ABSTRACT

Title of Document: COSTS AND BENEFITS OF COOPERATIVE INFANT CARE IN WILD GOLDEN LION TAMARINS (*LEONTOPITHECUS ROSALIA*).

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In cooperative breeding species, nonbreeding individuals typically delay dispersal, forego reproduction and provide care to infants that are not their own. All caregivers must therefore balance infant demands against their own self-interests. In this dissertation I investigate the costs and benefits of cooperative infant care in wild golden lion tamarins (*Leontopithecus rosalia*). In chapter 1, I examine what factors influence the distribution of infant care to clarify why helpers contribute care to infants. I find that reproductive status strongly influences infant caretaking patterns, with parents contributing significantly more infant carrying and food provisioning than helpers. Parental dominance in caretaking and the lack of variation in infant carrying or food transfers with caregiver age, sex or condition suggests that genetic relatedness dictates these caretaking decisions, with infant behavior also influencing food provisioning. In chapter 2, I investigate the effects of gestation and infant care on activity budgets and body mass to determine if infant care results in detectable short-term costs to caretakers. Tamarins are hypothesized to require assistance from nonreproductive helpers in raising offspring due to ecological (e.g. predation risk, foraging) and energetic costs of gestation and care of infants, usually twins. During gestation, reproductive females do not make behavioral changes that suggest an energy conservation strategy; however, all caregivers make behavioral changes while carrying infants to increase predator awareness and decrease energetic expenditure and are able to maintain a stable body mass throughout infant care. Cooperative infant carrying may allow individuals to balance energetic demands and mitigate predation risk, thus supporting the hypothesis that energetic costs have driven the evolution of cooperative caretaking. In chapter 3, I present the results of an acoustic playback experiment to determine the frequency and intensity of caregiver responses to infant begging vocalizations. Caregiver responses were influenced by reproductive status, sex, condition, experience, group size and activity level, but not familiarity or genetic relatedness. The variation in caregiver responses to infant vocalizations suggests that these responses are flexible and dynamic, shifting with changes in group composition and context and with individual reproductive status and physical condition.

COSTS AND BENEFITS OF COOPERATIVE INFANT CARE IN WILD GOLDEN LION TAMARINS (*LEONTOPITHECUS ROSALIA*)

By

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Preface

This dissertation contains an introduction section and three chapters. All chapters are presented in manuscript form, with abstract, introduction, methods, results, discussion and acknowledgements, followed by tables, figure legends and figures. A single bibliography is provided at the end.

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Introduction

Social systems describe the way animal societies are structured and often include characteristics of reproduction such as mating strategies and parental care (Trivers, 1972). One such social system, cooperative breeding, is defined by nonreproductive individuals who delay dispersal, forego reproduction and provide care to infants that may not be their own. Types of care include behaviors that directly increase infant growth and survival such as food provisioning, or behaviors such as defending a communal burrow which do not vary with infant number (Clutton-Brock, 1991). Explanations for this behavior focus on inclusive fitness benefits and direct benefits to nonbreeding individuals (Brown, 1987; Emlen, 1982; Hamilton, 1964), yet controversy exists over which benefits are realized and their role in the evolution of helping behavior. Studies on cooperative breeding birds and mammals have demonstrated that nonreproductive helpers can increase their inclusive fitness via improved survival or reproduction of related infants (Brown, 1987; Emlen and Wrege, 1989; Reyer, 1984), however an increasing number of studies have also shown that helpers provide care to unrelated infants (Dunn et al., 1995; Emlen and Wrege, 1988; Komdeur, 1994; Stacey and Koenig, 1990). Direct benefits that increase future reproductive success include emigration with other helpers (Ligon, 1983; Ligon and Ligon, 1978), improved infant care skills as a result of early experience with infants (Komdeur, 1996; Tardif, 1997), access to communal territories (Gaston, 1978) and improved access to limited reproductive opportunities (Cant and Reeve, 2002; Clutton-Brock et al., 2006; Taborsky, 1985; Tardif, 1997). However, helping behavior also has costs, including reduced growth in fish

(Taborsky, 1984) and meerkats, *Surricatta suricatta* (Russell et al., 2003) and weight loss in birds (Brown et al., 1982; Heinsohn and Cockburn, 1994), marmots (Arnold, 1990) and meerkats (Clutton-Brock et al., 1998).

The presence of nonreproductive helpers has both costs and benefits to reproductive individuals. Reproductives that allow helpers to remain in the group may face reproductive or foraging competition (Goldstein et al., 1998; Koenig et al., 1995; Mulder et al., 1994) or increase their risk of incest (Brown and Brown, 1998). However, helper presence may benefit reproductive individuals by increasing infant survival (Clutton-Brock, 1991; Malcolm and Marten, 1982; Mumme, 1992), allowing reproductives to reduce their own investment in care (i.e. load lightening) (Bales et al., 2000; Crick, 1992; MacGregor and Cockburn, 2002), reduce physical costs of care (Achenbach and Snowdon, 2002; Green et al., 1995; Schradin and Anzenberger, 2001), enhance mating opportunities elsewhere (Reyer, 1984) or increase their own survival (Crick, 1992; Koenig and Mumme, 1987; Reyer, 1984; Russell and Rowley, 1988). Studies that investigate costs and benefits of reproductive individuals and nonreproductive helpers simultaneously may provide a more complete explanation for the role of costs and benefits in the evolution of helping behavior.

Although cooperative breeding is relatively rare in mammals, the primate family Callitrichidae exhibits a high degree of cooperative breeding. The Callitrichidae consists of approximately 35 species in 5 genera: pgymy marmosets (*Cebuella*), marmosets (*Callithrix*), tamarins (*Saguinus*), Goeldi’s monkey (*Callimico*) and lion tamarins (*Leontopithecus*) (Martin, 1992). Callitrichids are the smallest of the anthropoid primates, ranging between 150g (marmosets) and 700g (lion tamarins). They are frugi-faunivores with a diet consisting of fruit and plant exudates along with animal prey (i.e. lizards, grasshoppers) (review by Kleiman et al., 1988). Callitrichids live in small groups that rarely exceed 10 individuals and defend territories of unusually large sizes given their small body size (Goldizen, 1987b; Snowdon and Soini, 1988). Although golden lion tamarin (*Leontopithecus rosalia*) groups typically contain only one reproductive pair and offspring of various ages, some groups contain two reproductive females or two adult males (Dietz and Baker, 1993). Both males and females disperse, typically by two years of age, but males are more successful at transferring directly into a new group (Baker and Dietz, 1996; Dietz and Baker, 1993).

Callitrichids are hypothesized to require assistance from nonreproductive helpers in raising offspring due to ecological (e.g. predation risk, foraging) and energetic costs of gestation and care of infants, usually twins (Goldizen, 1987a; Tardif, 1994). High levels of vigilance and cryptic behavior are the primary means of protection against both avian and terrestrial predators (Caine, 1993; Tardif, 1994; Terborgh, 1983), but these anti-predator behaviors often reduce foraging efficiency due to the visual attentiveness necessary to catch insect prey, the primary source of protein (Caine, 1996; Rylands and de Faria, 1993). Besides ecological constraints, callitrichids are considered energetically constrained due to their high energetic demands and small body size (Caine, 1998). Females in particular are described as energetically constrained due to twinning, high infant to adult weight ratios during both gestation and infant care, and temporal overlap of pregnancy and lactation in females that produce two litters per year (Kirkwood and Underwood, 1984; Tardif, 1994). In addition to lactation, infant care consists of physical transportation (carrying) and provisioning with solid food. Food transfers have been observed in 10 species of callitrichids, including all genera. In all species, infants will actively beg for food by vocalizing loudly and approaching another group member that has food (Baker, 1991; Roush and Snowdon, 2001; Ruiz-Miranda et al., 1999).

The goal of this dissertation is to explore the ecological and energetic costs associated with cooperative caretaking in wild golden lion tamarins, factors that may have shaped the evolution of the tamarin social system. To do this, I first examine the distribution of infant care within groups of wild golden lion tamarins and the variables that influence contributions to infant care. I then describe the short-term costs of gestation and infant caretaking to reproductive and nonreproductive individuals. Finally, I investigate how infant begging vocalizations influence frequency and intensity of responses by caretakers. Infant begging may reflect conflict over resource allocation and is predicted to occur between parents and their offspring, or between siblings, due to differences in relatedness (Parker and Macnair, 1979; Trivers, 1974).

In the first chapter, I examine how caregiver reproductive status, age class, sex, relative body mass, and group size influence the distribution of infant carrying and solid food transfers. My objective is to clarify why helpers contribute to care and determine how variation in infant care by helpers affects contributions to infant care by reproductive individuals. Variation in the distribution of infant care within cooperative breeding species is likely influenced by a complex suite of social, demographic and individual characteristics that differ between reproductive individuals and nonreproductive helpers. Determining how infant care is partitioned among individuals may allow me to identify the selective forces shaping infant care patterns in this cooperative breeding species. I find that infant caretaking patterns are strongly influenced by reproductive status, with parents contributing significantly more infant carrying (76% of total) and food provisioning (61% of total) than nonreproductive adult and subadult helpers. The lack of variation based on caregiver sex, age class or physical condition suggests that adult helpers do not help as payment to remain in the group or to court a dispersal partner and that they have the physical resources to make greater contributions to infant care. Parental dominance in caretaking and the lack of variation in infant carrying or solid food transfers suggests that genetic relatedness dictates these caretaking decisions. Evidence that food provisioning occurs primarily when infants beg for food suggests that infant behavior may also influence helper contributions to food provisioning.

The relatively small amount of infant care by nonreproductive helpers raises questions about the severity of ecological and energetic costs to reproductive individuals. In chapter 2, I investigate the effects of gestation and infant care on activity budgets and body mass to determine if infant care results in detectable short-term costs. I find that reproductive and nonreproductive golden lion tamarins employ different behavioral tactics to mitigate energetic costs of infant care, and these result in the absence of detectable differences in body mass, i.e., physiological costs. Reproductive females reduce prey foraging when heavily pregnant and reduce locomotion when carrying infants, changes that reduce energetic demands, while all infant carriers reduce time foraging and increase anti-predator behaviors. I suggest that reproductive females do not adopt an energy conservation strategy during gestation because the timing of reproduction coincides with the wet season when body masses are higher and trophic resources are more abundant. Reducing time spent in energetically expensive activities, such as traveling, while carrying infants allows reproductive females to invest resources in lactation without sacrificing body condition, a strategy made possible by multiple caregivers. Thus, cooperation in carrying infants allows individuals to balance energetic demands and mitigate predation risk, supporting the hypothesis that energetic costs have driven the evolution of cooperative caretaking.

In chapter 3, I present the results of an acoustic playback experiment to determine the frequency and intensity of caregiver responses to infant begging vocalizations. In early studies of parent-offspring interactions, infants were viewed as passive recipients of care while parents dictated resources. When parent-offspring conflict theory was developed, it posited that offspring maximize fitness by demanding more care than parents are predicted to give based on genetic relatedness (Trivers, 1974). Parents are expected to distribute resources equitably because they are equally related to all offspring but conflict is predicted to arise over the amount of care and the duration of care. In cooperative breeding species, conflict over care can occur not just with parents, but also with nonreproductive caregivers. I find that caregiver responses to infant begging vocalizations are influenced by reproductive status, sex, condition, experience, group size and activity level, but not familiarity or genetic relatedness. Reproductive individuals, especially males, are more likely to respond to infant calls, as are reproductive females who are either less-experienced or heavier than average for a reproductive female. Heavy nonreproductive males are also more likely to respond, as are reproductive individuals and adult male helpers from small groups and caregivers that are either travelling or stationary prior to the start of the playback stimulus presented. The variation in caregiver responses to infant vocalizations suggests that these responses are flexible and dynamic, shifting with changes in group composition and context and with individual reproductive status and physical condition. The fact that caregiver responses are not affected by familiarity or genetic relatedness to the calling infant is not surprising given the small number of infants present in each group and the high probability of relatedness in lion tamarin groups.

The results of these chapters make significant advances towards understanding what factors may have shaped the evolution of cooperative breeding within the family Callitrichidae. I provide evidence that the relative contribution to infant care by nonreproductive helpers is small but that all caregivers can accrue both indirect and direct benefits depending on reproductive status and caregiver sex. Distributing infant care among multiple individuals appears to balance short-term energetic demands and mitigate predation risk, thus supporting the hypothesis that energetic costs have driven the evolution of cooperative caretaking in this species. Infants achieve varying levels of success begging for care from all caregivers, suggesting that infants can exert control over resource distribution.

Chapter 1: Do helpers really help? Caregiver contributions to infant caretaking in a cooperative breeding primate

Abstract

Variation in the distribution of infant care within cooperative breeding species is likely influenced by a complex suite of social, demographic and individual characteristics that differ between reproductive individuals and nonreproductive helpers. I collected data on infant carrying and solid food transfers from six groups of wild golden lion tamarins at Poço das Antas Biological Reserve, Brazil to determine the effects of caregiver reproductive status, age class, sex, physical condition (i.e. body mass), and group size on caregiver contributions to infant care. Infant caretaking patterns were strongly influenced by reproductive status, with parents contributing significantly more infant carrying (76% of total) and food provisioning (61% of total) than nonreproductive adult and subadult helpers. All caregivers carried infants whereas only 45% of helpers contributed solid food to infants yet caregiver age class, sex, and physical condition did not influence the amount of infant care. Group size, however, influenced adult male contributions to infant carrying and reproductive female contributions to solid food transfers. The latter resulted in infants in larger groups receiving more food transfers than infants in smaller groups. The lack of variation based on caregiver sex, age class or physical condition suggests that adult helpers do not help as payment to remain in the group or to court a dispersal partner and that they have the physical resources to make greater contributions to infant care. Parental dominance in caretaking and the lack of variation in infant carrying or solid food transfers suggests that caretaking behavior may be explained by a single factor common to most individuals in the group: genetic relatedness to the infants. Evidence that food provisioning occurs primarily when infants beg for food suggests that infant behavior may also influence helper contributions to food provisioning as well as genetic relatedness. These data suggest that reproductive tamarins perform the majority of infant care, that helpers contribute to infant care to gain indirect fitness benefits and that infant behavior may be influencing helper contributions to food provisioning.

Introduction

In cooperatively breeding species, nonbreeding individuals typically delay dispersal, forego reproduction and provide care to infants that may not be their own. Explanations for this behavior by nonbreeding individuals include inclusive fitness benefits and direct benefits (Emlen, 1982; Hamilton, 1964). Nonreproductive helpers may increase their inclusive fitness via improved survival or reproduction of related infants (Brown, 1987; Emlen and Wrege, 1989; Reyer, 1984). They may also gain direct fitness benefits such as increased future reproductive success by emigrating with other helpers (Ligon, 1983; Ligon and Ligon, 1978), improved infant care skills as a result of early experience with infants (Komdeur, 1996; Tardif, 1997), inheritance of a breeding position as a result of caring for infants (Tardif, 1997) or improved access to limited reproductive opportunities (Cant and Reeve, 2002; Clutton-Brock et al., 2006; Taborsky, 1985; Tardif, 1997).

The presence of nonreproductive helpers has both costs and benefits to reproductive individuals. Reproductives that allow helpers to remain in the group may face reproductive or foraging competition (Goldstein et al., 1998; Koenig et al., 1995; Mulder et al., 1994) or increase their risk of incest (Brown and Brown, 1998). However, helper presence may benefit reproductive individuals by protecting infants from predators and increasing infant survival (Clutton-Brock, 1991; Malcolm and Marten, 1982; Mumme, 1992), allowing reproductives to reduce their own investment (i.e. load lightening) (Bales et al., 2000; Crick, 1992; MacGregor and Cockburn, 2002), maintaining physical condition during infant care (Achenbach and Snowdon, 2002; Green et al., 1995; Schradin and Anzenberger, 2001), enhancing mating opportunities elsewhere (Reyer, 1984) or increasing their own survival (Crick, 1992; Koenig and Mumme, 1987; Reyer, 1984; Russell and Rowley, 1988).

A complex suite of social, demographic and individual characteristics that differ between reproductive individuals and nonreproductive helpers, and perhaps across taxa, likely influences variation in the distribution of infant care in cooperatively breeding species (Heinsohn and Legge, 1999). For instance, while physical condition has been shown to influence the amount of care provided by golden lion tamarin, *Leontopithecus rosalia*, reproductive females and meerkat helpers, *Suricata suricatta*, (Bales et al., 2002; Clutton-Brock et al., 2002; Tardif and Bales, 2004), it has not been shown to influence the amount of care provided by cotton-top tamarin, *Saguinus oedipus*, reproductive males (Sánchez et al., 1999). Group size, or the number of helpers, has also been shown to influence the amount of care that mothers, fathers and helpers provide yet results differ within and across taxa.

For example, group size did not affect levels of maternal care in captive tamarins or marmosets (Price, 1992a; Santos et al., 1997) but smaller group sizes resulted in increased maternal care in wild tamarins (Bales et al., 2002). In large groups, helpers and reproductive males have been shown to decrease infant care (laughing kookaburra, *Dacelo novaeguineae*: Legge, 2000; superb fairy-wrens, *Malurus cyaneus*: Peters et al., 2002; cotton-top tamarins: Price, 1992a; genera *Leontopithecus* and *Callithrix*: Santos et al., 1997) but in other cases, group size did not affect infant care (apostlebird, *Struthidea cinerea*: Woxvold et al., 2006). There is also mixed evidence in support of genetic relatedness as an explanation for variation in infant care as reproductive males routinely care for unrelated infants (savannah baboons, *Papio cynocephalus*: Buchan et al., 2003; western bluebird, *Sialia mexicana*: Dickinson, 2003; Wied's black tufted-ear marmosets, *Callithrix kuhlii*: Ross et al., 2007; cotton-top tamarins: Tardif et al., 1990) as do helpers (superb fairy-wrens: Dunn et al., 1995; white-fronted bee-eater, *Merops bullockoides*: Emlen and Wrege, 1988; seychelles warbler, *Acrocephalus sechellensis*: Komdeur, 1994; Stacey and Koenig, 1990).

In addition to physical condition, group size and relatedness, contributions to infant care may also vary with helper age class and sex (Baker, 1991; Clutton-Brock et al., 2002; Gaston, 1978; Woxvold et al., 2006). Older helpers have been shown to provide more care than younger helpers based on evidence that young caregivers acquire foraging skills slowly and suffer disproportionate energetic costs when providing infant care (Boland et al., 1997; Heinsohn and Cockburn, 1994; Heinsohn et al., 1988; Ingram, 1977; Komdeur, 1996; Tardif et al., 1992). In addition to age class differences, the interests of male and female helpers may vary based on ecological constraints on successful dispersal. In cooperatively breeding avian societies, it is hypothesized that male helpers commonly provide more care than female helpers because of paternity uncertainty and female-biased dispersal (Cockburn, 1998; Stacey and Koenig, 1990). Both males and females disperse in cooperative breeding primates, which results in a more egalitarian system of potential costs and benefits for providing cooperative infant care (Baker, 1991; Pusey and Packer, 1987). However, differences in the amount of care between male and female helpers may exist if the cost of dispersal differs between the sexes. In golden lion tamarins, males are twice as likely to emigrate with same-sex relatives compared to females, are less likely to be the recipients of aggression by current group members, and are more likely to transfer directly into territorial groups, which results in shorter transition time for males than females (Baker and Dietz, 1996; Baker et al., 1993). The ability of males to emigrate with same-sex partners may explain why male helpers were more likely to care for litters containing at least one male infant than litters of all female infants (Baker, 1991).

The objectives of this study were to determine how caregiver reproductive status, age class, sex, relative body mass, and group size influence variation in infant care (carrying and solid food transfers) in wild golden lion tamarins. Determining how infant care is partitioned among individuals may allow me to identify the selective forces shaping infant care patterns in this cooperative breeding species. I chose to focus on infant carrying because it keeps infants close to the group and provides protection from predators. I chose food transfers because they are hypothesized to supplement infant nutrition, allow early weaning and/or ensure that infants obtain rare, nutritionally valuable items or items they would be unable to get themselves (Feistner and Chamove, 1986; Feistner and Mcgrew, 1989; Lefebvre, 1985; Price and Feistner, 1993). Since selection should favor individuals that provide care for their own offspring, I reasoned that reproductive individuals would provide more care than nonreproductive helpers. I also reasoned that adult helpers would provide more care than subadult helpers, who have not yet reached full body size and may still be developing foraging skills. Since female tamarins appear to face greater risk during dispersal, I reasoned that adult females would provide more care than male helpers in order to remain in the group. However, if male helpers provide infant care to improve their chances of successful dispersal, I reasoned that male helpers would be more likely to provide care for infant males, who are potential future dispersal partners, than for infant females. Previous research on golden lion tamarins suggests that reproductive females in good physical condition contribute more to early infant care (Bales et al., 2002), possibly because they have the physical resources necessary to do so. If that explanation were correct, I would expect all caregivers in relatively good condition, not just reproductive females, to contribute more to infant care. However, if reproductive individuals lack physical resources necessary to care for infants, the presence of helpers may allow them to reduce their own investment. Helpers may also benefit from a larger group size if they are able to distribute care among multiple individuals. If that were possible, I would expect reproductive individuals and helpers in small groups to provide more care than those in large groups.

Methods

Study Site and Species

This study was conducted at Poço das Antas Biological Reserve [22° 30–33´S, 42° 15–19´W] in the state of Rio de Janeiro, Brazil. The reserve is a 6,300 ha mixture of mature, secondary, and swamp forests and grasslands (Dietz and Baker, 1993; Dietz et al., 1997). Golden lion tamarins in this population have been captured semiannually since 1984 to fit at least one individual with a radio collar for tracking purposes. At this time, each tamarin is weighed, measured and receives a permanent tattoo and a temporary dye mark for field identification. Individuals in study groups are habituated to the presence of human observers. Approximately 50 tamarins are monitored at a given time with an estimated total population of 350 individuals within the Reserve (Ruiz-Miranda et al., 2008).

Golden lion tamarins live in groups ranging from 2-12 individuals with an average group size of 5.4 (Dietz and Baker, 1993). Reproduction in the wild peaks in October and again in February if females conceive during postpartum estrous, which occurs 2-3 weeks after giving birth (Dietz et al., 1994). Infant care consists of nursing and carrying infants from birth to 12 weeks of age along with providing solid food from 4 to 36 weeks of age (Baker, 1991; Ruiz-Miranda et al., 1999). Although tamarin groups typically contain only one reproductive pair and offspring of various ages, some groups contain two reproductive females or two presumably unrelated adult males (Dietz and Baker, 1993).

I categorized individual tamarins into classes based on reproductive status, sex and age class (Table 1). Data on growth and behavior of lion tamarins in captivity suggested that sexual maturity occurs between 15-20 months of age (Hoage, 1982). Therefore, I defined adults as individuals over the age of 19 months, which was the earliest known age of successful dispersal during this study. Fourteen individuals were classified in multiple categories because their age or reproductive status changed over time. If two females in the group produced infants, both were classified as reproductive if they produced litters during the same breeding season. Otherwise, the female that did not produce infants was reclassified as a nonreproductive adult female because she was caring for another female's infants. In 12 of 26 litters, only one adult male was present in the group at the time of conception and paternity was attributed to that male. In multi-male groups, I assigned paternity to the male who dominated copulations during the time of conception, identified by counting back 130 days from the infant's date of birth (Baker et al., 1993). Due to the presence of genetic chimerism in both blood and hair samples, I was unable to assign paternity based on genetic data.

Data Collection

I collected 1300 hours of infant care data on 54 tamarins in six groups from August through January in 2004, 2005 and 2006. Average group size was 4.9 individuals with a range of 3 to 13 individuals per group excluding unweaned infants. As soon as possible after birth, I weighed, sexed and marked infants (n=32) for identification using a baited trap (Bales et al., 2002). I continuously collected data on transfers of carried infants and on transfers of solid food to infants ≤ 12 weeks of age. For infant carrying transfers, I recorded which caregiver retrieved the infant and the length of time the infant was carried. For solid food transfers, I recorded the food donor, the recipient, the food type (animal or plant), whether the transfer was successful and the type of transfer (infant steals food, infant begs for food or adult offers food without infant begging).

I weighed all individuals in the study groups at weekly intervals during infant care. To obtain body masses without capture, I placed an electronic scale with a bamboo platform attached to the scale plate near the group. I suspended a banana above the scale and recorded body mass when individuals climbed onto the platform. I recorded several masses during each weighing attempt for each tamarin to determine a weekly average (n=1240 average masses from 39 individuals). This research complied with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws.

Statistical Analyses

Infant carrying data were analyzed using generalized linear mixed models in Proc Mixed in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA). Tamarin identity was included in the model as a random factor to account for repeated observations of the same subjects. Variances were partitioned by tamarin group and litter in the repeated statement and estimate statements were written to make *a priori* pairwise comparisons. The dependent variable was the percentage of infant carrying each caregiver provided to a particular infant in a litter. The independent variables were caregiver status, sex and age class, group size and body mass (i.e. condition). For the analysis of condition dependence, I calculated an average body mass for each sex and status category to determine relative condition of individuals. Tamarins that weighed more than the average for their sex and status group were considered heavy while those below the average were considered light. I excluded subadults from analyses of body mass because they were growing throughout the study. I analyzed the relationship between infant sex and proportion of infant carrying or solid food transfers by male helpers using paired t-tests on litters containing one male and one female infant (n = 6 litters).

To determine which type of solid food transfer was most prevalent (i.e. infant begging, caregiver offers, infant steals), I conducted a chi-square goodness of fit test. I then analyzed data on solid food transfers using permutation tests in Microsoft Excel using 1000 randomizations of the number of food transfers given to an infant from each caregiver. Dependent variables were caregiver status, sex and age classes, relative condition and group size. I used the same criteria for the categories of condition in both infant carrying and solid food transfers. The significance level for all statistical analyses was set at $\alpha = 0.05$. Probability values above this threshold indicate failure to reject the null hypothesis, thus no p-values are reported in these cases except for permutation tests.

Results

Infant Carrying

Infant carrying was strongly influenced by reproductive status, with parents contributing 76% of the total carrying that the infant received ($F_{2, 48.9} = 66.64$, $p < 0.0001$; Figure 1). Reproductive individuals contributed more infant carrying than adult helpers ($t_{51.6} = 10.6$, $p < 0.0001$) and subadult helpers ($t_{44.5} = 8.8$, $p < 0.0001$) but adult and subadult helpers did not differ from one another ($t_{47.9} = 1.81$). I did not find differences between sexes within reproductive classes (AF vs. AM: $t_{38.3}$=0.29; RF vs. RM: $t_{37.8}$=1.42; SF vs. SM $t_{45.1}$=0.44). In litters containing both a male and a female infant, infant sex did not affect infant carrying by adult male helpers (t_7=0.60) or by subadult male helpers (t_4=0.28). Thus, I found no evidence that male helpers carry male infants more so than female infants. Within each caregiver sex and reproductive status category, relatively heavier caregivers did not provide more infant carrying than relatively light individuals (AF: $t_{42.4}$=1.18; AM: $t_{44.1}$=0.10; RF: $t_{51.9}$=0.76; RM: $t_{39.8}$=0.55; Figure 2).

Contrary to my predictions, group size did not influence infant carrying by adult female helpers ($t_{50.5}$=0.91), reproductive males ($t_{51.1}$=0.86), subadult female helpers ($t_{42.7}$=0.38) or subadult male helpers ($t_{49.9}$=0.59) but adult male helpers in small groups provided more infant carrying than those in large groups ($t_{43.5}$=2.02, p=0.04; Figure 3). Reproductive females in large groups provided more carrying than those in small groups ($t_{50.4}$=2.48, p=0.01), however, the latter result was driven by one female from a large group who contributed 75% of the infant carrying to her litter when the average for other reproductive females was 37.5%. When that female was excluded, I did not find a difference in carrying between reproductive females in small groups and those in large groups (t_{51}=0.04).

Food Transfers

Of the 199 food transfer attempts observed between caregivers and infants during the study period, 174 were successful and 61% of all successful transfers were contributed by reproductive individuals. Although 14 of 15 reproductive individuals were seen transferring food to infants, only 9 of 17 adult helpers and 8 of 15 subadult helpers were seen transferring food. Reproductive individuals transferred solid food to infants more often than did adult helpers (p=0.008) or subadult helpers (p=0.001) who did not differ from one another (p=0.45; Figure 4). Although reproductive status explained variation in the average number of food transfers per caregiver, caregiver sex did not. I did not find differences in the number of food transfers to infants between male and female reproductives (p=0.42) or male and female subadult helpers (p=0.74), however, there was a trend for adult male helpers to provide more solid food to dependent infants than adult female helpers (p=0.05). In litters containing both a male and a female infant, infant sex did not affect solid food transfers by adult male helpers (t_4=0.67) or subadult male helpers (t_2=0.74). Thus, I found no evidence that male helpers transfer more food to male infants.

Contrary to my predictions, relative physical condition did not influence the average number of solid food transfers from adult caregivers (Figure 5; AF p=0.29, AM p=0.32, RF p=0.72, RM p=0.29). However, group size did influence food transfers from reproductive females such that reproductive females in large groups provided more solid food transfers than reproductive females in small groups (Figure 6; p=0.006). Group size did not influence the number of food transfers from reproductive or nonreproductive males or from adult female helpers (AF p=0.28, AM p=0.24, RM p=0.66, SM p=0.97). I was unable to test for a difference in food transfers between subadult females in small versus large groups because subadult females were only present in large groups. Sample sizes were too small to statistically test for an interaction between group size and body condition within each sex and status class. However, when all caregivers in small groups were combined, individuals that were heavy for their sex and status class were not more likely to provide solid food transfers than individuals that were light ($p=0.69$). The same was true of individuals in large groups ($p=0.65$); however, infants in large groups did receive more food transfers than infants in small groups ($x^2=14.37$, $p=0.0002$). Infants were more likely to receive food transfers by begging than from caregiver offers or by stealing from caregivers (73% vs. 18.9% vs. 8.2%; $x^2=115.1$, $p<0.0001$).

Discussion

Marmosets and tamarins are hypothesized to require assistance from nonreproductive helpers in raising offspring due to ecological (e.g. predation risk, foraging) and energetic costs of gestation and care of infants, usually twins (Goldizen, 1987a; Tardif, 1994). Nonreproductive helpers may forego their own reproduction and assist reproductive individuals to increase their inclusive fitness via improved survival or reproduction of related infants (Brown, 1987; Emlen and Wrege, 1989; Reyer, 1984) or to gain direct benefits that can increase future reproductive success (Tardif, 1997). I examined the variation in infant carrying and food provisioning to determine how variation in infant care by helpers affects contributions to infant care by reproductive individuals.

In response to the question, “do helpers help?” the answer is yes, but not much. In this study, golden lion tamarin infants received approximately 75% of infant carrying and 61% of solid food transfers from their parents, and the remainder from nonreproductive helpers. The lack of differences in carrying and food transfers between subadult helpers, who were still growing and honing foraging skills, and adult helpers suggests that adult helpers may be physically capable of providing more care than they contribute. One explanation for why helpers did not contribute a greater amount of infant carrying is that the quantity of assistance may be less important to reproductives than the timing of assistance. Sharing infant care, even in small amounts, would allow reproductive individuals to perform activities that are incompatible with infant caretaking due to the energetic burden of carrying infants and the need to maintain anti-predator behavior (Caine, 1993; Tardif, 1994). These results are consistent with data on some species of cooperative breeding birds and mammals in which reproductive individuals provide more care than do nonreproductive individuals (banded mongoose, *Mungos mungo*: Gilchrist and Russell, 2007; long-tailed tits, *Aegithalos caudatus*: Hatchwell, 1999).

The lack of variation in infant caretaking is surprising if cooperative breeding in the Callitrichidae evolved as a result of energetic costs to reproductive individuals. Infant carrying has been considered energetically expensive because it compromises leaping ability (Schradin and Anzenberger, 2001; Tardif, 1997) and is associated with reduction in food intake and locomotion (Price, 1992b; Sánchez et al., 1999; Tardif and Bales, 1997). Reproductive females in particular may benefit from helper contributions to care if it reduces energy expenditure, as is the case in cooperative breeding meerkats (Scantlebury et al., 2002). However, being the largest of the callitrichids, lion tamarin females may require less help than other callitrichids. Tardif (1994) demonstrated that the energetic costs of lactation and infant transport were lowest for *Aotus* and *Callicebus*, both of which are considerably heavier than *Saguinus* and *Callithrix*, the species that exhibited the highest costs. Therefore, lion tamarin helpers may provide a relatively small amount of care because of less immediate energetic constraints on reproductive females.

In another study, lion tamarin reproductive females in better physical condition carried infants more often in the first three weeks of infancy than individuals in relatively poor condition, presumably because they have the resources to do so (Bales et al. 2002). If that explanation were correct, I would expect all caregivers in relatively good condition, not just reproductive females, to contribute more to infant care. However, my results suggest that caregiver condition does not influence the distribution of infant carrying from birth through weaning, nor does it influence their contribution to solid food transfers. Reproductive females are the primary caretakers the first three weeks postpartum but reduce their contribution as infants age (Baker, 1991; Hoage, 1982; Kleiman, 1977). Therefore, female condition may be more important during early infant care, when the energetic burden is greater, as compared to closer to weaning. Although reproductive males and females provide equal amounts of infant carrying through weaning, males tend to provide more care when infants are older and thus heavier (Baker, 1991).

Sex differences in helping contributions in cooperative breeding birds and mammals are predicted to occur due to paternity uncertainty and ecological constraints on successful dispersal (Clutton-Brock et al., 2002; Cockburn, 1998; Stacey and Koenig, 1990). In lion tamarins, female helpers suffer greater costs during dispersal because they are more likely to be the recipients of aggression by current group members than males, are less likely to transfer directly into territorial groups and tend to disperse as singletons, whereas male helpers tend to leave in same-sex pairs (Baker and Dietz, 1996; Baker et al., 1993). Contrary to my prediction that adult female helpers would provide more infant care than male helpers due to greater constraints on successful dispersal, female helpers did not carry infants more than adult male helpers and they tended to provide fewer food transfers than adult male helpers. If the threat of eviction is minimal for an adult female helper, then providing infant care may not affect the female's chance of remaining in the group. Theoretical models predict that when there is no threat of eviction, helpers should only provide infant care if they receive direct fitness benefits (Hamilton and Taborsky, 2005).

Since males often disperse in same-sex pairs, adult male helpers are predicted to provide more carrying and more solid food to male infants in order to improve their chances of successful dispersal with that infant in the future. However, the evidence that neither adult nor subadult male helpers preferentially carried or transferred solid food to male infants over female infants suggests that male helpers do not provide care in order to improve their chances of successful dispersal. Interestingly, the trend for adult male helpers to do more provisioning than adult female helpers is consistent with findings on other callitrichid primates. Cotton-top tamarin infants are not carried more by male helpers than female helpers (Tardif et al., 1992), but infants solicit significantly more food transfers from adult male helpers and are more successful at getting food from adult males than other group members (Roush and Snowdon, 2001). In the current study, infants initiated 73% of food transfers whereas only 19% of food transfers were offered to infants. Therefore, the disproportionate amount of food transfers by adult males may occur because infants are preferentially soliciting food from specific caregivers, as occurs in other cooperative breeding mammals (Hodge et al., 2007).

The presence of helpers may allow reproductive individuals in large groups to reduce their investment. Studies on callitrichids show reduced care by reproductive males in the presence of multiple helpers (review in Bales et al., 2000) and by reproductive females when infants are 2-3 weeks old (Bales et al., 2002). In contrast to the aforementioned studies, I found that group size did not influence contributions to infant carrying by reproductive males or females, a finding consistent with data on captive golden-headed lion tamarins (Tardif et al., 2002; Van Elsacker et al., 1992). The conflicting results for females are likely due to variation in the distribution of infant care in weeks two and three compared to the full 12 weeks of dependency. As infants age, they reduce both nursing and time being carried, which allows females to reduce their investment over time and reduces the need for additional caretakers (Tardif et al., 2002). Group size did affect carrying by adult male helpers, with those in small groups carrying infants more than did adult males in large groups. Anecdotal evidence suggests that adult males in small groups, but not large groups, may provide more infant care to gain access to the reproductive female. In one of our study groups, which contained a single female and two unrelated males, the female spent an equal amount of time within 1m of both males yet the males were three times more likely to be next to the female than to each other. The subordinate male helper contributed 23% of infant carrying whereas the average adult male helper only contributes 11%.

If infant care is not distributed equally across all group members, infants in large groups may receive more resources than infants in small groups. In the study population, infants in large groups received more food transfers than infants in small groups due to the significantly higher number of food transfers from reproductive females in large groups. The additional food provided in large groups may convey inclusive fitness benefits to caregivers if it results in increased infant condition or survival, as in the Florida scrub jay (*Aphelocoma coerulescens*) in which nestlings with helpers achieve faster growth rates (Mumme, 1992).

Why do helpers help? Since adult and subadult helpers provide such a small amount of care in comparison to reproductive individuals, indirect fitness benefits may influence a helper's decision to provide care rather than its physical condition, likelihood of staying in the group or influencing a future dispersal partner. Anecdotal evidence in my study suggests that degree of relatedness to infants dictates helper contributions to infant carrying and solid food transfers. One large study group contained two reproductive females (mother/daughter) who each gave birth to twins one week apart. The average contribution of a reproductive female in the study population to infant carrying is 37.5% yet the subordinate female in this group contributed 75% of infant carrying to her litter. Both reproductive females had adult sons who preferentially carried and provided solid food to the litter of their mother, while the dominant male in the group only carried and only transferred food to the infants of the dominant female. This evidence suggests that group members are making caretaking decisions based on paternity certainty and relatedness to infants, which may dictate the amount of care required by the reproductive female as shown by the subordinate female in the aforementioned group.

In conclusion, infant caretaking patterns were strongly influenced by reproductive status with parents contributing significantly more care than helpers. Helpers may not contribute a greater amount of infant care because being the largest of the callitrichids, lion tamarin females may require less help than other callitrichids, or, the quantity of assistance may be less important to reproductives than the timing of assistance. Infant carrying is critical for infant survival and caregiver reproductive success because it keeps infants with the group and provides protection from predators. The lack of variation based on caregiver age class and physical condition in infant carrying and solid food transfers suggests that this behavior may be explained by a single factor common to most helpers in the group: genetic relatedness to the infants. In contrast, the absence of food transfers by 55% of helpers but only 7% of reproductives suggests that this behavior may be explained by infant behavior as well as genetic relatedness. Evidence from the present study as well as others, illustrate that caregivers rarely give food transfers to infants unless the infants beg for them (Price and Feistner, 2001; Ruiz-Miranda et al., 1999). Taken together, these data suggest that reproductives perform the majority of infant caretaking, that helpers contribute to infant care to gain indirect fitness benefits and that infant behavior may be influencing helper contributions to food provisioning.

Acknowledgements

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Tables

Table 1. Age, status and sex classes of golden lion tamarins in the study population.

Classification	Sample Size	Definition
Reproductive female (RF)	8	females ≥ 19 months of age that show physical evidence of pregnancy or lactation
Reproductive male (RM)	7	males ≥ 19 months of age that are unrelated to the reproductive female and are either the dominant male or the only male in the group
Non-reproductive adult female (AF)	8	females ≥ 19 months of age that do not show physical evidence of pregnancy or lactation
Non-reproductive adult male (AM)	9	males ≥ 19 months of age that are the descendants of the reproductive female and/or are subordinate to the dominant male
Sub-adult female (SF)	5	females between 8 and 18 months of age
Sub-adult male (SM)	10	males between 8 and 18 months of age

Figure Legends

Figure 1. Mean percentage (±SE) of infant carrying by lion tamarins based on caregiver sex and reproductive status. Reproductive individuals provided significantly more carrying than adult or subadult helpers regardless of caregiver sex ($F_{48.9}=66.64$; $p<0.0001$).

Figure 2. Mean percentage (±SE) of infant carrying by lion tamarins based on caregiver relative body condition. Within each sex and status category, heavier caregivers did not provide more infant carrying than lighter caregivers.

Figure 3. Mean percentage (±SE) of infant carrying by lion tamarins according to group size. Adult male helpers contributed more infant carrying if they were in small groups ($t_{43.5}=2.02$, $p=0.04$) whereas reproductive females provided more carrying if they were in large groups. However, the latter result was driven by one reproductive female who provided 75% of the carrying to her infants. An (*) denotes significance at $\alpha=0.05$.

Figure 4. The effect of caregiver sex and reproductive status on the mean number of solid food transfers (±SE). Reproductive males and females provided significantly more food transfers than adult helpers ($p=0.008$) or subadult helpers ($p=0.001$). There was a trend for adult male helpers to provide more solid food transfers than adult female helpers ($p=0.05$). An (*) denotes significance at $\alpha=0.05$.

Figure 5. Mean number of food transfers (±SE) by lion tamarins according to relative body condition. Heavy individuals within their age and sex class did not provide more food transfers than light individuals.

Figure 6. The effect of group size on the distribution of solid food transfers. Reproductive females transferred more solid food if they were in large groups rather than small groups ($p=0.006$), however, group size did not influence food transfers by reproductive or nonreproductive males or from adult female helpers. I was unable to test for a statistical difference in subadult female helpers. An (*) denotes significance at $\alpha=0.05$.

Figures

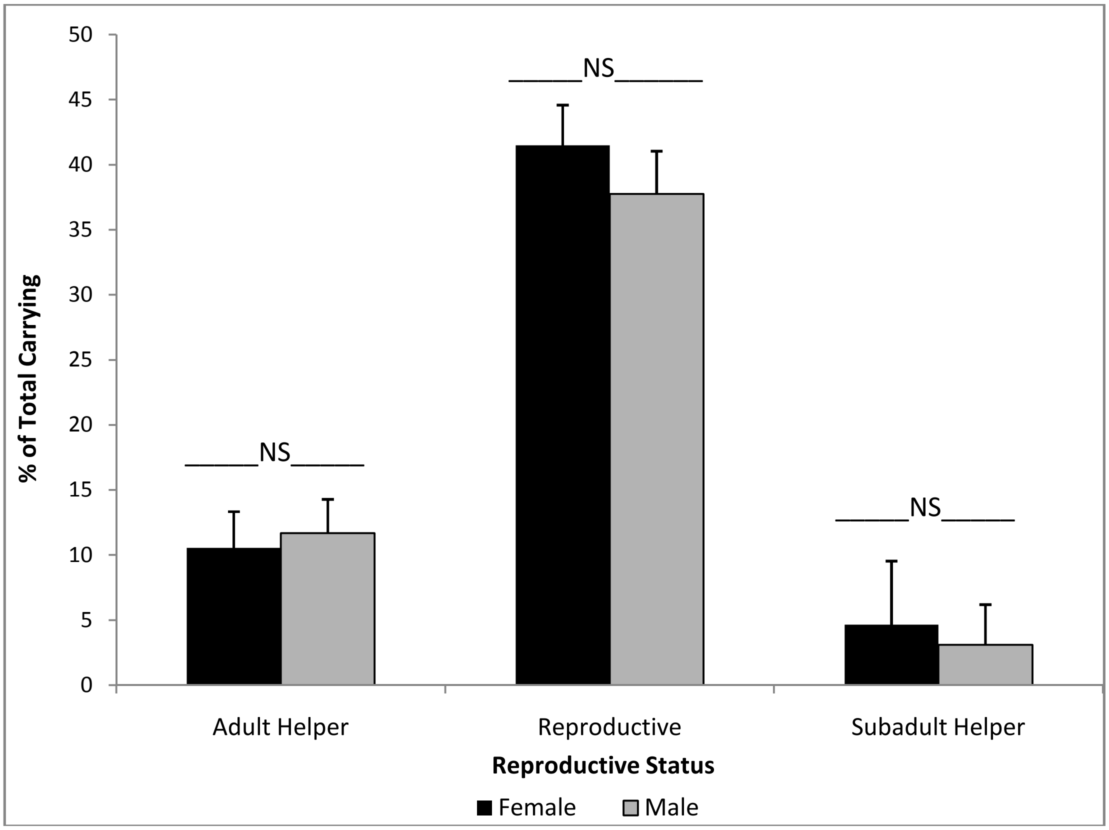


Figure 1.

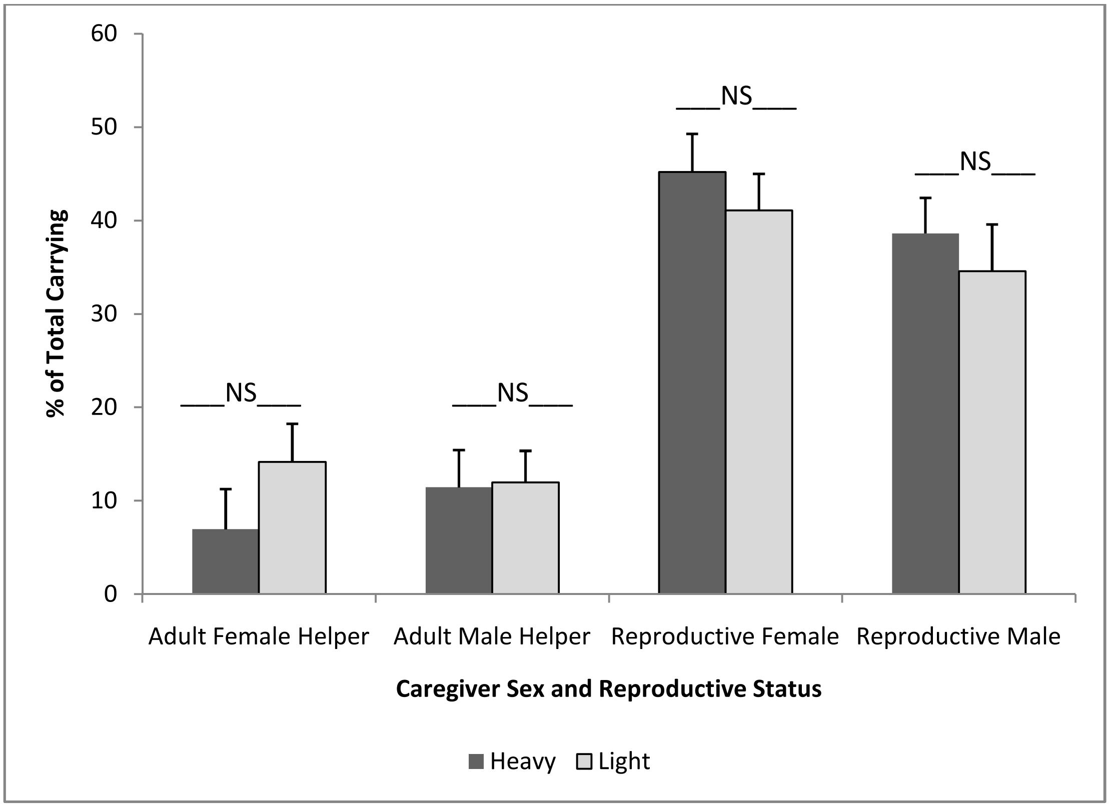
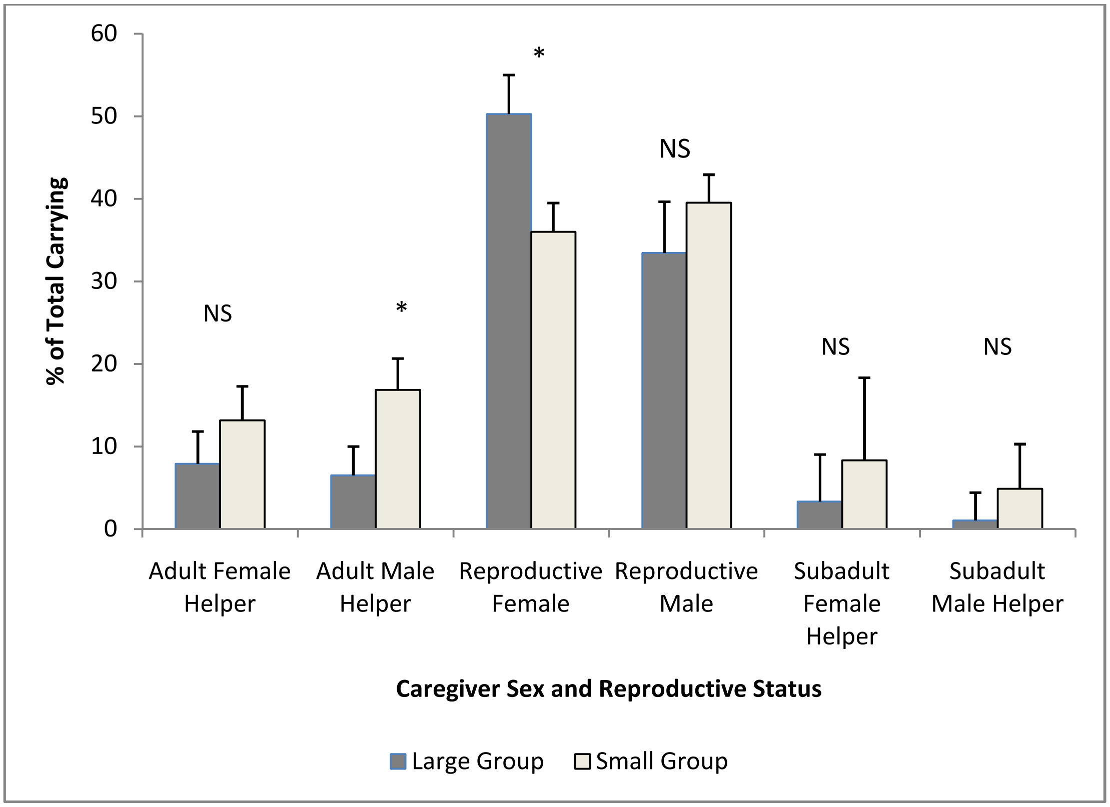

60
50
40
30
20
10
0
% of Total Carrying
____NS____
____NS____
____NS____
____NS____
Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Caregiver Sex and Reproductive Status
■ Heavy
□ Light

Figure 2.



60
50
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% of Total Carrying
*
NS
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NS
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Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Subadult Female Helper
Subadult Male Helper
Caregiver Sex and Reproductive Status
Large Group
Small Group

Figure 3.

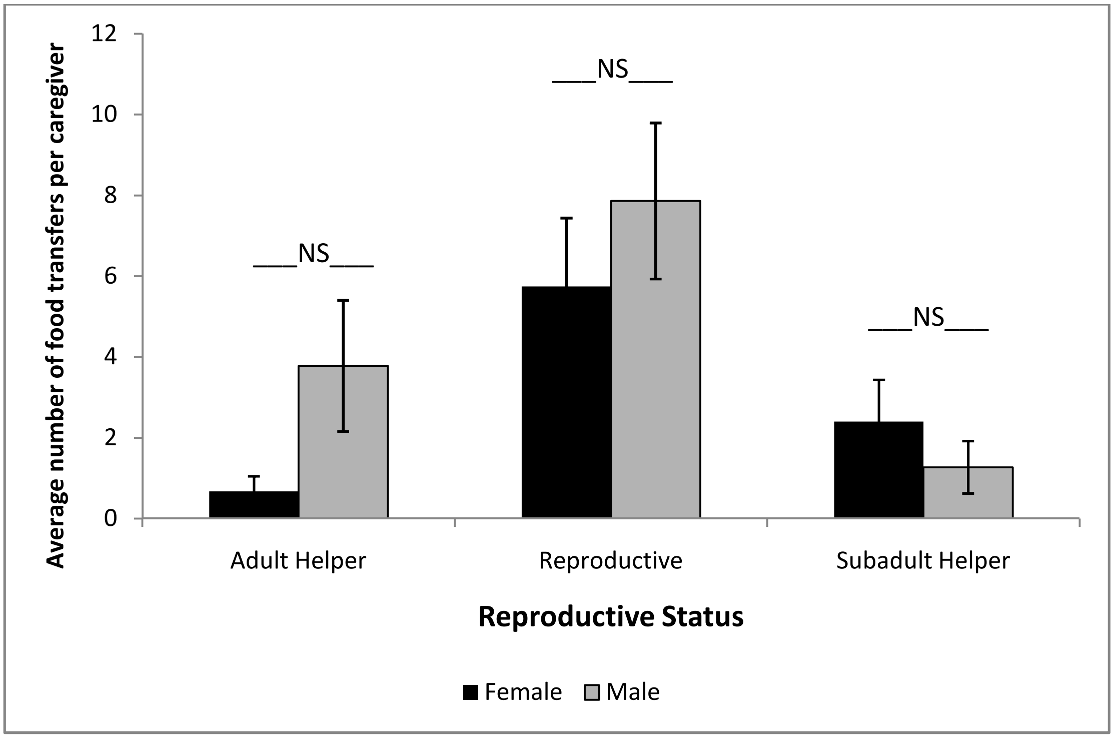
12
10
8
6
4
2
0
Average number of food transfers per caregiver
____NS____
____NS____
____NS____
Adult Helper
Reproductive
Subadult Helper
Reproductive Status
■ Female
□ Male

Figure 4.

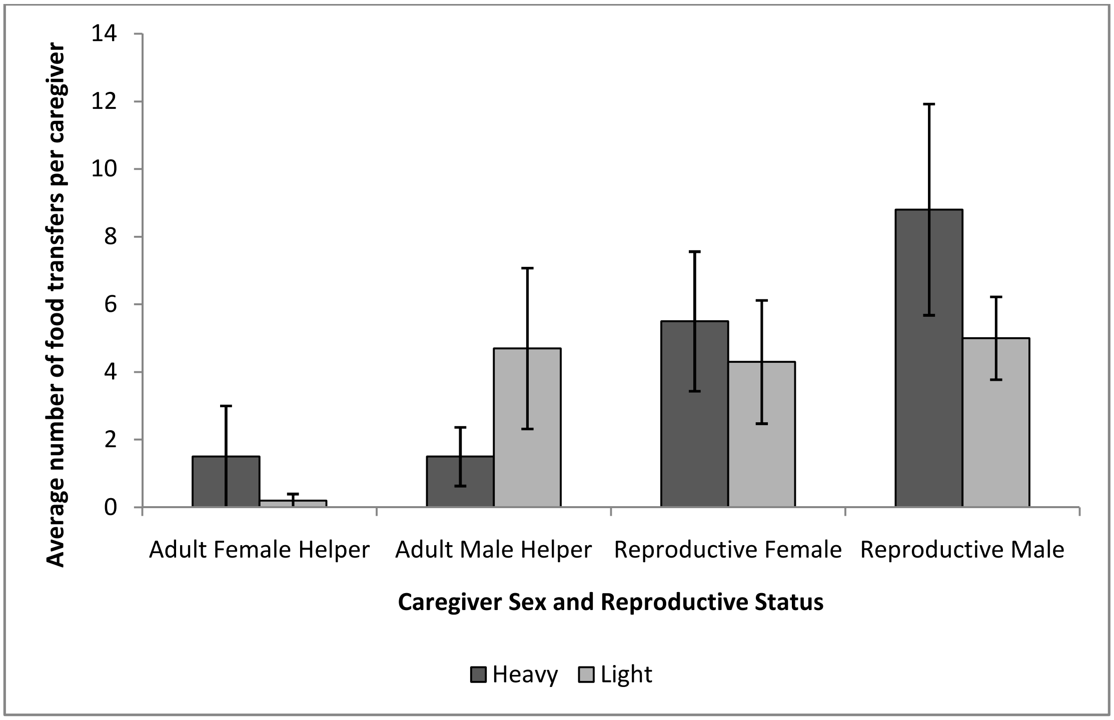
Average number of food transfers per caregiver
14
12
10
8
6
4
2
0
Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Caregiver Sex and Reproductive Status
Heavy
Light

Figure 5.

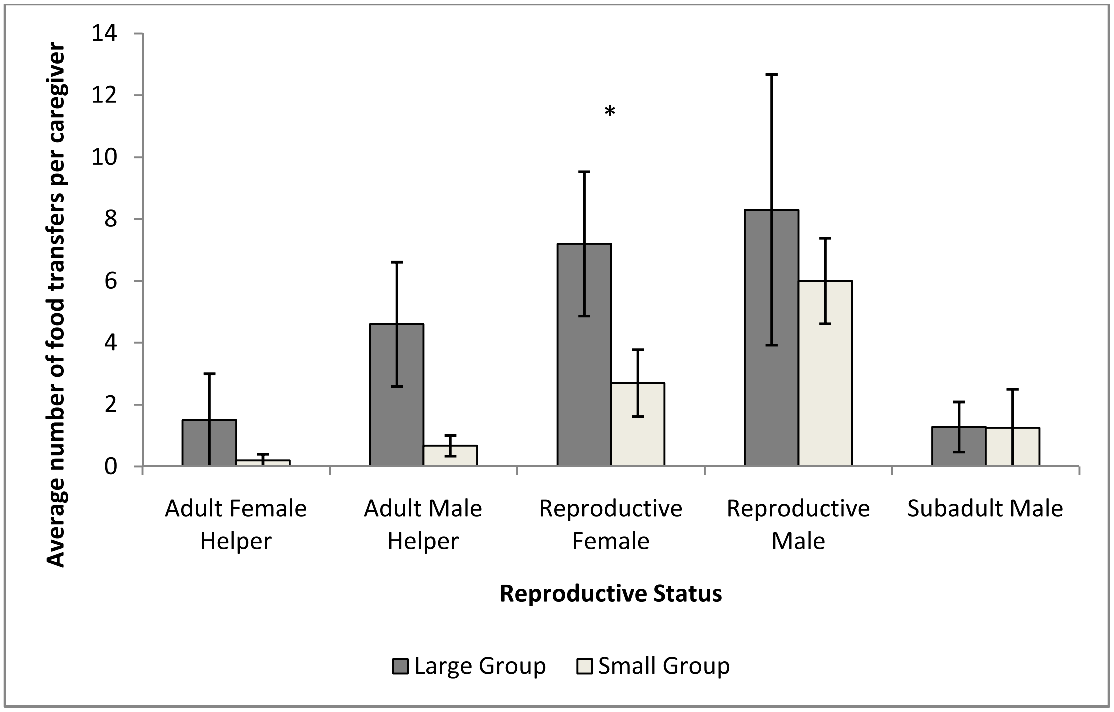
Average number of food transfers per caregiver
14
12
10
8
6
4
2
0
*
Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Subadult Male
Reproductive Status
Large Group
Small Group

Figure 6.

Chapter 2: Short-term costs of gestation and infant care in wild golden lion tamarins

Abstract

Cooperatively breeding vertebrates are hypothesized to require assistance by nonreproductive helpers in raising offspring due to ecological (e.g. predation) and/or energetic costs of gestation and infant care. To determine if infant care resulted in detectable short-term costs to caregivers, I investigated the effects of gestation and infant care on activity budgets and body mass in wild golden lion tamarins. I predicted that reproductive females would display energy conserving behaviors during late pregnancy and in infant care and that all caregivers would adopt a similar strategy when carrying infants. For 36 consecutive months, I collected data on behavior, infant carrying (n=42 infants), and body mass of 54 tamarins in six groups. Although reproductive females decreased their level of prey foraging in late pregnancy, they did not make other predicted adjustments to their activity budgets, nor did their activity budgets differ from those of nonreproductive adult females. During the period of infant care, reproductive females neither reduced time spent in high-energy activities nor did they increase time spent in low-energy activities, behavioral changes which would indicate an energy conservation strategy. When carrying infants, however, reproductive females, as well as other caretakers, did appear to adopt an energy conserving strategy. Infant carriers spent less time plant and prey foraging and more time being vigilant and social. By remaining stationary, infant carriers avoid expending energy foraging, and increase predator detection. With the exception of reproductive females, caregivers had higher rates of locomotion when carrying infants, yet all individuals maintained or increased body mass during infant dependency. I suggest that reproductive females do not adopt an energy conservation strategy during gestation because the timing of reproduction coincides with the wet season when body masses are higher and food resources are more abundant. Reducing time spent in energetically expensive activities while carrying infants allows reproductive females to invest resources in lactation without sacrificing body condition, a strategy made possible by the presence of multiple caregivers. Cooperation in carrying infants allows individuals, especially reproductive females, to balance energetic demands and manage predation risk, thus supporting the hypothesis that energetic costs have driven the evolution of cooperative caretaking.

Introduction

Research on the costs of reproduction has focused on fitness costs, such as reduced survival, fecundity and future reproductive success, as a function of current reproduction (Clutton-Brock, 1991; Harshman and Zera, 2007; Williams, 1966). Though less common, studies of immunocompetence (e.g. parasite load, disease susceptibility) has also shown physiological tradeoffs in energy allocation between self-maintenance and reproductive effort (Daan and Tinbergen, 1993; Svensson et al., 1998). Reproductive costs, however, may also include short-term tradeoffs in energy allocation within a reproductive season. Constraints of energetic demands may be reflected by changes in behavior patterns and physical condition during gestation and infant care. Studies on a variety of taxa describe annual activity budgets in relation to demographic and environmental variables (Caraco, 1979; Di Fiore and Rodman, 2001; Hanya, 2004; Huang et al., 2003; Isbell and Young, 1993; Koprowski and Corse, 2005; Li and Rogers, 2004; Sharpe and Rosell, 2003; Teichroeb et al., 2003; Vasey, 2005) but less is known about the interaction of behavioral patterns and physical condition, and the resulting effect on short-term costs of reproduction in the wild.

The cost of producing and caring for infants can be expressed in currencies including risk, time, and/or energy changes (Knapton et al., 1984). Cooperatively breeding marmosets and tamarins (family Callitrichidae) are hypothesized to require assistance in raising offspring by nonreproductive helpers due to ecological costs (e.g. predation risk, foraging) and energetic costs of gestation and infant care (Goldizen, 1987a; Tardif, 1994). Infant caretaking behaviors are not always compatible with other activities, possibly due to the energetic burden of carrying infants and the need to maintain anti-predator behaviors (Caine, 1993; Tardif, 1994). In callitrichids, high levels of vigilance and cryptic behavior are the primary means of protection against both avian and terrestrial predators (Caine, 1993; Tardif, 1994; Terborgh, 1983) but these anti-predator behaviors often reduce foraging efficiency due to the visual attentiveness necessary to catch insect prey, the tamarin's primary source of protein (Caine, 1996; Rylands and de Faria, 1993). Besides ecological constraints, callitrichid females are also described as energetically constrained due to twinning, high infant to adult weight ratios during both gestation and infant care, and temporal overlap of pregnancy and lactation in females that produce two litters per year (Kirkwood and Underwood, 1984; Tardif, 1994). Lactation is the most energetically expensive phase of the reproductive cycle (Altmann, 1980; Tardif et al., 2001) with caloric demand almost equal to maintenance costs (Kirkwood and Underwood, 1984). Though lactating females in captivity increased food intake (Kirkwood and Underwood, 1984; Nievergelt and Martin, 1999; Sánchez et al., 1999), some females gained weight during lactation (Sánchez et al., 1999) or remained the same (Tardif et al., 2001), while others lost weight (Nievergelt and Martin, 1999; Tardif et al., 2001). Taken together, these studies present no clear pattern for maintenance of female weight during lactation, but do suggest the need for additional investigation in a natural setting where trophic resources may be limited.

While reproductive individuals will bear some cost of reproduction, nonreproductive helpers in cooperatively breeding systems may also need to make tradeoffs in resource allocation to mitigate costs of infant care. Helping behavior has been associated with reduced growth in fish (Taborsky, 1984) and meerkats, *Surricatta suricatta* (Russell et al., 2003) and with weight loss in birds (Brown et al., 1982; Heinsohn and Cockburn, 1994), marmots (Arnold, 1990) and meerkats (Clutton-Brock et al., 1998). Variation in meerkat helping behavior has been shown to be dependent on body mass (Clutton-Brock et al., 2002). In captivity, callitrichid infant carriers show reduced food intake (Price, 1992b; Sánchez et al., 1999; Tardif and Bales, 1997), copulations (Tardif and Bales, 1997), affiliative behaviors, vigilance and locomotion (Price, 1992b) and decreased leaping ability (Schradin and Anzenberger, 2001; Tardif, 1997). Although weight loss during infant care has not been found in marmosets (Schradin and Anzenberger, 2001), it has been shown in captive tamarins (Achenbach and Snowdon, 2002; Sánchez et al., 1999). The prediction that weight loss resulting from infant care will be greater in the wild than in captivity is supported by observations that tamarins in larger, more naturalistic captive settings lose more weight while caring for infants (Morcillo et al., 2003; Sánchez et al., 2005).

Relatively little is known of the impact of infant care on activity budgets and physical condition in wild Callitrichidae. A study of saddle-back tamarins, *Saguinus fuscicollis*, found that the reproductive female increased feeding time when lactating but not when pregnant and that one of the two infant carriers reduced feeding and locomotion (Goldizen, 1987a). In contrast, *S. mystax* infant carriers did not alter their locomotion but they did increase time spent resting (Huck et al., 2004). In golden lion tamarin females, energy intake was lower in the wet season when females were in mid to late stages of pregnancy or lactating (Miller et al., 2006) but female body mass did not vary during lactation (Dietz et al., 1994). Miller and Dietz (2005) suggested that females were using two strategies: energy conservation when pregnant or lactating and energy maximization at other times.

The objective of this study was to determine if reproduction and infant care in golden lion tamarins results in energetic costs detectable as changes in behavioral patterns across reproductive stages, between reproductive and nonreproductive individuals or as changes in body mass. To test the hypothesis that energetic costs are greater for reproductive females, I predict that reproductive females, but not nonreproductive adult females, will adopt an energy conservation strategy during late pregnancy and infant care. Specifically, I expect lower levels of high-energy activities (e.g. locomotion) and higher levels of low energy activities (e.g. resting) by reproductive females, but not nonreproductive females, during both gestation and infant care. I also expect that differences in activity levels will be absent when reproductive females are not pregnant. To evaluate the costs of infant carrying, I predict that caregivers will adopt an energy conservation strategy when carrying infants and that they will increase time spent in predator detection behaviors. Specifically, I expect lower levels of high-energy activities and higher levels of low-energy activities, primarily vigilance, when individuals are carrying infants compared to when they are not carrying infants. If infant care is energetically costly, body masses of carriers should be lower when infants are in the group; individuals that perform most of the carrying will lose weight during the infant care period.

Methods

Study site and species

This study was conducted at Poço das Antas Biological Reserve [22° 30–33´S, 42° 15–19´W] in the state of Rio de Janeiro, Brazil. The reserve is a 6,300 ha mixture of mature, secondary, and swamp forests and grasslands (Dietz and Baker, 1993; Dietz et al., 1997). Golden lion tamarins in this population have been captured semiannually since 1984 to fit at least one individual with a radio collar for tracking purposes. At this time, each tamarin is weighed, measured and receives a permanent tattoo and a temporary dye mark for field identification. Individuals in study groups are habituated to the presence of human observers. Approximately 50 tamarins are monitored at a given time with an estimated total population of 350 individuals within the Reserve (Ruiz-Miranda et al., 2008).

Golden lion tamarins live in groups ranging from 2-12 individuals with an average group size of 5.4 (Dietz and Baker, 1993). Reproduction in the wild peaks in October and again in February if females conceive during postpartum estrous, which occurs 2-3 weeks after giving birth (Dietz et al., 1994). Infant care consists of nursing and carrying infants from birth to 12 weeks of age along with providing solid food from 4 to 36 weeks of age (Baker, 1991; Ruiz-Miranda et al., 1999).

Data Collection

I collected 840 hours of behavioral data from August through January of 2004, 2005 and 2006. In addition, three local field assistants collected 1185 hours of behavioral data year-round from January 2004 through December 2006, for a total of 2025 hours of behavioral data on 54 tamarins in six groups. Average group size was 4.9 individuals with a range of 3 to 13 individuals per group excluding nursing infants. I observed tamarins for 10-min focal periods conducted every 20 min. Observed behaviors were divided into six activity categories (Table 1). When infants of 12 weeks of age or younger (n = 42) were present in the groups, I continuously collected data on transfers of infants between carriers.

I weighed all individuals in the study groups at weekly intervals during periods when a female was pregnant or infants were present. To obtain body masses without capture, I placed an electronic scale with a bamboo platform attached to the scale plate near the group (Bales et al., 2002). I suspended a banana directly above the scale and recorded body mass when an individual climbed onto the platform. I recorded several masses for each tamarin and averaged them (n = 2138 masses on 45 tamarins). To obtain body mass at other times of the year, I used data from semiannual group captures (n=96 masses on 33 individuals).

I categorized individual tamarins into age, status and sex classes (see Table 1, Chapter 1). Data on growth and behavior of lion tamarins in captivity suggest sexual maturity occurs between 15-20 months of age (Hoage, 1982). Fourteen individuals were classified in multiple categories because their age or reproductive status changed over time. If two females in the group produced infants, both were classified as reproductive if they produced litters during the same breeding season. In groups containing two reproductive females, there was evidence that several pregnancies were lost pre-term. These females were reclassified as nonreproductive adult females following the loss. Females were categorized as pregnant based on palpation at annual capture and/or an increase in body mass over consecutive weeks. Pregnant females were categorized as being in the early (conception to 56 days), mid (57-78 days), or late stage of pregnancy (79-130 days). Weights of nongravid tamarin females and those in early pregnancy were not significantly different (Bales et al., 2001; Hankerson, 2008) and these data were combined in the current study. For analyses, the reproductive period was categorized into nongravid, late pregnancy or infant care (i.e. lactation and infant carrying) stages. Activity budgets of males and nonreproductive females were divided into time categories corresponding to the reproductive stage of that group's reproductive female. Infant care was categorized as early (birth-4 weeks), mid (5-8 weeks) or late (9 weeks-weaning). For 12 of 26 litters, only one adult male was present in the group at the time of conception and paternity was attributed to that male. In multi-male groups, paternity was assigned to the male who dominated copulations during the time of conception, identified by counting back 130 days from the infant's date of birth (Baker et al., 1993). Due to the presence of genetic chimerism in both blood and hair samples, I was unable to assign paternity based on genetic data. This research complied with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws.

Statistical Analyses

Data were analyzed using generalized linear mixed models in Proc Mixed in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA). I included tamarin identity as a random factor in the model to account for repeated observations of the same subjects. Variances were partitioned by tamarin group in the repeated statement, and estimate statements were written to make *a priori* pair-wise comparisons. Seasons were categorized as wet and dry based on weather station data obtained from NOAA and compiled in Hankerson (2008). A preliminary analysis was run to determine if seasonal differences existed within each activity category. Season was then included as a factor in analyses of activities that showed significant differences between the wet and dry season. Independent variables were stages of reproduction, infant carrying, and sex and status categories. Dependent variables were activity categories and body mass. Seasonal and reproductive data were arcsine transformed and infant transport data were square root transformed to meet assumptions of normality and then back transformed to report means and standard errors. I eliminated subadults from analyses of body mass because they had not yet reached full body size. The significance level for all statistical analyses was set at $\alpha = 0.05$. Probability values above this threshold indicate failure to reject the null hypothesis, thus no p-values are reported in these cases.

Results

Activity Budgets

The tamarins spent 40% of their time foraging for plants and animals (27% and 13% respectively), 23% resting, 17% stationary and vigilant, 15% locomoting and 6% engaged in social activities. Season explained variation in time spent foraging for plant material, resting, and social activities (Figure 1) and was included as a factor for further analyses of reproductive stages for those activities. In the dry season, caregivers spent more time foraging for plant material ($F_{1, 133} = 48.81$, $p < 0.0001$) but less time resting ($F_{1, 138} = 20.19$, $p < 0.0001$) and engaging in social activities ($F_{1, 89.3} = 19.67$, $p < 0.0001$) compared to the wet season.

Reproductive stage explained variation within the activity budgets of reproductive and nonreproductive females (Figure 2). In late pregnancy, reproductive females spent less time foraging for prey than when they were nongravid ($t_{128} = 2.24$, $p = 0.02$). I did not find differences in nonreproductive female activity levels between the nongravid and the late pregnancy reproductive stages. Both reproductive and nonreproductive adult females spent less time foraging for plant material (RF: $t_{134} = 3.49$, $p = 0.0006$; AF $t_{134} = 4.76$, $p = 0.001$) and more time in social activities (RF: $t_{112} = 2.72$, $p = 0.007$; AF $t_{112} = 3.14$, $p = 0.002$) during the infant care reproductive stage than the nongravid stage. Although not statistically significant, there was also a trend for both reproductive and nonreproductive females to spend more time being vigilant during infant care (RF: t_{134}=1.72, p=0.08; AF t_{134}=1.83, p=0.06). Nonreproductive females, but not reproductive females, spent more time locomoting during infant care (t_{134}=4.53, p=0.0001).

As predicted, reproductive and nonreproductive female activity budgets did not differ from one another during the nongravid reproductive stage (Figure 3). Contrary to my predictions, their activity budgets did not differ in the late pregnancy reproductive stage (Figure 3) though there was a trend for reproductive females to spend less time prey foraging than nonreproductive females (t_{128}=1.72, p=0.08) during the late pregnancy stage. During infant care, reproductive females spent less time locomoting than nonreproductive females. (t_{134}=2.43, p=0.01).

As predicted, tamarin activity budgets varied significantly during infant care (Figure 4). Individuals carrying infants spent less time foraging for either plants ($F_{1, 29.2}$=13.65, p=0.0009) or animal prey ($F_{1, 35.3}$=81.19, p<0.0001) and engaged less in social activities ($F_{1, 43.3}$=1.23, p=0.003) than when they were not carrying infants. Although resting rates did not differ ($F_{1, 41.4}$=2.27, p=0.14), tamarins spent more time being vigilant ($F_{1, 37}$=77.77, p<0.0001) when they were carrying infants. Tamarins also spent more time locomoting when carrying infants ($F_{1, 35.8}$=32.01, p<0.0001); however, there was a significant interaction for age, reproductive status and carrying ($F_{2, 26.5}$=8.47, p=0.001). In contrast with individuals in all other age and sex categories, reproductive females did not spend more time locomoting when carrying infants. Activity budgets of reproductive and nonreproductive adult females did not differ when the females were not carrying infants (Figure 5a) but nonreproductive females locomoted more ($t_{47.6}$=5.49, p<0.0001) and rested less when carrying infants ($t_{79.9}$=3.48, p=0.0008) than reproductive females (Figure 5b).

Physical Condition

I found a significant interaction effect on tamarin body mass between reproductive status and sex (interaction: $F_{1, 923}$=36.38, p<0.0001). Reproductive individuals were significantly heavier than nonreproductive individuals and the difference was more pronounced in females. Nongravid reproductive females were significantly heavier than nonreproductive adult females (t_{770}=13.73, p<0.0001) with an average non-pregnant weight of 609g compared to 562g. Reproductive males were heavier than nonreproductive adult males (t_{428}=4.63, p<0.0001) with an average weight of 602g compared to 585g. These differences persisted across seasons and reproductive stages (Figure 6). Reproductive females were significantly heavier than nonreproductive adult females in both seasons (dry season: t_{1056}=11.26, p<0.0001; wet season: t_{793}=11.17, p<0.0001) and reproductive stages (nongravid: t_{752}=6.36, p<0.0001; infant care: t_{935}=10.99, p<0.0001). Reproductive males were also significantly heavier than nonreproductive males in both seasons (dry season: t_{649}=5.10, p<0.0001; wet season: t_{509}=2.87, p=0.005) and the nongravid stage (t_{709}=3.65, p=0.0003) but not during infant care (t_{701}=1.50). With the exception of reproductive males, adult tamarins were heavier in the wet season than the dry season (adult females t_{631}=6.16, p<0.0001; adult males t_{817}=4.30, p<0.0001; reproductive females t_{925}=2.56, p=0.01).

Contrary to my predictions, reproductive and nonreproductive tamarins did not weigh less during the period of infant care. Body mass during nongravid stages did not differ from body mass during infant care for nonreproductive females (t_{353}=1.15) or reproductive males (t_{601}=0.94) and both reproductive females (t_{739}=2.41, p=0.01) and nonreproductive adult males (t_{532}=3.17, p=0.001) were heavier during the infant care stage than the nongravid stage. There was no difference in body mass of reproductive males or females, or of nonreproductive females at the end of infant care compared to the beginning (RF: t_{982}=0.59; RM: t_{837}=0.27; AF: t_{654}=0.5). Nonreproductive adult males, however, weighed significantly more at the end of infant care than at the beginning (t_{813}=2.19, p=0.02; Figure 7).

Discussion

In cooperatively breeding species such as golden lion tamarins, all group members spend time and energy raising infants and may bear any costs associated with infant care. Studies of reproductive costs typically focus on effects on fitness, such that less is known regarding short-term costs to individuals. The objective of this study was to determine if reproduction and infant care in golden lion tamarins results in energetic costs detectable as changes in behavioral patterns across reproductive stages, between reproductive and nonreproductive individuals or as changes in body mass within a breeding season. I tested the hypotheses that reproductive females would adopt an energy conserving strategy during late pregnancy and infant care, and that all caregivers would adopt this strategy when carrying infants.

Reproductive females did not appear to adopt an energy conservation strategy during late pregnancy. Although they spent less time prey foraging while in late pregnancy than when they were nongravid, their prey foraging level was not significantly different from that of nonreproductive females. Prey foraging returned to nongravid levels following the birth of infants, suggesting that reduced foraging during late pregnancy may be the result of physical limitations related to the size of the fetuses rather than an effort to conserve energy. To compensate for lost protein from reduced prey foraging, wild females may be supplementing their diet with animal prey received from other group members. Of the 16 observed food transfers in which a reproductive individual received a food item, 14 went to the reproductive female when she was in late pregnancy. Other studies on lion tamarins have shown that pregnant females are the adult group members most likely to receive food transfers (Rapaport, 2001; Ruiz-Miranda et al., 1999). Provisioning of pregnant females also occurs in birds (Jawor and Breitwisch, 2006; Lack, 1940; Poiani, 1992), vampire bats (Wilkinson, 1990) and cooperatively breeding canids (Moehlman and Hofer, 1997) and may alleviate the energetic stress of reproduction on females.

In addition to the absence of energy conservation during pregnancy, reproductive females did not appear to adopt an energy conservation strategy during infant care. Their levels of prey foraging, resting and locomoting remained unchanged from nongravid levels. When lactating, females spent less time plant foraging and more time being social. However, nonreproductive females made the same behavioral changes, which suggest they were not the result of energetic demands of lactation. More likely, this behavioral change is a result of greater resource availability during the period of infant care. As fruit becomes more plentiful, individuals can reduce time searching for fruit and are able to spend more time engaged in social activities.

Reproductive females did, however, adopt an energy conservation strategy while carrying infants. Reproductive females contributed 18-75% of infant carrying, whereas nonreproductive females contributed 1-31%, yet activity budgets while carrying infants only differed in rates of locomotion and resting, and both reproductive and nonreproductive females maintained a stable body mass regardless of carrying percentage. Reducing locomotion and increasing resting may allow reproductive females to allocate energy for lactation by contributing to infant carrying when it is energetically inexpensive, which allows females to maintain activity levels and body mass. The presence of helpers to perform the energetically taxing activity of locomotion while carrying infants would allow reproductive females to reduce their residual energy expenditure as is the case in cooperatively breeding meerkats (Scantlebury et al., 2002).

As predicted by my second hypothesis, all infant carriers adopted a behavioral strategy to conserve energy and increase predator detection by increasing energetically inexpensive activities and vigilance. Although studies in captivity showed a reduction in vigilance while carrying infants (Price, 1992b), this behavior would put both the infant and the carrier at a greater risk of predation in the wild and did not occur in the current study. Increased vigilance is likely a necessity when lion tamarin infants are present because they vocalize frequently and loudly, thus increasing the likelihood of attracting predators (Ruiz-Miranda et al., 1999).

Although infant carriers spent less time in high-energy foraging behaviors, individuals other than reproductive females did not spend less time locomoting while carrying infants. However, even with elevated levels of locomotion, neither reproductive males nor nonreproductive males or females lost weight during infant care. In fact, nonreproductive adult males gained weight during infant care regardless of their individual contribution to carrying. Since infant carriers maintained a stable body mass during infant care, they may be compensating for energy lost during traveling by performing high-energy foraging behaviors after transferring infants to other caregivers or placing infants on tree branches where they may still be supervised. The latter behavior typically increases in frequency as infants approach weaning (Siani, personal observation).

In addition to the benefits of helpers, female tamarins may mitigate energetic demands of infant care and increase their reproductive success by timing reproduction to occur when resources allow them to reach greater body mass. As with other callitrichids, the majority of births and subsequent infant care occurs during the wet season when food resources are considered relatively abundant (Dietz et al., 1994; Goldizen et al., 1988; Snowdon and Soini, 1988). Timing of births during the wet season may facilitate stable energy intake by coinciding with optimal availability and/or nutrition of trophic resources (Miller et al., 2006; Miller and Dietz, 2005; Peres, 1994). I found that reproductive females, nonreproductive males and nonreproductive females were heavier in the wet season. Breeding individuals, especially females, were heavier than nonreproductive helpers. Heavier callitrichid females have higher ovulation numbers (Tardif and Jaquish, 1997), are more likely to have live-born infants (Bales et al., 2001) and are more likely to provide a greater amount of early infant care (Bales et al., 2002). Likewise, a meta analysis of 33 species of cooperatively breeding canids found that larger females had larger neonates, larger litter mass and larger numbers of offspring per breeding attempt (Moehlman and Hofer, 1997). Though all species included could breed in the first year, age of sexual maturity was not related to growth (Moehlman and Hofer, 1997) with nonbreeding females having a lower average body mass than breeding females of the same age (Mech, 2004; Sacks, 2005).

In conclusion, reproductive and nonreproductive golden lion tamarins employ different behavioral tactics to mitigate energetic costs of infant care, and these result in the absence of detectable differences in body mass, i.e., physiological costs. Reproductive females reduce prey foraging when heavily pregnant and reduce locomotion when carrying infants, changes which decrease energetic demands, while all infant carriers reduce time foraging and increase anti-predator behaviors. I suggest that reproductive females do not adopt an energy conservation strategy during gestation because the timing of reproduction coincides with the wet season when body masses are higher and trophic resources are more abundant. Reducing time spent in energetically expensive activities, such as traveling, while carrying infants allows reproductive females to invest resources in lactation without sacrificing body condition, a strategy made possible with multiple caregivers. Cooperation in the carrying of infants allows caregivers to balance energetic demands and mitigate predation risk, thus supporting the hypothesis that energetic costs have driven the evolution of cooperative caretaking.

Acknowledgements

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Tables

Table 1. Golden lion tamarin activities recorded during instantaneous focal animal sampling.

Activity	Definition
Plant Foraging	searching for and eating plant items (fruit, nectar)
Prey Foraging	searching for and eating prey items (insect, lizard, frog)
Locomotion	movement to a new location
Vigilance	stationary and alert, moving head to view surroundings
Rest	eyes are closed, body is relaxed in a curled or prone position
Social	aggressive (e.g. chasing) and affiliative behaviors (e.g. grooming)

Figure Legends

Figure 1. Seasonal differences in activity budgets of wild golden lion tamarins (Mean ±SE). An (*) denotes significance at the $\alpha=0.05$ level.

Figure 2. Activity budgets (mean ±SE) of reproductive females (a) and nonreproductive females (b) over reproductive stages. Reproductive females spent less time prey foraging during late pregnancy than during the nongravid reproductive stage. Both nonreproductive and reproductive females spent less time plant foraging and more time engaged in social activities in the infant care stage than in the nongravid stage. Nonreproductive females, but not reproductive females, also had higher rates of locomotion during infant care.

Figure 3. Activity budgets (mean ±SE) of nonreproductive adult (AF) and reproductive females (RF). Female activities did not differ from one another during the nongravid phase (a) or late pregnancy phase (b) with $p<0.05$ for all comparisons. However, nonreproductive adult females had higher rates of locomotion during the infant care phase (c) than reproductive females. An (*) denotes significance at $\alpha=0.05$.

Figure 4. Activity budgets (mean ±SE) of golden lion tamarins during the period of infant care. Individuals carrying infants spent less time foraging and engaging in social activities, and more time locomoting and vigilant. An (*) denotes significance at $\alpha=0.05$.

Figure 5. Activity budgets (mean ±SE) of nonreproductive adult females (AF) and reproductive adult females (RF) when they were (a) not carrying infants or (b) carrying infants. An (*) denotes significance at α=0.05. Activity budgets did not differ significantly when females were not carrying infants. Only locomoting and resting rates differed when females were carrying infants.

Figure 6. Mean body mass (in grams) ±SE of female (a) and male (b) tamarins across seasons and reproductive stages. Reproductive females were significantly heavier than adult females regardless of season or reproductive stage. Reproductive males were significantly heavier than adult males in both seasons and in the nongravid reproductive stage but not during the infant care stage. An (*) denotes significance at α=0.05.

Figure 7. Mean body mass (in grams) of nonreproductive and reproductive adult tamarins during stages of reproduction and infant care. Infant care and lactation occurred in weeks 1-12. Individuals did not show significant differences in body mass during infant care at α=0.05.

Figures

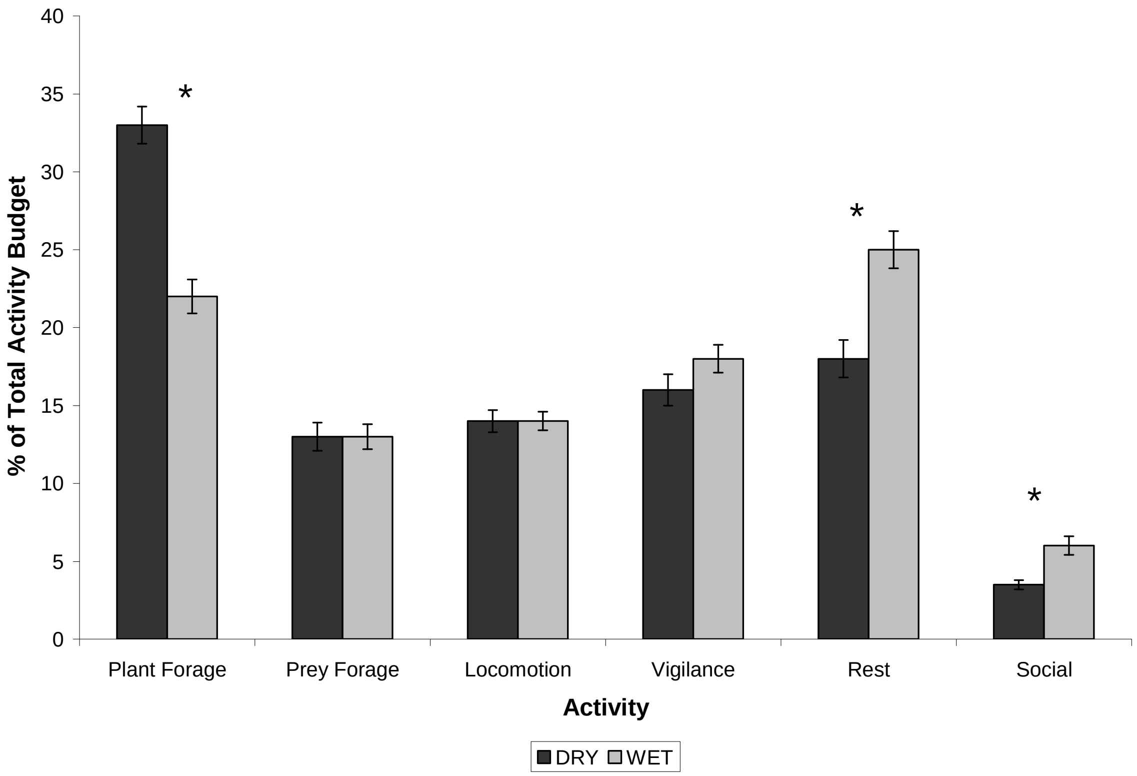
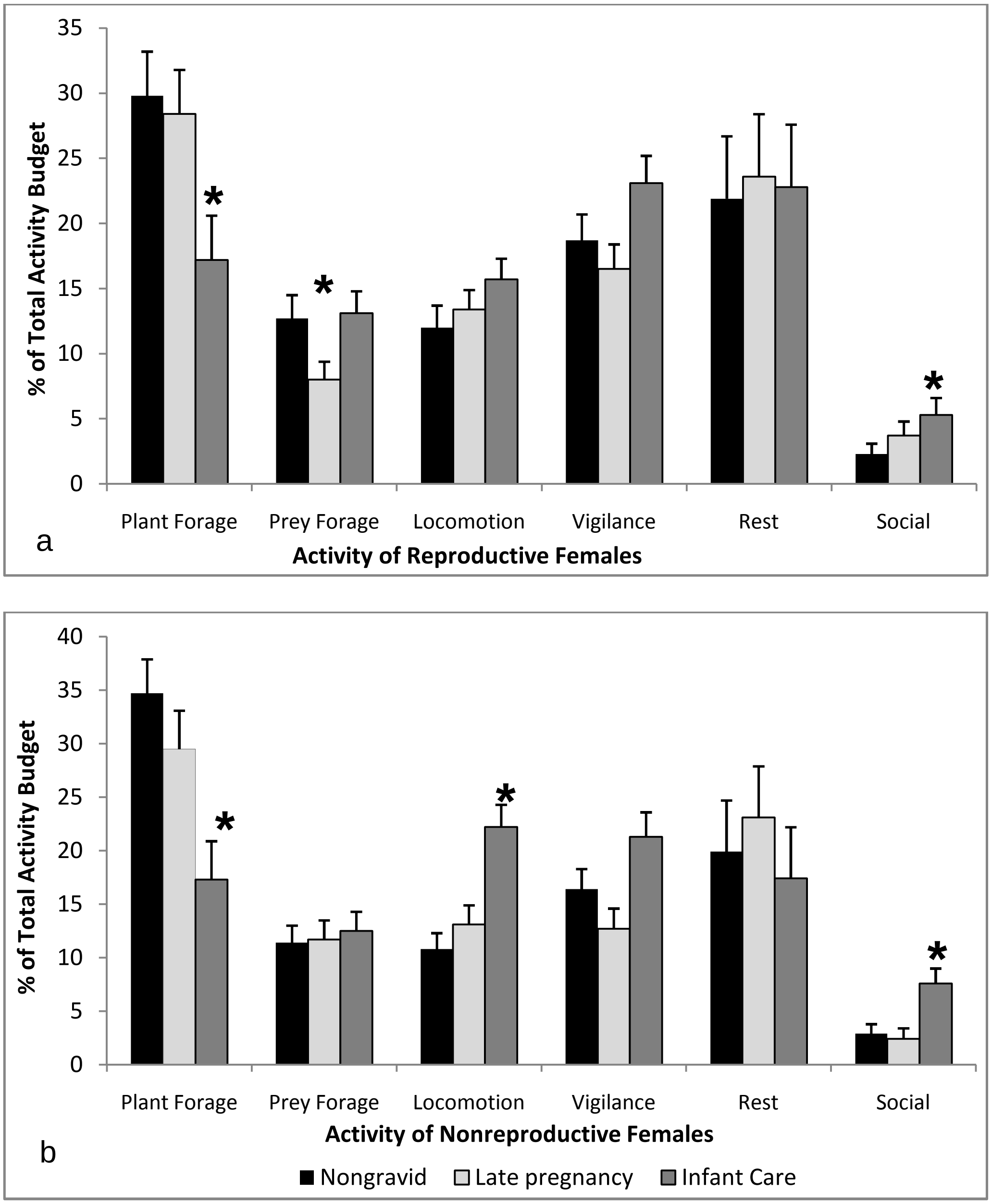


Figure 1.


35
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% of Total Activity Budget
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Plant Forage
Prey Forage
Locomotion
Vigilance
Rest
Social
a
Activity of Reproductive Females
40
35
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% of Total Activity Budget
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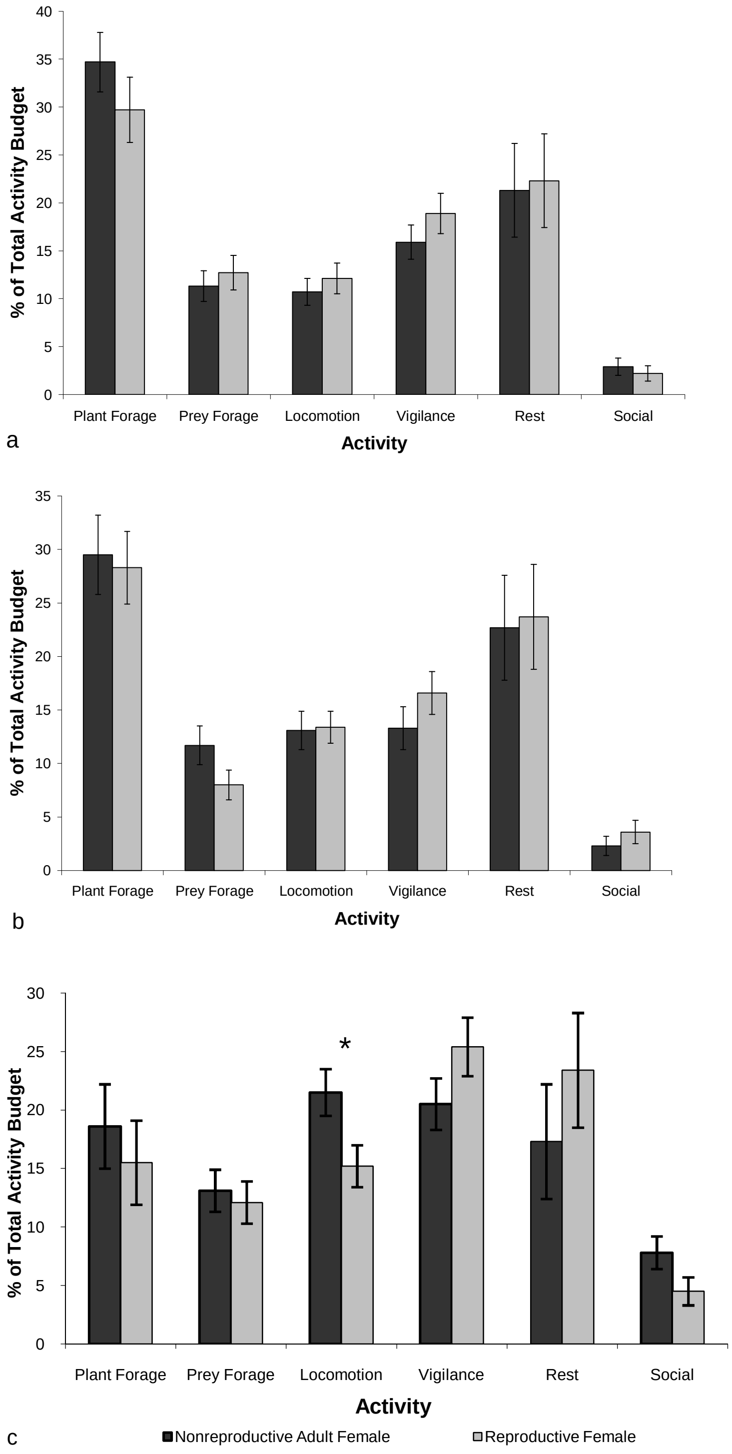
Plant Forage
Prey Forage
Locomotion
Vigilance
Rest
Social
Activity of Nonreproductive Females
b
■ Nongravid
□ Late pregnancy
▨ Infant Care

Figure 2.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Plant Forage
Prey Forage
Locomotion
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Social
Activity
b
% of Total Activity Budget
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Plant Forage
Prey Forage
Locomotion
Vigilance
Rest
Social
Activity
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% of Total Activity Budget
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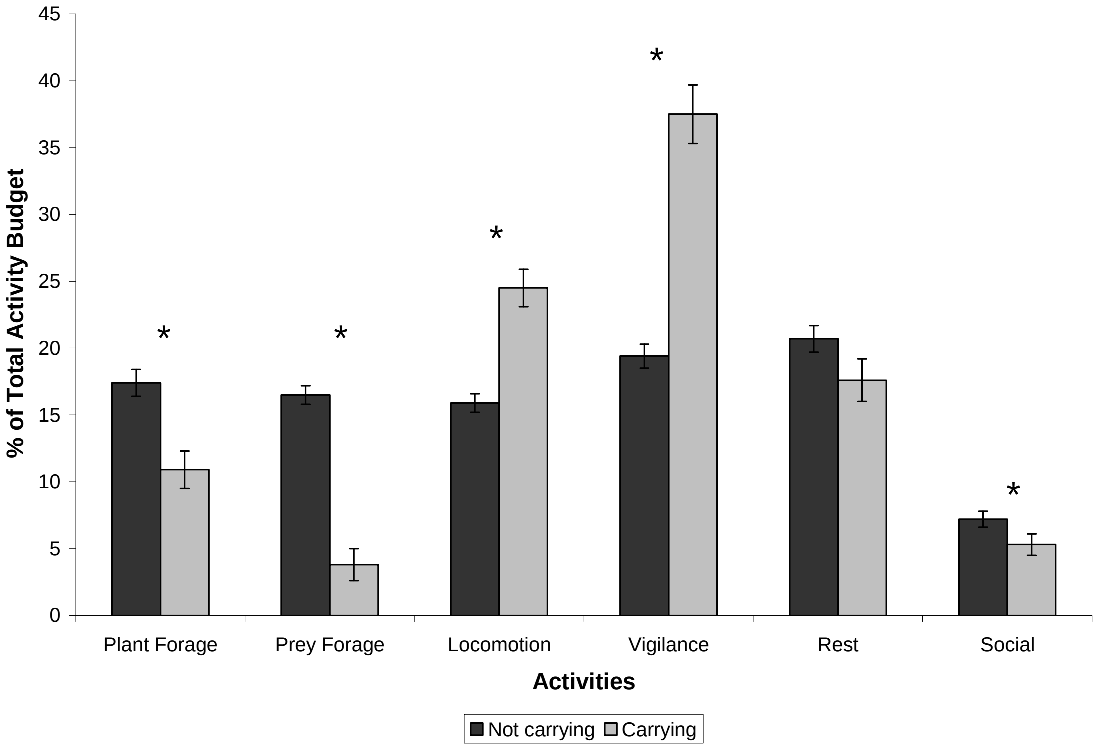
Plant Forage
Prey Forage
Locomotion
Vigilance
Rest
Social
Activity
■Nonreproductive Adult Female
□Reproductive Female

Figure 3.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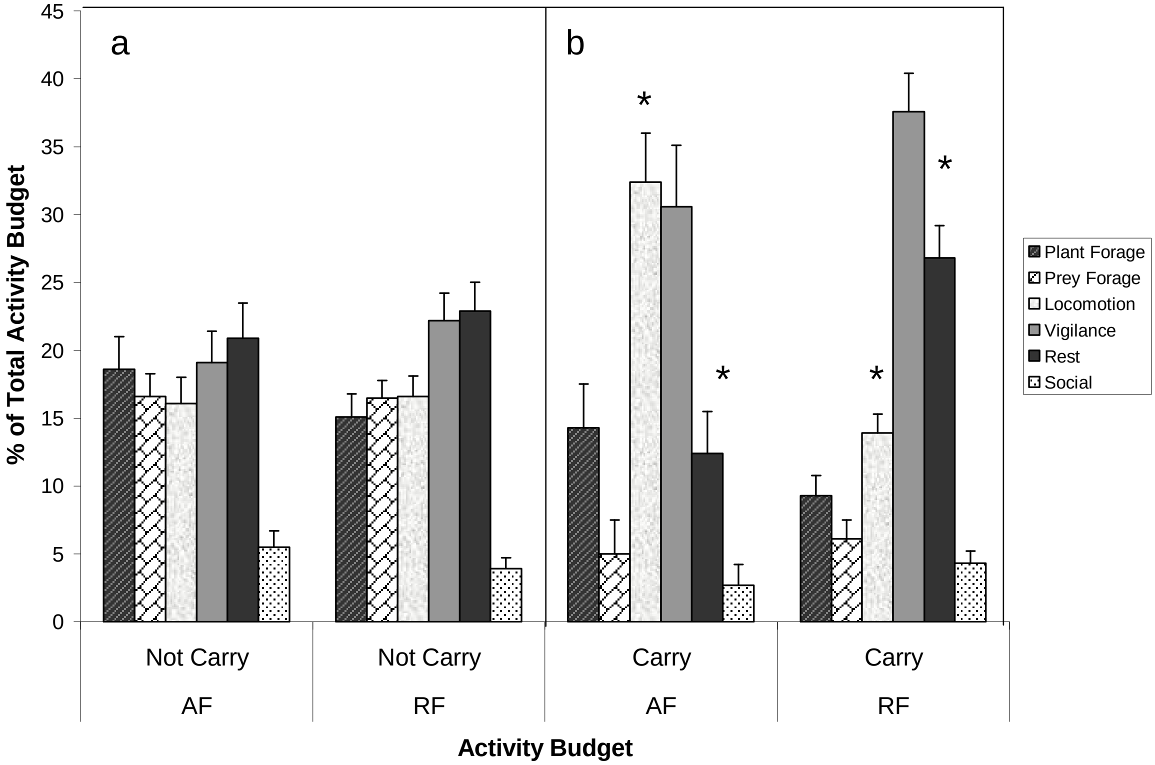
Plant Forage
Prey Forage
Locomotion
Vigilance
Rest
Social
Activities
■ Not carrying
□ Carrying

Figure 4.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Plant Forage
Prey Forage
Locomotion
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Not Carry
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Carry
AF
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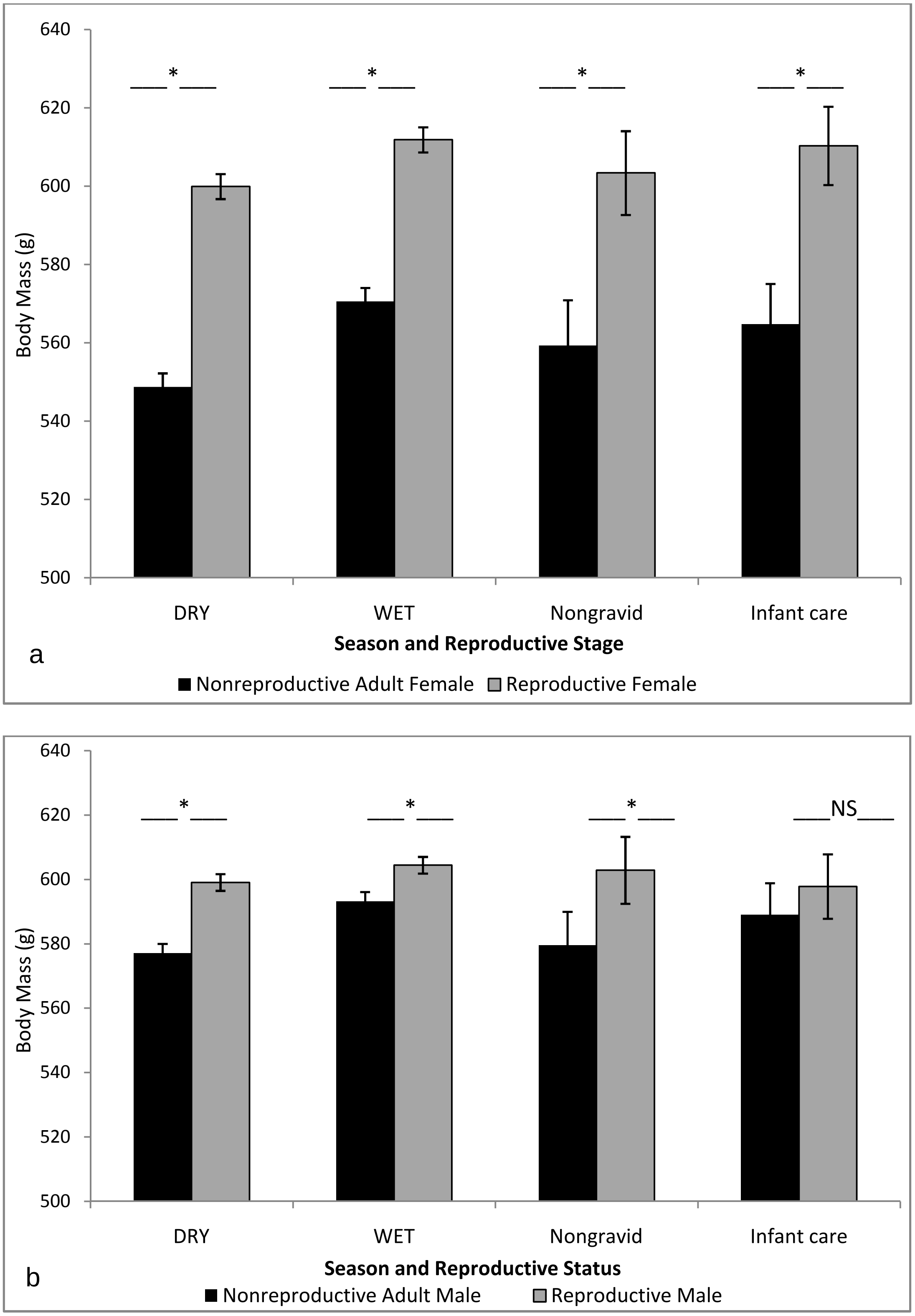
AF
RF
Activity Budget

Figure 5.


640
620
600
580
560
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520
500
Body Mass (g)
*
*
*
*
DRY
WET
Nongravid
Infant care
Season and Reproductive Stage
a
■ Nonreproductive Adult Female
□ Reproductive Female
640
620
600
580
560
540
520
500
Body Mass (g)
*
*
*
NS
DRY
WET
Nongravid
Infant care
Season and Reproductive Status
b
■ Nonreproductive Adult Male
□ Reproductive Male

Figure 6.

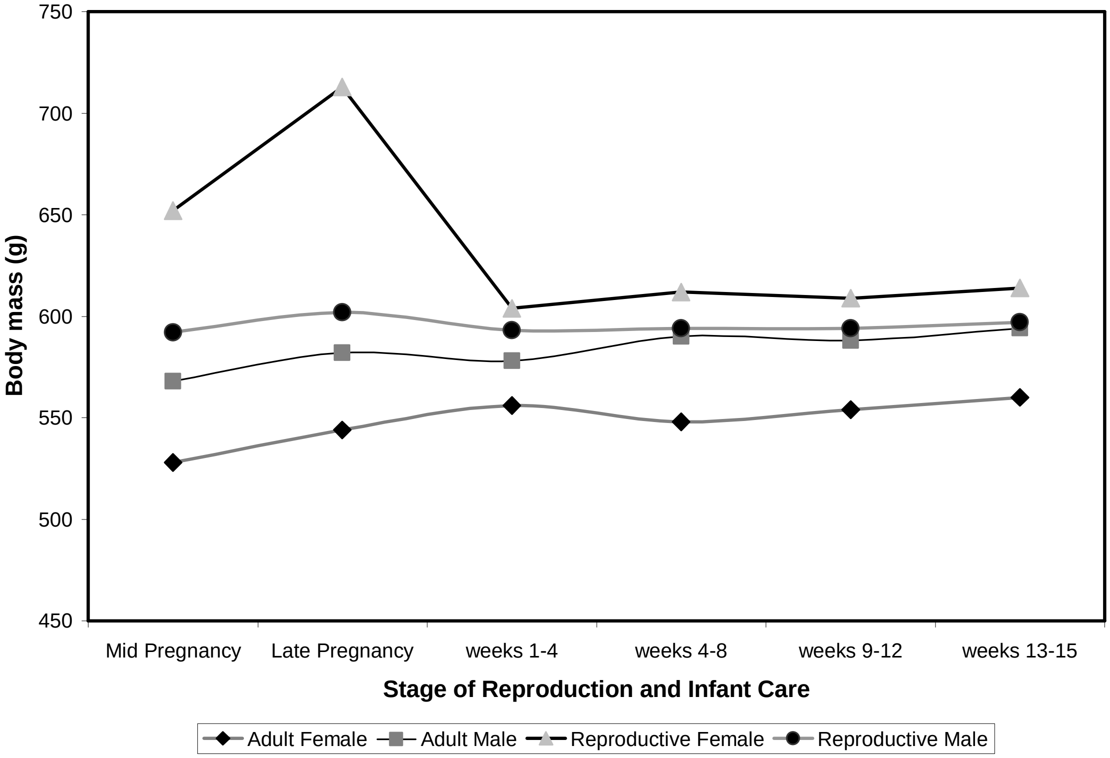
750
700
650
600
550
500
450
Body mass (g)
Mid Pregnancy
Late Pregnancy
weeks 1-4
weeks 4-8
weeks 9-12
weeks 13-15
Stage of Reproduction and Infant Care
Adult Female
Adult Male
Reproductive Female
Reproductive Male

Figure 7.

Chapter 3: Caregiver responses to infant lion tamarin begging vocalizations are influenced by group size and individual age, sex, and reproductive status

Abstract

Infant begging vocalizations may increase resource allocation if caregivers attend to this behavior. In cooperatively breeding birds and mammals, begging vocalizations may not solicit care equally as the distribution of infant care differs among caregivers. In this field experiment, I evaluated the extent to which caregiver responses to infant vocalizations varied with genetic, behavioral, morphological, reproductive and ecological conditions. The study was conducted on five groups of wild golden lion tamarins at Poço das Antas Biological Reserve, Brazil. Once per week I presented caregivers with rasps and trills recorded from infants between two to nine weeks of age from the same social group and from neighboring groups. Although I did not find a difference in caregiver response rate or intensity based on familiarity or relatedness to the infant, response rate was influenced by reproductive status, sex, condition, experience, group size and activity level. At both high and low response intensities, reproductive individuals, especially males, were more likely to respond to infant calls as were less-experienced reproductive females or those that were heavier than average for their sex and age class. Heavy nonreproductive males were also more likely to respond, as were reproductive individuals and adult male helpers from small groups and caregivers that were either travelling or stationary prior to the start of the

playback stimulus. The diversity of non-genetic factors effecting variation in caregiver responses to infant vocalizations suggests that these responses are flexible and dynamic, shifting with changes in group composition and context and with individual reproductive status and physical condition.

Introduction

Infant begging may reflect conflict over resource allocation and is predicted to occur between parents and their offspring, or between siblings, due to differential relatedness (Parker and Macnair, 1979; Trivers, 1974). The use of conspicuous signals, such as begging vocalizations, is hypothesized to induce parents to invest more resources than would be optimal for those parents (Kilner and Johnstone, 1997; Redondo and Castro, 1992; Wright and Leonard, 2002). Although begging may increase parental resource allocation, the potential disadvantages such as increased predator susceptibility and/or metabolic costs of begging behaviors (Harper, 1986), have generated a great deal of research on the evolution of infant begging strategies, namely whether begging is an honest signal of nutritional need (Godfray, 1991; Godfray, 1995; Grafen, 1990; Royle, 2002). Empirical evidence has shown that nestling birds alter call rates, duration and intensity in accordance with hunger levels, which results in corresponding changes in parental food provisioning (reviewed by Mondloch, 1995). Using experimental manipulations of begging rates, nestlings have been shown to gain weight if parents increase provisioning in response to begging intensity (Price, 1998) but there is mixed evidence for increased nest predation and reduced nestling growth as costs of begging (reviewed by Moreno-Rueda, 2007).

Although infants that beg may gain the benefits of additional care, the benefits that parents or other caregivers, in the case of cooperatively breeding species, receive by responding to these vocalizations are not well understood. Vocalizations may be used to share information with caregivers for mutual benefit such as when caregivers can allocate resources based on infant need (Smith, 1969; Zahavi, 1975) or to manipulate caregivers to respond and provide resources that caregivers could have invested elsewhere (Maynard-Smith, 1974). In cooperative breeding birds and mammals, the amount of care provided by each individual has been shown to vary with factors including relatedness (Komdeur, 1994; Ross et al., 2007; Tardif et al., 1990), reproductive status (Siani, Chapter 1, this dissertation), age and sex (Baker, 1991; Clutton-Brock et al., 2002; Cockburn, 1998; Woxvold et al., 2006), group size (Digby, 1995; Washabaugh et al., 2002; Woxvold et al., 2006), physical condition (Bales et al., 2002; Clutton-Brock et al., 2002; Tardif and Bales, 2004), and number of helpers (Bales et al., 2002; Creel and Waser, 1994; Jaquish et al., 1997; Price, 1991; Santos et al., 1997; Tardif et al., 1990). However, there is considerable variation across taxa in how these factors affect the likelihood of individual response to infant vocalizations. For example, in Arabian babblers, *Turdoides squamiceps,* both helpers and parents have been shown to respond to playback experiments of infant calls and provision equally (Wright, 1998) whereas bell miner fathers, *Manorina melanophrys,* increased provisioning much more than did helper males in response to playbacks (McDonald et al., 2009). In cooperatively breeding meerkats and mongooses, sex differences were not found in response rate to playback calls but sex and condition influenced food provisioning following calling bouts (Bell, 2008; English et al., 2008).

Like meerkats and mongooses, infants from the primate family Callitrichidae are highly mobile and beg incessantly throughout infancy. For instance, when left alone on a branch golden lion tamarin infants emit loud, broad-band rasping and trilling calls at over 80 dB at 10m (Ruiz-Miranda et al., 1999) (Figure 1), apparently soliciting nursing, which occurs from birth to 12 weeks of age, solid food, which begins at 4 weeks of age, or soliciting to be carried, which occurs from birth to 12 weeks of age (Baker, 1991; Ruiz-Miranda et al., 1999). Calling bouts range from a single vocalization up to 400 consecutive vocalizations lasting 16 minutes (Ruiz-Miranda and Kleiman, 2002). Begging declines in rate at 9 months of age when the frequency of food transfers declines (Ruiz-Miranda et al., 1999). Behavioral observations suggest that lion tamarin infants that vocalize the most receive the most food transfers (Ruiz-Miranda and Kleiman, 2002) and that these vocalizations also may be used to display discomfort or to seek social contact (Kleiman et al., 1988). Although adult tamarin contact calls contain information on individuality and familiarity (Matasaka, 1987; Miller et al., 2001), it is unknown whether infant calls also contain this type of information.

In the present research, I conducted experiments involving in situ playbacks of recorded golden lion tamarin infant vocalizations to investigate the variation in factors affecting caregiver responses. My objectives were to determine the effects of familiarity, relatedness, reproductive status, age class, caregiver sex, female caregiving experience, physical condition, group size and activity on the likelihood and intensity of caregiver responses. Determining how these genetic, physiological and/or ecological factors affect caregiver response may allow us to identify the selective forces shaping infant care patterns in this cooperative breeding species. I reasoned that if selection favors caregivers that provide more care for their own or closely related infants, then caregivers should be able to recognize and preferentially respond to vocalizations from infants to which they are closely related. In addition, selection should favor caregivers that provide more care for infants that are familiar but not necessarily related, as bonds and alliances may be formed (e.g. when two tamarins from the same group co-emigrate). Thus, caregivers with a high degree of relatedness to the calling infant are predicted to respond more often than caregivers with a low degree of relatedness, and caregivers are predicted to respond more often to infants from their own social group than neighboring groups.

In some cooperatively breeding species, older helpers are better at providing care than younger helpers based on evidence that young caregivers acquire foraging skills slowly and suffer energetic costs when providing infant care (Boland et al., 1997; Heinsohn and Cockburn, 1994; Heinsohn et al., 1988; Komdeur, 1996; Tardif et al., 1992). Since subadult tamarins are still growing and have not had as much time as adults to develop foraging skills, I reasoned that adult helpers should respond more often to infant calls than subadult helpers. In addition to age differences, the interests of male and female helpers may vary based on ecological constraints of dispersal (Cockburn, 1998; Stacey and Koenig, 1990). If this explanation holds for golden lion tamarins, as a way to remain in the group, female helpers would be more likely to respond to infant calls than male helpers because of the higher risks that females face during dispersal (Baker and Dietz, 1996). Age and experience also play roles in establishing effective mothering techniques and enhancing breeding performance (Clutton-Brock, 1988; Fleming and Sarker, 1990; Levy and Poindron, 1987; Newton et al., 1981), especially if learning is required (Komdeur, 1996). Inexperienced lion tamarin females carried infants more than experienced females (Baker, 1991) and less-experienced cotton-top tamarin reproductive females retrieved infants from both other carriers and when infants were alone more often than experienced females (Washabaugh et al., 2002). If infant begging vocalizations influence caretaking, then I would expect reproductive females with little caregiving experience to respond more frequently to infant vocalizations as compared to females with extensive caregiving experience.

Previous research suggests that helpers and reproductive females that are in good physical condition contribute more to infant care (Bales et al., 2002; Clutton-Brock et al., 2002) possibly because they have the physical resources necessary to do so. If that explanation were correct, I would expect caregivers in relatively good condition to respond more often to infant vocalizations. If caregivers lack physical resources for infant care, they may benefit from the presence of helpers that allow them to reduce their own investment (i.e. load lightening) (Bales et al., 2000; Crick, 1992; MacGregor and Cockburn, 2002). For instance, lion tamarin mothers in groups with relatively few helpers per infant contribute more to infant carrying (Bales et al., 2002), reportedly because they must compensate for work not done by helpers. If the number of caregivers affects the distribution of infant care, I would expect caregivers from small groups to respond more often to infant vocalizations as compared to caregivers in large groups containing more helpers. Finally, caregivers may be less inclined to respond to infant begging when it interrupts behaviors that would increase the caregiver's direct fitness (e.g. foraging); however, selection should also favor caregivers that are vigilant to potential threats to their direct or indirect fitness. Thus, I expect that all caregivers will respond more often to infant calls when infants are potentially at greater risk (i.e. when the group is traveling and risks leaving the infant behind).

Methods

Study site and species

This study was conducted at Poço das Antas Biological Reserve [22° 30–33´S, 42° 15–19´W] in the state of Rio de Janeiro, Brazil. The reserve is a 6,300 ha mixture of mature, secondary, and swamp forests and grasslands (Dietz and Baker, 1993; Dietz et al., 1997). Golden lion tamarins in this population have been captured semiannually since 1984 to fit at least one individual with a radio collar for tracking purposes. On these occasions, each tamarin is weighed, measured and receives a permanent tattoo and a temporary dye mark for field identification. Individuals in study groups are habituated to the presence of human observers. Approximately 50 tamarins are monitored at a given time with an estimated total population of 350 individuals in the Reserve (Ruiz-Miranda et al., 2008). Groups are typically composed of 1-2 reproductive females which produce twins once or twice per year, 1-2 adult males unrelated to the reproductive females and infants of various ages with an average group size of 5.4 (Dietz and Baker, 1993). While only reproductive females nurse, all individuals carry and provide solid food to infants.

In the present study, I classified individuals from five groups into the following age class, status and sex categories: reproductive female (n=6), reproductive male (n=5), nonreproductive adult female (n=5), nonreproductive adult male (n=6), subadult female (n=3) and subadult male (n=8). Data on growth and behavior of lion tamarins in captivity suggest sexual maturity occurs between 15-20 months of age (Hoage, 1982). Therefore, I defined adults as individuals over the age of 19 months, which was the earliest known age of successful dispersal from a natal group during this study. Less-experienced reproductive females were those that had given birth to one or two litters of infants whereas experienced females had given birth to at least three litters and upwards of ten litters. I could not divide the females based on parity because all but one female had already produced infants during the study period. All relatively inexperienced females in the study population had been observed carrying infants prior to becoming reproductives.

Between August and December of 2005 and 2006, 19 infants from the study groups were weighed, sexed and marked for identification as soon as possible after birth using a baited live-trap (Bales et al., 2000). Fifteen of the 19 infants survived to weaning age. During periods when infants received care from parents and helpers, we weighed all individuals in the study groups at weekly intervals. To obtain body masses without capture, I placed an electronic scale with a bamboo platform attached to the scale plate near the group. I suspended a banana above the scale and recorded body mass when individuals climbed onto the platform. I recorded several masses for each tamarin and averaged them (n=1240 measures from 33 individuals).

I determined the relatedness between each caregiver and infant dyad based on known maternal lineages. I used behavioral data to determine paternity since paternal genetic relatedness could not be determined due to evidence of genetic chimerism in both blood and hair samples. If one adult male was present in the group at the time of conception, paternity was attributed to that male. In multi-male groups, I assigned paternity to the male that dominated copulations during the time of conception, identified by counting back 130 days from the infant's date of birth (Baker et al., 1993).

Recordings

I recorded vocalizations of all study infants each week using a PMD-660 digital recorder and a Sennheiser ME67 long gun microphone (with K6 power module). The distance between the caller and the microphone ranged from 2-8 m. Spectrograms of infant calls were viewed using Raven 1.2.1 interactive sound analysis software (Cornell Lab of Ornithology). For each infant, I selected 10-14s segments of rasps and trills from longer calling bouts for use as playback stimuli. I selected segments with limited background noise; however, due to overlapping frequencies, noise from insect calls could not be eliminated and was present in the majority of recordings. Non-predatory bird calls were recorded monthly for use as control stimuli for playback experiments. To avoid habituation to individual playback calls, I used a total of 136 recordings throughout the course of the playback experiments.

Experimental Protocol

My assistants and I conducted playback experiments once per week with each study group (n=38 days) beginning when infants were two weeks of age (i.e. beginning to move independently) and ending when they were ten weeks of age (i.e. spending about 80% of their time moving independently). We conducted each trial after verifying the composition of the group and ensuring that the infants were not vocalizing and located out of the focal caregiver's sight. We selected a focal caregiver that was distant from the infant. We mounted a camouflaged speaker on a tree at approximately 1.5m height and 5–15m distance from the subject. The playback sounds, which included infant vocalizations from both focal and neighboring groups, were played in a random order. The subject's behavior was recorded by a field assistant (who was not informed of the call context) immediately before, during and after the sound was played. The field assistant noted if, when and how the subject responded (see data analysis, below). If at any time during the playback an infant in the group began vocalizing or moved behind the speaker or between the speaker and the focal subject, the playback experiment was terminated. We played up to 10 calls to the focal subject and then repeated this protocol with a new focal caregiver after at least two hours had passed and experimental criteria could be met. This research complied with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws.

Data analysis

I defined response rate as the number of positive responses to the playback stimulus divided by the total number of times the stimulus (control or experimental) was played for each dependent variable. I then ranked positive responses to playback stimuli to determine response intensity. Low-rank responses included head turns toward the speaker and/or a single vocalization toward the speaker. Moderate-rank responses included head turns combined with movement toward the speaker; high-rank responses were head turns combined with both movement and vocalizations directed toward the speaker. I characterized a subject as non-responsive to the sound played when it continued the activity exhibited prior to the playback or changed the direction of its behavior but not toward the speaker (e.g., originally traveling and then stopping to forage while the sound was playing). Activities were divided into six categories: eating and foraging for plant material, eating and foraging for animal prey, traveling, resting, stationary and social behaviors (e.g., chasing, allogrooming). Statistical analyses of response rate and intensity were conducted using chi square tests with the number of responses weighted to account for differences in the number of times a particular call was played (SAS version 9.1; SAS Institute, Cary, North Carolina, USA). Response rate and response intensity rank were the dependent variables while reproductive status, age and sex class, prior caregiving experience, group size, the activity interrupted and body mass (i.e. condition) were independent variables. For the analysis of condition, I calculated an average body mass for each sex and status category to determine the relative condition of individuals as either heavier or lighter than average. I excluded subadults from analyses of body mass because they were growing throughout the course of the experimental protocol. The significance level for all statistical analyses was set at $\alpha = 0.05$. Probability values above this threshold indicate failure to reject the null hypothesis, thus no p-values are reported in these cases.

Results

Familiarity and Relatedness

Caregivers responded to experimental sounds significantly more often than control sounds at all levels of intensity (x^2 = 128.9, $p<0.0001$) and the mean positive response rate to all experimental sounds was 38.9%. Caregivers did not respond differently to calls from infants in their own social group compared to infants in neighboring groups (x^2 = 2.2; Figure 2) nor did I find a difference in response rates for caretakers that were related vs. unrelated to the infant calling (x^2 = 1.5; Figure 3).

Reproductive status, age class, sex and experience

Response rate was influenced by reproductive status, age, sex and condition. Reproductive individuals responded significantly more often than nonreproductive helpers at all levels of intensity (x^2 = 85.8, $p<0.0001$), and adult helpers responded significantly more often than subadult helpers (x^2 = 16.9, $p<0.0001$; Figure 4). Sex differences existed within all three status classes (x^2 = 107.1, $p<0.0001$; Figure 5). Adult female helpers responded significantly more often than adult male helpers (x^2 = 15.1, $p<0.0001$), reproductive females responded significantly less often than reproductive males (x^2 = 9.8, $p=0.002$), and subadult females responded less often than subadult males (x^2=7.3, $p=0.007$). Reproductive females that were less-experienced, having produced only 1 or 2 litters, responded significantly more often to recorded infant calls than did females that had produced more than two litters of infants (47.5% vs. 26%; $x^2 = 19.9$, $p<0.0001$). In this comparison, the response rate differed significantly at both low intensity and high intensity responses ($x^2 = 25.6$, $p<0.0001$; Figure 6).

Condition, group size and activity level

Individuals that were heavier than the average body mass within their status and sex class responded significantly more often than individuals that were lighter than average ($x^2 = 4.6$, $p=0.03$). However, this was not true for all age and sex classes as condition did not influence response rates of nonreproductive adult females ($x^2 =0.13$) or reproductive males ($x^2 = 3.5$, $p=0.06$; Figure 7). Heavier nonreproductive adult males ($x^2 = 7.5$, $p=0.006$) and reproductive females ($x^2 = 3.9$, $p=0.04$) responded more frequently than lighter individuals. Individuals in small groups were twice as likely to respond to infant calls as those in large groups (48.2% vs. 20.3%; $x^2 = 163.8$, $p<0.0001$) and also responded more often at all levels of intensity ($x^2 = 176.6$, $p<0.0001$). Although group size did not influence the response rate of adult female helpers ($x^2 = 1.6$), caregivers in small groups responded more often than caregivers in large groups (AM: $x^2 = 34.24$, $p<.0001$; RF: $x^2 = 30.56$, $p<.0001$; RM: $x^2 = 57.79$, $p<.0001$; Figure 8). Caregivers were more likely to respond to infant calls when they were either traveling or stationary prior to the playback sound than if they were engaged in foraging or social activities or resting ($x^2 = 56.8$, $p<0.0001$; Figure 9).

Discussion

My results indicate that reproductive status, age class, caregiver sex, experience, condition and group size influence lion tamarin caregiver responses to infant begging vocalizations. However, caregivers did not respond more often to vocalizations of infants that were in their own social group (i.e. familiar infants) or related to them, suggesting that infant vocalizations do not contain recognition information or that caregivers do not exhibit preferences based on these factors. There is evidence in cooperative breeding birds and mammals, including in the primate family Callitrichidae, that the amount of infant care provided by each individual varies with relatedness (Komdeur, 1994; Ross et al., 2007; Tardif et al., 1990 but see Dunn, 1995). Thus, it is more likely that tamarin infant vocalizations do not contain recognition information. Recognition is more prevalent when there is a need to differentiate among multiple infants within the group or when the likelihood of physical separation exists (Beecher, 1981, 1991; Falls, 1982). Since tamarin groups typically contain one litter comprised of 1or 2 infants, the need to differentiate among multiple infants is minimal. In addition, tamarin groups remain in close proximity throughout the day such that infants are rarely distant from adults. In a study of intra-group communication in adult and subadult golden lion tamarins, differences were rare within age, sex and reproductive classes, which the authors suggested maintained honest group participation in communication (Boinski et al., 1994), an explanation that could be extended to infant calls as well. Although familiarity, sex and identity have been found in the long-distance contact calls of other tamarin species (Matasaka, 1987; Miller et al., 2001), those are salient calls used extensively throughout the animal’s lifetime whereas infant vocalizations are rarely emitted as adults. An exception is that adult tamarins frequently use infant vocalizations when attempting to enter a new group as a transient individual (personal observation). In this relatively rare circumstance, conveying individual-specific information via infant vocalizations may not be beneficial to the potential immigrant.

Since reproductive lion tamarins contribute more to infant care than nonreproductive helpers (Siani, Chapter 1, this dissertation), I predicted that they would also respond more frequently to infant vocalizations. While reproductive males were the most frequent responders to infant begging calls, adult female helpers responded as frequently as reproductive females and more so than adult male helpers. High response rates by adult female helpers may be explained as appeasement to allow them to remain in the group. Adult female helpers rarely transferred solid food to infants but they provided approximately 10% of infant carrying (Siani, Chapter 1, this dissertation) and are more likely than other caregivers to be traveling while carrying infants (Siani, Chapter 2, this dissertation). Thus, females may contribute to infant care by retrieving infants prior to group movement, which may alleviate energetic demands placed on reproductive individuals. In addition, male helpers are more likely to remain in their natal group and transfer directly into an adjacent group whereas female helpers face aggression from both resident males and females, typically resulting in a longer transition period between groups and a higher mortality risk (Baker and Dietz, 1996). Since the cost of dispersal is higher for females, they may be more willing to pay “rent” in the form of responding to infant begging to retain the benefits associated with group membership (e.g. time to enhance survival skills, improve condition, inherit the breeding position). “Pay to stay” is predicted to occur to varying degrees according to relatedness, the cost of helping, and ecological constraints on successful dispersal (Kokko et al., 2002).

In cooperative breeding meerkats, infant care is condition-dependent for male and female helpers and is suggested to occur based on differences in philopatry and direct benefits between the sexes (Clutton-Brock et al., 2002). In golden lion tamarins, physical condition does not influence infant carrying or solid food transfers by male or female adult helpers (Siani, Chapter 1, this dissertation). However, heavy adult male helpers respond more often to infant vocalizations than light adult male helpers, possibly due to differences in the threat of eviction between light males and heavy males who may be viewed as more threatening reproductive competitors. If this is the case, high response rates to infant begging by heavy adult male helpers may then be explained as appeasement to reduce the risk of eviction and allow these males to remain in the group by demonstrating productivity (Emlen, 1982).

Whereas ecological constraints on successful dispersal may explain sex differences by helpers, variation in the response rate of reproductive females may be explained by caregiving experience. Although females will have experience carrying young as helpers, until they reproduce they will not have experienced the energetic burden of lactation or of being the primary caretaker during early infancy when infants are most dependent on caregivers. Subordinate female marmosets have been shown to extend the time of sole caretaking whereas dominant females allowed other group members to carry on the day of parturition (Digby, 1995). Thus, less-experienced females may not be as adept at responding appropriately to infant signals as females with more caregiving experience, especially if females must learn to respond to vocal cues accurately. In macaques, young, inexperienced females spent more time handling infants while older, experienced females showed less interest and responded on only 1/3 of occasions in which infants exhibited distress (Schino et al., 2003) and less-experienced cotton-top females retrieved infants more frequently than their more experienced counterparts (Washabaugh et al., 2002).

Previous research suggests reproductive females that are in good physical condition contribute more to early infant care (Bales et al., 2002) possibly because they have the physical resources necessary to do so. In contrast, physical condition does not influence infant carrying beyond week three of infant dependency, nor does it influence food provisioning (Siani, Chapter 1, this dissertation); however, physical condition may influence nursing. Heavy reproductive females may have responded more often to infant vocalizations because they are capable of providing a more nutritious supply of milk. Smaller than average marmoset females rearing twins had lower milk fat and gross energy and had reduced fertility in subsequent breeding attempts (Tardif et al., 2001). Thus, light lion tamarin females may limit their responses to infant begging to discourage nursing in an attempt to conserve energy.

Caregivers may benefit from the presence of helpers if it allows them to reduce their own investment (i.e. load lightening) (Bales et al., 2000; Crick, 1992; MacGregor and Cockburn, 2002). The findings that reproductive males and females and adult male helpers respond less frequently in large groups support this hypothesis. Individuals in larger groups are able to divide the responsibility of caretaking among more individuals whereas individuals in small groups cannot. All individuals responded to infant calls regardless of the behavior that was interrupted by the playback, however, they were more likely to respond when they were either traveling or vigilant while stationary. Individuals tend to be in close proximity when eating, foraging and resting, which reduces the likelihood of physical separation of infants and adults. Ignoring infant calls when there is a risk of leaving the infant behind or when the risk of predation is elevated may decrease the caregiver's inclusive fitness if the infant is more susceptible to injury or death. Thus, individuals may attend to vocalizations based on their perceived threat level.

In conclusion, variation in caregiver responses to infant vocalizations suggests that these responses are flexible and dynamic, shifting with changes in group composition and context and with individual reproductive status and physical condition. For instance, caregivers will adjust their response rates according to group size by dividing caregiving responsibilities among multiple individuals, but caregivers must weigh this investment against their own physical condition. The fact that caregiver responses were not affected by familiarity or genetic relatedness to the calling infant is not surprising given the small number of infants present in each group and the high probability of relatedness in lion tamarin groups and neighboring areas.

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Figure Legends

Figure 1. Wave forms and spectrograms of infant rasps (a) and infant trills (b).

Figure 2. Comparison of the response rate and intensity of tamarin caregiver responses to playback calls of infants in the same group, neighboring group or to bird vocalizations (control). Caregivers responded to experimental calls significantly more often than control sounds at all levels of intensity; however, their response rate to infant calls from their own social group did not differ from the response rate to infant calls from neighboring groups ($x^2 = 2.2$).

Figure 3. The effect of relatedness on caregiver response rate. Caregivers respond equally to infant calls regardless of the level of relatedness between caregiver and calling infant ($r = 0$ reflects unrelated dyad; $r = 0.25$ reflects cousin or grandparent; $r = 0.5$ reflects parent or sibling).

Figure 4. The effect of reproductive status on caregiver response rate and intensity. Reproductive individuals responded significantly more often than adult helpers and subadult helpers at all levels of intensity.

Figure 5. The effect of reproductive status and sex on response rate and intensity of caregivers. Reproductive status and sex significantly influenced response rate to playback calls. Nonreproductive adult females responded significantly more often than nonreproductive adult males ($x^2 = 15.1$, $p < 0.0001$) yet reproductive females

responded less often than reproductive males (x^2 = 9.8, p=0.002) and subadult females responded less often than subadult males (x^2=7.3, p=0.007). * = significant differences in response rate between males and females within each status class.

Figure 6. The effect of female caregiving experience on response rate and intensity. Reproductive females that had produced only 1-2 litters (i.e. inexperienced) responded significantly more often at low and high intensities (x^2 = 25.6, p<0.0001).

Figure 7. The effect of caregiver relative body mass on their response rate and intensity. Relative condition influences response rate differently within reproductive status and sex classes (x^2 = 4.6, p=0.03). Heavy reproductive females (x^2 = 3.9, p=0.04) and heavy adult male helpers (x^2 = 7.5, p=0.006) responded more frequently than light individuals. Condition did not influence response rate of adult female helpers (x^2 =.13) or reproductive males (x^2 = 3.5, p=0.06). NS = no significant differences in response rate between heavy and light individuals within each class. * = significant differences in response rate between heavy and light individuals within each class.

Figure 8. The effect of group size on caregiver response rate and intensity. Large groups contained 5-7 individuals; small groups contained 3-4 individuals. With the exception of adult female helpers (x^2 = 1.6), caregivers in small groups responded more often than caregivers in large groups (AM: x^2 = 34.24, p<0.0001; RF: x^2 = 30.56, p<0.0001; RM: x^2 = 57.79, p<0.0001). NS = no significant differences in

response rate between heavy and light individuals within each class. * = significant differences in response rate between heavy and light individuals within each class.

Figure 9. The effect of prior activity on caregiver response rate. Caregivers were more likely to respond to infant calls when caregivers were either traveling or stationary (e.g. vigilant) prior to playback of the vocalization.

Figures

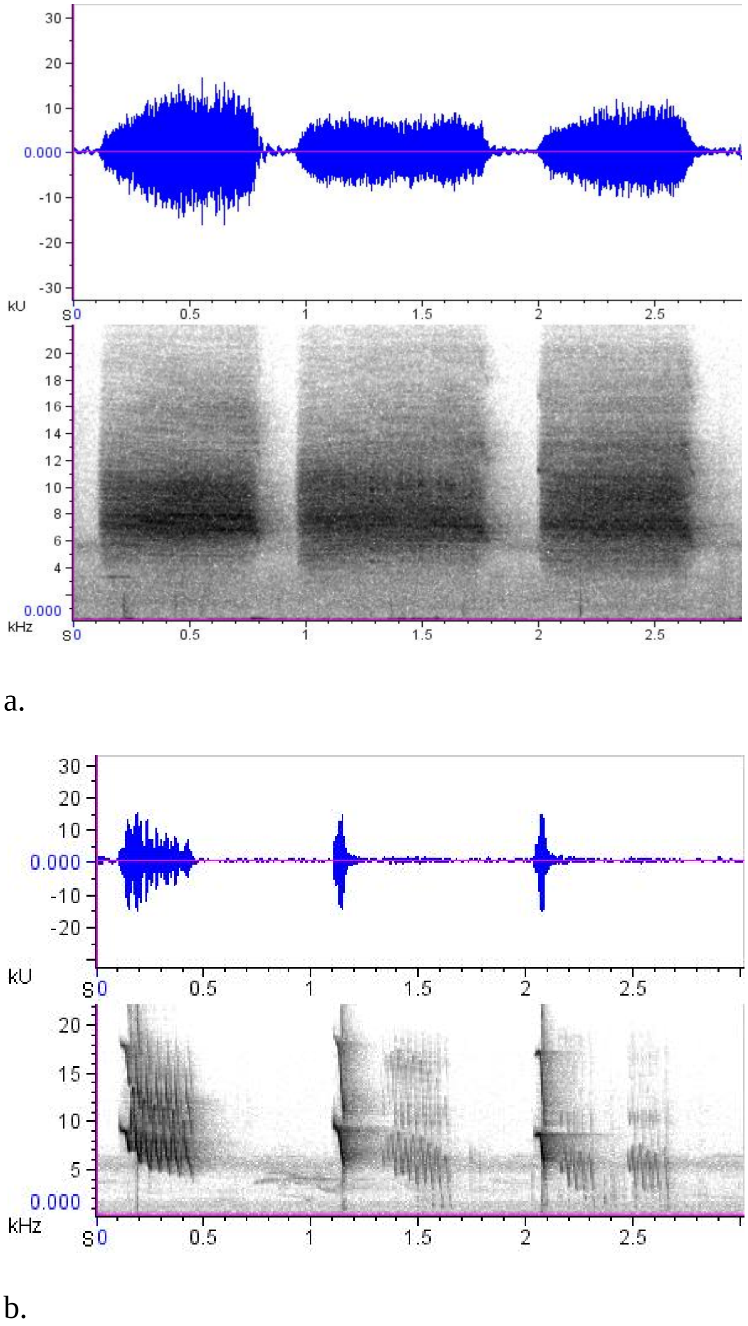
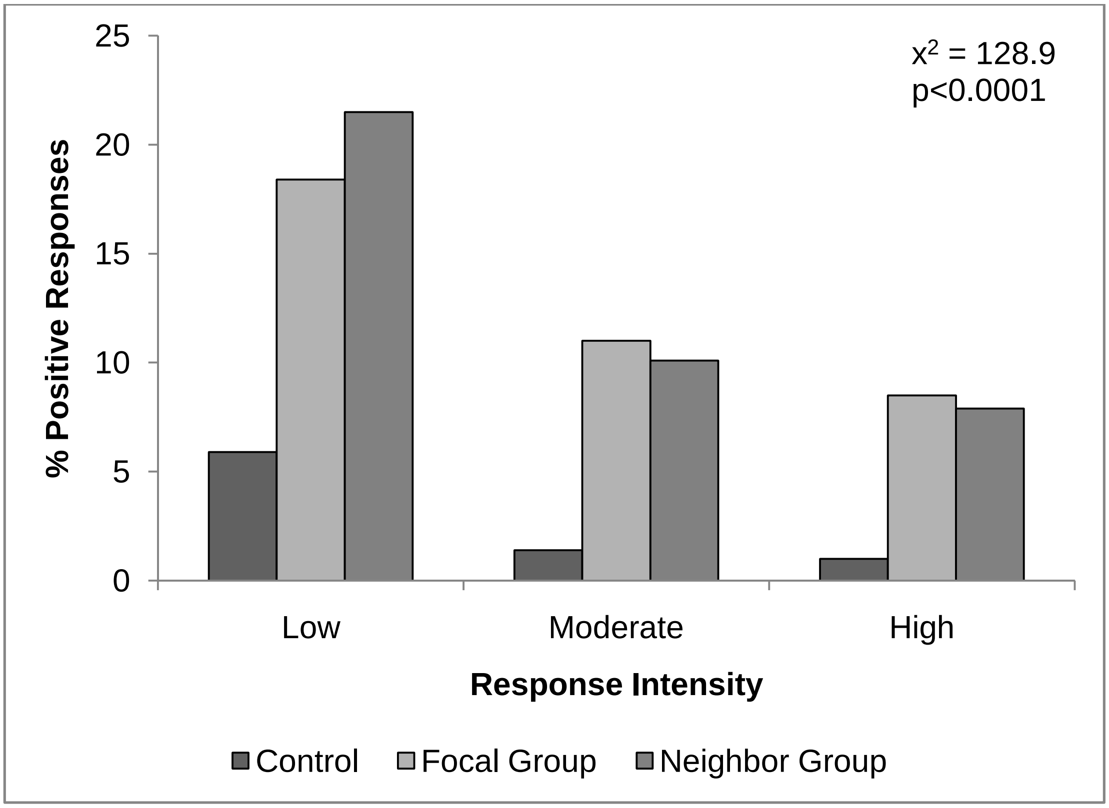


Figure 1.


x2 = 128.9
p<0.0001
% Positive Responses
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5
10
15
20
25
Low
Moderate
High
Response Intensity
Control
Focal Group
Neighbor Group

Figure 2.

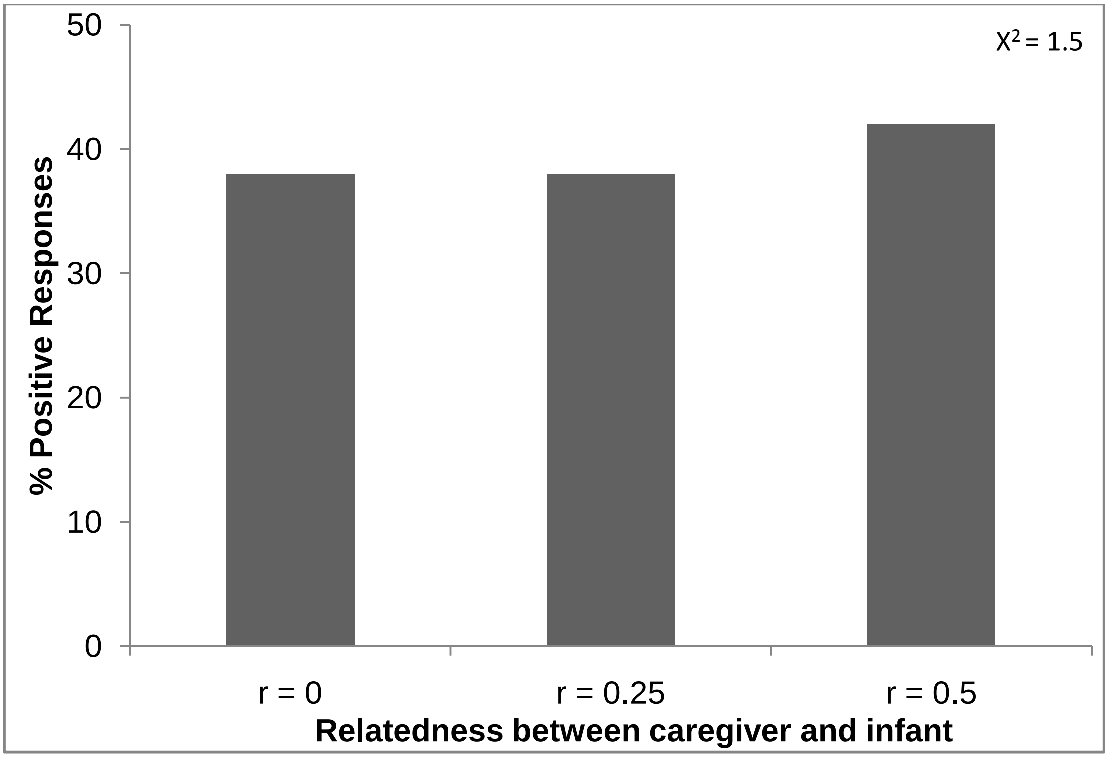
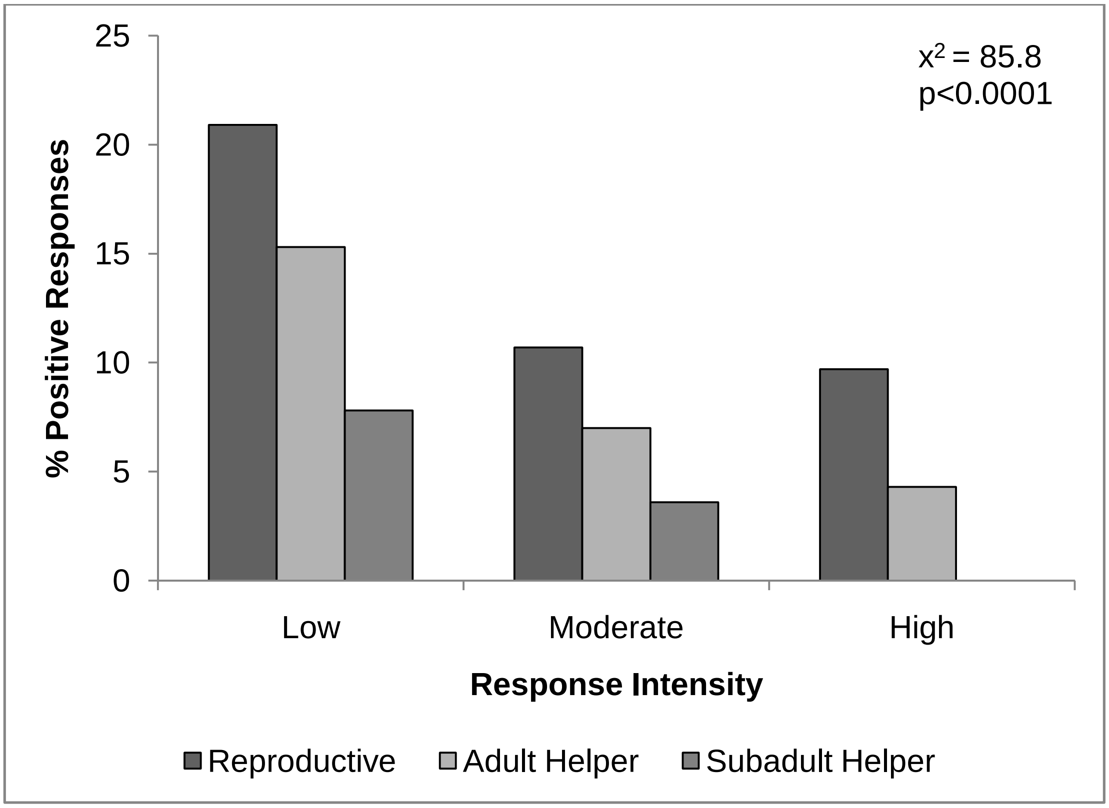

50
40
30
20
10
0
% Positive Responses
X² = 1.5
r = 0
r = 0.25
r = 0.5
Relatedness between caregiver and infant

Figure 3.


25
20
15
10
5
0
% Positive Responses
x² = 85.8
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Low
Moderate
High
Response Intensity
Reproductive
Adult Helper
Subadult Helper

Figure 4.

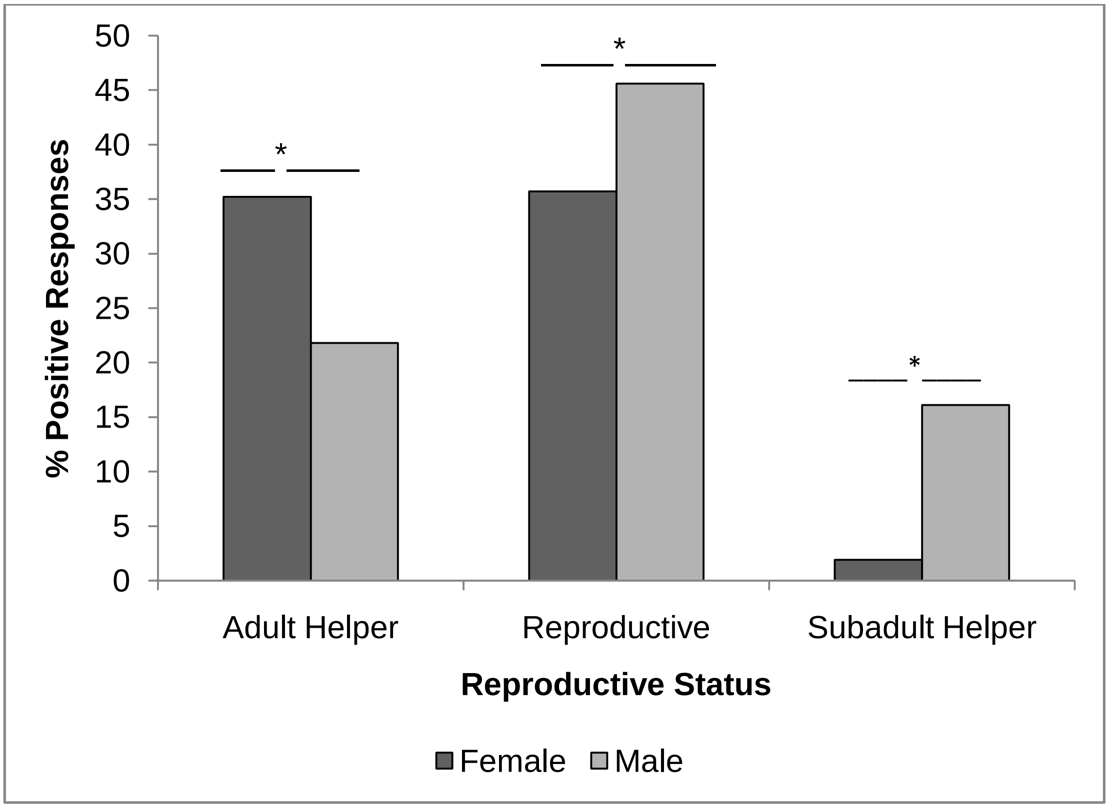
50
45
40
35
30
25
20
15
10
5
0
% Positive Responses
*
*
*
Adult Helper
Reproductive
Subadult Helper
Reproductive Status
■ Female
□ Male

Figure 5.

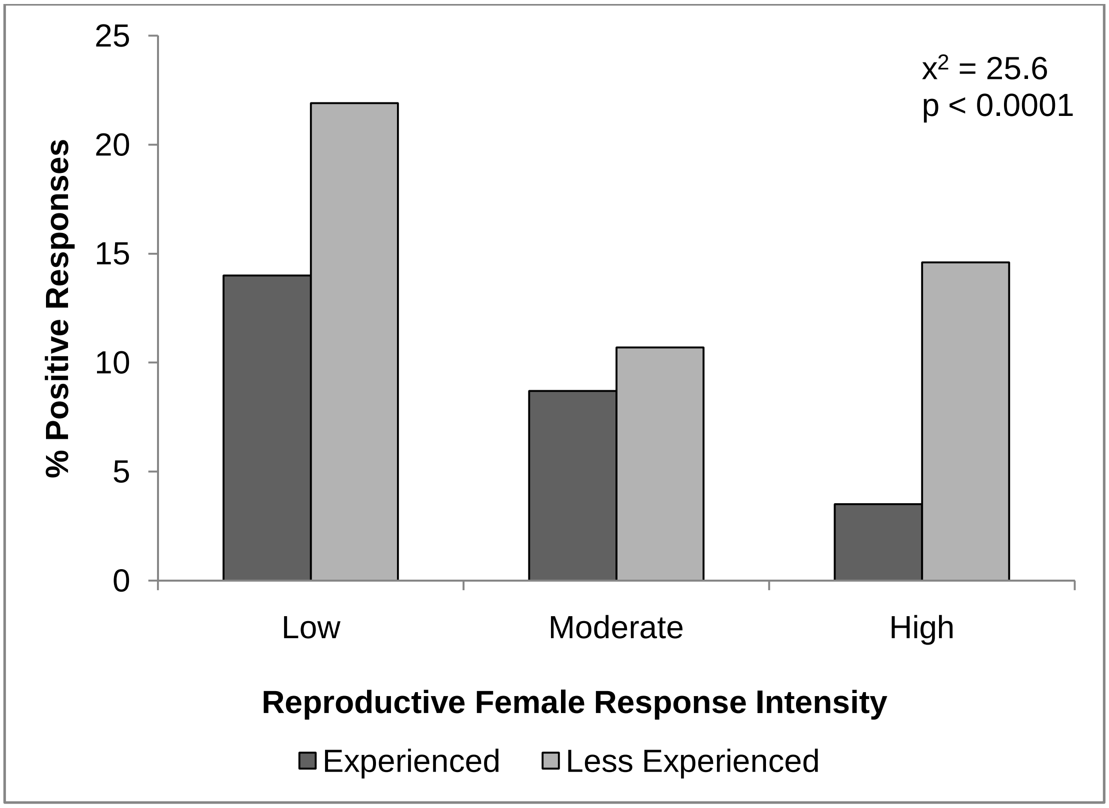
25
20
15
10
5
0
% Positive Responses
$x^2 = 25.6$
$p < 0.0001$
Low
Moderate
High
Reproductive Female Response Intensity
Experienced
Less Experienced

Figure 6.

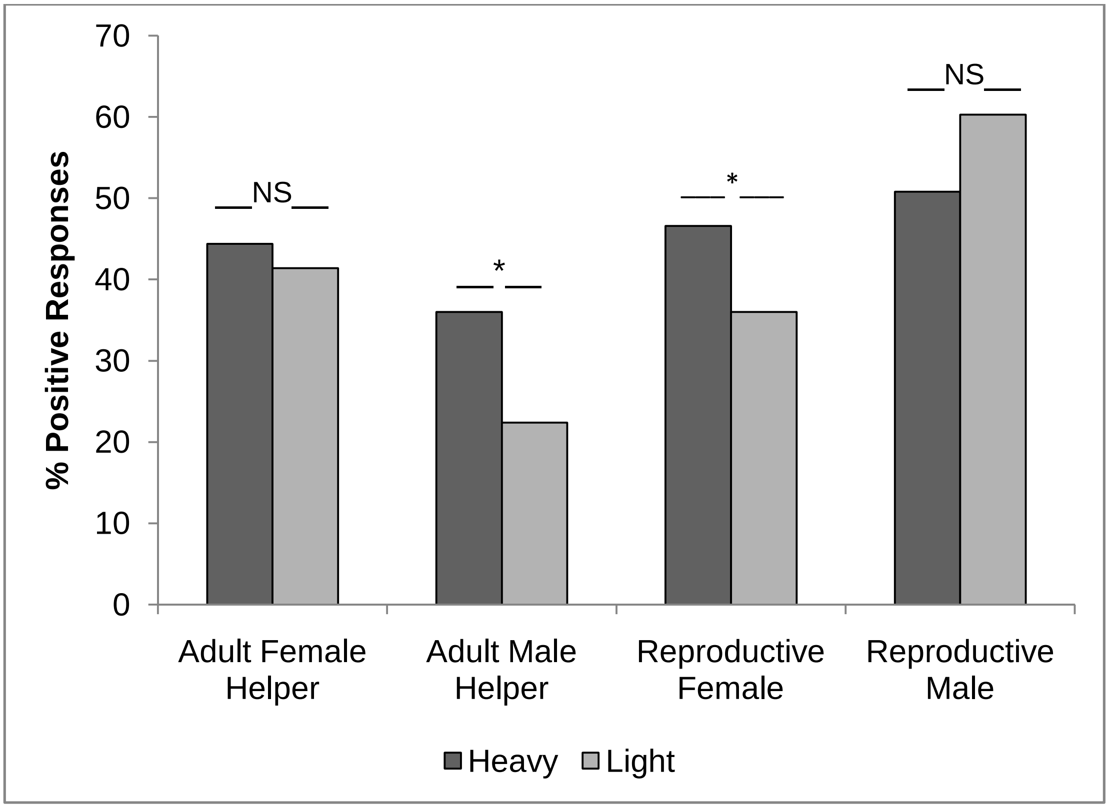
70
60
50
40
30
20
10
0
% Positive Responses
__NS__
__*__
__*__
__NS__
Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Heavy
Light

Figure 7.

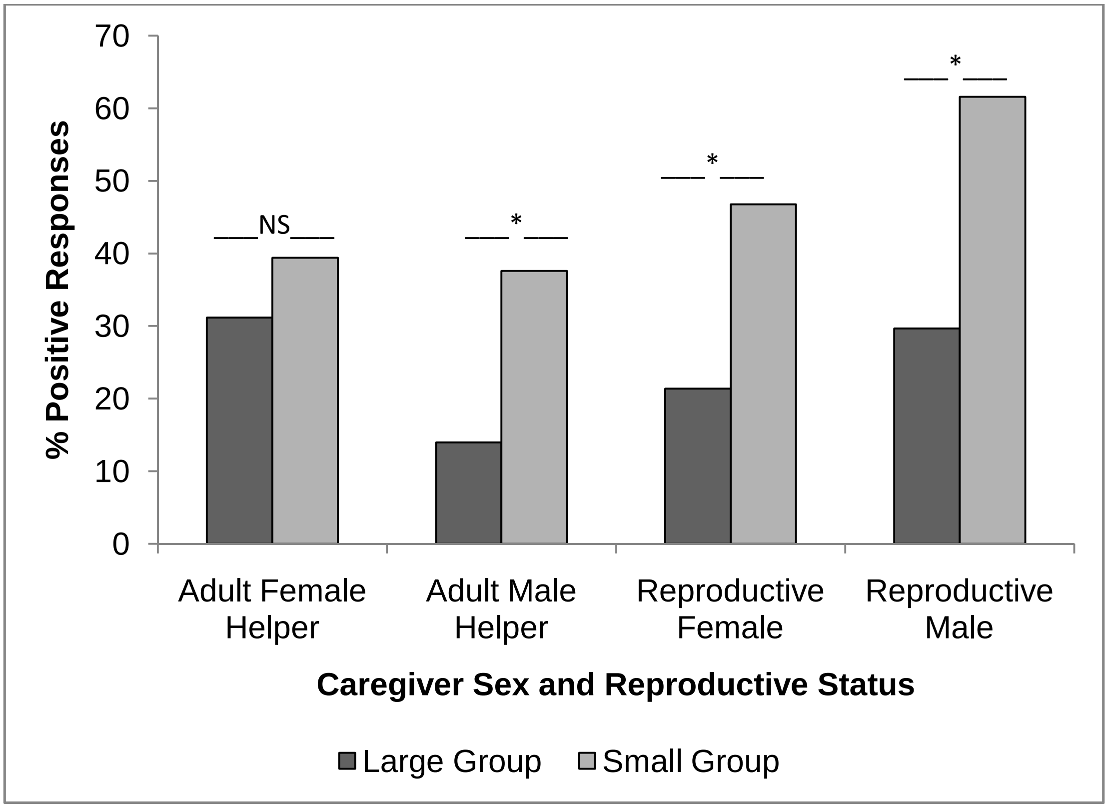
70
60
50
40
30
20
10
0
% Positive Responses
NS
*
*
*
Adult Female Helper
Adult Male Helper
Reproductive Female
Reproductive Male
Caregiver Sex and Reproductive Status
■ Large Group
□ Small Group

Figure 8.

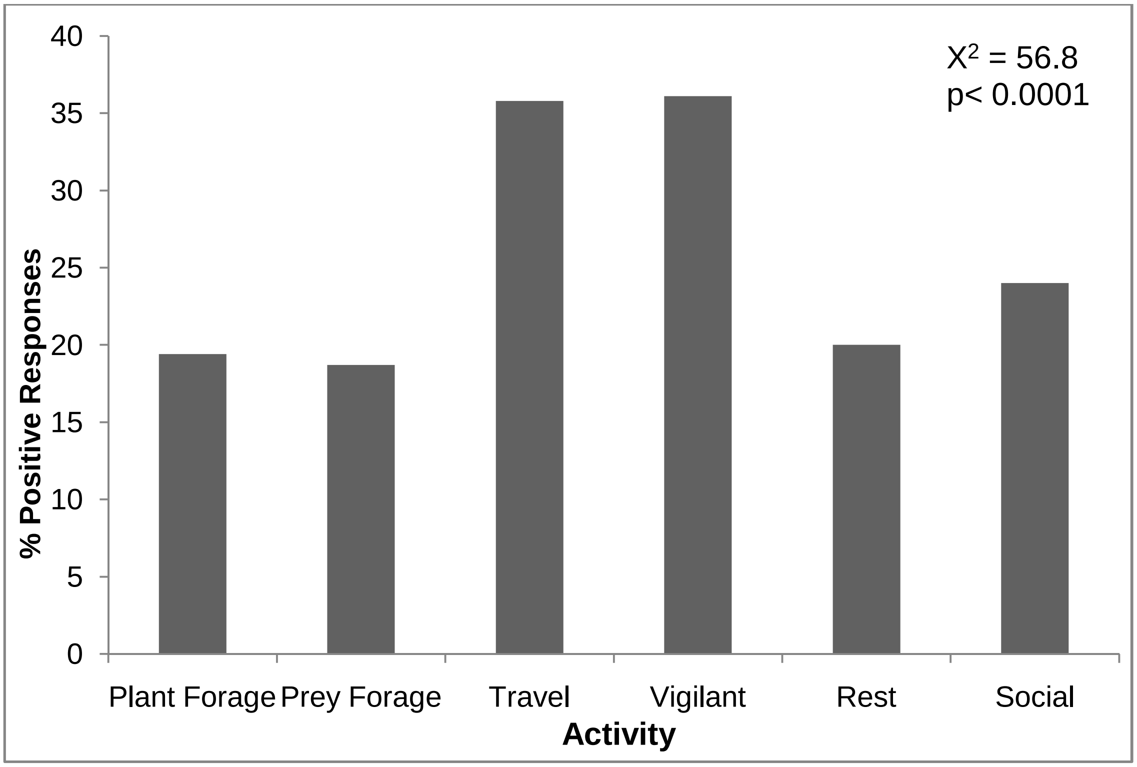
40
35
30
25
20
15
10
5
0
% Positive Responses
X2 = 56.8
p< 0.0001
Plant Forage
Prey Forage
Travel
Vigilant
Rest
Social
Activity

Figure 9.

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