection from adverse weather and reproductive state may all affect the choice of sites (Chivers 1974; Dawson 1979; Aquino & Encarnación 1986; Kappeler 1998; Anderson 2000). Although tree holes may provide thermoregulatory benefits compared to other types of primate sleeping site, size constraints may restrict their use to smaller taxa. Indeed whilst noting exceptions, Kappeler (1998) predicts that tree holes will be used more frequently by smaller taxa. Mixed-species troops of tamarins allow this to be tested without the need to control for differences in habitat variables. It would be expected that in troops of saddleback and mustached tamarins the smaller saddleback tamarins would use tree holes more frequently. Reproductive state may also influence the choice of sleeping site as there may be increased pressure to choose safer sites when infants are present. For example Reichard (1998) found that female white-handed gibbons with infants selected taller sleeping sites which were inferred as safer. Infants may also be more at risk from cold or inclement weather, and this too may affect choice of sleeping sites. Consequently it may be expected that there will be a difference in the sites chosen when infants are present. Independent of the presence of infants, it has been suggested that protection from rain plays a part in selection of sleeping sites (Chivers 1974; Aquino & Encarnacion 1986). If so, it would be expected that sites chosen either during the wet season or on rainy days would be different to those at other times.

Within its home range or territory an animal may choose to sleep either within a core area of exclusive use or towards the periphery in a zone of overlap (Ramirez 1989). The former strategy would allow access to exclusive resources and potentially avoid boundary disputes around the time of being in the sleeping site, whilst the latter may be viewed as assisting with range defense either through early access to contested resources or detection of neighboring troops (Dawson 1979). Since all wild callitrichids have been described as being “typically neighbor-intolerant” (Peres 1992) and the majority of intergroup encounters occur early in the day (Dawson 1979; Peres 1992; Smith et al in prep) predominantly in a peripheral boundary zone (Peres 1986; 1992; Buchanan-Smith 1991; Smith and Buchanan-Smith in prep) it may be expected that the sleeping sites also will be more frequently located in this zone.

Sleeping sites may also be chosen the basis of proximity to food resources (Chapman et al 1989; Heymann 1995; Day & Elwood 1999). An animal may choose to return to a central place to sleep (central place foraging) (Giraldeau & Kramer 1982) or may utilize one of a number of limited central sites, typically proximate to their last feeding site (multiple central place foraging) (Sigg & Stolba 1981; McLaughlin & Montgomery 1989). Given the relatively long overnight fast period and relatively small body size of callitrichids, 564g and 352g for mustached and saddleback tamarins respectively (Garber and Teaford 1986; Soini, 1990), tamarins may be under physiological pressure to sleep close to feeding sites and as such may be expected to employ a multiple central place foraging strategy.

Few researchers have examined the times at which primates enter or leave their sleeping sites in any depth. Ramirez (1989) and Reichard (1998) have both suggested that time of entry and exiting of sleeping sites would be effected by seasonal changes in photoperiod due to latitude. It may thus be predicted that seasonal variation in the times of sunset and sunrise would have the greatest influence on the times of entry to and exit from sleeping sites. Further, Gibbons and Menzel (1980) present limited data for a group of captive saddleback tamarins to show that time of exiting from a sleeping site is more tightly linked to sunrise than the time of entry is to sunset. It may also be expected that mustached tamarins would enter their sleeping sites later than their associating saddleback tamarins since they may take longer to fulfil their greater energetic needs based on their larger body size. The time of leaving a sleeping site may be influenced by the time it was entered the previous night (Dawson 1979).

From the preceding rationale the following hypotheses can be made regarding the sleeping habits of associating saddleback and mustached tamarins. The times of entry to, and from, sleeping sites will be correlated with seasonal variation in the times of sunset and sunrise (H1), with the closest correlation being between the time of exit and sunrise (H2). The time of exiting a sleeping site will be correlated with the time it was entered the previous night (H3). Mustached tamarins will enter their sleeping sites later than saddleback tamarins (H4). Both species will use many different sleeping sites and switch frequently between them (H5), but this will be more pronounced for mustached tamarins (H6). With respect to type of sleeping site, saddlebacks will use tree holes more frequently than the

mustached tamarins (H7). The presence of infants will affect the types of sites chosen (H8), as will season or weather conditions (H9). Sleeping sites will be located towards the periphery of the home range (H10), and the tamarins will employ a multiple central place foraging strategy (H11).

## **METHODS**

Three mixed-species troops of saddleback and mustached tamarins were observed at the Estación Biológica Quebrada Blanco (EBQB) (4°21'S, 73°09'W). The site is located approximately 1 km northwest from the right bank of the Quebrada Blanco in north-eastern Peru. The Quebrada Blanco is a white water tributary of the Río Tahuayo, which is in turn primarily a black water tributary of the Río Amazonas (for details see Heymann & Hartmann, 1991). The climate at EBQBII can be divided into wet and dry seasons. The wet season, characterized by higher rainfall, runs from February until May, and the dry season from June to January (see Smith et al. 2004).

Troop 1 consisted of five mustached (an adult male, two adult females, a juvenile male and a juvenile female born in January 1994) and five saddleback tamarins (three adult males and two adult females) at the beginning of the study. Twin mustached tamarins, a male and a female, were born at the end of December 1994. A single infant saddleback tamarin was born at the beginning of March; it disappeared, presumed dead, two weeks later before we were able to determine its sex. Between March and July 1995 the composition of the saddleback tamarin group varied due to a series of emigrations and immigrations before stabilizing at three adult males and two adult females (see Smith 1997). Troop 2 comprised four saddleback (one adult female, two adult males, and one sub-adult female) and five mustached tamarins (two adult females, two adult males and one sub-adult male) at the beginning of the study. Neither of the female saddleback tamarins was observed to be pregnant during the study, whereas both female mustached tamarins gave birth in February 2000. Female 1 was seen with a single infant that died on the same day that it was born. Female 2 gave birth to twin males the following day that were raised by both their mother and Female 1 (see Smith et al. 2002). Female 2 emigrated 15<sup>th</sup> October 2000. Female 1 gave birth to a single male infant in February 2001 which survived for six weeks (see Löttker et al 2004 for details). The composition of the saddleback tamarin group

remained constant over the course of the study. Although comprising of totally different individuals Troops 1 and 2 occupied almost the same home range as each other approximately 5 years apart. Troop 3's home range was adjacent to that of Troop 2's. Troop 3 contained eight saddleback (two adult females, two adult males, one juvenile female, one juvenile male, one infant female and one infant male) and eight mustached tamarins (three adult females, three adult males, and two infant males born May 2000) at the start of observations. Twin male and female infants were born in January 2001, and two adult females emigrated in September 2001 (see Löttker et al 2004 for details).

Troops were observed as follows: Troop 1 from March 1994 until November 1995, Troop 2 from January 2000 until December 2001 and Troop 3 from July 2000 until December 2001. Data were always collected from both species within Troop 1 whenever possible, and for Troops 2 and 3 until December 2000. Between January and December 2001 data were collected solely from the mustached tamarins. The tamarins were observed for approximately 12 consecutive days per month, except between January and December 2001 when the mustached tamarins in Troops 2 and 3 were observed almost every day. The time that the tamarins entered and left their sleeping sites and the height at which they slept were recorded. Their behavior before entering sleeping sites was also noted. Light levels upon entering and exiting sleeping sites were recorded at ground level beneath the sleeping site using a hand-held light meter (Jessops Model D-3 series).

The trees used as sleeping sites were mapped onto known reference points; this was not possible for Troop 3. Their height, circumference at breast height, canopy dimensions were recorded. The locations at which the tamarins slept were classified into one of five categories following Heymann (1995):

- *Ungurahui palm* - sleeping site in the cavity formed by the branching-off of living palm leaves, remains of dead palm leaves and epiphytic growth.
- *Tree hollow* - hollow in dead or living tree trunk.
- *Tangle* - dense tangle formed by epiphytic growth and foliage.
- *Crotch* - ramification of tree trunk or major branches.
- *Branch* - horizontal branch in a tree crown without dense cover by epiphytes or foliage.

The times of sunrise and sunset at the Estacion Quebrada Blanco II were calculated using the United States Naval Observatory Astronomical Applications Department's computer programme for the exact longitude and latitude co-ordinates. The program is located on the World Wide Web; address "[http://aa.usno.navy.mil/data/docs/RS\\_OneDay.html](http://aa.usno.navy.mil/data/docs/RS_OneDay.html)".

### **Data analysis and statistics**

Times of entry to and exit from sleeping sites and the type and location of sleeping were not always available for each night, nor were data for both associating species always able to be collected on a given night. The number of data points used in each analysis is indicated accordingly. Data from each night are treated as independent sample points as the tamarins' choice of sleeping site on a given night is deemed to be uninfluenced by their choice on a preceding night. Where sample sizes or variance were unequal comparisons were made using unequal variance t-tests to account for this. Where G-tests were used if expected values were less than five, categories were collapsed to achieve values of five or greater.

## **RESULTS**

### **Time of entry to, and exit from sleeping sites**

Sleeping records were noted for a total of 1,391 tamarin nights, 517 for Troop 1 (saddleback n=263; mustached n=254), 485 for Troop 2 (saddleback n=77; mustached n=408) and 389 (saddleback n=20; mustached n=369) for Troop 3. Monthly mean times of entry to and exit from sleeping sites (calculated between years) were compared using an ANOVA (Troop 2's saddleback tamarins were excluded from this analysis as records were only available between July and December). Neither time of entry to, or exiting from a sleeping site were significantly effected by species (entry  $F=1.09$ , 1,54 d.f.,  $p>0.05$ ; exit  $F=0.75$ , 1,54 d.f.,  $p>0.05$ ), troop (entry  $F=1.10$ , 2,54 d.f.,  $p>0.05$ ; exit  $F=1.59$ , 2,54 d.f.,  $p>0.05$ ) nor their interaction (entry  $F=0.25$ , 1,54 d.f.,  $p>0.05$ ; exit  $F=0.10$ , 1,54 d.f.,  $p>0.05$ ) (Table 1). For subsequent analyses troops were combined. The time of sunrise accounted for a significant amount of the variation in the time of exiting sleeping sites for both species (saddleback  $r^2=0.136$ ,  $F=41.7$ , 1,266 d.f.,  $p<0.001$ ; mustached  $r^2=0.357$ ,  $F=483.4$ , 1,870 d.f.,  $p<0.001$ ). Similarly the time of sunset accounted for a significant amount of the

variation in the time of entry to sleeping sites for both species (saddleback  $r^2=0.032$ ,  $F=10.89$ , 1,334 d.f.,  $p<0.001$ ; mustached  $r^2=0.106$ ,  $F=110.91$ , 1,936 d.f.,  $p<0.001$ ) (Fig. 1).

**Table 1:** about here & **Figure 1:** about here

Both species left their sleeping sites significantly later than sunrise (saddleback  $0609 \pm 26\text{min}$  vs.  $0550\text{h} \pm 11\text{min}$ ,  $t=13.26$ , 267 d.f.,  $p<0.05$ ; mustached  $0600\text{h} \pm 21\text{min}$  vs.  $0549 \pm 11\text{min}$ ,  $t=18.4$ , 863 d.f.,  $p<0.001$ ) and entered them significantly before sunset (saddleback  $1556\text{h} \pm 29\text{min}$  vs.  $1753\text{h} \pm 8\text{min}$ ,  $t=-110.17$ , 335 d.f.,  $p<0.05$ ; mustached  $1549 \pm 25\text{min}$  vs.  $1754 \pm 9\text{min}$ ,  $t=163.4$ , 933 d.f.,  $p<0.001$ ). Both species also entered them significantly longer before sunset than they left them after sunrise (saddleback  $183.6 \pm 41.6\text{min}$  vs.  $19.8 \pm 24.4\text{min}$ ,  $t=-66.50$ , 259 d.f.,  $p<0.05$ ; mustached  $122.8 \pm 36.2\text{min}$  vs.  $10.8 \pm 17.1\text{min}$ ,  $t=-108.6$ , 792 d.f.,  $p<0.001$ ). The time of entry to a sleeping site did not account for a significant amount of the variation in the time of leaving it the following morning for either species when corrected for the time of sunrise (saddleback  $r^2=0.001$ ,  $F=0.2$ , 1,259 d.f.,  $p>0.05$ ; mustached  $r^2=0.002$ ,  $F=1.7$ , 1,791 d.f.,  $p>0.05$ ).

### Light levels at entry to, and exit from sleeping sites

There was no difference in the level of light (measured as exposure level, EV) between the two species for either troop when entering (Troop 2 saddleback  $5.2 \pm 1.6\text{EV}$ ,  $n=73$ , mustached  $5.2 \pm 1.7\text{EV}$ ,  $n=84$ ;  $t=0.15$ , 155 d.f.,  $p>0.05$ ; Troop 3 saddleback  $5.5 \pm 2.4\text{EV}$ ,  $n=18$ , mustached  $6.1 \pm 1.8\text{EV}$ ,  $n=20$ ;  $t=-0.86$ , 36 d.f.,  $p>0.05$ ) or leaving (Troop 2 saddleback  $0.7 \pm 1.3\text{EV}$ ,  $n=65$ , mustached  $0.7 \pm 1.1\text{EV}$ ,  $n=71$ ;  $t=-0.04$ , 134 d.f.,  $p>0.05$ ; Troop 3 saddleback  $2.6 \pm 2.5\text{EV}$ ,  $n=18$ , mustached  $1.2 \pm 1.6\text{EV}$ ,  $n=16$ ;  $t=1.92$ , 32 d.f.,  $p>0.05$ ) a sleeping site. The species were then pooled and the light levels at entry and exit compared. Light levels were significantly higher when entering a sleeping site than when leaving it for both troops (Troop 2  $5.2 \pm 1.7$  vs.  $0.7 \pm 1.2\text{EV}$ ;  $t=-25.97$ , 291 d.f.,  $p<0.0001$ ; Troop 3  $5.9 \pm 2.1$  vs.  $2.0 \pm 2.2\text{EV}$ ;  $t=-7.61$ , 70 d.f.,  $p<0.0001$ ). Data were unavailable for Troop 1.

### Behaviour before entering sleeping trees

Before entering their sleeping trees both species showed characteristic, species typical behaviours. The saddlebacks spent prolonged periods, occasionally in excess of 30 minutes, clinging to vertical trunks, or resting on low branches at a height of 2-3 m, close to the sleeping site. They then travelled rapidly and directly to the sleeping site, often using single file “cling and leap” locomotion. This final bout of travel was interspersed by short pauses, during which visual scanning of the environment was prevalent. The moustached tamarins also often showed extended periods of relative inactivity before suddenly and with some speed, running to their sleeping site. The vocalisations of both species were subdued prior to entering the sleeping tree, with only soft, low intensity calls being given. These were more frequently heard from the saddlebacks; this may be due to the greater distance from which the moustached tamarins were observed due to their greater flight distance from the observer. At this time, the calls of both species were very quiet, and so the distance over which they carried was relatively short. The greater distance between the observer and moustached tamarins would result in a reduced probability of their calls being heard, with respect to those of the saddlebacks’.

### **Number of sleeping sites**

The number of nights observed, number of sleeping sites and exclusivity of use by either species are given in Table 2. Sixteen trees were shared by both species, with each using a different sleeping site within the tree. Only on two nights were both species observed to use the same tree concurrently. The number of new sleeping trees for both species continued to increase over the study periods for all three troops (Fig. 2). The rates of increase in new sleeping sites were compared using the number of new trees used for each subsequent 10 nights (values were paired for block of 10 nights). The rate of increase in new sleeping sites shown by Troop 2’s saddleback tamarins was significantly higher than that of their associating mustached tamarins ( $6.0 \pm 1.8$  vs.  $4.6 \pm 1.8$  new trees / 10 nights,  $n=7$  blocks;  $t=2.71$ , 6 d.f.,  $p<0.05$ ), but those of troop 1 were not ( $3.2 \pm 1.9$  vs.  $2.8 \pm 1.8$  new trees / 10 nights,  $n=25$  blocks;  $t=1.31$ , 24 d.f.,  $p>0.05$ ). There were insufficient data for this to be examined within Troop 3. Within species, Troop 2’s saddlebacks showed a significantly faster rate of increase in new sleeping sites than those of Troop 1 ( $6.0 \pm 1.8$  vs.  $3.0 \pm 2.2$  new trees / 10 nights,  $n=7$  blocks;  $t=-3.00$ , 6 d.f.,  $p<0.05$ ), but there was no

difference between troops for the mustached tamarins ( $3.2 \pm 1.9$  vs.  $3.3 \pm 2.0$  vs.  $3.2 \pm 2.1$  new trees / 10 nights,  $n=25$  blocks;  $F=0.58$ , 1,73 d.f.,  $p>0.05$ ).

**Table 2:** about here and **Figure 2:** about here

### **Frequency of use of sleeping sites**

Both species showed a similar pattern in their use of sleeping trees, with the greatest number of sleeping sites being used for a single night independent of the number of nights for which they were observed (Table 3). The distribution of repeated use was compared between species within Troop 1 and between the three groups of mustached tamarins for which >250 records were available. The distribution was not significantly different between species (Troop 1:  $G=3.2$ , 4 d.f.  $p>0.05$ ; 5 & 5+ nights collapsed), or between groups of mustached tamarins ( $G=3.1$ , 6 d.f.  $p>0.05$ ; 4, 5 & 5+ nights collapsed).

Four consecutive nights, occurring three times for Troop 1's saddleback tamarins, was the longest run for which a sleeping site was reused. The probability of selecting the same sleeping site on consecutive nights was then used to calculate expected frequencies for consecutive reuse from the total number of sleeping sites and the number of runs of consecutive nights. These were then compared to the frequencies for which runs of two, three and four consecutive nights were observed. Troop 1's saddlebacks used the same sleeping sites on two, three and four consecutive nights significantly more often than chance. Troop 1's mustached tamarins similarly reused the same site on two consecutive nights significantly more often than chance (Table 4).

**Table 3:** about here and **Table 4:** about here

### **Characteristics of sleeping sites**

In order to circumvent the problem of unequal sample sizes when comparing the mean heights of both the trees themselves and the sites within the trees where the tamarins slept monthly means were used. Data from Troop 3 were excluded from the analysis as they were only available for limited months for the saddleback tamarins. Further, data from Troops 1 and 2 were restricted to those months when data were available for both species.

The trees used by the saddleback tamarins were significantly shorter than those used by the mustached tamarins ( $F=72.51$ , 1,43 d.f,  $p<0.01$ ), and those used by troop 1 were significantly shorter than those used by troop 2 ( $F=5.81$ , 1,43 d.f,  $p<0.05$ ), but the interaction of species and troop was not significant ( $F=0.90$ , 1,43 d.f,  $p>0.05$ ). The mean height at which the saddleback tamarins slept was significantly lower than that for the mustached tamarins ( $F=11.0$ , 1,43 d.f,  $p<0.05$ ), but neither troop ( $F=0.1$ , 1,43 d.f,  $p>0.05$ ) nor the interaction of troop and species ( $F=0.1$ , 1,43 d.f,  $p>0.05$ ) were significant (Fig. 3). For subsequent analyses on sleep heights data from Troops 1 and 2 were pooled.

**Figures 3 and 4:** about here

The height at which the mustached tamarins slept was not affected by whether the group had infants (mustached  $t=1.3$ , 273.0 d.f.,  $p>0.05$ ). This was not able to be examined for the saddleback tamarins as the single infant that was born during the observation period did not survive. Sleeping height was similarly unaffected by either season (saddleback  $t=1.1$ , 142.1 d.f.,  $p>0.05$ ; mustached  $t=1.0$ , 303.0 d.f.,  $p>0.05$ ) or daily rainfall  $>10\text{mm}$  (saddleback  $t=-1.1$ , 55.2 d.f.,  $p>0.05$ ; mustached  $t=-1.7$ , 93.1 d.f.,  $p>0.05$ ).

The frequency of the tamarins' use of the various categories of sleeping sites was first compared to the number of sites in each category that they used (Table 5). The frequency of use was significantly different from the distribution of the number of sleeping sites for all of the mustached tamarin groups (Group 1  $\chi^2=45.4$ , 3 d.f.  $p<0.01$ ; Group 2  $\chi^2=92.3$ , 3 d.f.  $p<0.01$ ; Group 3  $\chi^2=66.0$ , 3 d.f.  $p<0.01$ ) but for neither of the saddleback tamarin groups for which sufficient data were available (Group 1  $\chi^2=7.6$ , 3 d.f.  $p>0.05$ ; Group 2  $\chi^2=1.1$ , 3 d.f.  $p>0.05$ ). Troop 1's mustached tamarins used crotches more often than expected at the expense of tangles, branches and palms. In addition to crotches those of Troop 2 also used branches more frequently, whilst those of Troop 3 slept in tangles more often than expected and in palms and crotches less often.

**Table 5** about here

The frequencies with which the two species used each type of sleeping site were significantly different from one another for both Troop 1 ( $G=382.2$ , 4 d.f.,  $p<0.0001$ ) and Troop 2 ( $G=56.2$ , 3 d.f.,  $p<0.0001$ : hollows and epiphyte tangles collapsed). Both saddleback troops spent the majority of nights in epiphyte tangles, and tree hollows were also important for those in Troop 1, whereas mustached tamarins favored crotches and branches, and those in Troop 1 also used ungurahui palms frequently. Saddlebacks never used branches and conversely mustached tamarins never slept in tree hollows. Data were unavailable for this to be examined for Troop 3.

There was also a significant difference in the distribution of use of sites between troops for saddleback tamarins ( $G=18.7$ , 2 d.f.,  $p<0.05$ : branches excluded since they were used by neither group and crotch and tangle collapsed). Troop 1's saddlebacks used hollows more frequently than those of Troop 2, which used crotches more often. Similarly there was also a difference in the distribution between categories of sleeping sites between troops for the mustached tamarins  $G=135.5$ , 6 d.f.,  $p<0.0001$ : hollows excluded since they were used by neither group). Troop 1's mustached tamarins favored crotches, ungurahui palms or branches, whereas those of Troop 2 spent the majority of nights in a crotch, and Troop 3 in a tangle.

The distribution of use between categories of sleeping sites was not significantly different in the wet and dry seasons for any of the groups tested (Troop 1 saddleback  $G=4.4$ , 2 d.f.,  $p>0.05$ , branches excluded since they were used by neither group; mustached  $G=2.8$ , 3 d.f.,  $p>0.05$ : Troop 2 mustached  $\chi^2=5.7$ , 3 d.f.,  $p>0.05$ , hollows excluded since they were used by no mustached group; there were insufficient data for this to be examined for saddleback tamarins or for Troop 3's mustached tamarins). It was not significantly different for either species in Troop 1 (saddleback ( $G=1.1$ , 2 d.f.,  $p>0.05$ : mustached  $G=1.0$ , 2 d.f.,  $p>0.05$ : crotches and tangles collapsed) on when daily rainfall was  $>10\text{mm}$ , but it was for Troop 2's mustached tamarins ( $G=9.7$ , 3 d.f.,  $p<0.05$ ) with more palms being used on rainy days. The effect of the presence of infants under 5 months old was examined for the mustached tamarins. They had no significant effect for either group (Group 1  $G=2.5$ , 3 d.f.,  $p>0.05$ ; Group 2  $G=3.6$ , 2 d.f.,  $p>0.05$ , crotch and tangle collapsed). This was not examined

for the saddleback tamarins as the single infant born during the observation period did not survive.

A series of Kruskal-Wallis ANOVAs were then used to determine if there were any differences in rainfall, and maximum and minimum temperatures when each type of sleeping site was used. There were no significant differences in any of the variables examined for either saddleback (branches excluded) or mustached (hollows excluded and crotch and tangle collapsed) (Table 6).

**Table 6:** about here

### **Spatial distribution of sleeping sites**

The distribution of the sleeping sites within the tamarins' home range showed no clear pattern of preference for one location over another (Fig. 5) (location data were unavailable for Troop 3); but with few exceptions they did not sleep at the periphery of their home range. The number of sleeping sites within and outside 100m of the boundary was compared to that expected based on the area of the two zones. Both species in both troops had significantly fewer sleeping sites in the peripheral zone and more in the core zone than expected based on area (Troop 1 saddleback  $\chi^2=46.8$ , 1 d.f.  $p<0.05$ ; mustached  $\chi^2=50.5$ , 1 d.f.  $p<0.05$ ; Troop 2 saddleback  $\chi^2=22.9$ , 1 d.f.  $p<0.05$ ; mustached  $\chi^2=28.6$ , 1 d.f.  $p<0.05$ ). Where the tamarins slept within their home ranges was compared between species and troops using the centrality, a measure of the distance from the centre of the home range, of the sleeping sites. The saddleback tamarins slept significantly further from the centre of their home range than the mustached tamarins ( $F=5.0$ , 1,790 d.f.,  $p<0.05$ ). Troop 2 slept significantly further from the centre of their home range than Troop 1 ( $F=21.3$ , 1,790 d.f.,  $p<0.0001$ ). The interaction between species and troop was not significant ( $F=0.05$ , 1,790 d.f.,  $p>0.05$ ) (Fig. 6).

**Figure 5:** about here and **Figure 6:** about here

The location of known sleeping sites was then examined with respect to the location of last feeding tree used before entering each sleeping site. This was possible for 361

sleeping sites for Troops 1 (saddleback n=117; mustached n=115) and 2 (saddleback n=55; mustached n=74). On 16.9% of nights the tamarins entered the sleeping site closest to their last feeding site (Troop 1 saddleback 12.0%, mustached 13.9%; Troop 2 saddleback 20.0%, mustached 27.0%). Troop ( $F=40.3$ , 1,357 d.f.,  $p<0.0001$ ), species ( $F=5.4$ , 1,357 d.f.,  $p<0.05$ ) and their interaction ( $F=7.0$ , 1,357 d.f.,  $p<0.01$ ) all had a significant effect on the distance between the last feeding site and the sleeping site entered. The observed distance between the last feeding site and the sleeping tree was then compared to that between the last feeding site and the nearest sleeping site (multiple central place foraging, MCPF) and between the last feeding site and the mean sleeping site (as indicated by the arithmetic mean of the coordinates of the sleeping sites used) (central place foraging, CPF) for each group of tamarins (Fig. 7). Whilst all comparisons were significant except that for the distance between the observed and mean sites for Troop 2's saddlebacks, the sleeping sites used were significantly closer to those expected by a multiple central place foraging strategy than by a central place foraging strategy for all except Troop 2's saddleback tamarins (Table 7).

**Figure 7:** about here and **Table 7:** about here

The distance between the sleeping site and the last feeding site of the day was then compared to that between the sleeping site and the first feeding tree of the next day. There was no significant difference for any of the groups of tamarins, except for Troop 1's saddlebacks who slept significantly closer to their last feeding site than their next feeding site (Table 8).

**Table 8:** about here

The distance between the sleeping sites used by both tamarin species on the same night was compared between Troops 1 & 2 ; there were insufficient data for this to be examined for Troop 3. For Troop 1 the sites used by both species were located on 223 nights, and for Troop 2 on 32 nights. For these nights the tamarins in Troop 1 used 181 pairs of sleeping trees, and those in Troop 2 used 31 pairs. The majority of these pairs were used on only a single occasion (Troop 1 n= 152; Troop 2 n=25). For Troop 1, 19 pairs were used twice, seven pairs three times and three pairs for each of four, five and six times. For Troop

2 two pairs were used twice and one pair was used three times. The mean distance between the two species' sleeping sites was not significantly different between troops (Troop 1  $110.0 \pm 100.5$  m,  $n=223$  nights vs Troop 2  $142.3 \pm 138.5$  m,  $n=32$  nights;  $t=-1.3$ , 35.8 d.f.,  $p>0.05$ ). The tamarins slept within 100 m of the other species in 57.8 & 50.0% of cases for Troops 1 & 2 respectively. This distribution was not significantly different between troops ( $G_{\text{Williams's}}=0.69$ , 1 d.f.,  $p>0.05$ ).

## **DISCUSSION**

### **Time of entry to, and exit from sleeping sites**

The times that the tamarins entered and left their sleeping sites and the length of the intervening activity period were in accordance with other studies (Table 9). The hypothesis that the times of entry to, and from, sleeping sites will be correlated with seasonal variation in the times of sunset and sunrise (H1) was supported in line with the findings of seasonal differences for mustached tamarins at a nearby location (Ramirez 1989). However, it is in contrast to the lack of variation reported by Dawson (1979) for Panamanian tamarins, which being further from the equator will experience greater changes in photoperiod associated with latitude.

#### **Table 9:** about here

As predicted, H2, the correlation between the times of exit and sunrise was closer than that between the times of entry and sunset. The tamarins left their sleeping site soon after sunrise, with the earliest time of leaving in any given month very seldom being earlier than sunrise, yet they showed much greater variation in the times at which they entered them typically about two hours before sunset. Predation and foraging or energetic constraints are most likely the primary factors influencing when the tamarins entered and left their sleeping sites. It is suggested that physiological pressure to feed following the long night-time fast causes the tamarins to leave their sleeping sites as soon as they are released from the threat posed by nocturnal or crepuscular predators. The time of entry to sleeping sites may not so strongly influenced by physiological pressures as it does not follow a fast period.

Two alternative hypotheses for why tamarins do not leave their sleeping sites earlier have been proposed. Dawson (1979) suggested that the orthopteran prey of tamarins do not become sufficiently warm to emerge from their nocturnal resting places until well after dawn. However Nickle and Heymann (1996) and Smith (2000) showed the majority of the prey species taken to be nocturnal, spending the day inactive at a roost site, which would refute this hypothesis. Alternatively the efficiency of foraging before sunrise, in low intensity light, may not be adequate for a small bodied primate, especially following the relatively long fast of the night. This has also been disputed (Caine 1987) on the basis of Garber's (1986) finding that tamarins are capable of traveling efficiently between fruit trees rather than simply "searching" for them. Indeed many cebids have been recorded to forage and feed on fruits before sunrise and to continue until well after sunset (Thorington, 1967; Baldwin and Baldwin, 1972). However, the relatively higher metabolic requirements of smaller-bodied callitrichids may constrain foraging in the early morning below certain efficiency thresholds. Since foraging efficiency in tamarins, in terms of the detection and selection of ripe fruits, is affected by color vision capability (Smith et al 2003) the time at which tamarins can begin foraging may be limited by the light intensity threshold for retinal cone cells. Support for this comes from the fact that the sleeping sites were seldom left until light levels within the forest were sufficient for photopic (cone-based) vision (pers. obs.), ca 1 candela/m<sup>2</sup> (Harris, pers. comm.). The hypothesis that the time of exit is influenced by the time of entry (H3) was not supported when seasonal changes in photoperiod were controlled for. This is perhaps surprising as it implies that going longer without food on nights when entry to sleeping sites was early does not result in a need to rise sooner in order to forage. However, it should be noted that as tamarins may visit their last fruiting tree anywhere between several minutes and in excess of an hour before entering their sleeping sites the time of their last meal is not accurately indicated by time of entry to a sleeping site.

The reason tamarins enter their sleeping sites approximately two hours before sunset whilst light levels were well above the threshold for photopic vision is less clear. Moynihan (1970) suggested an early retirement may reduce competition with dusk-active insectivorous bird but this has been disputed on the basis that the birds and tamarins do not share the same prey (Dawson 1979). An alternative hypothesis is that the risk of drawing a

predator's attention to a sleeping site that is about to be entered is greater than drawing it to one that has just been left. By entering well before the active period of nocturnal predators begins the chance of being seen by such a predator would be greatly reduced, and any scent trail would have longer to dissipate. No evidence was found to support the hypothesis that mustached tamarins would enter their sleeping sites later than saddlebacks (H4).

As has been noted for these and other tamarin species (*S. geoffroyi*, Dawson, 1979; *S. fuscicollis*, Yoneda, 1984b; Soini, 1987; *S. fuscicollis* & *S. labiatus* Buchanan-Smith, 1991) weather often greatly influenced the time of entry to and leaving from sleeping sites. A heavy shower or an impending rainstorm in the afternoon would cause the tamarins to rapidly enter their sleeping site. The two most dramatic examples of this during the present study were when the saddlebacks in Troops 2 and 1 entered their sleeping trees at 1:14pm and 2:12 pm respectively, immediately after the onset of a second heavy shower in the afternoon. The second example is identical in time and circumstance to that reported for Panamanian tamarins (Dawson, 1979). In a similar manner the tamarins delayed leaving their sleeping tree in response to rain, mist or exceptional cloud or cold in the early morning.

### **Number of sleeping sites & frequency of reuse**

The findings that both species used many sleeping sites, and that sites were seldom used for more than two consecutive nights supports H5. A similar strategy has been reported for a range of primates (e.g. black and white colobus, *Colobus guereza*, von Hippel 1998; yellow baboons, *Papio cynocephalus*, Hausfater & Meade 1982; Central American or black-handed spider monkeys, *Ateles geoffroyi*, Chapman 1989; brown capuchins, *Cebus apella*, Zhang 1995; black-and-white snub-nosed monkeys, *Rhinopithecus bieti*, Cui et al 2006) in addition to the same (Ramirez 1989) and other callitrichid species of (Weid's black-tufted-ear marmosets, *Callithrix kuhli*, Rylands 1989; golden-handed tamarins, *S. midas*, Day & Elwood 1999). Such a strategy indicates a high pressure not to reuse the same sites. Of particular significance is that there was no indication of an asymptote being reached in sleeping site recruitment for any of the groups observed, despite some having been observed for 300 nights and having used more than 80 different sites. The driving force for this may be either the need to minimize the build up of odor or other cues

(Reichard 1998), the potential for a predator to develop a search image for a particular site type (Sonerud 1985) or to minimize infection with parasites or other diseases (Hausfater & Maede 1982; Day & Elwood 1999; Cui et al 2006).

The prediction that the mustached tamarins would use more sites or switch sites more frequently (H6) was not supported. Similar patterns of site use between the species suggest they face similar predation risks. Moreover, the risks associated with drawing a predators attention through giving a long-call to reform the association may be split equally since contrary to Norconk's (1990) findings, other workers (Heymann 1990; Peres 1991; Smith 1997) have shown neither species to be more likely to be the first to call. However there was a difference between troops in the frequency with which they used the same sleeping sites on consecutive nights, with this happening more often than expected only for Troop 1 (both species). This implies that differences in habitat and resource availability or perhaps predation pressure exert a stronger influence on patterns of reuse than does species. Interestingly, Franklin (2004) found predation pressure did not significantly effect the rate of change of sleeping sites in golden lion tamarins (*Leontopithecus rosalia*), although as he notes his results may be atypical due to the founders of the population being reintroduced animals.

Despite a general similarity in the pattern of usage of sleeping in accordance with Heymann's (1990) shorter study, none of the mustached tamarin groups used the same sleeping site for more than two consecutive nights despite in excess of 150 opportunities whereas it was observed five times for one group of saddlebacks in 157 opportunities. The repeated use of sites by the saddlebacks may be part of a species-specific complex of behaviors that Heymann (1995) terms 'risky'.

### **Characteristics of sleeping sites**

As predicted, saddlebacks used tree holes more frequently than the mustached tamarins (H7). In fact despite being known to use closed nest boxes with circular entrances in captivity mustached tamarins were never observed to use them on any of the 486 nights for which data were available. Whilst sleeping sites may be a contested resource (Aquino & Encarnación 1986), exclusion can be discounted since as Heymann (1995) notes the larger

mustached tamarins are consistently dominant in disputes (Norconk, 1986; Heymann, 1990; Peres, 1991; Smith 1997). It is possible that the larger size of the mustached tamarin groups' may have limited their ability to use tree cavities, although this is unlikely to have been a major factor as in Heymann's (1995) study both groups of mustached tamarins were smaller than those of the saddlebacks with which they associated. It has been proposed that the difference between the two species may stem from mustached tamarins avoiding cavities *per se*, since they also do not forage in cavities as saddlebacks do (Heymann 1995). Consistent interspecific differences between troops also included a lack of use of branches by saddlebacks and a greater use of ungurahui palms by mustached tamarins.

The preference for tangles shown by saddlebacks in Troops 1 and 2 and mustached tamarins in Troop 3 is similar to that reported for golden-handed tamarins (Day & Elwood 1999), despite as Day and Elwood note, they may also provide hiding places for snakes such as tree boas (*Corralus* spp), rainbow boas (*Epicrates cenchria*) and some vipers (*Bothrops* spp.). However, a preference for such tangles or cavities may reduce the rate of malaria infection through containment of the cues by which mosquitoes locate hosts (Heymann 1995; 2000a; Nunn & Heymann 2005). Whilst all groups used ungurahui palms, they were not the most frequent sites used by either species as reported by Heymann (1995). Within the current study differences between groups of the same species may have been due to variations in the availability of resources including the various types of sleeping sites. However, since Troops 2 & 3 bordered each other, and Troop 2 occupied the majority of the home range that Troop 1 used five years previously these factors were controlled for to a higher degree than in comparisons between sites. Consequently it is possible that the choice of sleeping sites may be influenced by individual preferences, which may be socially learnt.

No support was found for the hypotheses that the presence of infants (H8) or season or weather conditions (H9) would affect the types of sites chosen. The former finding suggests that predation pressure may be sufficiently high that the safest sites available are being chosen even when no infants are present. The hypothesis was based on Reichard's (1998) observation that female white-handed gibbons with infants chose taller trees to sleep in. The sleeping habits of gibbons are potentially more flexible compared to tamarins. Whereas members of gibbon groups may sleep in different trees or at different heights in

the same tree, a group of tamarins all sleep together in a huddle in the same discrete site. Thus whilst a female gibbon with infants can choose the tallest tree in the location that the group will sleep or the highest position within a given tree, a female tamarin with infants would have to transfer her whole group to her preferred site. Moreover, since the majority of infant carrying is done by other group members (Goldizen 1987), it may not be the female who carries the infants when the group enters their sleeping site. However, given the high degree of relatedness in wild tamarin groups (Huck et al 2005) kin selection would predict the majority of group members to benefit from any increase in infant survival. It may be useful, if not easy, to examine the position of the female tamarin and her infants within the sleeping huddle.

That the sites chosen during the wet season or on days with >10mm of rain were not different from those chosen at other times suggests that all sites chosen offer suitable protection from the weather. Further, there were no differences in rainfall or temperature on days when each type was used. Of the five categories hollows, tangles and ungurahui palms are all relatively enclosed sites, and crotches, being next to the trunk, would also offer protection from overhead rain. Only branch sites which by definition lacked epiphytic cover and were used exclusively by mustached tamarins may be considered as exposed. The general choice of enclosed sites may be driven by a baseline need for sites that offer good insulation since callitrichids allow their metabolism to fall at night (Thompson *et al.*, 1994), or that reduce the potential for infection with simian malaria (Heymann 1995; 2000a; Nunn & Heymann 2005). Further choice between types of sleeping sites related to weather or the presence of infants may be limited by other factors such as the spatial location of food resources and the sleeping sites themselves.

### **Spatial distribution of sleeping sites**

Contrary to the prediction that sleeping sites would be located towards the periphery of the home range (H10), more than expected were located in the core area of exclusive use. Although contrary to reports from Norconk (1986) and Ramirez (1989) with many sites located towards the home range boundary, as Day & Elwood (1999) note these findings are difficult to evaluate as the proportion of the home range accounted for by each of these zones is not provided. Their study of golden-handed tamarins revealed no preference when

each zone's relative area had been controlled for. That the central area was used more often than expected in the present study is in-line with findings for cotton-top tamarins (*Saguinus oedipus*, Savage 1990), brown capuchins (Zhang 1995) and black and white colobus (von Hippel 1998) and suggests that exclusive access is more important than priority of access to contested resources or the early detection of neighboring groups. Moreover sites towards the centre of the home range allow shorter travel times to a greater part of the home range, for reasons which may include range defense, than do sites located at the periphery.

The hypothesis that tamarins employ a MCPF strategy (H11) was only partially supported, and is in contrast to Pontes and Soares (2005) who provide evidence that common marmosets in a fragmented habitat sleep close to food resources. However, food resources in fragmented habitats may be more limited than in primary forest, and thus pressure to sleep closer to them may be higher. In agreement with Day and Elwood's (1999) findings for golden-handed tamarins, the saddleback and mustached tamarins in the current study were intermediate between multiple central place and central place foragers, although the strategy they adopted was closer to that of multiple central place foragers than central place foragers. This may be expected since their pattern of using a very large number of sleeping sites with a relatively low level of reuse is in almost direct contrast to the idea of returning to a central place to sleep.

The proportion of times that the sleeping site closest to the last feeding site was used was similar to that observed for golden-handed tamarins (15-33% vs 12-27%) (Day and Elwood 1999). As Day and Elwood note, this may be explained in terms of a trade-off between favored sleeping sites and proximity to food resources. The suggestion that tamarins may decide where they will sleep before they reach their last feeding site presents the interesting possibility that tamarins may be deciding where to sleep based on where they plan to forage or at least travel to the following day. This was examined in the current study through the comparison of the distance between the sleeping site and the last feeding tree and that of the first used the following morning. No evidence was found that sleeping sites were chosen to be closer to future feeding sites than to past ones, in contrast one group of saddlebacks slept closer to their last feeding site than to their subsequent one. However this does not rule out the possibility that choice of site is influenced by a need to minimize

subsequent travel distances for either foraging or range defense. Further, patterns of reuse linked to predation risks may also influence the site used on a given night.

The mean distance between pairs of heterospecific sleeping sites, when weighted for frequency of use, was greater than has been reported in previous studies of these and other associating tamarin species (Table 10). Territory size may influence the maximum spatial separation between the two species before contact is lost. For example, without leaving the boundaries of a small territory, the maximum distance can be larger as there is a greater probability that once separated the two species would be reunited by chance, than in a larger territory. The index of defensibility is the ratio of the mean daily path length to the diameter of a circle of area equal to that of the home range (Mitani and Rodman, 1979). It provides a convenient measure analogous to the degree to which the two species would be expected to encounter each other by chance within their joint territory. As can be seen from Table 10, it is higher for Troops 1 and 2 than in either of the two other studies for which data are available (Norconk, 1986; Peres, 1991). Hence, it may be that the tamarins slept further apart because they would be more liable to re-establish contact by chance should they lose it. A number of other factors may also influence the distance between heterospecific sleeping sites. For example, differences, both at an intra and interspecific level, in resource distribution and availability between study sites may have an effect; but these factors have seldom been assessed, or measured in a comparable manner between studies. It also must be pointed out that whilst the distance between the heterospecific sleeping sites was greater than in other studies, it was within the range covered by contact long calls, 100-200 m (Pook and Pook, 1982; Ramirez, 1989; Norconk, 1990; ACS pers. obs.).

**Table 10:** about here

Although this study has addressed many questions about the sleeping habits of tamarins a few remain to be answered. For example, the differences found between groups in their preferences for different types of site raise the possibility of social transmission of preferences through the immigration of individuals into groups. Individuals may also differ in their order of entering or leaving sleeping sites based on real or perceived predation risk, which may be linked to perceptual capabilities such as color vision status (Smith et al

2004). It would also be of interest to know more about the microclimates provided by each type of site, and how these may relate to thermoregulation and metabolism in these small primates.

In summary the three groups of saddleback and mustached tamarins observed in this study showed a clear pattern of sleeping site use consistent with a strategy to avoid crepuscular or nocturnal predators. For example, they utilized a large number of trees as sleeping sites, seldom slept in the same site on consecutive nights, entered their sleeping sites well before sunset in a manner consistent with minimizing the probability of a predator following their progression, and left them relatively soon after sunrise. Further, the physical characteristics of the sites used were not related to the season, rainfall, or presence of infants. However, whilst overall the results indicate the clear importance of predation, other factors including access to food resources and range boundaries for defense may well act in combination with predation to determine the pattern of sleeping site use in primates, including early homids.

## **ACKNOWLEDGMENTS**

We thank the Dirección General Forestal y de Fauna of the Peruvian Ministry of Agriculture in Lima and the Dirección Regional de Recursos Naturales y de Medio Ambiente of the Regional Government of Loreto in Iquitos for permission to carry out field research at the Estación Biológica Quebrada Blanco. We are indebted to the late Jaime Moro S. and to Enrique Montoya G., Filomeno Encarnación C., and Luis Moya I. for help and logistic support. Arsenio Calle Cordova, Camilo Flores Amasifuén, Emérita R. Tirado Herrera, Jenni Pérez Yamacita, Juan Huanaquiri H., Marcos Overslijis Vásquez and Ney Shahuano all provided invaluable assistance in the field. Studies by ACS were supported in part by the Department of Psychology, The University of Reading and by the BBSRC (98/S11498 to HMB-S). Studies by CK, EWH, and MH and PL were supported by the Deutsche Forschungsgemeinschaft (HE1870/3-3; HE1870/10-1,2 and HE1870/3-1,3).

## LITERATURE CITED

- Altmann SA. 1974. Baboons, space, time, and energy. *Am Zool* 14: 221-248.
- Anderson JR. 1984. Ethology and ecology of sleep in monkeys and apes. *Adv Stud Behav* 14:165-229
- Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *Am J Primatol* 46:63-75
- Anderson JR. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Med Rev.* 4:355-373
- Aquino R, Encarnación F. 1986. Characteristics and use of sleeping sites in *Aotus* (Cebidae: Primates) in the Amazon lowlands of Peru. *Am J Primatol* 11:319-331.
- Baldwin JD, Baldwin J. 1972. The ecology and behaviour of squirrel monkeys (*Saimiri oerstedii*) in natural forest in western Panama. *Folia Primatol* 18:161-184.
- Banks P, Norrdahl, K, Korpimäki, E. 2000. Non-linearity in the predation risk of vole mobility. *Proc R Soc Lond B* 267:1621-1625.
- Bartecki, U & Heymann EW. 1990. Field observations on scent-marking behaviour in saddle-back tamarins, *Saguinus fuscicollis* (Callitrichidae, Primates). *J Zool Lond* 220:87-99.
- Blaffer-Hrdy S. 1977. The langurs of Abu. Cambridge, Massachusetts: Harvard Univ. Press.
- Brownlow AR, Plumptre AJ Reynolds V, Ward R. 2001. Sources of variation in the nesting behavior of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo forest, Uganda. *Am J Primatol* 55:49-55.
- Buchanan-Smith HM. 1991. A field study on the red-bellied tamarin, *Saguinus l. labiatus*, in Bolivia. *Int J Primatol* 12:259-276.
- Caine N G. 1984. Visual scanning by tamarins: A description of the behaviour and tests of two derived hypotheses. *Folia Primatol* 43:59-67.
- Caine NG. 1987. Vigilance, vocalizations, and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *Am J Primatol* 12:241-250.
- Carpenter CR. 1985. Behavior of red spider monkeys in Panama. *J Mammal* 16:171-180.
- Chapman C. 1989. Spider monkey sleeping sites: use and availability. *Am J Primatol* 18:53-60.
- Chapman CA, Chapman LJ, McLaughlin R. 1989. Multiple central place foraging in spider monkeys: Consequences of using many sleeping sites. *Oecologia* 79:506-511.

- Chivers DJ. 1974. The Siamang in Malaya. Basel: Karger.
- Coimbra-Filho AF. 1978. Natural shelters of *Leontopithecus rosalia* and some ecological implications. In: Kleiman DG, editor. The Biology and Conservation of the Callitrichidae. Washington DC: Smithsonian Institution Press. P 79-90.
- Cui L -W, Quan R -C, Xiao W. 2006. Sleeping sites of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Baima Snow Mountain, China. J Zool 270:192-198
- Dawson GA. 1979. The use of time and space by the Panamanian tamarin *Saguinus oedipus*. Folia Primatol 31:253-284.
- Day RT, Elwood RW. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas* : The role of predation risk, proximity to feeding sites, and territorial defence. Ethology 105:1035-1051.
- Di Bitetti MA, Vidal EML, Baldovino MC, Benesovsky V. 2000. Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*) Am J Primatol 50:257-274.
- Dow H, Fredga S. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. J Anim Ecol 52:681-695.
- Erkert HG. 1989. Characteristics of the circadian activity rhythm in common marmosets (*Callithrix j. jacchus*). Am J Primatol 17:271-286.
- Franklin SP. 2004. Predator influence on golden lion tamarin nest choice and presleep behavior. MSc Thesis University of Maryland, Maryland, USA
- Garber PA, Teaforde MF. 1986. Body weights in mixed species troops of *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* in Amazonian Peru. Am J Phys Anthropol 71:331-336.
- Garber PA. 1986. The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). Am J Primatol 10:155-170.
- Gautier-Hion A. 1970. L'organisation sociale d'une bande de talapains (*Miopithecus talapoin*) dans le nord-est du Gabon. Folia Primatol 12:116-141.
- Gibbons EF, Menzel. 1980. Rank orders of arising, eating, and retiring in a family group of tamarins (*Saguinus fuscicollis*). Primates 21:44-52.
- Giraldeau L.-A, Kramer DL. 1982. The marginal value theorem: a quantitative test using load size variation in a central place forager, the eastern chipmunk, *Tamias striatus*. Anim Behav 30:1036-1042.
- Goldizen AW. 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). Behav Ecol Sociobiol 20: 99-109.

- Goodall J. 1962. Nest building behaviour in the free ranging chimpanzee. *Ann N Y Acad Sci* 102:455-467.
- Hamilton WJ, Buskirk RE, Buskirk WH. 1976. Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology* 57:1264-1272.
- Hampton JK. 1973. Diurnal heart rate and body temperature in marmosets. *Am J Phys Anthropol* 38:339-342.
- Hausfater G, Meade BJ. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23:287-297.
- Hetherington CM. 1978. Circadian oscillation of body temperature in the marmoset, *Callithrix jacchus*. *Lab Anim* 12:107-108.
- Heymann EW. 1990. Interspecific relations in a mixed- species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Platyrrhini: Callitrichidae) at the Rio Blanco, Peruvian Amazonia. *Am J Primatol* 21:115-127.
- Heymann EW. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia; Primates; Callitrichidae), in north-eastern Peru. *J Zool Lond* 237:211-226.
- Heymann EW. 2000a. Malaria infection rate of Amazonian primates: the role of sleeping habits. *Folia Primatol.* 72:153.
- Heymann EW. 2000b. Spatial patterns of scent marking in wild moustached tamarins, *Saguinus mystax*: no evidence for a territorial function. *Animal Behaviour* 60:723-730
- Heymann EW, Hartmann G. 1991. Geophagy in moustached tamarins, *Saguinus mystax* (Platyrrhini: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *Primates* 32:533-537.
- Izawa K. 1979. Studies on peculiar distribution pattern of *Callimico*. Kyoto University Overseas Research Reports of New World Monkeys.1-19.
- Huck M, Löttker P, Böhle UR, Heymann EW. 2005. Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). *Am J Phys Anthropol* 127:449-464
- Kappeler PM. 1998. Nests, tree holes, and the evolution of primate life histories. *Am J Primatol* 46:7-33.
- Löttker P, Huck M, Heymann EW. 2004. Demographic parameters and events in wild moustached tamarins (*Saguinus mystax*). *Am J Primatol* 64:425-449
- Lopez MA, Ferrari SF. 1994. Foraging behaviour of a tamarin group (*Saguinus fuscicollis weddelli*) and interactions with marmosets (*Callithrix emiliae*) *Int J Primat* 15:373-387.

- McLaughlin RL, Montgomery RD. 1989. Brood dispersal and multiple central place foraging by Lapland longspur parents. *Behav Ecol Sociobiol* 25:207-216.
- Meddis R. (1983). The evolution of sleep. In: Mayes A, editor. *Sleep Mechanisms and Functions in Humans and Animal*. Wokingham: Van Nostrand. p 57-95
- Mitani JC, Rodman PS. 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol* 5:241-251.
- Moynihan M. 1970. Some behavioural patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contrib Zool* 28:1-77.
- Moynihan M. 1976. *The New World Primates*. Princeton, New Jersey: Princeton Univ. Press.
- Neyman PF. 1978. Aspects of the ecology and social organisation of free ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: Kleiman DG, editor. *The biology and conservation of the Callitrichidae*. Washington, DC: Smithsonian Institution Press. p 39-72.
- Nickle DA, Heymann EW. 1996. Predation on Orthoptera and other orders of insects by tamarin monkeys, *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* (Primates: Callitrichidae), in north-eastern Peru. *J Zool Lond* 239:799-819.
- Nilsson SG, Johnsson K, Tjernberg. 1991. Is avoidance by black woodpeckers of old nest holes due to predators? *Anim Behav* 41:439-441.
- Norconk MA. 1986. Interactions between primate species in a neotropical forest: Mixed species troops of *Saguinus mystax* and *S. fuscicollis* (Callitrichidae) PhD thesis. University of California, Los Angeles, USA.
- Norconk MA. 1990. Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. *Am J Primatol* 21:159-170.
- Nunn CL, Heymann EWH. 2005. Malaria infection and host behavior: a comparative study of Neotropical primates. *Behav Ecol Sociobiol* 59:30-37.
- Patterson JD. 1973. Ecologically differentiated patterns of aggressive and sexual behaviour in two troops of Ugandan boboons, *Papio anubis*. *Am J Phys Anthropol* 33:641-648.
- Peres CA. 1986. *Costs and benefits of territorial defense in golden lion tamarins, Leontopithecus rosalia*. Unpubl. M.Sc. dissertation, University of Florida, Gainesville, USA.

- Peres CA. 1991. Ecology of mixed-species groups of tamarins in Amazonian terra firme forests. Unpubl. PhD thesis, University of Cambridge, UK.
- Peres CA. 1992. Consequences of joint-territoriality in a mixed species group of tamarin monkeys. *Behaviour* 123:220-246.
- Peres CA. 1993. Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian terra firme forest. *J Zool Lond* 230:567-592.
- Petry VH, Riehl I, Zucker H. 1986. Energieumsatzmessungen an Weissbuscheläffchen (*Callithrix jacchus*) *Anim Physiol Anim Nutr* 55:214-224.
- Pontes ARM, Soares ML. 2005. Sleeping sites of common marmosets (*Callithrix jacchus*) in defaunated urban forest fragments: a strategy to maximize food intake. *J Zool* 266:55-53.
- Pook A, Pook AG. 1982. Polyspecific association between *Saguinus fuscicollis* and *Saguinus labiatus*, *Callimico goeldii* and other primates in north western Bolivia. *Folia Primatol* 38:196-21.
- Ramirez MM. 1989. Ecology and demography of the moustached tamarin, *Saguinus mystax* in north eastern Peru. PhD thesis, City University of New York, New York, USA.
- Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*) *Am J Primatol* 46:35-62.
- Rylands AB. 1989. Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. *J Human Evol* 18:679-95.
- Savage A. 1990. The reproductive biology of the cotton-top tamarin (*Saguinus oedipus oedipus*) in Colombia. Ph.D dissertation, University of Wisconsin. 166 p.
- Schnell CR, Wood JM. 1993. Measurement of blood pressure and heart rate by telemetry in conscious, unrestrained marmosets. *Am J Physiol* 264:1509-1516.
- Sigg H, Stolba A.. 1981. Home Range and Daily March in a Hamadryas Baboon Troop. *Folia Primatol* 36:40-75.
- Smith AC. 1997. Comparative ecology of saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins. PhD thesis, University of Reading, UK
- Smith AC. 2000. Interspecific differences in prey captured by associating saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins. *J Zool, Lond* 251:315-324.

- Smith AC, Buchanan-Smith HM, Surridge AK, Osorio D, Mundy NI. 2003. The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.) J Exp Biol 206:3159-3165.
- Smith AC, Kelez S, Buchanan-Smith HM. 2004. Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*) Behav Ecol Sociobiol, 56:18-25.
- Smith AC, Buchanan-Smith HM. In prep. Factors effecting intergroup encounters between wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*)
- Smith AC, Tirado ER, Buchanan-Smith HM, Heymann EW. 2002. Multiple breeding females and allo-nursing in a wild group of moustached tamarins (*Saguinus mystax*) Neotrop Primates 9:67-69.
- Soini P. 1987. Ecology of the saddle-back tamarin *Saguinus fuscicollis illigeri* on the Rio Pacaya, northeastern Peru. Folia Primatol 49:11-32.
- Soini P. 1988. The pygmy marmoset, Genus *Cebuella*. In: Mittermeier RA, Coimbra-Filho AF, da Fonseca GAB, editors. Ecology and behavior of neotropical primates, Volume 2. Washington DC: World Wildly Fund. p 79-129.
- Soini P. 1990. Ecológia y dinámica poblacional de pichico común *Saguinus fuscicollis* (Callitrichidae, Primates) La Primatología en el Perú, Investigaciones primatólogicas (1973-1985) Lima, Peru
- Sonerud GA. 1985. Nest hole shift in Tengmalm's owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. J Anim Ecol 54:179-192
- Sonerud GA. 1989. Allocation of prey between self-consumption and transport in two different-sized central place foragers. Ornis Scand 20:69-71.
- Struhsaker TT. 1967. Social structure among vervet monkeys (*Cercopithecus aethiops*). Behaviour 29:83-121.
- Sussman RW, Kinzey WG. 1984. The ecological role of the Callitrichidae: a review. Am. J Phys Anthropol 64:419-449.
- Terborgh J. 1983. Five New World Primates. A study in comparative ecology. Princeton: Princeton Univ. Press.
- Thompson S. 1988. Thermoregulation in the water opossum (*Chironectes minimus*): An exception that 'proves' the rule. Physiol Zool 61:450-460.

- Thompson S. 1991. Biotelemetric studies of mammalian thermoregulation. In Asa C, editor. Biotelemetry applications for captive animal care and research. Wheeling: American Association of Zoological Parks and Aquariums. p19-28.
- Thompson SD, Power ML, Rutledge CE, Kleiman DG. 1994. Energy metabolism and thermoregulation in the golden lion tamarin (*Leontopithecus rosalia*). *Folia Primatol* 63:131-143.
- Thorington RW. 1967. Feeding and activity of *Cebus* and *Saimiri* in a Columbian forest. In Starck, Schneider and Kuhn, editors. Progress in Primatology. Proc. 1st Int. Congr. Primatol. Stuttgart: Fischer. p 180-184.
- von Hippel. 1998. Use of sleeping trees by black and white Colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *Am J Primatol* 45:281-290.
- Wasburn SL, Devore I. 1961. The social life of baboons. *Sci. Am.* 204:62-71.
- Yoneda M. 1981. Ecological studies of *Saguinus fuscicollis* and *S. labiatus* with reference to habitat segregation and height preference. *Kyoto Universities Overseas Reports* 2:43-50.
- Yoneda M. 1984a. Comparative studies on vertical separation, foraging behaviour and traveling mode of saddle-backed tamarins (*Saguinus fuscicollis*) and red-chested moustached tamarins (*Saguinus labiatus*) in northern Bolivia. *Primates* 25:414-422.
- Yoneda M. 1984b. Ecological study of the saddle backed tamarins (*Saguinus fuscicollis*) in northern Bolivia. *Primates* 25:1-12.
- Zhang S. 1995. Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guiana. *Am J Primatol* 36:327-335.

**Table 1:** Times of entry to and exit from sleeping sites in three mixed species troops of saddleback and mustached tamarins

**Figure 1:** Seasonal variation in mean times A) saddleback and B) mustached tamarins entered and left their sleeping sites. Grey line indicates sunrise and sunset. Error bars indicate the earliest and latest times of entry and exit.

**Table 2:** Exclusivity of use of sleeping sites by saddleback and mustached tamarins

**Figure 2:** Cumulative frequency of new sleeping trees used by three troops of saddleback and mustached tamarins

**Table 3:** Frequency of use of individual sleeping trees by three mixed-species troops of saddleback and mustached tamarins

**Table 4:** Differences in the observed and expected frequency of runs of two, three and four consecutive nights spent in the same sleeping site by saddleback and mustached tamarins

**Figure 3:** Differences in the sleeping heights of saddleback and mustached tamarins within three mixed species troops

**Table 5** Frequency of the different types of sleeping sites and their intensity of use by saddleback and mustached tamarins

**Table 6:** Test of difference in meteorological variables when different categories of sleeping sites were used by saddleback and mustached tamarins (Kruskal-Wallis ANOVAs)

**Figure 4:** Location of sleeping sites for two mixed-species troops of saddleback and mustached tamarins (scale bars indicate co-ordinates / m)

**Figure 5:** Mean centrality of two mixed species troops of saddleback and mustached tamarins whilst in their sleeping sites

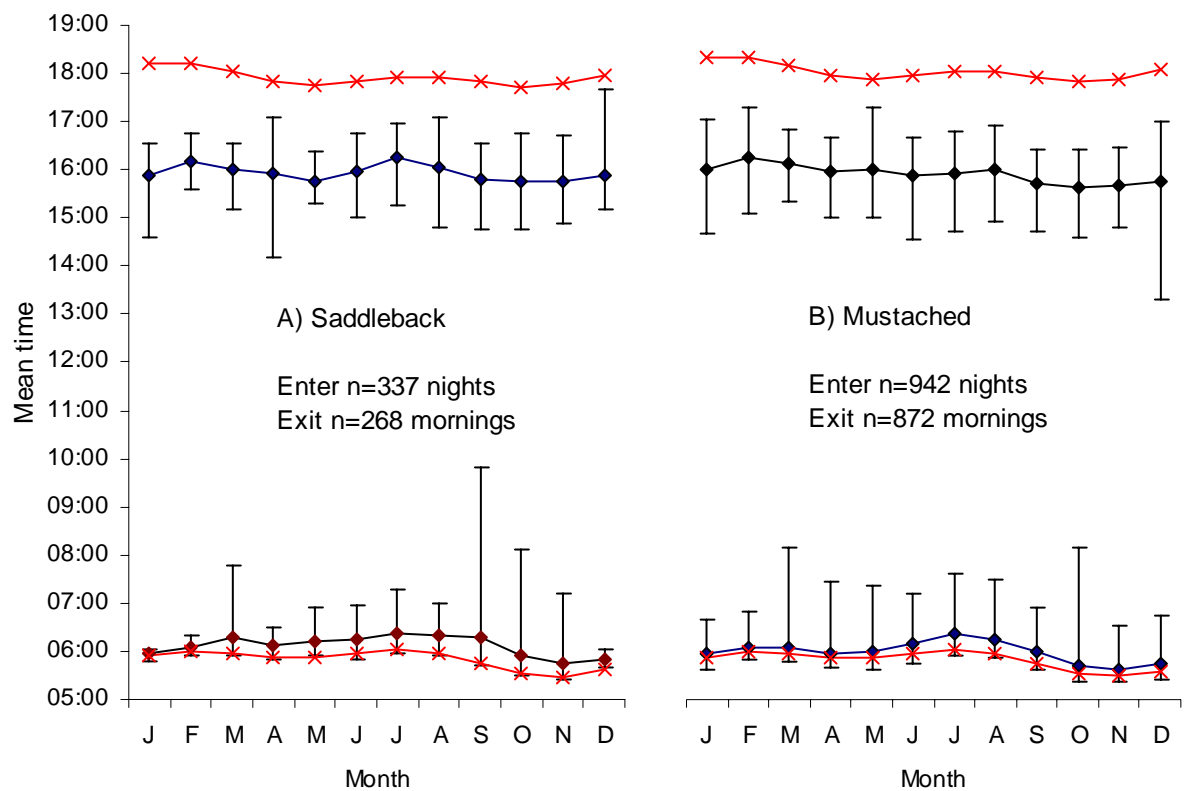
**Figure 6:** Mean distance between the last feeding site of the day and the observed sleeping site, the nearest sleeping site (multiple central place foraging, MCPF) and the mean sleeping site (central place foraging, CPF) in two mixed species troops of saddleback and mustached tamarins.

**Table 7:** Differences between the distance from the last feeding site of the day and the observed sleeping site and the nearest sleeping site (multiple central place foraging, MCPF) and the mean sleeping site (central place foraging, CPF) in two mixed species troops of saddleback and mustached tamarins (paired t-tests)

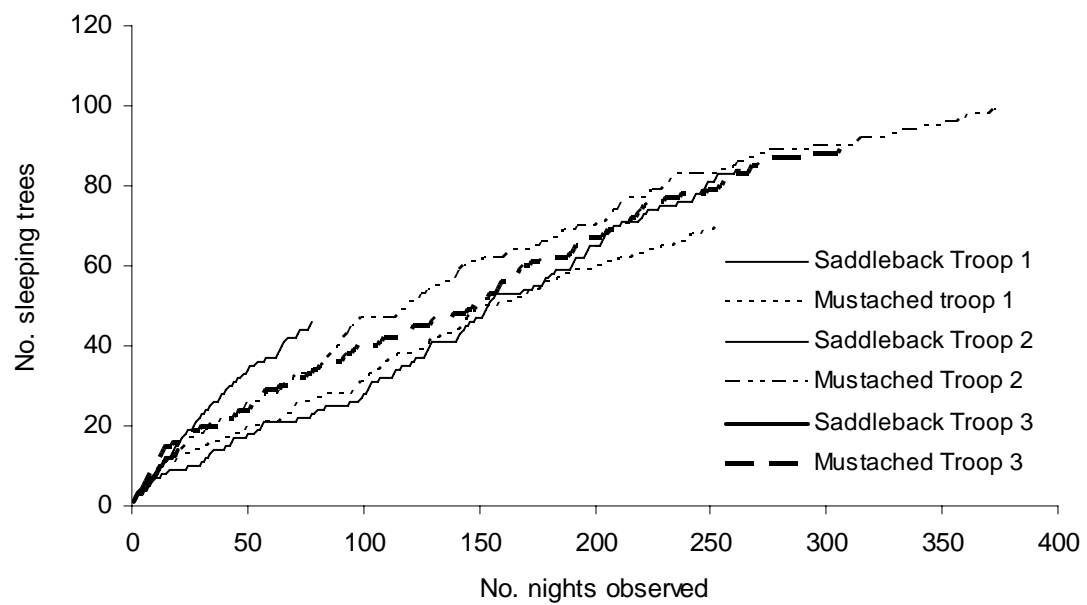
**Table 8:** Difference between the distance from the sleeping site and the last and first feeding sites in two mixed species troops of saddleback and mustached tamarins

**Table 9:** Times of entering and leaving sleeping sites, and length of active period in wild tamarins

**Table 10:** Distance between pairs of heterospecific sleeping sites in associating wild saddleback and mustached tamarins.  $D$  = index of defensibility (Mitani and Rodman, 1979)



**Figure 1**



**Figure 2**

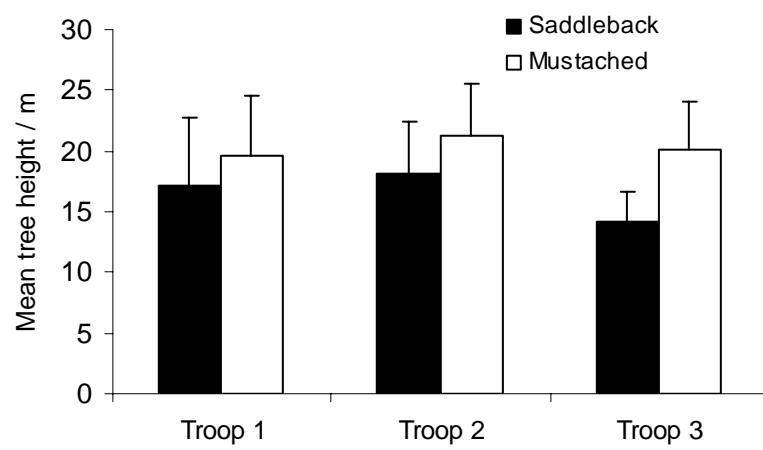
**Table 3:** Frequency of use of individual sleeping trees by three mixed-species troops of saddleback and mustached tamarins

No. of nights	Troop 1		Troop 2		Troop 3	
	Saddleback	Mustached	Saddleback	Mustached	Saddleback	Mustached
1	38	24	28	45	10	35
2	11	14	8	13	2	15
3	9	9	10	14	2	11
4	8	5	1	6	0	5
5	6	2	0	7	0	5
5+	11	16	0	14	0	18
Mean nights	3.1 ± 3.3	3.6 ± 4.0	1.7 ± 0.9	3.8 ± 2.0	1.4 ± 0.8	3.5 ± 3.8
n	263	254	78	373	20	311

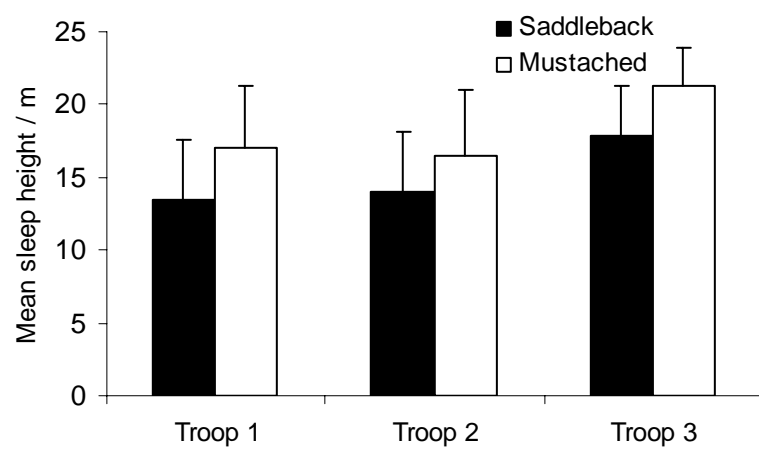
**Table 4**

Troop	Species	2 nights			3 nights			4 nights		
		O	E	n	O	E	n	O	E	n
1	Saddleback	33*	2.45	203	5*	0.023	157	3*	0.0002	119
	Mustached	11*	2.83	198	0	0.031	153	0	0.0003	116
2	Saddleback	2	1.04	48	0	0.014	30	0	0.0001	13
	Mustached	4	3.19	313	0	0.028	265	0	0.0002	224
3	Saddleback	0	0.93	13	0	0.036	7	0	0.0004	1
	Mustached	4	2.83	252	0	0.026	207	0	0.0002	168

\* Binomial test  $P < 0.05$



**Figure 3**



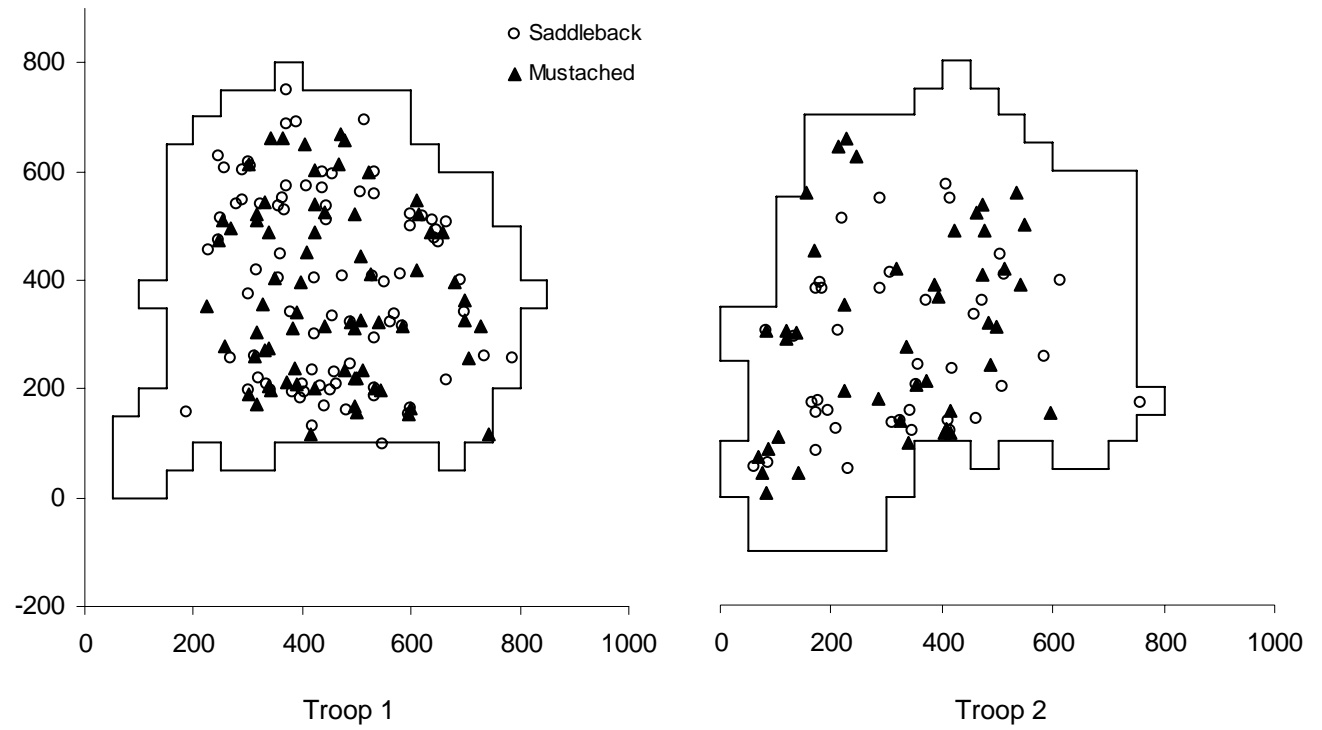
**Figure 4**

**Table 5**

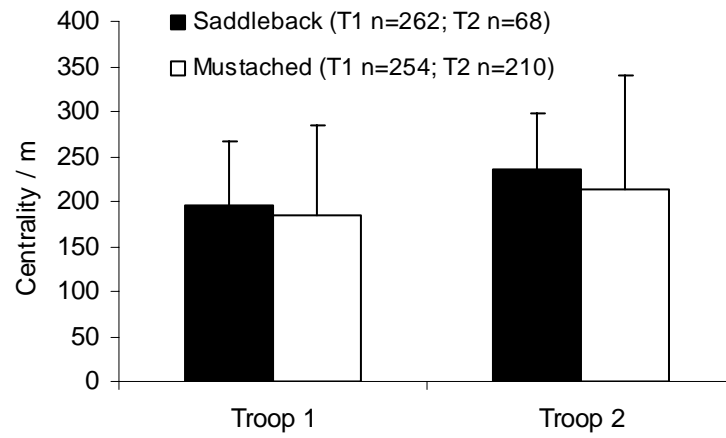
		Troop 1		Troop 2		Troop 3
		Saddleback	Mustached	Saddleback	Mustached	Mustached
Branch	Number	0.0%	26.6%	0.0%	8.1%	4.4%
	Use	0.0%	20.2%	0.0%	17.3%	4.6%
Crotch	Number	2.8%	21.9%	17.4%	27.0%	8.7%
	Use	2.1%	39.3%	19.0%	54.5%	5.7%
Hollow	Number	29.2%	0.0%	4.3%	0.0%	0.0%
	Use	36.1%	0.0%	7.1%	0.0%	0.0%
Palm	Number	13.9%	39.1%	17.4%	35.1%	69.6%
	Use	15.5%	33.9%	14.3%	16%	39.8%
Tangle	Number	54.2%	12.5%	60.9%	29.7%	17.4%
	Use	46.2%	6.6%	59.5%	12.2%	50.0%
n	Number	72	64	23	37	23
	Use	238	242	42	156	88

**Table 6**

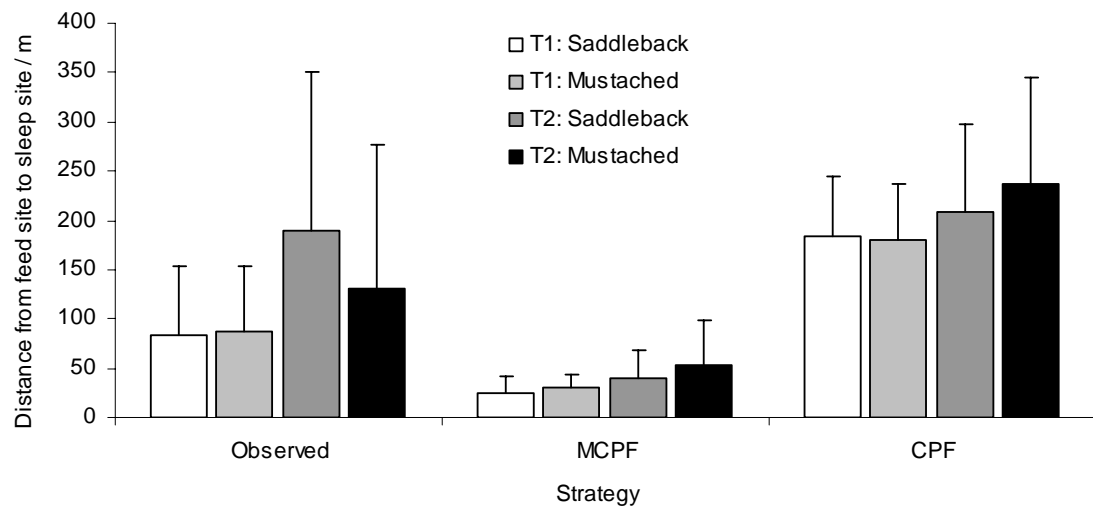
		Rainfall			Max temp			Min temp		
		$\chi^2$	d.f.	P	$\chi^2$	d.f.	P	$\chi^2$	d.f.	P
Troop 1	Saddleback	2.5	3	>0.05	0.05	3	>0.05	2.9	3	>0.05
	Mustached	0.39	2	>0.05	3.1	2	>0.05	2.0	2	>0.05
Troop 2	Saddleback	1.1	3	>0.05	4.6	3	>0.05	1.6	3	>0.05
	Mustached	5.3	2	>0.05	8.7	2	>0.05	.23	2	>0.05
Troop 3	Mustached	4.2	2	>0.05	0.56	2	>0.05	2.2	2	>0.05



**Figure 5**



**Figure 6**



**Figure 7**

**Table 7**

		Observed vs. MCPF			Observed vs. CPF			Diff: Obs-MCPF vs. Obs-CPF		
		t	d.f.	P	t	d.f.	P	t	d.f.	P
Troop 1	Saddleback	9.3	116	0.001	-11.1	116	0.001	-5.4	116	0.001
	Mustached	9.5	114	0.001	-12.4	114	0.001	-4.9	114	0.001
Troop 2	Saddleback	7.3	54	0.001	-1.0	54	>0.05	1.5	54	>0.05
	Mustached	5.6	73	0.001	-6.3	73	0.001	-4.3	73	0.001

**Table 8**

		Distance between sleeping site and last feeding site		t	d.f.	P
Troop 1	Saddleback	83.4 ± 69.3	109.0 ± 93.0	-3.1	96	<0.01
	Mustached	87.3 ± 66.4	99.6 ± 82.4	-1.6	91	>0.05
Troop 2	Saddleback	189.0 ± 161.4	185.7 ± 179.6	0.1	48	>0.05
	Mustached	130.6 ± 145.7	133.2 ± 144.5	0.2	54	>0.05

**Table 9**

Species	Location	Time of exit (Range)	Time of entry (Range)	Active period (Range)	Reference
<i>Saddleback</i>	4°40'S, 73°00'W	0604 (0530 - 0927)	1600 (1412 – 1646)	9:54 (8:00 - 10:55)	Smith (1997)
<i>Mustached</i>		0604 (0528 - 0733)	1557 (1456 – 1712)	9:52 (8:53 - 11:02)	
<i>Saddleback</i>	4°5' S, 65°16' W	0631	1540	8:51	Peres (1991)
<i>Mustached</i>		(Both sp.)	(Both sp.)	(Both sp.)	
<i>Saddleback</i>	4°40'S, 73°00'W	-	1609	-	Heymann (1995)
<i>Mustached</i>		-	1607	-	
<i>Saddleback</i>	8°58'S, 63°14'W	-	-	9:20 <sup>wet</sup> 9:55 <sup>-dry</sup>	Lopes and Ferrari (1994)
<i>Red-bellied</i>	11°11'S, 68°42'W	0615 (0600 - 0900)	1623 (1445 – 1745)	10:08	Buchanan-Smith (1991)
<i>Saddleback</i>	5°26'S, 74°34'W	(0535 - 0620)	(1700 – 1755)	11:06	Soini (1987)
<i>Saddleback</i>	4°40'S, 73°W	(0600 - 0637)	(1520 – 1703)	-	Bartecki and Heymann (1990)
<i>Saddleback</i>	4°40'S, 73°W	0603 (0535 - 0628)	1606	-	Heymann (1990)
<i>Mustached</i>		-	1545	-	
<i>Cotton-top</i>	Panama Canal Zone	Sunrise + 11 min.	Sunset - 34 min	11:16 (7:06 - 12:11)	Dawson (1979)
<i>Mustached</i>	4°15'S, 73°04'W	0620 (0555 - 0710)	1656 <sup>wet</sup> 1606 <sup>dry</sup>	10:10 (8:59 - 11:30)	Ramirez (1989)
<i>Saddleback</i>	11°02'S, 69°05'W	0623	1646	10:23	Yoneda (1981)
<i>Red-bellied</i>					
<i>Red-bellied</i>	11°02'S, 69°05'W	(0600 - 0640)			Yoneda (1984a)

**Table 10**

Distance $\pm$ s.d. / m	N	D	Reference
110.0 $\pm$ 100.5	223	2.37 <sup>1</sup>	Current study Troop 1
142.3 $\pm$ 138.5	32	2.46 <sup>2</sup>	Current study Troop 2
45.8 $\pm$ 22.6	84	1.43	Peres (1991)
33 $\pm$ 26	18	1.98 <sup>3</sup>	Heymann (1990)
40 $\pm$ 28	31	2.09 <sup>3</sup>	Heymann (1995)
25 - 75		1.84	Norconk (1986)
25 - 75			Ramirez (1989)

<sup>1</sup> from Smith 1997, <sup>2</sup> Smith unpublished data, <sup>3</sup> taken from Heymann (2000b)

