

ABSTRACT

Title of Dissertation: PREDATOR INFLUENCE ON GOLDEN LION
TAMARIN NEST CHOICE AND PRESLEEP
BEHAVIOR

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Primate sleeping site choices and cryptic pre-retirement behaviors presumably aid survival by reducing a predator's ability to find and access prey. I examined presleep behaviors in a population of golden lion tamarins (*Leontopithecus rosalia*) that recently suffered heavy losses from predators. I analyzed existing sleeping site data to determine whether groups at higher risk of predation, as measured by the number of observed encounters with potential predators, changed den sites more frequently than groups at lower risk. Additionally, I evaluated scent marking data to resolve whether study individuals decreased scent marking just prior to retiring. The predator encounter interval was not a significant predictor of the rate with which social groups changed den sites and study individuals significantly increased scent marking just prior to retiring. Consequently, it appears that after multiple generations without exposure to heavy predation pressure the tamarins in this isolated population fail to alter their behavior appropriately to mitigate predation risk.

PREDATOR INFLUENCE ON GOLDEN LION TAMARIN
NEST CHOICE AND PRESLEEP BEHAVIOR

by

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Thesis Submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Master of Science
2004

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ACKNOWLEDGEMENTS

During the course of my graduate study I learned that the completion of this dissertation depended on a number of things: luck, hard work, and most importantly, a great deal of help from other people. I want to thank all those individuals without whom I could not have completed this research.

Among the people to whom I must offer great thanks are my advisor and the members of my committee. My advisor, Dr. James Dietz, provided invaluable guidance during the course of this project and was always willing to help me whenever I needed. Similarly, Dr. David Inouye and Dr. Gerald Wilkinson provided helpful advice and instruction.

In addition to guidance from faculty members within the Biology Department, I also received a great deal of statistical assistance from other faculty members. Drs. Estelle Russek-Cohen, Larry Douglass, and Bahram Momen all dedicated their time to helping me.

Fellow graduate students from the Dietz laboratory, past and present, were also of considerable help. Dr. Karen Bales provided valuable statistical advice, Dr. Becky Raboy shared useful ideas, and Dr. Kimran Miller contributed data, scientific advice, and time reviewing this thesis. Similarly, Sarah Hankerson provided help formulating testable hypotheses and entering data. MaLinda Henry and Jennifer Siani provided editing advice and help with data entry. Annie Bush taught me how to use GIS and was patient whenever I had to ask the same questions repeatedly. Undergraduate laboratory members Sheri Coutermarsh and Britt Burtner provided hours of assistance in entering data that I used for this project.

In addition to help from students within the Dietz lab, graduate students from other laboratories were also helpful. Most notably, Dr. Chris Swann and Holly Menninger contributed advice on my statistical procedures.

Beyond the University of Maryland many other people contributed to this thesis. Several Brazilian office assistants and field workers were instrumental in providing guidance and support during the time that I was working in Brazil. Furthermore, their tireless efforts in the field resulted in the accumulation of many data, including those used in this project.

Aside from those individuals who assisted directly with this project I need to thank two individuals who guided me during the course of my study. Both Dana Purcell and Lois Reid were always patient and helpful when I needed their instruction on how to handle the numerous bureaucracies associated with completing a graduate degree.

Finally, I know that without the support of friends and family I would not be where I am today. They were always encouraging when I needed them most.

TABLE OF CONTENTS

LIST OF FIGURES	V
LIST OF TABLES	V
INTRODUCTION.....	1
CHAPTER 1: PREDATION PRESSURE DOES NOT EXPLAIN SLEEPING SITE USE BY GOLDEN LION TAMARINS (<i>LEONTOPITHECUS ROSALIA</i>).....	8
<i>Introduction.....</i>	8
<i>Methods.....</i>	14
Study Site and Data Collection.....	14
Analysis.....	14
<i>Results.....</i>	17
<i>Discussion.....</i>	18
<i>Tables and Graphs.....</i>	22
CHAPTER 2: DO THE BENEFITS OF SCENT MARKING SLEEPING SITES BY A CAVITY-NESTING PRIMATE OUTWEIGH THE POTENTIAL RISK OF PREDATION?.....	24
<i>Introduction.....</i>	24
<i>Methods.....</i>	31
Study Site and Data Collection.....	31
Data Analysis.....	32
<i>Results.....</i>	33
Hypotheses Tested.....	33
<i>Discussion.....</i>	34
<i>Tables and Graphs.....</i>	38
LITERATURE CITED	41

LIST OF FIGURES

CHAPTER 1. FIGURE 1. Den Change.....22

CHAPTER 1. FIGURE 2. Predator Effect on GLT
Patterns of Sleeping Site Use.....23

CHAPTER 2. FIGURE 1. Scent Marking at Sleeping Sites38

CHAPTER 2. FIGURE 2. Daily Patterns of Scent Marking.....39

CHAPTER 2. FIGURE 3. Seasonal Patterns of Scent Marking39

CHAPTER 2. FIGURE 4. Seasonal Patterns of Scent Marking
Just Prior to Retirement.....40

LIST OF TABLES

CHAPTER 1. TABLE 1. Number of sleeping site records,
unique den sites, and frequency of movement
among sleeping sites.....22

CHAPTER 1. TABLE 2. Predator encounters and
predator encounter interval.....23

INTRODUCTION

The golden lion tamarin (*Leontopithecus rosalia*; GLT) is a small, endangered primate endemic to the Atlantic Rainforest of Brazil. Since most of the Atlantic rainforest was cleared and fragmented in the last century little habitat exists and these monkeys persist only in a few small and relatively isolated populations. The largest population of wild GLTs is found in the Poço das Antas (PDA) Biological Reserve in the state of Rio de Janeiro, Brazil. This population has been monitored continuously from 1983 through the present time. Between the years 1995 and 2000 predation on tamarins increased significantly, reducing this population from approximately 347 to 220 individuals.

Most of the increased predation on GLTs in PDA occurred in the proximity of GLT sleeping sites. On at least 16 occasions between 1995 and 2000, an unidentified carnivore(s) located the tamarins in their den tree. Most of these den trees were hollow and the tamarins often entered the tree at some height above the ground before descending through the hollow trunk to sleep at ground level inside the tree. The trees either had an opening that permitted the predators to enter the tree hollow or the predators were able to create a hole through which they could enter. After gaining access to the GLTs the carnivores killed and ate them in the den or captured them as they attempted to flee in the dark. In the majority of these cases the predator killed multiple GLTs and sometimes the entire social group. Many of these predation events occurred at dens that GLT groups used repeatedly.

The majority of diurnal species are at increased risk of predation during their period of sleep. Primates are among those species considered most vulnerable to

predators at night. However, observing predators successfully attacking primates is exceedingly difficult (Stanford 1988) and confirmed reports of predators capturing primates at sleeping sites are rare. Further, population declines caused by predation at den sites, such as that observed with the GLTs in PDA, have not been documented for other primates. One of the reasons there are few observations of predation is that predators are often secretive species that are difficult to see at any time. Witnessing predation at night is even more difficult because it becomes increasingly challenging to see predators as light levels diminish. Finally, primates presumably attempt to minimize the chances of predation at sleeping sites by employing anti-predator behaviors (see Anderson 1984).

Prey can reduce the likelihood of predation at sleeping sites in a variety of ways. Choosing sleeping sites that prevent predator access is one of the primary ways by which prey can avert predation. Many primates choose to sleep in large trees that emerge from the canopy, presumably because carnivores cannot easily access the sleeping tree from surrounding trees (Reichard 1998, Di Bitetti et al. 2000, Ramakrishnan and Coss 2001). Some primates, birds, squirrels, and bats frequently nest in tree cavities (Coimbra-Filho 1977, Tidemann and Flavel 1987, Vonhof and Barclay 1996, Carey et al. 1997, Kappeler 1998, Aitken et al. 2002). Using tree holes may offer better protection from predators than sleeping on branches or in open nests by restricting predators too large to enter the den site. Similarly, various primates and bats sleep as high in a nest tree as possible (Sugardjito 1983, Betts 1998, Ramakrishnan and Coss 2001). Sleeping high within a tree, either in the open or in cavities, limits the ability of terrestrial predators to reach them as they sleep.

Prey may also mitigate predation risk at sleeping sites by attempting to remain hidden from their potential predators. In order to conceal their location while resting many primates typically avoid vocalizing while in their den tree or on their way to the den tree (Dawson 1979, Caine 1987, Day and Elwood 1999). Additionally, primates reduce the likelihood that predators will find them by remaining hidden or motionless while resting (Reichard 1998, Ramakrishnan and Coss 2001, Radespiel et al. 2003). Further, some primates demonstrate a tendency to move more rapidly during their approach to or departure from their den than during other times of day (Neyman 1977, Day and Elwood 1999). By moving quickly to their den sites prey apparently reduce the chances that predators will be able to follow them from their last feeding site to their den. Similarly, brown bats (*Tadarida sp.*) dive rapidly towards the ground immediately after exiting their tree hollow before flying away (Czechura 1983). Such behavior could be an attempt to evade detection so that the location of the roost remains unknown to local predators.

In addition to remaining quiet and moving quickly to and from the den, prey might conceal their sleeping location by changing dens frequently. By changing dens, they can minimize the accumulation of olfactory cues that may reveal their location. Relatively stationary voles suffered higher predation at their runways than individuals that moved more frequently (Banks et al. 2000). The authors suggested that sedentary individuals accumulated scent, urine, and feces that attracted mustellids. In addition to preventing an accumulation of scent that could attract predators, changing dens could limit the success of predators that routinely return to profitable nesting sites or that have developed a search image for a specific nest type (Sonerud 1985). Black woodpeckers

(*Dryocopus martius*) that nested in older tree cavities suffered greater predation and had significantly lower fledgling success than individuals that fledged in new nests (Nilsson et al. 1991). Similarly, Tengmalm's owl (*Aegolius funereus*) clutches laid in nest boxes that were previously the site of predation were significantly more likely to be preyed upon than nest boxes that had successfully fledged young the previous year (Sonerud 1985). Further, Tengmalm's owl nest boxes that were moved experimentally between subsequent breeding seasons had higher fledgling success, compared to the boxes that were not moved, because predators more frequently raided the boxes that remained at the same location (Sonerud 1989). A potential explanation is that predators had learned where older and more profitable nesting sites were situated and returned to them regularly.

Although changing den sites regularly may reduce the conspicuousness of a den site, and could mitigate predation in some situations, such behavior might also be detrimental. The fledgling success of goldeneyes (*Bucephala clangula*) that remained in the same nest box between breeding seasons was higher than that of females that changed dens between seasons (Dow and Fredga 1983). When changing dens regularly, individuals may have begun using dens that were less secure from predators, thus predisposing them to increased predation. Conversely, frequent re-use of the same sleeping sites may have improved the individual's knowledge of and ability to detect resident predators, thus leading to lessened predation risk (Dow and Fredga 1983). In the same way, repeated use of a single site could foster an intimate familiarity with a particular site and the best escape routes from the den (Struhsaker 1967).

Whether frequent reuse of the same sleeping sites or regular movement among sites is advantageous depends upon the degree to which individual sites are predator proof and the availability of secure sites. In an ideal situation, prey can move frequently among a plethora of equally secure sleeping sites. However, it is unlikely that a scenario exists in which all sites offer equal inaccessibility to predators. Hence, there is a tradeoff between the advantages conferred by using many sites infrequently and using one or a few sites regularly (Day and Elwood 1999). The strategy that maximizes prey safety and shapes the prey's pattern of sleeping site use may be influenced by habitat characteristics that affect the distribution of secure sites within a prey's territory (Hamilton 1982). If predator proof sites are not available individuals may benefit from changing den sites frequently in order to minimize the likelihood that predators will find them (Hrdy 1977). Conversely, if a limited number of predator proof sites are available the best strategy may involve use of a few dens despite the increased risk that predators will identify the location of the dens.

The distribution and availability of secure sleeping sites might affect other behaviors in addition to patterns of movement among den sites. If available sleeping sites are not predator proof, individuals may not be concerned with defending individual sites from conspecifics. Additionally, because insecure sleeping sites are relatively common (Humphrey 1975), marking dens to facilitate their relocation may not be necessary. Scent marking of low quality sites may increase predation risk in that such behavior could notify predators of the sleeping site location (Koivula and Korpimäki 2001). In contrast, if secure sites are available and offer protection from predators, prey need to be able to relocate and potentially defend these sites from conspecifics in order to

re-use them (Bartecki and Heymann 1990). The risk of advertising den location to predators by scent marking such a site for the purposes of relocation or defense may be outweighed by benefits derived from its reuse.

In summary, prey may employ a variety of behaviors to diminish predation risk at their sleeping sites. Prey may choose sleeping sites that are inaccessible to predators, thereby preventing predators from capturing them while they are asleep and vulnerable. Additionally, prey may attempt to conceal their sleeping sites by behaving cryptically and using many different den sites. Alternatively, if few predator proof dens are available prey may use the secure sites routinely to avoid vulnerability associated with sleeping in less secure locations. Depending on their pattern of den site use, prey may actively mark their sleeping sites to facilitate their relocation and to defend them from conspecifics. If however, marking of sleeping sites advertises the den location to predators then prey may refrain from marking their nests.

The objective of my research is to use previously collected data to determine which of the aforementioned strategies GLTs use to minimize predation. In the first chapter of this thesis, I analyze GLT use of den sites and their movement among sites. More specifically, I examine how GLT groups respond to variable predation risk to determine whether groups increase or decrease their movement among dens in response to a heightened threat. Additionally, I incorporate habitat characteristics into the assessment of the GLT patterns of den use to resolve how the availability of secure sites may affect GLT behavior. In the second chapter, I discuss the potential advantages and disadvantages of GLT scent marking in the proximity of the den site. I evaluate scent marking to establish whether GLTs increase or decrease scent marking near their den

relative to this behavior at other times of day. The purpose of the study is to determine whether GLTs mark their dens to defend/relocate them or whether they refrain from marking their dens to avoid attracting predators. Finally, I compare the scent marking behavior with their pattern of den site use to assess whether the two behaviors are consistent with a common anti-predator strategy, either a strategy to re-use valuable sleeping sites or a strategy dependent on crypsis and frequent movement among many sites.

CHAPTER 1: PREDATION PRESSURE DOES NOT EXPLAIN SLEEPING SITE USE BY GOLDEN LION TAMARINS (*Leontopithecus rosalia*)

Introduction

Predation has a substantial impact on the behavior of prey species (see Krebs and Davies 1984). One aspect of prey ecology influenced by predation pressure is choice and pattern of use of sleeping sites (Sonerud 1985, Nilsson et al. 1991). Diurnal mammalian prey are usually most vulnerable to predation at night because they are less capable of detecting and responding appropriately to a predatory threat. As a result, losses to predators may have selected for prey behaviors that minimize predation risk at night.

Prey can behave in various ways to reduce the chances of predation at den sites. The most obvious behavior that could minimize predation is choosing sleeping sites that predators are unable to enter. Numerous studies report primate use of large emergent trees that have few low limbs, stand apart from neighboring trees, or overhang water (Anderson and McGrew 1984, Chapman 1989, Reichard 1998, Di Bitetti et al. 2000, Ramakrishnan and Coss 2001). Similarly, cavity-nesting bats prefer to roost high in large trees that are distant from other large trees (Vonhof and Barclay 1996, Betts 1998). Presumably, these sites are advantageous for primates and bats because they are difficult for terrestrial predators to climb or enter laterally. Similarly, tree cavities with small openings provide their users with protection from predators too large to enter the cavity and from predatory birds that can capture individuals asleep on open branches.

Once an individual has discovered a sleeping site that is inaccessible to predators it may return to this location routinely. Numerous primates, cavity-nesting birds, and bats demonstrate a tendency to return frequently to familiar sleeping site locations (Humphrey 1975, Sussman and Tattersal 1981, Hamilton 1982, Aitken et al. 2002).

Female goldeneyes (*Bucephala clangula*) that returned to the same nest box in two successive breeding seasons were more likely to fledge young than females who used a new den in the second year (Dow and Fredga 1983). A potential explanation for increased breeding success of individuals returning to the same nest is that these animals were more cognizant of resident predators (Dow and Fredga 1983). Additionally, the routine use of a few favored sleeping sites may foster an intimate knowledge of the best escape routes and thus contribute to an individual's ability to escape attack (Struhsaker 1967). Finally, some sleeping sites are passed from parents to offspring indicating fidelity for successful sites that extends beyond the individual (Humphrey 1975). In summary, fealty for secure sleeping sites could be a defense strategy that enhances an individual's survival and reproductive success.

Although consistent re-use of a few secure sleeping sites may mitigate predation risk, there are caveats to this anti-predator strategy. Primarily, the routine use of a few sleeping sites may increase the likelihood that predators discover the dens. Banks et al. (2000) demonstrated that sedentary voles suffered greater mortality due to predation when compared to individuals that moved with intermediate frequency. The authors suggest that the sedentary individuals accumulated scent marks, urine, and feces that facilitated discovery by small mustellids. Even for prey species that use relatively safe nesting sites, such as cavity-dwellers, fealty for the most secure dens may be disadvantageous. The frequency with which predators successfully raided the nest boxes of Tengmalm's owls (*Aegolius funereus*) increased significantly with the age of the nest box (Sonerud 1985). Further, the chances that a predator discovered a nest box were significantly greater if the nest box was the site of predation the previous year. Similarly,

black woodpeckers (*Dryocopus martius*) that nested in old tree cavities suffered significantly lower breeding success due to predation compared to individuals that nested in newly excavated tree cavities (Nilsson et al. 1991). Great crested flycatchers (*Myiarchus crinitus*) and tree swallows (*Tachycineta bicolor*) that used nest boxes suffered lower nest success due to predation in the second year of 2-year studies than individuals that nested in natural tree cavities (*Myiarchus crinitus*, Miller 2002a; *Tachycineta bicolor*, Robertson and Rendell 1990). These results suggest that predators are more likely to learn the location of frequently used nesting sites and will return to profitable sites (Sonerud 1985).

Even if sleeping sites, such as tree cavities, are completely predator proof, frequent re-use may enable predators to locate their prey and learn their habits of entry and exit from the den site (Day and Elwood 1999). Predators can then wait to ambush individuals as they enter or exit the den. Carnivorous birds such as cracticids wait outside roosts to capture bats as they exit the roost (Young 1980). Similarly, Australian hobbies capture *Mormopterus* individuals as they exit their roost site (Czechura 1983). In these situations, the accessibility of the sleeping site is irrelevant to the prey's safety and the prey could benefit from the use of a greater number of less secure sites that are unknown to the predators.

Since regular re-use of 'safe' sleeping sites might reveal a group's resting location, prey may profit from adopting an alternative strategy that conceals their sleeping site. By using many den sites in a shifting, unpredictable pattern, prey could minimize predators' ability to discover their dens and learn their habits of entry/exit (see Hrdy 1977). To maximize chances for long-term survival, prey should move randomly

among many predator-proof sleeping sites. In so doing, prey would minimize the chances that a predator will find them while maximizing their likelihood of survival even if predators discover where they are nesting. In reality, not all sleeping sites are equally inaccessible to predators and individuals using many sleeping sites will likely use some sites that are less secure than others are. Therefore, there is a potential trade-off between using a few relatively secure sites repeatedly and many less secure sites sparingly (Reichard 1998, Day and Elwood 1999).

Habitat characteristics can influence the availability and quality of sleeping sites and thus how frequently groups move between different dens. Di Bitetti (2000) noted that his study troops of tufted capuchin monkeys (*Cebus apella nigrinus*) in Argentina used fewer den sites than capuchin groups observed by Terborgh (1983) in Manu, Peru. However, the tufted capuchin monkeys in Argentina used more trees than white-faced capuchins (*Cebus capucinus*) in Costa Rica (Di Bitetti et al. 2000). Di Bitetti (2000) suggested that the differences in patterns of den use were attributable to the differences in availability of safe sites among the dry seasonal forest of Costa Rica where suitable sites were rare, the pristine Amazon in Peru with its abundance of sites, and the forest in Argentina where adequate sleeping trees were neither sparse nor abundant.

Habitat type can have a particularly great effect on the density and distribution of sleeping sites available for cavity-nesting species that depend on natural decay or excavating species to create usable tree holes. In many locations, logging has reduced the number of mature trees that are likely to have appropriate cavities (Conner 1976, Coimbra-Filho 1977, Saunders 1979). As a result, habitat characteristics may influence

how frequently cavity-dwellers move among different den sites to minimize predation at their resting places.

The endangered golden lion tamarin (*Leontopithecus rosalia*; GLT) is a small, cavity-nesting primate endemic to the Atlantic Rainforest in Brazil. The largest population of wild GLTs is in the Poço das Antas Biological Reserve (PDA). This population recently suffered intense predation, most of which took place at sleeping sites. As a result, the population decreased from approximately 350 to 220 individuals between 1995 and 2000 (Franklin 2001). On at least 16 occasions during this period, an unidentified carnivore(s) attacked tamarins in their den trees. Most of these den trees were hollow and the tamarins entered the tree at some height above the ground before descending through the hollow trunk to sleep at or near ground level inside the tree. Predators gained access to the tamarins at night by entering an existing hole or digging a new one. After gaining access to the GLTs the predator(s) killed and ate them in the den or captured them as they attempted to flee in the dark. In the majority of these cases, the predator(s) killed several individuals and sometimes the entire social group. Many of these predation events occurred at dens used repeatedly by GLT groups. A variety of mammalian predators are known to take small primates (see Ferrari 1990) but the identity of those responsible for the recent predation on Poço das Antas lion tamarins is unknown.

In this research we examine the relationship among encounters with potential predators, habitat quality, and tamarin patterns of sleeping site use to test two non-mutually exclusive hypotheses: GLTs attempt to mitigate predation at sleeping sites by using sites that are secure and/or GLTs use sites in a pattern that reduces the chances predators will locate them.

If GLTs attempt to mitigate predation by only using safe den sites, we expect that they will use relatively few dens. That is, groups will select the most secure dens from the array of available dens. Further, we predict that as predation pressure increases GLT groups will continue to use only these favored sleeping sites and may become even more selective, restricting sleep to the most secure dens. Since secure dens are probably more prevalent in areas of mature forest (Coimbra-Filho 1977), those groups that have more mature forest in their territories may change sites more frequently and use a greater number of secure sleeping sites. Conversely, groups with little mature forest may be limited to use of fewer secure sleeping sites.

If GLTs attempt to avert predation at sleeping sites by avoiding detection, we predict that they will use many sleeping sites. Further, we expect the GLTs to move among their sleeping sites in a random, unpredictable pattern. In response to increased predation pressure groups should increase the number of den sites they use and the frequency with which they move among them. Groups moving frequently among many dens, some of which are relatively accessible to predators, would not be confined to using secure tree cavities in areas of mature forest but could use dens located in secondary scrub forest. In this case, we would not expect to see a relationship between how frequently groups move among different dens and the amount of mature forest in their territory.

Methods

Study Site and Data Collection

This study was conducted in the Poço das Antas Biological Reserve (PDA), Rio de Janeiro State, Brazil (22°30-33'S, 42°15-19'W). PDA is a 6,300-hectare remnant of Atlantic Coastal rainforest covered by forests in varying states of succession, large tracts of secondary swamp forest, and exotic grasses (Dietz et al. 1997). The topography ranges from 20 to 200 meters above sea level and precipitation is seasonal (Dietz 1994).

We collected data on ten reproductive groups of GLTs from January 1995 through March 2003. Group size varied from 2 to 8 individuals and, due to increased predation, the mean number of individuals per group declined from 5.6 to 3.4 during the course of the study. Groups were live-trapped biannually to reapply dye marks and tattoo newly captured individuals. We placed radiocollars on one or two adult individuals per group to facilitate location. Groups were monitored on average two to three times per week. We recorded the location of a group every twenty minutes during observation and we noted the position of sleeping sites. Finally, we recorded data on all encounters with predators *ad libitum*.

Analysis

We first determined the continuous 2-year period of most extensive observation for each of the ten GLT study groups and restricted the analysis to these periods. We chose a 2-year study period in order to avoid including many emigration/immigration events while permitting inclusion of a substantial number of encounters between GLTs and their predators.

We quantified the rate with which groups changed den sites by first identifying all unique sleeping sites used by each group. We then created a scatter plot for each group with the number of distinct sleeping sites on the abscissa and the cumulative number of sleeping records on the ordinate. We fitted a linear trend line to the plot that was neither constrained to include the origin nor the final data point. We used the slope of the line (nights/unique den tree) as the measure of GLT fidelity for favored sleeping sites.

We estimated predation pressure by calculating the predator encounter interval for each GLT group. We divided the number of hours the group was observed during the 2-year study period by the number of times the group was observed encountering potential predators. Predator encounters included any situation in which a carnivore that poses a potential threat to GLTs was seen near the group. Medium and small-sized felids including ocelots (*Leopardus pardalis*), jaguarundis (*Herpailurus yagouaroundi*), and margays (*Leopardus wiedii*) were considered potential predators because they are known to prey on primates including callitrichids (see Emmons 1987, Murray 1997, de Oliveira 1998a, b). We also considered tayra (*Eira barbara*) potential predators because they have been observed attempting to prey on GLTs in PDA (Dietz, unpublished) and one was seen carrying a dead marmoset at another location (Moynihan 1970). Similarly, coatis (*Nasua nasua*) consume small mammals (see Gompper and Decker 1998) and GLTs demonstrate avoidance behavior in their presence (Dietz, unpublished) so we considered them a threat. Capuchin monkeys (*Cebus apella nigrinus*) are omnivores known to prey on small animals including coati nestlings (Perry and Rose 1994, Rose 1997). Further, we have observed capuchins attempting to capture GLTs in PDA (Dietz, unpublished). Snakes, including constrictors and pit vipers were counted because they

have been observed killing callitrichids (Correa and Coutinho 1997, Kierulff et al. 2002b). Additionally, we included large raptors as potential predators because they are known to prey on primates in the New World tropics (Terborgh 1983). If the GLTs reacted as if a predator were close by, such as by alarm calling or mobbing, even if the human observer was unable to see the threat we included this as a predator encounter. Finally, we included all instances in which an individual died and evidence indicated that a predator was responsible.

We quantified the size and amount of mature forest in each group's home range during the 2-year observation period by randomly sampling one x,y point from the series of coordinates collected each day that a group was followed. With these points we calculated a 95% home range estimator using the Adaptive Kernel Method in ArcView (ESRI ArcView 3.2, Animal Movement Extension to ArcView 1.1). We then superimposed the home range perimeter on top of vegetation maps of PDA and calculated the amount of each habitat type in each home range.

We used multiple linear regression (SAS System, Version 8.2, Cary, N.C.) to assess GLT nest site selection as a function of predator risk and habitat quality. Reuse of preferential sleeping sites (slope: nights/unique den tree) was the response variable. The predator encounter interval, size of a group's home range, and amount of mature forest (hectares) within a home range were the explanatory variables. We performed the regression under two scenarios. In the first, we included encounters with all aforementioned predator species in the analysis. In the second, we omitted encounters with coatis, raptors, and unidentified predators. We omitted these species because the

threat they pose to GLTs at den sites remains more dubious than that of the other predatory species.

Results

We found only moderate variation among GLT groups in the rates with which they changed sleeping sites (Figure 1). The minimum and maximum rates of den change were 2.23 and 7.29 nights/den as calculated from the trend lines fit to the graphs. The mean for all groups was 4.48 (± 0.48) nights/den. Data on the number of sleeping site records, unique den trees, and the rate of den change for all groups are in Table 1.

We also found little variation in the frequency with which groups encountered predatory species. With the exception of one group, 3M, all groups were observed encountering predators on average once every 75 to 215 hours of observation (mean=180.8, ± 52.39). Table 2 shows how much time was spent observing each group and describes which predatory species were encountered.

The regression analysis indicated that the three explanatory variables were not significant predictors of variation in patterns of movement among sleeping sites. Results were not significant when encounters with all potential predators were included in the model ($F_{3,5}=1.29$, $p>0.37$) or when encounters with coatis, raptors, and unidentified threats were omitted ($F_{3,5}=1.39$, $p>0.34$). Additionally, visual inspection of the graph depicting the association between sleeping site use and predator encounters (Figure 3) suggests that no relationship exists between the predator encounter interval and the frequency with which groups changed den sites.

Discussion

All GLT study groups continuously acquired new den sites throughout the study period. Further, although some groups retired to the same den site on numerous consecutive observation nights before proceeding to use unique sites for several subsequent observation nights, the majority of groups changed dens at a rather constant rate throughout the study period (Figures 1 and 2). However, when compared to other callitrichids for which sleeping records have been collected GLT groups spent more nights on average at each of their sleeping locations. Day and Elwood (1999) calculated the average number of nights that three groups of golden-handed tamarins (*Saguinus midas midas*) slept at each of their den sites by dividing the number of nights they were observed entering a den by the number of distinct den sites used: 1.7 (44 observation nights/26 sites), 2.3 (55/24), and 3.4 (108/32) nights per tree. If we compute the same statistic using data collected on Panamanian tamarins (*Saguinus oedipus geoffroyi*) we find that groups used each tree an average of 2.5 (61/24) nights (Dawson 1979). Three groups of saddleback and moustached tamarins used their trees 2.3 (35/15), 2.4 (34/14), and 2.1 (33/16) nights on average (Heymann 1995). If we perform the same calculation for the GLTs in PDA we find that groups average 4.38 (± 0.52) nights per den (Table 2). The other studies used fewer records of sleeping sites, potentially biasing their calculations to indicate more frequent movement. However, even when we limit the calculation for GLTs to the first 53 nights of observation, the average number of observation nights for the aforementioned callitrichid studies, the GLTs appear to spend more time at each site than these other species, (4.57, ± 1.17). Hence, the data suggest that although GLTs routinely incorporate new sleeping sites in their pattern of use they

do not change den sites with great frequency in order to alleviate predation risk. The regression analysis bolsters this conclusion. We failed to find either a significant positive or negative relationship between the predator encounter interval and the regularity with which groups incorporated new sleeping sites into their pattern of den site selection.

Our failure to detect a relationship between the risk of predation and the rate of den change lends some support to the hypothesis that GLTs rely on the safety provided by reusing secure sites. However, our failure to detect a relationship between the frequency with which groups changed sleeping sites and the amount of mature forest in their home range contradicts our expectations for this strategy. In addition, although we were unable to quantify the security of sleeping sites, on many occasions we observed GLTs using dens that apparently were accessible to the predators listed above. Further, several times during the study period predators entered den sites and captured GLTs, indicating that GLTs used some sites that were not secure. Unfortunately, we observed few encounters with predators and our ability to determine whether GLTs respond to increased predator threat by restricting sleep to safe dens or by increasing movement among den sites may be limited as a result. We tentatively conclude that GLTs switch dens less frequently than other callitrichids for which data are available, but there is not strong support for either rapid switching or exclusive use of secure sites as predator avoidance strategies in this population.

Our data and the recent population decline indicate that GLTs in Poço das Antas do not behave in ways that effectively reduce the likelihood of predation at sleeping sites. Several factors may explain why tamarins in this population fail to respond appropriately to predation risk. Many prey species need experience and social influence to learn how

to cope with predation (Griffin et al. 2000, Griffin et al. 2001). Captive bred GLTs do not employ appropriate anti-predator behaviors and predation is the second greatest cause of mortality for reintroduced individuals aside from human inflicted mortality (Kierulff et al. 2002a). The observation that captive bred GLTs without regular predator contact do not respond appropriately to predator threats indicates that GLTs may require experience with predators in order to retain anti-predator behaviors. Coimbra Filho (1977) suggested that waves of deforestation drastically reduced the abundance of predators in PDA. We speculate that limited contact with predators over a period of several decades may have diminished GLTs' ability to evaluate predator risk and respond appropriately to mitigate that risk. The ability to evaluate the safety provided by sleeping sites and the frequency with which they should change dens may be two of the behaviors that GLTs failed to retain.

Alternatively, despite infrequent exposure to predators, tamarins in Poço das Antas may continue selecting den sites in a manner that would have minimized predation in the past when suitable sites were readily available. Captive red-bellied tamarins (*Saguinus labiatus*) continued to decrease vocalizations and increase vigilance just prior to retirement, presumably to reduce predation, even in the complete absence of predators (Caine 1984, Caine 1987). This observation suggests that callitrichids may retain anti-predator behaviors in the absence of predator contact. Tamarins in PDA may use few den sites because such behavior might have been advantageous when secure tree cavities were abundant. Degradation of the forest in PDA could have decreased the availability of secure sleeping sites. Hence, GLTs may continue to rely on a few den sites as an anti-

predator strategy but the sites they use may not be predator proof and could leave them vulnerable to predation.

In summary, although GLTs continuously incorporated the use of new sleeping sites during the course of the study, they accumulated new sites at a relatively slow rate and used each sleeping site longer than other callitrichids for which data are available. Further, GLTs did not show a tendency to change their use of sleeping sites in response to changes in predation risk. GLT rates of den change were not related to habitat characteristics, suggesting that den change was not affected by the availability of secure sites. These results suggest that GLTs neither change dens frequently nor use only a few secure sites to minimize the risk of predation. We speculate that GLTs in this degraded forest lost some ability to modify their behavior in response to predators during the extended period in which risk of predation was artificially low.

Tables and Graphs

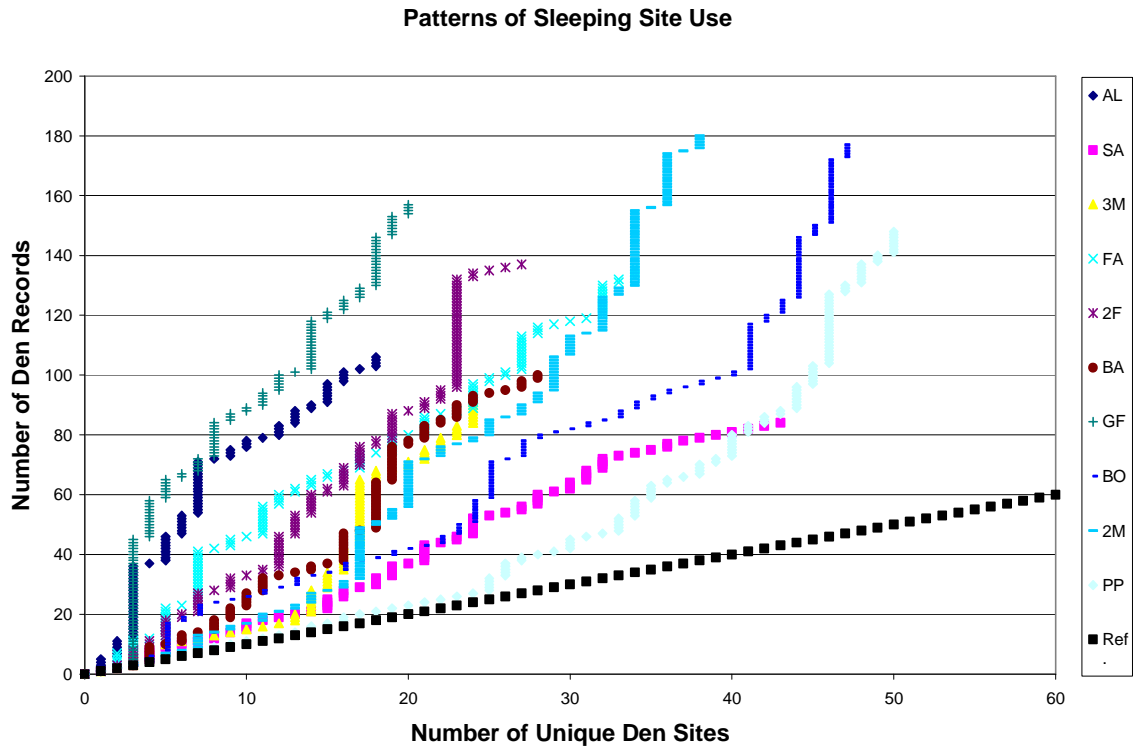


Figure 1. Acquisition of new sleeping sites by all study groups. A reference line is included to indicate the maximum rate of acquisition, equivalent to the use of a new den every night.

Group	24-Month Period		No. of Den Records	Unique Sleeping Sites	Nights/Den	Slope of Trend Line (Nights/ Den)
AL	Aug-00	Jul-02	106	18	5.9	5.99
SA	Feb-95	Jan-97	84	43	2.0	2.23
3M	Feb-98	Jan-00	91	24	3.8	4.09
FA	Jun-98	May-00	136	34	4.0	3.86
2F	Dec-96	Nov-98	137	27	5.1	5.5
BA	Jul-97	Jun-99	100	28	3.6	4.19
PP	Nov-98	Oct-00	148	50	3.0	3.04
2M	Feb-00	Jan-02	180	38	4.7	5.2
BO	Aug-98	Jul-00	177	47	3.8	3.42
GF	Dec-98	Nov-00	157	20	7.9	7.29

Table 1. Number of sleeping site records, unique den sites, and average number of nights a group used each den site during the 2-year period.

Group	Hours of Observation	Felids	Coati	Tayra	Capuchin	Raptor	Snake	Unknown	Total	Encounter interval: hrs/encounter
AL	562	0	0	1	0	3	0	0	4	141
SA	606	0	0	0	2	1	0	1	4	152
3M	637	0	0	0	0	0	0	1	1	637
FA	799	0	1	0	3	0	1	2	7	114
2F	825	0	0	0	6	0	1	0	7	118
BA	847	0	0	0	0	1	0	3	4	212
PP	896	0	0	0	3	2	0	0	5	179
2M	939	0	1	3	5	1	1	1	12	78
BO	942	0	0	1	6	2	0	1	10	94
GF	1055	0	0	3	6	1	1	1	12	88

Table 2. Predator encounters and predator encounter interval.

Predator Effect on GLT Patterns of Sleeping Site Use

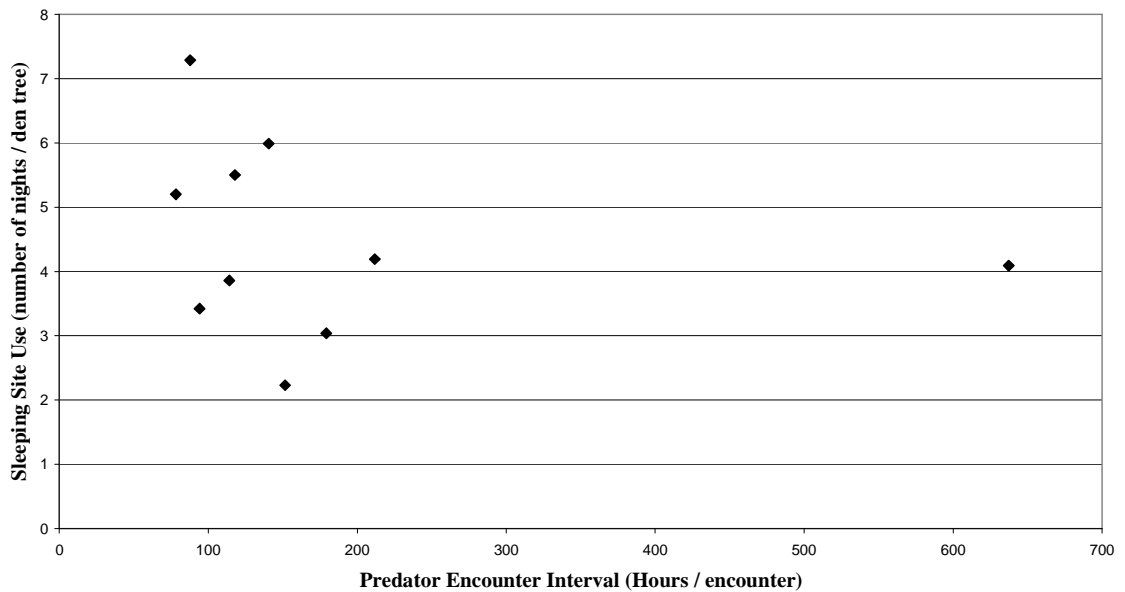


Figure 2. Predator encounter interval and the frequency with which GLT groups changed den sites.

CHAPTER 2: DO THE BENEFITS OF SCENT MARKING SLEEPING SITES BY A CAVITY-NESTING PRIMATE OUTWEIGH THE POTENTIAL RISK OF PREDATION?

Introduction

In addition to providing a location for daily rest, the sites where animals choose to sleep may serve a variety of other functions in both solitary and social species. For social species, suitable den sites may facilitate intragroup social interaction such as infant care, grooming, and sexual reproduction (see Anderson 1984). The location and spacing of sleeping sites may facilitate intergroup communication (Kinzey et al. 1977) and detection of conspecific incursions into the home range. Badgers (*Meles meles*) appear to locate their main sleeping sites close to territory boundaries because this facilitates territory defense (Doncaster and Woodroffe 1993, Stewart et al. 2001). Some animals prefer den sites close to food resources so that they can maximize feeding time and minimize energy expenditure while traveling to and from their den to obtain food (Langham 1992). For example, whooping cranes (*Grus americana*) in Colorado typically choose roosting sites that are in close proximity to feeding areas (Shenk and Ringelman 1992). Finally, sleeping sites may provide protection from predators and inclement weather. Pregnant or lactating silver-haired bats (*Lasionycteris noctivagans*) choose roosting sites high in tall trees distant from other tall trees. These sites are suspected to deter terrestrial predators from reaching their roost while enhancing insulation and warming that is beneficial for rearing of pups (Betts 1998). Given their potential to improve individual survival and reproductive success, high-quality sleeping sites are valuable resources worth re-using and defending.

Lion tamarins (*Leontopithecus spp.*), small monkeys endemic to Brazil's Atlantic forest, are unique among New World primates in their near exclusive use of tree holes as sleeping sites. Unlike many other primates that nest in trees, the small size of lion tamarins permits entire groups to enter tree cavities too small to accommodate larger animals (*Leontopithecus rosalia*, Coimbra Filho 1977; *Leontopithecus chrysomelas*, Rylands 1989; *Leontopithecus caissara*, Valladares-Padua and Prado 1996). Golden lion tamarins (*Leontopithecus rosalia*; GLT) frequently nest in tree holes created by decay or excavated by primary cavity-dwellers (Dietz, unpublished). GLTs spend approximately fourteen hours a day sleeping, the vast majority of this in their evening tree hole (Miller 2002b).

The quality of dens may have important implications for individual survival in cavity-nesting species. Tree cavities used by birds may reduce predation: Nilsson (1986) demonstrated that total nest failures, most of which are caused by predation (Nilsson 1984), were less frequent in cavity-dwellers compared to open nesting species. Additionally, huddling together at sleeping sites reduces the amount of energy expended in thermoregulation. Local heating of the nest environment was greater and individual's consumption of oxygen lower for field voles (*Microtus agrestis*) that huddled as opposed to those that were isolated (Hayes et al. 1992). Like other callitrichids, the small body size of GLTs makes them susceptible to a wide array of both nocturnal and diurnal predators (Sussman and Kinzey 1984, Cheney and Wrangham 1987) and increases the difficulty of maintaining a positive energy balance (Thompson et al. 1994). Tree cavities used by GLTs provide refuge from foraging predators and help them conserve heat and

energy by shielding the monkeys from wind and rain while allowing individuals to huddle together.

Tree cavities are frequently a limiting resource for cavity-dwelling species and can limit population size (see Newton 1994). Tree cavities that provide lion tamarins with protection from weather and predators have become a scarce resource in nature (see Rylands 1993). GLTs are endemic to the highly degraded lowland Atlantic forest of Rio de Janeiro State, in which virtually all primary forest has been eradicated. Most GLTs live in areas containing a patchwork of forest in early stages of regeneration and little mature forest. Relative to primary forest, existing GLT habitat contains few trees with cavities large enough to accommodate entire social groups. As a result, groups may have difficulty finding adequate den sites (Coimbra-Filho 1977). Black lion tamarins at one location in the state of São Paulo, Brazil sleep primarily in vine tangles because tree cavities are not available (Mamede-Costa 1998). Lion tamarins that have the ability to locate and defend tree cavities from conspecifics could improve their fitness and that of their kin by increasing the likelihood that they will avert predation and conserve energy.

Once a GLT group has identified a suitable sleeping site they have a tendency to reuse that site (Franklin, Chapter 1 of this thesis). Like other callitrichids, GLTs have well developed glands on their sternum and circumgenital region that produce pungent secretions (Epple et al. 1993). Study of captive common marmosets (*Callithrix jacchus*) indicates that these monkeys scent mark their sleeping boxes more frequently than other parts of their enclosure (Sutcliffe and Poole 1978). However, research on wild GLTs has shown that individuals scent mark throughout their home range, including their den sites

(Dietz, unpublished), and under a variety of social contexts (Miller et al. 2003). The functional significance, if any, of scent marking den sites is unclear.

Several hypotheses might explain why GLTs would scent mark their den sites. The first is that scent marking aids in relocation of the den. Studies with insects indicate that carpenter bees (*Xylocopa pubescens*) and crickets (*Hyalogryllacris sp. 14*) identify their nests by means of olfactory cues from feces, oral secretions, or secretions from Dufour glands (Hefetz 1992, Lockwood and Rentz 1996). Likewise, nocturnal petrels use olfactory cues to locate their underground burrows (Minguez 1997, Bonadonna and Bretagnolle 2002). Hoary marmots escape pursuing predators by quick recognition of burrows marked with their own scent (Taulman 1990). Plethodontid salamanders (*Plethodon jordani*) and newts (*Taricha rivularis*) use olfactory signals, potentially airborne cues, to locate previously attended nests (Grant et al. 1968, Madison 1969, Madison and Shoop 1970). Black rhinoceros (*Diceros bicornis*) use fecal scent trails to navigate through their territory (Goddard 1967 in Johnson 1973). Likewise, GLT scent marking might facilitate relocation of previously used den sites.

The second hypothesis explaining the function of scent marking near dens relates to defense. GLTs are territorial and aggressively defend their home ranges from incursion by conspecifics (Peres 1989). Intensive scent marking on and near a den may identify ownership and dissuade neighboring groups from assuming these sites. Although clear evidence of individuals using scent marks as a sleeping site defense mechanism does not exist, two studies provide support for such a function. Foxes (*Vulpes vulpes*) in Poland focus winter scent marking in forested areas, presumably to claim ownership of locations that they will use the subsequent spring for dens and rearing

of pups (Goszczynski 1990). Similarly, yellow-bellied marmots (*Marmota flaviventris*) focus cheek marking within 3 meters of the burrow system in order to signal site occupancy (Brady and Armitage 1999). Several studies suggest that scent marking is important in territorial defense. Many mammalian carnivores use scent marking to identify or defend territory boundaries or resources (brown hyaenas, *Hyaena brunnea*, Gorman and Mills 1984; coyotes, *Canis latrans*, Allen et al. 1999; gray wolves, *Canis lupus*, Briscoe et al. 2002; Ethiopian wolves, *Canis simensis*, Sillero-Zubiri 1998; black-footed cats, *Felis nigripes*, Molteno 1998; *Meles meles*, Stewart et al. 2001). Likewise, ungulates such as antelope (*Oreotragus oreotragus*) use scent marking to defend resource rich territories (Roberts and Lowen 1997, Roberts 2000). Amphibians such as plethodontid salamanders (*Plethodon cinereus*) and alpine salamanders (*Salamandra lanzai* and *Salamandra atra*) also rely on fecal scents to delineate territory boundaries (Jaeger 1986, Gautier and Miaud 2003).

The third hypothesis explaining scent marking of sleeping sites relates to reproduction and the efficacy of signal transmission. Dominant individuals of social species generally scent mark more frequently than subordinates scent mark, potentially to assert their authority and monopolize breeding opportunities (*Canis lupus*, Macdonald 1985; *Leontopithecus rosalia*, Kleiman 1978, Kleiman and Mack 1980, Miller et al. 2003; *Callithrix jacchus*, Epple 1970). Dominant females of some callitrichid species in captivity use scent to suppress ovulation in fellow group members (*Callithrix jacchus*, Barrett et al. 1990; *Saguinus oedipus*, Savage et al. 1988). In a variety of mammals, the secretions of females advertise ovulatory status and may function in coordinating copulations with males at times of fertility (*Canis simensis*, Sillero-Zubiri 1998; *Felis*

nigripes, Molteno 1998; *Saguinus Oedipus*, French et al. 1984, Ziegler et al. 1993, Washabaugh and Snowdon 1998; *Callithrix jacchus*, Dixson 1993, Smith 1998). If scent marking has social functions for GLTs, individuals may concentrate scent in a location, such as at nest holes or food sources, where group members will likely encounter the signal. Rylands (1985) concluded that common marmosets frequently mark tree holes at which they feed on exudates because conspecifics were certain to smell these areas. By enhancing the probability of successful signal transmission individuals increase the efficacy of scent marking, whether its purpose is inhibition of subordinates or self-advertisement.

Although scent marking near a den site may enhance individual fitness, such behavior may also have substantial fitness costs. Most notably, the accumulation of scent in or near the den could advertise the den location to predators. Numerous studies have demonstrated that insect predators exploit olfactory cues to locate prey (see Zuk and Kolluru 1998). In mammals, addition of scent to treatment plots resulted in significantly higher mortality levels for voles due to enhanced predation by small mustellids (Koivula and Korpimaki 2001). Snakes use olfactory cues and their well-refined sense of smell to locate potential prey (Bellairs 1969). Finally, raptors see fluorescence of scent marks in ultraviolet light and use scent marks to focus their hunting activities in areas of higher prey density (Viitala et al. 1995, Koivula and Viitala 1999, Koivula and Korpimaki 2001). A variety of felids, mustellids, and snakes that prey on GLTs may use tamarin scent marks to locate dens. In response to a perceived predatory threat, dominant male mice (*Mus musculus*) decreased their rate of scent marking (Roberts et al. 2001).

Similarly, GLTs may minimize their deposition of scent near the den to mitigate the risk of predation.

The need to relocate or defend sleeping sites, maintain social relationships, and yet avoid predators may all influence the extent to which GLTs scent mark near sleeping sites. In order to determine the function of scent marking in these contexts we first document whether GLTs deposit scent near their dens and then we examine patterns of scent marking during different times of day and across seasons.

We predict that if GLTs use scent marking to relocate or defend den trees then scent marking rates just prior to retiring should be greater than rates of marking during other times of day (see Figure 1). On the other hand, if GLTs avoid scent marking at dens to reduce the risk of predation, the marking rate should decrease prior to retiring. If den relocation or defense is an important function of scent marking, we expect to observe either no seasonal difference in scent marking or an increase in scent marking during the wet season. Since heavy rains during the wet season may decrease persistence of scent marks, GLTs may need to mark more frequently to relocate/defend their dens.

In contrast with the predictions for den relocation or predator avoidance, if scent marking serves to maintain social hierarchies or coordinate reproduction we expect to see a significant seasonal difference in scent marking behavior. GLTs should increase their rate of scent marking during the dry season months when most fertile copulations occur and competition for reproductive opportunities is greatest (Baker et al. 1993). Likewise, if scent marking serves to coordinate reproductive bouts when females are fertile, female scent marking should increase during the dry season. If a high concentration of scent is needed to enhance signal transmission, either to establish dominance or to advertise

fertility, GLTs may increase scent marking near dens since this is a location where they congregate.

Methods

Study Site and Data Collection

We conducted this study on golden lion tamarins (*Leontopithecus rosalia*) in the Poço das Antas Biological Reserve (PDA) from May 1998 through April 1999. PDA is a 6,300-hectare remnant of Atlantic Coastal rainforest in the state of Rio de Janeiro, Brazil (22°30-33'S, 42°15-19'W). This region was heavily logged prior to creation of the reserve and PDA is now covered by forests in various phases of secondary succession, swamp forest, and exotic grass (Dietz et al. 1997). The topography ranges from 20 to 200 meters above sea level and precipitation is seasonal (Dietz 1994). The dry season months during this study included May-August 1998 and April 1999 while the wet season extended from September 1998 through March 1999.

We collected data on 37 individuals in eight social groups of GLTs. Study groups varied in size from 2 to 8 individuals with a mean of 4.6. We collected behavioral data on all animals in these groups except infants (0-3 months of age) and two adults not habituated to observation. Groups were located using radio telemetry and all individuals were identifiable by dye marks applied after live-capture (Dietz et al. 1997). We followed groups on 125 days: 58 full-day follows (dawn to dusk) and 67 half-day follows during which individuals were observed only in the morning. We recorded all instances of scent marking during 15-minute observation periods on randomly selected focal individuals. Additionally, we collected data on sleeping site characteristics including the type of den used and the time of group entry/egress from the sleeping site.

Data Analysis

We classified observations as occurring during the wet or dry season and during one of four time periods relative to a group's entry into their den site. If the 15-minute observation period commenced less than 30 minutes before a GLT group entered their sleeping site any scent marking observed during that period was considered 'pre-retirement'. If the observation period started between 30 and 60 minutes prior to a group's retirement the observed scent marking was categorized as 'intermediate'. If the observation period began more than 60 minutes prior to the group's entry into their den site the behavior was deemed 'baseline'. If the time of entry into the den was not known for a particular day any behavior noted during an observation period that commenced before 14:00 was considered baseline since GLTs rarely enter their sleeping site before 15:00 (Dietz, unpublished). Finally, any observation period that started after 14:00 on a day when the time of retirement was not known was considered 'unknown'. We excluded observation periods classified as 'intermediate' or 'unknown' from all analyses.

Following preliminary analysis, we also deleted observations of juveniles, defined as individuals less than one year of age. Juveniles marked only eight times during the study, an average rate of scent marking of 0.003 scent marks/hour (\pm SE 4.96×10^{-5} , 0.14). In comparison, the average rate of scent marking for individuals one year or older was 1.70 scent marks/hour (\pm SE 1.48, 1.96) across all seasons and times of day.

Since we conducted multiple observations of individuals throughout the study, we used a repeated measures regression analysis to determine the effect of season and time of day on scent marking rates. We used a generalized linear mixed model (GLIMMIX macro, SAS version 8.2, SAS Institute Inc., Cary, N.C.) We selected the GLIMMIX

macro because the data were counts of scent marks with an overdispersed Poisson distribution. This macro calculates a coefficient of overdispersion and adjusts the tests accordingly. Additionally, since our observations on GLTs were not spaced evenly in time, the GLIMMIX macro was appropriate because we could specify a spatial covariance matrix based upon the calculated time between repeated observations.

We first modeled the number of scent marks per observation period as a function of two explanatory variables: the season during which the observation was conducted (wet versus dry) and the time category of the observation. In order to compare scent marking before retirement between the two seasons we included the interaction between season and time of day in a second model. We used a pre-planned contrast to evaluate this difference. Finally, we included the time that the study animal was visible during the observation period as a covariate in both models. We included this covariate because occasionally animals were not in view throughout the duration of the observation period.

Results

Hypotheses Tested

Hypothesis 1: scent marking of sleeping sites is used to aid in their relocation or defense

Hypothesis 2: scent marking of sleeping sites is used to defend den sites from conspecifics

Relative to baseline levels, GLTs increased their rate of scent marking just prior to repose. The mean rate of scent marking less than 30 minutes prior to retiring was 3.33 ($\pm 1.88, 5.90$) scent marks per hour while the baseline rate was 0.94 ($\pm 0.78, 1.13$). This difference was statistically significant ($t_{25}=-2.15, p<0.05$). See Figure 2.

Hypothesis 3: scent marking functions to establish dominance or advertise reproductive/ovulatory status

GLTs significantly increased their rate of scent marking during the wet season. The mean rate of scent marking across all time categories was 0.63 marks/hr ($\pm 0.42, 0.95$) in the dry season and 4.93 ($\pm 3.62, 6.71$) during the wet season. This difference was significant ($t_{25}=-5.58, p<.0001$). See Figure 3.

The rate of GLT scent marking just prior to retirement in the wet season was 11.58 marks/hr ($\pm 6.09, 21.99$). This was greater than the rate of scent marking before retirement in the dry season, 0.63 ($\pm 0.19, 2.09$). This difference was marginally significant ($t_{10}=-2.15, p<0.06$). See Figure 4.

Hypothesis 4: GLTs decrease scent marking near sleeping sites to reduce the potential cost of attracting predators

GLTs did not decrease their rate of scent marking during the period just before they entered their den. In fact, they significantly increased their rate of scent marking near sleeping sites (see Hypothesis 1).

Discussion

Our observations suggest that establishment of social hierarchies and advertisement of ovulatory status are not the primary factors affecting GLT scent marking behavior at sleeping sites. If the primary function of GLT scent marking at dens were social, we would expect that scent marking would be most frequent during the dry South American winter when female tamarins are fertile and most breeding takes place (Dietz et al. 1994, French 1996, De Vleeschouwer 2003). In contrast with this prediction, the rate of scent marking was significantly greater during the wet season. These results are interesting considering that several studies on captive callitrichid species have demonstrated the importance of scent marking in status advertisement and inhibition of

subordinates (French et al. 1984, Savage et al. 1988, Abbott et al. 1993, Dixson 1993, Ziegler et al. 1993).

Although studies of captive callitrichids create the expectation that GLTs should increase scent marking during the breeding season, our observation that GLTs increase scent marking during the wet season is not surprising. In a study of free-ranging common marmosets Lazaro-Perea et al. (1999) reported an increase in rates of scent marking during the wet season. These authors suggested that individuals compensate for decreased scent longevity in the wet season by scent marking more frequently. GLTs may also increase their scent marking during the rainy season to replenish scent that has faded due to rain.

While increased scent marking during the wet season has been observed in other primates, increases in scent marking just prior to retirement was unanticipated and suggests that GLTs are not attempting to conceal their sleeping site location from predators. This finding is noteworthy considering that predation exerts a profound pressure on various behaviors in callitrichid species (Terborgh 1983, Cheney and Wrangham 1987, Caine 1993). For example, several studies have suggested that predation may explain the rapid movement, reduced vocalizations, and increased vigilance of multiple callitrichid species en route to their den site (see Caine 1987). These monkeys were thought to behave more cryptically in order to evade predators and/or to prevent predators from finding their den.

One possible explanation for the observed increase in scent marking near dens is that predator pressure on GLTs in Poço das Antas may have been relatively low in recent decades. GLTs reside in the Atlantic forest where anthropogenic habitat destruction,

hunting of animals on which carnivores prey, and killing of carnivores, has reduced the prevalence of many predators (Coimbra-Filho 1977). During the first fifteen years of study on GLTs in PDA (1983-1998) there were relatively few noted predation events and the predator community was assumed to be depauperate in this forest island (Dietz, unpublished). An artificially low risk of predation over the course of multiple generations might have allowed these monkeys to adopt behaviors that would prove costly in geographic locations where predators are abundant. The potential exists to clarify this issue by examining the scent marking behavior of golden-headed lion tamarins (*Leontopithecus chrysopygus*). One population of this congener to GLTs lives in mature forest with a relatively intact predator community.

Alternatively, despite a recent history of relatively infrequent exposure to predators in Poço das Antas, tamarins may continue to behave in ways that minimize predation risk. Support for this possibility comes from the observation that captive red-bellied tamarins significantly decrease vocalization and increase vigilance just prior to retirement, even in the complete absence of predators (Caine 1984, Caine 1987). One explanation for how increased scent marking near sleeping sites may mitigate predation risk relates to the near exclusive use of tree cavities as sleeping sites by GLTs. In comparison with other kinds of sleeping sites (bromeliads, tangles of vines, open branches, etc.), tree holes are relatively predator proof. Since mature trees with adequate cavities are not abundant in PDA, GLTs probably cannot depend on finding a new tree hole wherever they end their daily activities. Returning to a previously used site might reduce predation risk. GLTs may scent mark frequently near their den to facilitate a rapid return in the late afternoon when crepuscular predators are most active and pose a greater

threat. Additionally, scent marking heavily near their den may inhibit competitors from using their preferred sleeping sites.

In summary, daily and seasonal patterns do not support the hypothesis that scent marking at den sites serves a social or reproductive function. Since GLTs do not increase their scent marking during the breeding season, it does not appear that individuals focus scent marking near the den primarily to establish dominance hierarchies or to advertise reproductive/ovulatory status. Rather, the significant increase in scent marking just prior to retirement suggests that individuals scent mark favored sleeping sites either to facilitate rapid relocation of predator proof dens or to defend them from conspecifics. For either purpose, individuals increase their scent marking during the wet season and may do so to replenish scent that rain has washed away. Data on the efficacy of scent marks as a deterrent against den use by other tamarin groups would address whether den site relocation or den defense is a more likely explanation for GLT scent marking behavior.

Tables and Graphs

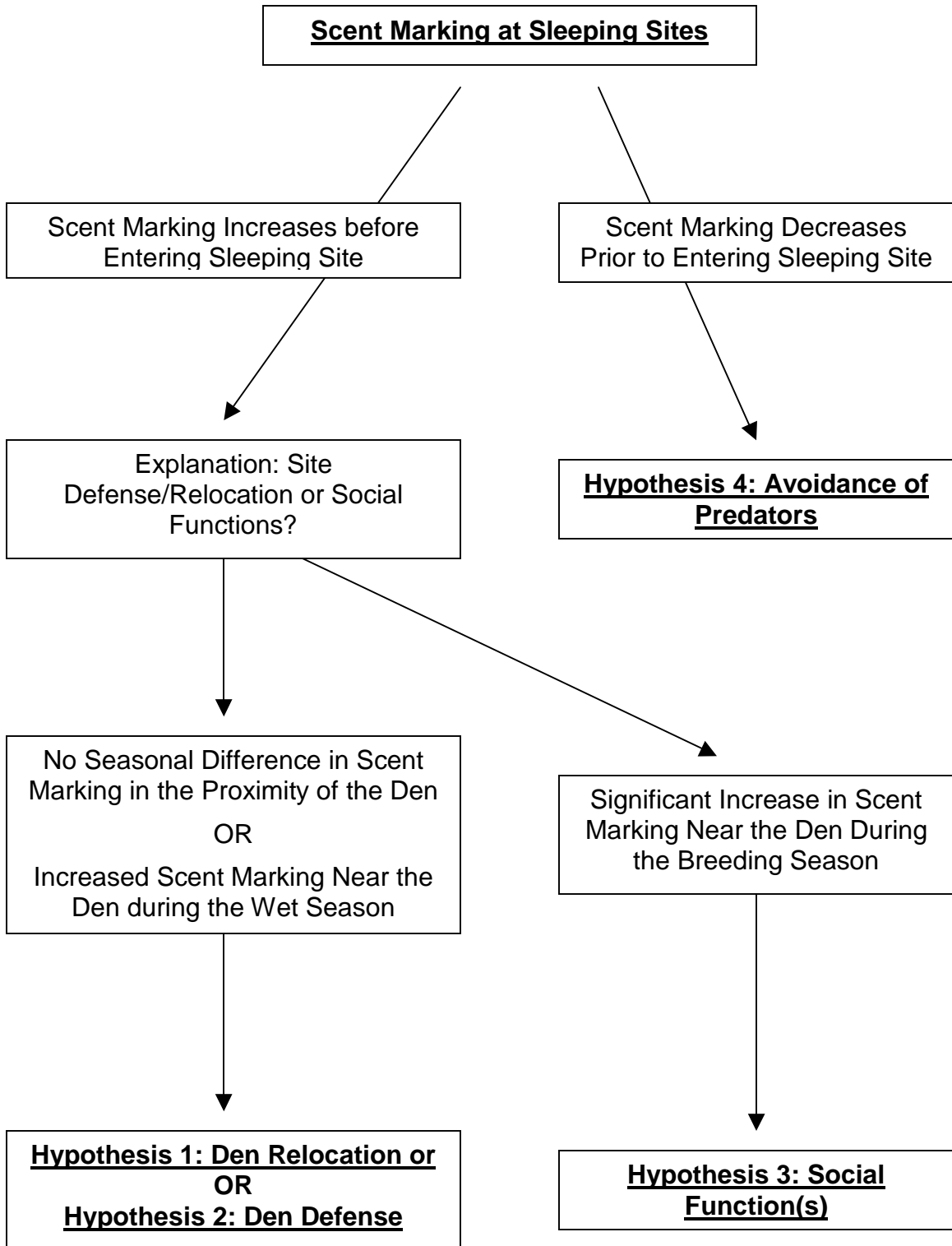


Figure 1. Predictions for the hypothesized functions of scent marking sleeping sites.

Time of Day Effect on Scent Marking Behavior

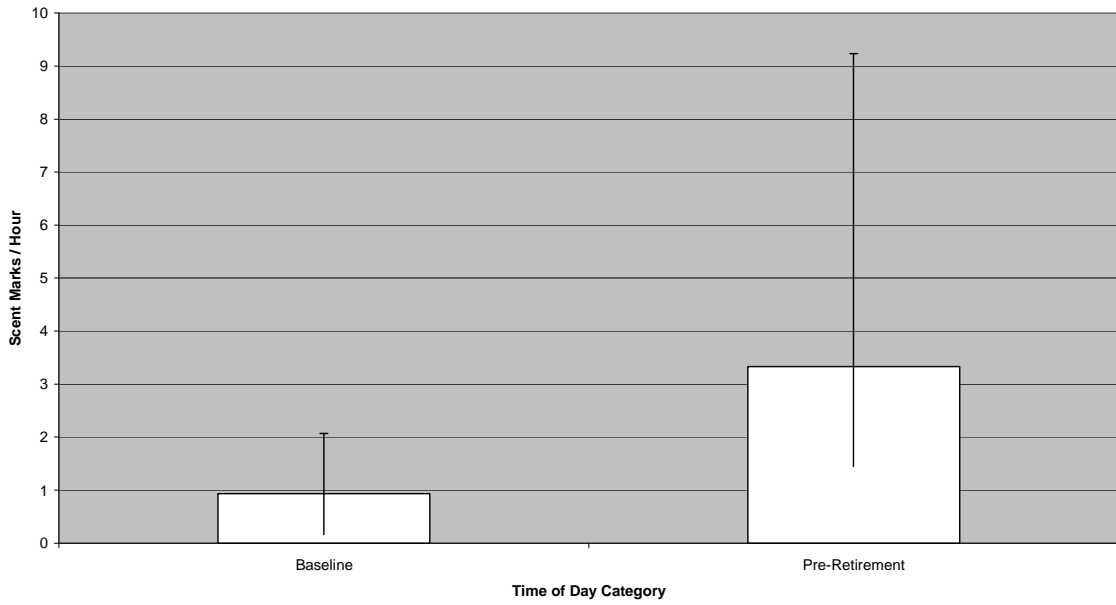


Figure 2: Scent marking rates (\pm SE) observed during two different times of day.

Seasonal Scent Marking

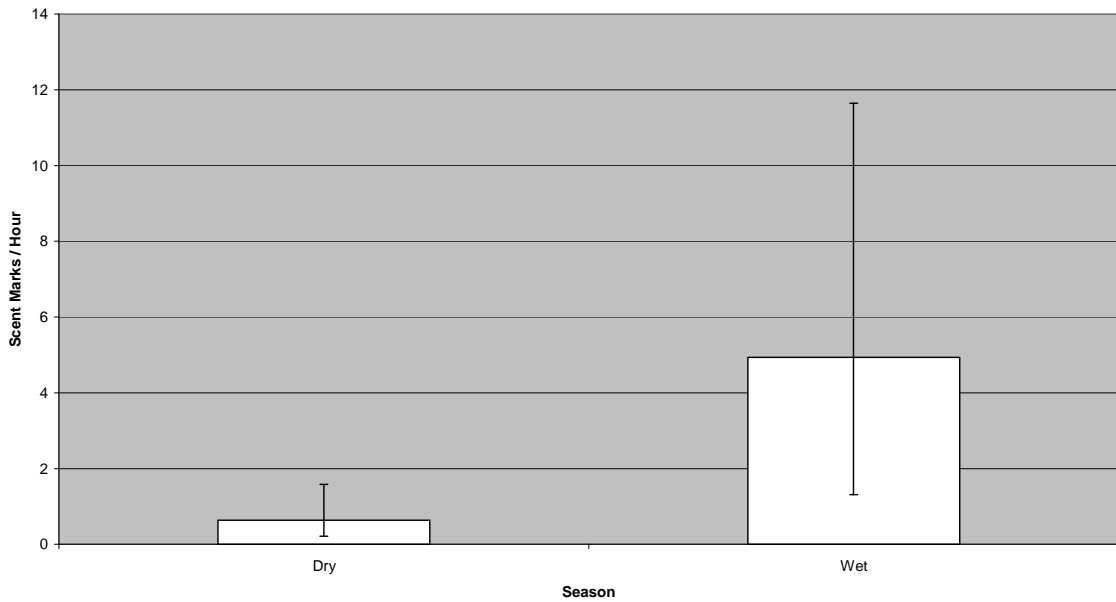


Figure 3. Mean rate of scent marking (\pm SE) during the dry and wet seasons.

Scent Marking Prior to Retiring

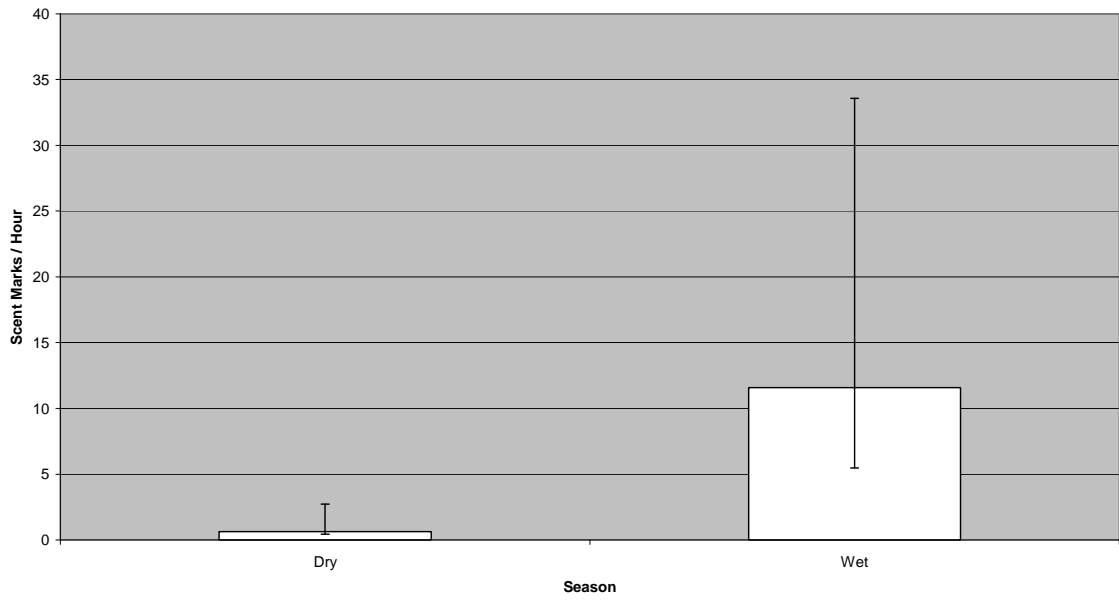


Figure 4: Pre-retirement scent marking (\pm SE) during the dry and wet seasons.

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