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Is Fatter Sexier? Reproductive Strategies of Male Squirrel Monkeys (*Saimiri sciureus*)

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Abstract Sexually dimorphic traits can evolve through male–male competition or female choice. Squirrel monkeys (genus *Saimiri*) live in large multimale, multifemale groups and are seasonal breeders with concealed ovulation. In several species of the genus, females are dominant to males. Males show weight gain preceding and during the mating season, which produces a “fattened” appearance in the upper arms, shoulders, and torso. Although much is known about the physiology of fattening, the evolutionary function(s) of this sexually dimorphic trait, including possible benefits and costs, remain(s) unknown. This unusual reproductive physiology of males is suggestive of sexual selection. Here I present data on wild *Saimiri sciureus* studied in Brazil to describe male reproductive investment in the species and to examine the hypothesis that male fattening is a product of sexual selection. I observed at least nine adult males via focal animal sampling and *ad libitum* observations during four mating seasons and during an additional 10 nonbreeding season months for comparison. Compared to less robust males, fatter males spent significantly more time near females and less time alone. These males also spent more time engaged in sociosexual activities and less time feeding/foraging, suggesting a trade-off between maintenance and reproductive behaviors. The 2-mo mating season accounted for 62% of all male–male agonism observed over one 12-mo period. These results are suggestive of male–male competition for females. However, males did not coerce females to mate and females often rejected males; this pattern suggests female choice. It is possible that male fattening in *Saimiri* is a product of both intra- and intersexual selection. Males experience intense reproductive costs related to agonism with other males, and related to time and energy invested in the pursuit of females. Although fattening may mitigate

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some of these costs by aiding in male–male competition and in female preference, this phenomenon is likely not without physiological costs to adult males.

Keywords Fattening · Intersexual selection. Intrasexual selection · Reproduction · *Saimiri sciureus*

Introduction

Sexual selection is the process by which sexually dimorphic traits, which serve no purpose in survival, evolved to enhance access to mates (Darwin 1871). These traits could increase competitive abilities against rivals (intrasexual selection) or enhance attractiveness to mates (intersexual selection). Traits selected by intrasexual selection are often called “weapons” and can be used in direct male combat or intimidation (Andersson 1994). Classic examples of secondary sexual characteristics include larger body size and antlers in male ungulates (Malo *et al.* 2005), and larger canines in male baboons (*Papio* sp.) and macaques (*Macaca* sp.: Plavcan and van Schaik 1992). Traits selected by intersexual selection are often called “ornaments,” such as the peacock’s tail (*Pavo crissatus*: Petrie *et al.* 1991).

Sexual size dimorphism (*sensu* Blanckenhorn 2005) is widespread among polygynous mammals, as large body size often increases male mating success (Andersson 1994). Traditionally, researchers have regarded sexual dimorphism in primates as a product of male–male competition (Plavcan 2004). For example, body size dimorphism correlates strongly with the intensity of male–male competition in primates (Plavcan and van Schaik 1997). Other secondary sexual characteristics may also reflect male–male competition. Recent data in humans, for instance, suggest that beards signal status and aggressiveness among males (Dixon and Vasey 2012). Evidence of direct female choice in primates remains scarce (Kappeler and van Schaik 2004; Setchell and Kappeler 2003), mainly because quantifying choice has been challenging. Female mate choice in gorillas (*Gorilla gorilla gorilla*) appears to be based on male crest size (Caillaud *et al.* 2008). Stumpf and Boesch (2006) have demonstrated that proceptive and resistance behaviors by female chimpanzees (*Pan troglodytes verus*) can significantly affect male copulation success, even though males dominate females (cf. Mueller *et al.* 2011). Female choice is predicted to be even more effective when males are unable to coerce females, such as in taxa where females are dominant, e.g., *Lemur catta* (Pereira and Weiss 1991; Sauther 1991), suggesting that female choice is effective in this species. In addition, in seasonally breeding species, many females will be receptive simultaneously, reducing the ability of a single male to monopolize access to them (Emlen and Oring 1977; Ims 1989).

An unusual and poorly understood sexually dimorphic trait in primates is “male fattening” (seasonal increase in male body size, preceding and during the mating season). This phenomenon, first reported in squirrel monkeys (genus *Saimiri*: DuMond and Hutchison 1967) was subsequently also reported in captive rhesus macaques (*Macaca mulatta*: Bercovitch 1992). In the latter species, Bercovitch (1992) suggested that seasonal fat mobilization allows males to engage in mate guarding and sociosexual behaviors while buffering the costs of any reduced feeding time. In contrast, mandrills (*Mandrillus sphinx*) show dimorphism specifically in “rump fattenedness” and in sexual skin coloration, though these traits do not vary

seasonally and are thus not considered equivalent to the seasonal fattening of squirrel monkeys (Setchell and Dixon 2001a,b). Male mouse lemurs (*Microcebus murinus*) also gain weight seasonally, but this is specifically due to proliferation of testicular tissue (Schmid and Kappeler 1998).

Squirrel monkeys are small neotropical primates (700–1000 g; Smith and Jungers 1997) that live in large multimale, multifemale groups (25–75 individuals; Boinski 1999). These primates are characterized by highly seasonal breeding (Di Bitetti and Janson 2000), concealed ovulation, presence of several breeding females in a group, and weak male–female associations because males remain at the periphery of troops during most of the year (Zimble-DeLorenzo and Stone 2011). Females often are dominant to males (Mitchell 1990; Izar *et al.* 2008) and may or may not immigrate from their natal group, depending on the species (Blair and Melnick 2012; Boinski 1999; Mitchell 1990). Therefore, one might expect that opportunities for female choice occur in squirrel monkeys, as the chances for female monopolization by males are low. The “fatted male phenomenon” has been documented in all *Saimiri* spp. studied to date in the wild and in captivity, and is highly suggestive of sexual selection. Males show weight gain (85–222 g; DuMond and Hutchison 1967) during the brief mating period (2–8 wk; Izar *et al.* 2008) due to fat deposition and water retention, which produces a “fatted” appearance in the upper torso, arms, and shoulders (Boinski 1987; Mendoza *et al.* 1978a; Mitchell 1990; Stone 2004). This response is controlled by a seasonal increase in testosterone and its conversion to estrogen, and by high levels of thyroid hormones (Coe *et al.* 1985; Nadler and Rosenblum 1972). Increases in plasma cortisol also occur (Schiml *et al.* 1996, 1999), indicating a potential physiological cost to fatter males. The fattening response always precedes sexual activity and is not related to increased food consumption (Mendoza *et al.* 1978a; Stone 2004). Fattening also coincides with seasonal spermatogenesis (DuMond and Hutchison 1967), and dominance interactions among males become more intense during the mating season (Baldwin 1968).

Although much is known about the physiology of male fattening, its functional significance remains unclear. Boinski (1987, 1992) suggested that such a seasonal increase in body size is a product of sexual selection, but this hypothesis has not been tested. If fatter males have a mating advantage, does it result from male intrasexual competition, female choice, or both? Anecdotal observations suggest that females in Costa Rica (*Saimiri oerstedii*) preferentially solicit copulations from the most fattened males in the troop (Boinski 1987, 1992). In Peru, fattening in *Saimiri boliviensis* appears to aid in male–male competition for access to females (Mitchell 1990). In captive groups of *Saimiri sciureus*, males are more frequently approached by females once they are fattened (Mendoza *et al.* 1978b). Like their Peruvian counterparts, *Saimiri sciureus* are characterized by large, sexually segregated groups and female dominance (Izar *et al.* 2008). Overt physical female signals of estrus, e.g., sexual swellings, are absent in the genus.

In this article, I investigate the mating strategies of male squirrel monkeys (*Saimiri sciureus*) in the wild, with particular attention to the phenomenon of “male fattening.” I first examine and describe the reproductive costs and trade-offs that males face, such as time spent pursuing females and time spent on maintenance activities. Based on previously reported data in the wild and in captivity (Mendoza *et al.* 1978a, b; Mitchell 1990; Stone 2004), I predict that male squirrel monkeys face high levels of male–male aggression and injury costs during the breeding season. I predict that because of female dominance, males will not coerce or be aggressive toward females,

thus increasing the opportunity for female choice. I also hypothesize that fattening confers mating benefits to more robust males, and that these benefits are due both to male–male competition and to female choice. I predict that increased male fattening will be associated with the following behaviors: 1) more time spent in proximity to adult females; 2) less time spent alone in the periphery of the social group; 3) more time spent in sociosexual behaviors; and 4) less time spent on maintenance activities, indicating a trade-off between foraging/resting and reproduction.

Methods

Study Area

I conducted this study near the village of Ananim (VA), 150 km east of Belém, Brazil (01°11 S, 47°19 W). The 800-ha site consists of privately owned ranches that include primary forest and adjacent secondary forests. Rainfall is highly seasonal, with a wet season from January to June and a dry season from July to December (Stone 2007a). Mating in this population of squirrel monkeys (based on observations of three groups) occurs during an 8-wk period from mid-July to mid-September and births occur in January and February of each year (Stone 2006). I collected the behavioral data presented here during four mating seasons (2000, 2002, 2011, 2012), in one study group. In addition, I also collected behavioral data on this group, including social behaviors, during the remainder of 2002 during nonmating periods, as part of a longer term study (Stone 2004).

Subjects

I observed one group of *Saimiri sciureus*, consisting of 44–50 individuals. Observations totaled 288 h, including *ad libitum* observations. Focal hours on adult males totaled 15 h of observation. I followed the group for ≥ 10 d/mo from 06:00 until *ca.* 16:00 h. I obtained accurate group counts on several occasions, especially when subjects were crossing the canopy over larger trails. The most reliable count of the group was as follows: 9 adult males (resident males), 16 adult females, and 19 juveniles and infants (census taken in June 2002). In August 2012, an accurate total group count totaled 50 individuals. The group count was likely higher in August as additional males from other groups may have been present at the periphery of the group at this time (Izar *et al.* 2008; *pers. obs.*). I classified individuals as adults when >5 yr of age (males) and 3 yr of age (females; Mitchell 1990; Stone 2004). Although not all 50 monkeys were individually identified, six males and seven females were, either by obvious physical characteristics or from having been marked with Nyanzol fur dye (Albany Dyestuffs International).

Male fattening in this population begins at the end of June (*pers. obs.*) and lasts until early September. All adult males in the group experience the fattening process, though the younger, subadult males (*ca.* <5 yr; Mitchell 1990) show minimal “plumping” (Scolly 1980), and are not included in the adult male sample. These males can be distinguished visually from fully adult males by their smaller body size, smaller testicle size, and more oval heads. During observations, I classified each adult male into a robustness category: Grade 1 (barely noticeable fattening response: upper arms and

torso area “plump”); Grade 2 (showing the fattening response in the upper arms and torso, but neck still visible); Grade 3 (fattening response very pronounced in the arms and torso, relative to the rest of the body which remains unfattened; neck barely visible). Observations were always made by the same individual (the author), and thus the classification system was as consistent as possible. I did not observe a male’s robustness category to change within the short mating season.

Behavioral Data Collection

Observations from the 2000 and 2002 mating seasons consisted primarily of all-occurrence observations of sociosexual behaviors and of agonistic interactions occurring in the context of mating. During the 2011 and 2012 mating periods, I also conducted 5- to 10-min (8 ± 3 min) focal animal samples on all nine adult males (Altmann 1974), with instantaneous observations taken at 1-min intervals ($N = 90$ focal samples). Observations were balanced by time of day (samples taken prior to 11:00 h and those taken after 11:00 h).

At each 1-min interval, I recorded the following variables: activity of the focal individual (eat, forage, rest, travel, social; Stone 2007a) and age–sex class of the nearest neighbor, within 5 m (another adult male; an adult female; a juvenile; alone). If the focal individual was engaged in a social behavior, I recorded the specific behavior, e.g., copulation, threat. Within the focal period, I also made continuous observations of any sociosexual behaviors that took place involving the focal male (see Table 1). I also noted initiation and directionality of social interactions between the focal male and other individuals (Gibson 2010). I collected all-occurrence data on less commonly seen behaviors such as copulations and aggressive male aggregations (involving more than two males) that occurred in the context of mating (see Results). During each instance, I noted the age–sex class (or identity) of the initiator and the recipient and the outcome when visible.

Although non-identification of all focal individuals is a potential limitation of the study, I took several steps to ensure adequate sampling. First, the order of observations of robustness grades was not completely random in order to avoid oversampling certain males. For example, if the first sample of the day was a Grade 2 (determined randomly), I often sampled a second Grade 2 male immediately after the first to avoid repetition of the same individual. Second, because the group was often spread over 50–150 m, I made a point of conducting successive samples on individuals that were distantly located. Third, during the 2011 and 2012 sampling periods, four of the nine males of the group were recognized.

Data Analyses

Using descriptive statistics on observed sociosexual behaviors (including copulations), I examined whether males coerced adult females during the mating season. To test the prediction that males experience high levels of male–male aggression and injury costs during the breeding season, I compared the mean agonism rate among males of different robustness grades, although the small sample size did not allow for statistical comparison. Using data from focal samples only, I examined the effect of male robustness on activity and on nearest neighbor, using a one-way ANOVA followed by *post hoc* tests. This allowed me to test the following predictions: fatter males will spend more time spent in proximity to adult females, less time alone in the periphery of

the social group, more time in sociosexual behaviors, and less time on maintenance activities.

Instantaneous observations within each male focal sample are not statistically independent. Therefore, I treated each adult male sample, rather than each individual observation within a sample, as a data point for analyses. Both categorical variables (activity and nearest neighbor) were converted to quantitative variables as the proportion of intervals a focal individual was engaged in that activity (Stone 2007b). Variables did not conform to a normal distribution and were arc-sine transformed before statistical tests. I also conducted a Spearman rank correlation to test whether time spent near females was associated with time spent in foraging activities. Statistical significance was set at $P < 0.05$ for all tests, and data are reported as the mean ± 1 SE of untransformed data.

Results

Sociosexual Behaviors in *Saimiri sciureus*

The complete behavioral mating sequence in this squirrel monkey group was characterized by males pursuing females, soliciting copulations with or without vocalizations, and mounting, followed by intromissions and ejaculation. I observed only males initiating sexual interactions. The mean duration of mounts was 5.2 s (range = 2–10 s; $N = 32$). Copulations (mounts accompanied by intromission; $N = 26$) had a mean of 11.1 s (range = 8–25 s). Multiple mounts always occurred during a copulatory sequence that led to ejaculation. After ejaculation ($N = 3$ observations), both males and females consumed any semen left on the branch on which the pair had copulated. Copulatory plugs were never observed, and I never observed males or females removing ejaculate from the vagina. I did not observe post-copulatory mate guarding.

Of the 26 copulations seen, 8 occurred in July, 12 in August, and 6 in September.

Table 1 Affiliative sociosexual interactions observed between adult male and adult female *Saimiri sciureus* in Brazil during four mating seasons (2000, 2002, 2011, 2012)

Behavior	Male initiated (counts)	Female initiated (counts)
Approach: Individual A comes within <0.5 m of individual B (which is stationary).	22	1
Branch sniff: Individual A sniffs branch that individual B had been sitting on immediately before.	11	0
Genital sniff: Individual A sniffs genital area of individual B.	38	0
Pursuit: Individual A travels alongside individual B (which is moving), attempting to maintain physical proximity.	99	6
Drape: Individual A positions itself sideways over individual B (which is stationary).	5	0
Mount: Male mounts female from the rear, without intromission.	12	0
Copulation: Mounts are accompanied by intromission, with or without ejaculation.	26	0

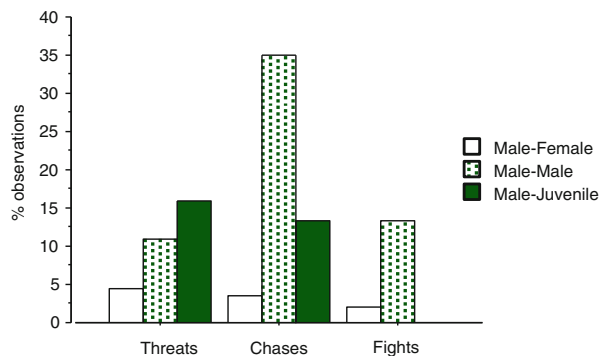
Consortships (spatial association of <3 m between a specific male and a female, accompanied by pursuits) occurred in 31% of the observed copulations. However, because I observed consortships only during *ad libitum* data collection, it is possible that more copulations occurred in this context. A consortship could last from 17 min to >4 h within a day (interspersing mounts with resting and foraging), with the female's youngest offspring (6–8 mo) accompanying the pair. Consortships started by a male approaching a female and remaining in close spatial proximity to her during foraging and travel. Males and females vocalized very little during these associations and sometimes remained at the back of the group, although they never completely left the group ($N = 15$ consortship observations).

Agonism and Affiliation

Males competed aggressively over access to females. In 2002, the 2-mo mating season accounted for 62% of all male–male agonistic interactions observed over the year ($N = 47$ observations). The level of agonism in the group was higher in the mating season (0.015 events/h per individual) than at other times of the year (0.008 events/h per individual). Most aggression (57%, $N = 137$ observations) occurred among adult males (Fig. 1). In addition to fights between two males, these interactions could involve three to five males in “pile-ups” (Baldwin 1968). Pile-ups occurred either when additional males joined two already fighting males, but most frequently seemed to involve several males chasing and fighting with a solitary male ($N = 12$ observations), possibly a strange male from a different group. Because these interactions occurred quickly and far from the observer, the males involved could not be classified reliably into fattenedness grades. In 87% of male–male aggression instances, an adult female was within <5 m from the fighting males, vocalizing, but not obviously supporting any particular male in the fight. Rates of aggression received according to male fattenedness were as follows: Grade 1 = 0.27 events/min of focal sample; Grade 2 = 0.24 events/min of focal sample; Grade 3 = 0.19 events/min of focal sample (these include threats received by adult females and juveniles). Owing to small sample sizes per male grade, I did not conduct inferential statistical analyses on aggression rates.

Qualitative observations indicated that injuries (cuts, gashes, even broken limbs) on adult males were common during the mating season compared to other times of the

Fig. 1 Agonistic interactions observed between *Saimiri sciureus* adult males and other group members during four mating seasons (2000, 2002, 2011, 2012) in Vila Ananiam, Brazil.



year. For example, in the 2000 mating season, an adult male lost a portion of his upper lip during a conflict with another male. I observed fighting males falling to the ground on six occasions. In contrast, injuries on adult females and juveniles were generally uncommon, and no more frequent during the mating period compared to other times of the year. During the 2012 mating period, I observed at least seven different males with injuries, including an individual with a broken hand.

Levels of agonism involving males and females were low, and consisted of females threatening or attacking males who were pursuing them, and then moving rapidly away. Males did not coerce females, with the males at the most pulling the tail of a female while she attempted to leave. However, this did not prevent females from leaving ($N = 3$ observations). Much of the agonism (27% of observations) involved the youngest offspring of the females (6–8 mo old) harassing, i.e., chasing and threatening, males who approached or copulated with their mothers. In nine cases, these juveniles blocked attempts of the male to mount the female by standing behind her and “mounting” her themselves.

Males approached/pursued females in 96% of instances ($N = 128$ approach and pursue observations), but were rarely approached/pursued by females. Females did not engage in soliciting, such as presenting hindquarters or vocalizing to males. After approaching females, males frequently sniffed the females or the branch on which she had been sitting before pursuing her or not. Males also engaged in a behavior I call “draping” in which they approached but did not mount the female, but sprawled over her sideways, in a relaxed manner (Table 1).

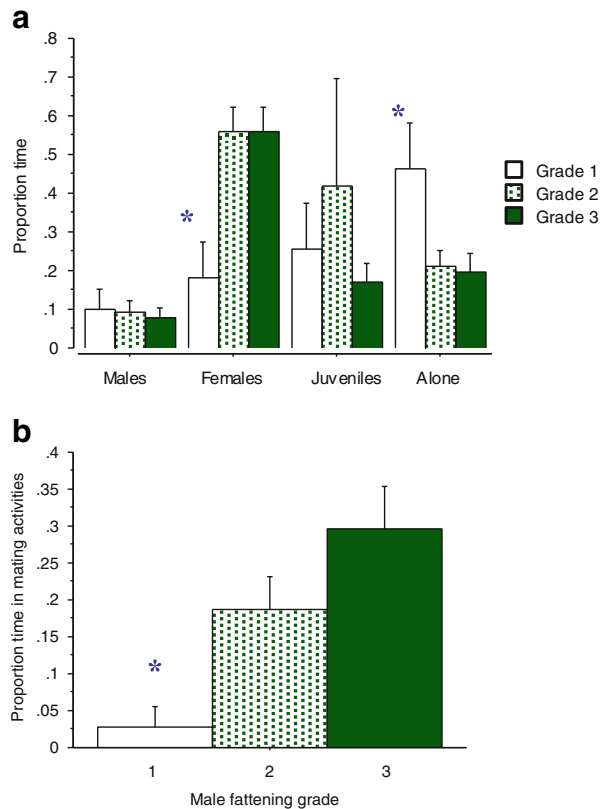
Effect of Male Fattening on Male Behaviors

Grade 1 males (less robust) spent significantly less time in proximity to adult females ($F_{2,72} = 5.62$, $P = 0.005$) and more time alone ($F_{2,72} = 4.27$, $P = 0.010$), compared to Grade 2 and Grade 3 males (Fig. 2a). Grade 2 and Grade 3 males did not differ from each other in their nearest neighbor associations ($P = 0.101$). These more robust males also spent significantly more time engaged in sociosexual behaviors ($F_{2,63} = 3.95$, $P = 0.02$; Fig. 2b). Grade 3 males spent 8% more time than Grade 2 males participating in sociosexual activities, though this difference was not statistically significant ($P = 0.070$). Grade 2 and Grade 3 males spent significantly less time eating/foraging compared to Grade 1 males ($F_{2,63} = 9.70$, $P = 0.002$); no difference existed between Grades 2 and 3 ($P = 0.160$; Fig. 3). Adult males that spent more time in proximity to adult females spent less time eating/foraging ($r_s = -0.47$, $N = 72$ observations, $P = 0.007$).

Discussion

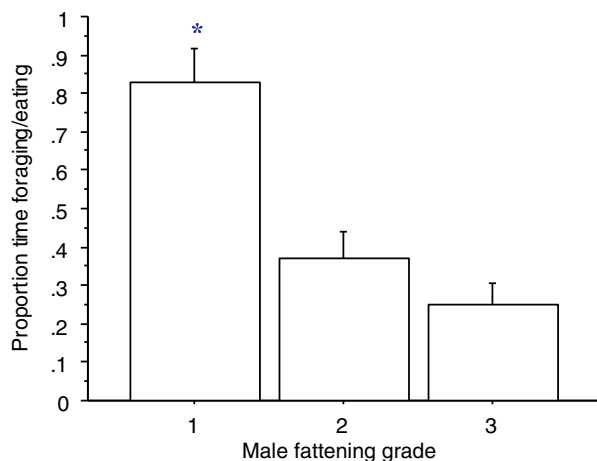
Data collected in this study show that adult male squirrel monkeys in this population are subject to various challenges and reproductive costs. First, as predicted, my results show that male–male aggression and injury risk during the mating season is high, not only within the social group, but also possibly among males from different social groups, as evidenced by pile-ups. Second, the finding that young juveniles/late infants often successfully harass adult males attempting to mate with their mothers creates an extra challenge to males (see Fig. 1). Sexual interference (any disturbance directed to a

Fig. 2 Effect of male fattening condition of *Saimiri sciureus* on (A) mean time spent in proximity to nearest neighbor (individual within 5 m) and (B) mean time spent in sociosexual social behaviors. Data are from four mating seasons (2000, 2002, 2011, 2012) in Vila Ananim, Brazil. $N=30$ focal samples for each male grade. Error bars represent standard errors.



mating pair by other individuals) is an effective behavioral tactic in reducing the mating success of rivals, e.g., *Rhinopithecus roxellana* (Qi *et al.* 2011); however, it is unclear how sexual interference would serve young juveniles. One possibility is that females continued to lactate at the start of the mating season (several juveniles were still suckling, but I could not determine whether their mothers were actually lactating),

Fig. 3 Effect of male fattening condition (Grades 1, 2, and 3) of *Saimiri sciureus* on mean time spent engaged in foraging/eating. Data are from four mating seasons (2000, 2002, 2011, 2012) in Vila Ananim, Brazil. $N=30$ focal samples for each male grade. Error bars represent standard errors.



and that successful pregnancy would result in full weaning. Regardless, juvenile harassment effectively prevented copulations in several cases, posing a cost to adult males. Third, as per my second prediction, male sexual coercion of females is nonexistent, as females are dominant and were free to refuse advances from approaching males and even attack them (one male fell to the ground when a female attacked him during a pursuit). Lastly, the seasonal breeding pattern and short mating season of squirrel monkeys means that fertile females are difficult to monopolize, particularly owing to the large number of females and high group dispersion (Stone 2007b). Females are characterized by concealed estrus and cycle every 8–10 d during the breeding period (Dukelow 1985), reducing monopolization chances by any single male in the group (Emlen and Oring 1977; Ostner *et al.* 2008; Say *et al.* 2001).

Within this context, male fattening appears to be adaptive. As expected, less robust males (Grade 1) spent less time near adult females and more time alone at the periphery of the group, and also spent less time engaged in sociosexual behaviors. This pattern suggests that these males may have low mating success and, possibly, low reproductive success. What is not yet clear is whether Grade 2 and Grade 3 males copulate more frequently, and whether they copulate during a female's fertile period. In captivity, higher ranking male *Saimiri* are often the first to show the fattening response (Coe *et al.* 1985), suggesting that these males may have the advantage of fertilizing females earlier (*cf.* strepsirrhines; Eberle *et al.* 2007). Unfortunately, such specific data on timing are not yet available from this wild population of squirrel monkeys. In addition, more data are needed to determine whether Grade 3 males have an advantage over Grade 2 males. Both grades spent equal time in proximity to adult females, which could mean that once a minimum fattenedness level is achieved there is little difference in benefits to males. Yet Grade 3 males spent more time engaged in sociosexual behaviors; one possibility to be examined is whether Grade 3 males are more tolerated by the females' offspring when approaching them.

Given that intrasexual competition occurs in *Saimiri sciureus*, fattening likely provides an advantage during competitive interactions with rival males, allowing them better access to females (Clutton-Brock 2007; Jordan *et al.* 2011). For example, mane length in lions (*Panthera leo*) is an important way to assess rivals, and therefore impacts male–male competition (West and Packer 2002). Setchell and Dixon (2001b) also suggest that the “rump fattening” seen in male mandrills is more likely to serve as a competitive signal among males than as a signal to females. Mitchell (1990) also reports that fattening in *Saimiri boliviensis* in Peru appears to aid in male–male competition, protecting males as they compete aggressively for access to females. The largest male in this population was responsible for 90% of long consortships (>6 h) observed (Mitchell 1990). In support of the intrasexual competition hypothesis, male canines are 47% longer than those of females (Stone, unpublished trapping data). However, because females are dominant in both *Saimiri* spp., they are not obliged to mate with males who win contests. For example, female choice in ring-tailed lemurs (*Lemur catta*), including preference for extra-group males, can be more important than male dominance relations in explaining male reproductive success (Pereira and Weiss 1991). In addition, male and female bonobos (*Pan paniscus*) are co-dominant, and therefore even males that win contests cannot force females to copulate, suggesting an element of female choice (Surbeck *et al.* 2012). Similarly, the ability of a male *Saimiri* to keep rivals away may not be the sole factor in monopolizing fertile females.

I did not observe direct and obvious female choice via proceptive behaviors such as pursuing males, calling to males or presenting hindquarters to males. In contrast, female Costa Rican *Saimiri oerstedii* appear to actively solicit copulations from the most fattened males in the troop, and these males appear to obtain the majority of copulations (Boinski 1987, 1992). In *Saimiri sciureus*, females perhaps choose more subtly, by permitting proximity and genital inspections by the males of their choice without threatening them. This “choice via receptivity” has been observed in chimpanzees (Stumpf and Boesch 2006), a species in which males dominate females, so the potential for such choice may be even greater in a female-dominant species such as *Saimiri sciureus*. In addition, because they do not show visible physical signs of estrus, female squirrel monkeys may control the timing and duration of matings. For example, females could mate with several males during the season, but only with their preferred one when they are ovulating, e.g., Hanuman langurs (*Semnopithecus entellus*; Heistermann *et al.* 2001). In addition, because many mount/intromission bouts occur before ejaculation, females could interrupt the mating sequence at any point (*cf.* chimpanzees; Stumpf and Boesch 2006).

More data are needed to verify that females prefer the fattest males, although we know that these males are more likely to be in proximity to females (Fig. 2). If the most robust males are also the ones that win in fights or intimidation against rivals, females may be exercising indirect female choice by allowing the winners to approach and mate with them. Females also may behave in ways that incite male fights, perhaps as a way of testing the consort male: if he is good enough to keep away other males, he is a good choice (Cox and Le Bouef 1977; Candolin 1999). Infanticide has never been reported in squirrel monkeys (Izar *et al.* 2008); because females are dominant over males and males stay at the periphery of the group (away from infants) during most of the year, infanticide is unlikely to occur. Therefore, females may not need to select mates on the basis of their potential to protect them, allowing females to focus on other possible indicators of fitness such as body condition, e.g., fattening.

More fattening could indicate desirable traits such as higher rank and aggressiveness, and these traits can be related to higher testosterone levels in fitness-enhancing contexts such as reproduction (Gould and Ziegler 2007; Setchell and Dixson 2001a; Sobolewski *et al.* 2012; Wingfield *et al.* 1990). For example, female lions prefer males with darker manes, because darker manes indicate higher circulating testosterone (West and Packer 2002). In primates, higher testosterone is associated with increased dominance in mating contexts, e.g., ring-tailed lemurs (*Lemur catta*; Bercovitch and Goy 1990; Gould and Ziegler 2007). The male fattening period in *Saimiri* correlates with a peak in testosterone (Schiml *et al.* 1996), though individual variation in testosterone levels according to fattenedness remains to be examined. Male–male dominance interactions in squirrel monkeys are still poorly understood in the wild, and need to be further elucidated to examine whether fattening is related to dominance rank. Captive work with *Saimiri* has shown that the dominant male often disrupts mounting attempts of subordinate males, although middle ranking males initiate sexual behavior more than do the other males (Mendoza *et al.* 1978b).

An alternative to the sexual selection hypothesis is that such a seasonal mobilization of lipid resources allows males to forego feeding in favor of reproduction (Bercovitch 1992). Indeed, male rhesus macaques lose *ca.* 10% of body weight during the mating season (Bercovitch 1997), and those males that have the highest copulatory success tend to be in the worst energetic condition by the end of the mating season (Higham

et al. 2011). This compensatory function of male fattening seems less likely for squirrel monkeys, because males do not lose weight as the mating season progresses, but rather gain up to 24% in water and fat (DuMond and Hutchison 1967). On the other hand, fatter males (Grades 2 and 3) do spend less time engaged in eating/foraging activities compared to Grade 1 males (Fig. 3), suggesting a potential trade-off if these fatter males are foregoing time spent in maintenance activities in favor of reproductive effort.

Several avenues for future research remain to be pursued with this population of squirrel monkeys. A recently initiated trapping program with the study group will allow additional variables to be examined, such as 1) a comparison of testicle size between fattened and less fattened males (fattening correlates with seasonal spermatogenesis; DuMond and Hutchison 1967), which could indicate sperm competition (Schmid and Kappeler 1998); and 2) absolute male weights. As pointed out by Dixson *et al.* (2005), one difficulty of studying sexual selection in primates often is the lack of quantitative measures on sexually dimorphic visual traits. Obtaining weights on all the males of the group will allow us to better quantify degree of fattening; in addition, photogrammetric methods also can be used (Caillaud *et al.* 2008; Rothman *et al.* 2008). Finally, examining individual variation in glucocorticoids and testosterone levels would also be informative to gauge physiological and stress costs to adult males that fatten more. Additional behavioral data on permanently marked adults will also allow for better and quicker identification of participants in agonistic interactions and possibly in clandestine copulations (Gibson 2010). This will allow us to obtain more detailed observations on rates of aggression given/received for Grade 1, 2, and 3 males, and on behavioral differences between Grades 2 and 3 males, which may be significant with larger sample sizes. Finally, as is true in many sexual selection studies, the relationship between behavioral mating success and genetic reproductive success is unclear (Di Fiore 2003; Kappeler and van Schaik 2004). Genetic analyses will allow us to examine whether interindividual variation in fattening is positively associated with paternity. High rank often leads to higher paternity in primates (Alberts *et al.* 2006; Jack and Fedigan 2006; Majolo *et al.* 2012; Muniz *et al.* 2010; *cf.* review by Cowlishaw and Dunbar 1991; Ohsawa *et al.* 1993). However, I suspect that seasonal breeding and female polyandry prevents a *single* dominant male from completely monopolizing paternity (Emlen and Oring 1977; Ims 1989; Ostner *et al.* 2008) and, therefore, male fattening could have a significant effect on male reproductive success.

In conclusion, the current study shows that male squirrel monkeys face several reproductive costs during the brief mating season. Consortships and pursuits of females are time and energy-consuming endeavors because females travel long distances within a short period (Stone 2007a) and consorting males must invest considerable effort in maintaining proximity to them (possibly foregoing foraging and feeding). They also must chase off other approaching males, and risk injuries from fights. Finally, they are frequently threatened and chased by the female's youngest offspring. Male fattening may be advantageous in helping to mitigate these socio-ecological costs, despite probably posing its own set of physiological costs.

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References

- Alberts, S., Buchanan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From mating opportunities to paternity success. *Animal Behaviour*, 72, 1177–1196.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Baldwin, J. D. (1968). The social behavior of adult male squirrel monkeys (*Saimiri sciureus*) in a seminatural environment. *Folia Primatologica*, 9, 281–314.
- Bercovitch, F. B. (1992). Estradiol concentrations, fat deposits, and reproductive strategies in male rhesus macaques. *Hormones and Behavior*, 26, 272–282.
- Bercovitch, F. B. (1997). Reproductive strategies of rhesus macaques. *Primates*, 38, 247–263.
- Bercovitch, F. B., & Goy, R. W. (1990). The socioendocrinology of reproductive development and reproductive success in macaques. In T. E. Ziegler (Ed.), *Socioendocrinology of primate reproduction* (pp. 59–93). New York: Wiley-Liss.
- Blair, M. E., & Melnick, D. J. (2012). Genetic evidence for dispersal by both sexes in the Central American squirrel monkey, *Saimiri oerstedii citrinellus*. *American Journal of Primatology*, 74, 37–47.
- Blanckenhorn, W. U. (2005). Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111, 977–1016.
- Boinski, S. (1987). Mating patterns in squirrel monkeys: Implications for seasonal sexual dimorphism. *Behavioral Ecology and Sociobiology*, 21, 13–21.
- Boinski, S. (1992). Monkeys with inflated sex appeal. *Natural History*, 101, 42–49.
- Boinski, S. (1999). The social organization of squirrel monkeys: Implications for ecological models of social evolution. *Evolutionary Anthropology*, 8, 101–112.
- Caillaud, D., Levrero, F., Gatti, S., Menard, N., & Raymond, M. (2008). Influence of male morphology on male mating status and behavior during interunit encounters in Western lowland gorillas. *American Journal of Physical Anthropology*, 135, 379–388.
- Candolin, U. (1999). Male-male competition facilitates female choice in sticklebacks. *Proceedings of the Royal Society of London B: Biological Sciences*, 266, 785–789.
- Clutton-Brock, T. (2007). Sexual selection in males and females. *Science*, 318, 1882–1885.
- Coe, C. L., Smith, E. R., & Levine, S. (1985). The endocrine system of the squirrel monkey. In L. A. Rosenblum & C. L. Coe (Eds.), *Handbook of squirrel monkey research* (pp. 191–218). New York: Plenum Press.
- Cowlishaw, G., & Dunbar, R. I. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, 41, 1045–1056.
- Cox, C. R., & Le Bouef, B. J. (1977). Female incitation of male competition: A mechanism in sexual selection. *The American Naturalist*, 111, 317–335.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: John Murray.
- Di Bitetti, M. S., & Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in neotropical primates. *American Journal of Primatology*, 50, 109–130.
- Di Fiore, A. (2003). Molecular genetic approaches to the study of primate behavior, social organization, and reproduction. *Yearbook of Physical Anthropology*, 46, 62–99.
- Dixson, A., Barnaby, D., & Anderson, M. (2005). Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes and human beings. *Annual Review of Sex Research*, 16, 1–19.
- Dixson, B. J., & Vasey, P. L. (2012). Beards augment perceptions of men's age, social status and aggressiveness, but not attractiveness. *Behavioral Ecology*, 23, 481–490.
- Dukelow, W. R. (1985). Reproductive cyclicity and breeding in squirrel monkeys. In L. A. Rosenblum & C. L. Coe (Eds.), *Handbook of squirrel monkey research* (pp. 169–190). New York: Plenum Press.
- DuMond, F. A., & Hutchison, T. C. (1967). Squirrel monkey reproduction: The “fatted” male phenomenon and seasonal spermatogenesis. *Science*, 58, 1067–1070.
- Eberle, M., Perret, M., & Kappeler, P. M. (2007). Sperm competition and optimal timing of matings in *Microcebus murinus*. *International Journal of Primatology*, 28, 1267–127.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection and evolution of mating systems. *Science*, 197, 215–223.

- Gibson, K. N. (2010). Male mating tactics in spider monkeys: Sneaking to compete. *American Journal of Primatology*, 72, 794–804.
- Gould, L., & Ziegler, T. E. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology*, 69, 1325–1339.
- Heistermann, M., Ziegler, T., van Schaik, C. P., Laundhardt, J., Winkler, P., & Hodges, J. K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 2445–2451.
- Higham, J. P., Heistermann, M., & Maestrieri, D. (2011). The energetics of male-male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, 81, 1001–1007.
- Ims, R. A. (1989). The potential for sexual selection in males: Effect of sex ratio and spatiotemporal distribution of receptive females. *Evolutionary Ecology*, 3, 338–352.
- Izar, P., Stone, A. I., Carnegie, S. D., & Nakai, E. (2008). Sexual selection, female choice and mating systems. In P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. Heymann, & K. Strier (Eds.), *South American primates: Testing new theories in the study of primate behavior, ecology and conservation* (pp. 157–198). New York: Springer Science+Business Media.
- Jack, K. M., & Fedigan, L. M. (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 367–386). New York: Springer Science + Business Media.
- Jordan, N. R., Mwanguhya, F., Furrer, R. D., Kyabulima, S., Ruedi, P., & Cant, M. A. (2011). Scent marking in wild banded mongooses: 2. Intrasexual overmarking and competition between males. *Animal Behaviour*, 81, 43–50.
- Kappeler, P. M., & van Schaik, C. P. (2004). In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 3–23). Cambridge, UK: Cambridge University Press.
- Majolo, B., Lehmann, J., de Bortoli, V., & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology*, 147, 652–660.
- Malo, A. F., Soldan, E. R. S., Garde, J., Soler, A., & Gomendio, M. (2005). Antlers honestly advertise sperm production and quality. *Proceedings of the Royal Society of London B: Biological Sciences*, 272, 149–157.
- Mendoza, S. P., Lowe, E. L., Davidson, J. M., & Levine, S. (1978a). Annual cyclicity in the squirrel monkey (*Saimiri sciureus*): The relationship between testosterone, fattening and sexual behavior. *Hormones and Behavior*, 20, 295–303.
- Mendoza, S. P., Lowe, E. L., Resko, J. A., & Levine, S. (1978b). Seasonal variations in gonadal hormones and social behavior in squirrel monkeys. *Physiology and Behavior*, 20, 515–522.
- Mitchell, C. L. (1990). *The ecological basis of female dominance: A behavioral study of the squirrel monkey (Saimiri sciureus) in the wild*. Ph.D. thesis, Princeton University.
- Mueller, M. N., Thompson, M. E., Kahlenberg, S. K., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, 65, 921–933.
- Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., & Gros-Louis, J. (2010). Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *American Journal of Primatology*, 72, 1118–1130.
- Nadler, R. D., & Rosenblum, L. A. (1972). Hormonal regulation of the “fatted” phenomenon in squirrel monkeys. *Anatomical Record*, 173, 181–187.
- Ohsawa, H., Inoue, M., & Takenaka, O. (1993). Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates*, 34, 533–544.
- Ostner, J., Nunn, C. L., & Schuelke, O. (2008). Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology*, 19, 1150–1158.
- Pereira, M. E., & Weiss, M. L. (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, 28, 141–152.
- Petrie, M., Halliday, T., & Sanders, C. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, 41, 323–331.
- Plavcan, J. M. (2004). Sexual selection, measures of sexual selection and sexual dimorphism in primates. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 230–252). Cambridge, UK: Cambridge University Press.
- Plavcan, J. M., & van Schaik, C. P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 87, 461–477.
- Plavcan, J. M., & van Schaik, C. P. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 103, 37–68.

- Qi, X., Yang, B., Garber, P. A., Ji, W., Watanabe, K., & Li, B. (2011). Sexual interference in the golden snub-nosed monkey (*Rhinopithecus roxellana*): A test of the sexual competition hypothesis in a polygynous species. *American Journal of Primatology*, 73, 366–377.
- Rothman, J. M., Chapman, C. A., Twinomugisha, D., Wasserman, M. D., Lambert, J. E., & Goldberg, T. (2008). Measuring physical traits of primates remotely: The use of parallel lasers. *American Journal of Primatology*, 70, 1–5.
- Sauther, M. L. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology*, 84, 463–477.
- Say, L., Pontier, D., & Natoli, E. (2001). Influence of oestrus synchronization on male reproductive success in domestic cats (*Felis catus* L.). *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 1049–1053.
- Schimid, P. A., Mendoza, S. P., Saltzman, W., Lyons, D. M., & Mason, W. A. (1996). Seasonality in squirrel monkeys (*Saimiri sciureus*): Social facilitation by females. *Physiology and Behavior*, 60, 1105–1113.
- Schimid, P. A., Mendoza, S. P., Saltzman, W., Lyons, D. M., & Mason, W. A. (1999). Annual physiological changes in individually housed squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, 47, 93–103.
- Schmid, J., & Kappeler, P. M. (1998). Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, 43, 125–132.
- Scollay, P. A. (1980). Cross-sectional morphometric data on a population of semi-free ranging squirrel monkeys (Iquitos). *American Journal of Physical Anthropology*, 53, 309–316.
- Setchell, J. M., & Dixon, A. F. (2001a). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior*, 39, 177–184.
- Setchell, J. M., & Dixon, A. F. (2001b). Circannual changes in the secondary sexual adornments of semifree-ranging male and female mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, 53, 109–121.
- Setchell, J. M., & Kappeler, P. M. (2003). Selection in relation to sex in primates. *Advances in the Study of Behavior*, 33, 87–170.
- Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution*, 32, 523–559.
- Sobolewski, M. E., Brown, J. L., & Mitani, J. C. (2012). Territoriality, tolerance and testosterone in wild chimpanzees. *Animal Behaviour*, 84, 1469–1474.
- Stone, A. (2004). *Juvenile feeding ecology and life history in a neotropical primate, the squirrel monkey* (*Saimiri sciureus*). Ph.D. thesis, University of Illinois at Urbana-Champaign.
- Stone, A. I. (2006). Foraging ontogeny is not linked to delayed maturation in squirrel monkeys. *Ethology*, 112, 105–115.
- Stone, A. I. (2007a). Responses of squirrel monkeys to seasonal changes in food availability in an Eastern Amazonian rainforest. *American Journal of Primatology*, 69, 142–157.
- Stone, A. I. (2007b). Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys. *Ethology*, 113, 782–792.
- Stumpf, R. M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Tai forest, Cote d'Ivoire. *Behavioral Ecology and Sociobiology*, 60, 749–765.
- Surbeck, M., Deschner, T., Schubert, G., Weltring, A., & Hohmann, G. (2012). Mate competition, testosterone and intersexual relationships. *Animal Behaviour*, 83, 659–669.
- West, P. M., & Packer, C. (2002). Sexual selection, temperature and the lion's mane. *Science*, 297, 1339–1343.
- Wingfield, J. C., Hegner, R. E., Duffy, A. M., & Ball, G. F. (1990). The challenge hypothesis: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136, 829–846.
- Zimble-DeLorenzo, H. S., & Stone, A. I. (2011). Integration of field and captive studies for understanding the behavioral ecology of the squirrel monkey, *Saimiri* sp. *American Journal of Primatology*, 73, 607–622.