Jealous of Mom? Interactions Between Infants and Adult Males during the Mating Season in Wild Squirrel Monkeys (Saimiri collinsi)

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JEALOUS OF MOM? INTERACTIONS BETWEEN INFANTS AND ADULT MALES DURING THE MATING SEASON IN WILD SQUIRREL MONKEYS (*SAIMIRI COLLINSI*)

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Abstract

Squirrel monkeys (*Saimiri collinsi*) are seasonal breeders that live in large social groups in which females are dominant to males. Females have one infant per year, and the nursing period lasts six to eight months. Preliminary observations in the wild indicated that during the mating period (eight weeks: July and August in our population), the infants show agonism directed at males who approach their mothers. This directed sexual interference by infants has rarely been reported for neotropical primates. Our study reports observations in a natural population of *Saimiri collinsi* with the aim of describing the social behavior of infants during the breeding season, especially with regard to adult males in the group. Infants of both sexes were observed during three mating periods (2011, 2012, 2013), to test hypotheses about the possible function of infant harassment directed at adult males. The behavior of infants (variables: activity and nearest neighbor) was sampled by the focal animal method as well as *ad libitum* observations. We recorded 99 cases of agonism and 17 cases of tolerance between nearby males and infants via the all-occurrence method. Thus, 85% of interactions between adult males and infants involved agonism. These results suggest that infant interference can present a cost to adult males during the breeding season.

Keywords: social conflict, sexual interference, nursing

Resumen

Los monos ardilla (*Saimiri collinsi*) procrean estacionalmente y viven en grandes grupos sociales en los cuales las hembras son dominantes sobre los machos. Las hembras paren una cría por año, y el período de lactancia dura entre seis y ocho meses. Observaciones preliminares en estado silvestre indicaron que durante el periodo de apareamiento (ocho semanas: Julio y Agosto en nuestra población), los infantes muestran comportamiento agonista dirigido a los machos que se acercan a sus madres. Esta interferencia sexual dirigida por los infantes ha sido raramente reportada para primates neotropicales. Nuestro estudio reporta observaciones en una población natural de *Saimiri collinsi* con el propósito de describir el comportamiento social de los infantes durante la estación de apareamiento, especialmente con relación a los machos adultos en el grupo. Infantes de ambos sexos fueron observados durante tres períodos de apareamiento (2011, 2012, 2013), para probar la hipótesis acerca de la posible función de hostilidad de los infantes dirigida a los machos adultos. El comportamiento de los infantes (variables: actividad y vecino más cercano) fue muestreado por el método de animal focal, así como mediante observaciones *ad libitum*. Registramos 99 casos de agonismo y 17 casos de tolerancia entre machos cercanos e infantes mediante el método de registro de todos los eventos. Así, 85% de las interacciones entre machos adultos e infantes involucraron agonismo. Estos resultados sugieren que la interferencia de los infantes puede presentar un costo para los machos adultos durante la estación de apareamiento.

Palabras clave: conflicto social, interferencia sexual, lactancia

Introduction

Social conflict between adult males and unrelated infants/juveniles is often reported in primates. For example, juvenile yellow baboons (*Papio cynocephalus*) are not tolerated by adult males at feeding sites (Pereira, 1988, 1989). The most extreme form of aggression of males toward infants is evidenced by infanticide, a male reproductive strategy shown by many primates (Agoramoorthy and Rudran, 1995; Borries et al., 1999; Beehner and Bergman, 2008; Rimbach et al., 2012), when males recently immigrated to a social group attack and kill unrelated unweaned infants. However, in squirrel monkeys (*Saimiri collinsi*, formerly classified as *S. sciureus*; Lavergne et al., 2010), an inverse and seldom reported type of agonism occurs between males and infants. In this species, it is the infants who show agonism toward the adult males, usually in the presence of their mothers, and without any retaliation from the males (Stone, 2014). This behavior occurs primarily during the mating season (approximately eight weeks; Stone, 2006), and appears to consist mostly of sexual interference. Specifically a female's youngest dependent offspring (here called "infant") shows agonism toward males who approach and attempt to copulate with its mother.

"Sexual interference" is considered any disruption that other individuals direct toward a copulating pair, whether through contact or no-contact (Nishida, 1997). Usually this behavior occurs among adults in a group, and consists of behaviors by a third individual that can interrupt the pair's copulation. Intra-sexual competition among males is the most common form of sexual interference seen in primates, although female competition also results in sexual interference (Qi et al., 2011). Males also may direct aggression toward ovulating females, attempting to prevent their mating with subordinate or non-resident males (Smuts and Smuts, 1993). To our knowledge, however, sexual interference by infants (in particular, targeted agonism toward adult males) has not been reported in primates, and this phenomenon merits investigation in order to understand the context in which it occurs, and its possible ecological and adaptive function.

Squirrel monkeys are polygamous neotropical primates that live in large multi-male, multi-female groups of 25-75 individuals (Zimbler-de Lorenzo and Stone, 2011). Groups show female-biased sex ratios (Stone, 2004) and are characterized by weak male-female associations, with males remaining at the periphery of the group during most of the non-breeding periods (Izar et al., 2008). In addition, adult female *S. collinsi* are dominant to adult males (Izar et al., 2008). Squirrel monkeys are highly seasonal breeders (Di Bitetti and Janson, 2000) and males show weight gain (85 to 222 g; DuMond and Hutchison, 1967) during the brief mating period (two to eight weeks; Izar et al., 2008). The weight gain results from fat deposition and water retention, which produces a "fatted" appearance in the upper torso, arms and shoulders (Mendoza et al. 1978; Boinski, 1987;

Mitchell, 1990; Stone, 2004). Male fattening in this species appears to be related to sexual selection (Stone, 2014). Gestation in *Saimiri* lasts five months (Garber and Leigh, 1997) and lactation lasts from six to eight months in *S. collinsi*, with the end of weaning coinciding with the start of the next mating season (Stone, 2006).

This study addresses the following questions: (1) what is the possible adaptive significance of infant sexual interference/agonism toward adult males (hereby called IMA) seen in *S. collinsi*? (2) in which social and ecological contexts do these events occur? Several hypotheses (not mutually exclusive) could explain the behavior of the infants. For example, the weaning conflict (Trivers, 1974) could result in nursing infants trying to prevent pregnancy in their mothers, which would reduce investment in themselves. Alternatively, due to the pattern of female dominance in this species, female infants rather than male infants may be the main aggressors toward adult males, in order to establish dominance over them (Smale et al., 1995). Finally, the possibility exists that infants preferentially direct agonism toward certain males, either lower-quality males who try to copulate with their mothers, or males who are not their fathers. In order to shed light on these hypotheses, this study investigates: whether there is an association between IMAs and nursing bouts; the effect of sex on activity budgets and nearest neighbors of infants; and whether male robustness affects the frequency of IMAs. We also examine whether the infants are successful at blocking copulation attempts by adult males; that is, whether this infant behavior represents a cost to adult males.

Methods

Study Area

This study was conducted in near the village of Ananim (municipality of Peixe-Boi), 150 km east of Belém, state of Pará, Brazil (01°11'S, 47°19'W). The 800-hectare site consists of privately owned ranches that include primary forest and adjacent secondary forests. Rainfall is seasonal, with a wet season from January to June and a dry season from July to December. Fruit availability is highest during the wet season (Stone, 2007). Mating in this population of squirrel monkeys occurs during an 8-week period from mid-July to mid-September, and births occur in January and February of each year (Stone, 2006). Therefore, the wet season corresponds to births and lactation, and the dry season corresponds to mating and gestation. We collected the behavioral data presented here during three mating seasons (2011, 2012 and 2013).

Study Animals

We collected behavioral data on one social group of squirrel monkeys, with approximately 46 individuals (*ca.* nine adult males, 15 adult females, 12 juveniles and seven infants). Although most adult females give birth every year, infant mortality accounts for a reduction in the number of infants in the group by the next mating season (Stone, 2004). We

classified individuals as adults when over five years of age (males) and three years of age (females; Mitchell, 1990; Stone, 2004). We define individuals observed nursing on their mothers, even if sporadically, as infants (between six and eight months of age during this time period). Four individuals (two adult males and two adult females) were individually recognized, either by natural marks or by beaded identification collars. During observations involving adult males, we classified each individual into a robustness category (see Stone, 2014): Grade 1 (barely noticeable fattening response; n=2 in 2013); Grade 2 (showing the fattening response in the upper arms and torso, but neck still visible; n=4 in 2013); Grade 3 (fattening response very pronounced in the arms and torso, relative to the rest of the body which remains unfattened; neck barely visible; n=3 in 2013).

Behavioral Data Collection
Observations in the three mating seasons totaled 129 hours. We followed the group for at least 10 days per month from 06:00 until approximately 14:00 hours (2011 and 2012) and between 11:00 and 15:00 hours (2013). In all mating periods, we collected all-occurrence data on infant-adult male interactions (whether agonistic or tolerant; see Table 1) and on nursing bouts, timing the duration of the latter whenever possible. We also always attempted to sex the infant and to classify the adult male into the aforementioned robustness categories. Specifically in the 2013 mating season, we also collected 64 10-min focal-animal samples (Altmann, 1974) on infants. During the focal period, we classified the infant into male, female or unknown. At each 1-min interval, we recorded the following variables: activity of the focal animal (eat, forage, rest, travel, social) and age-sex class of the nearest neighbor (hereafter NN), within 5 m (adult male; adult female; juvenile or infant; alone). Within the focal period, we also made continuous observations of any social behaviors that took place involving the focal infant (*e.g.*, nursing, threatening adult male), noting initiation and directionality of interactions. We timed the duration of any nursing bouts observed.

Although non-identification of focal infants is a potential limitation of the study, we took steps to minimize any pseudoreplication. The order of observations of infants based on sex was not random, to avoid oversampling some of the infants. For example, if the first sample of the day was a female infant (determined randomly), we often sampled a second female infant immediately after the first in order to avoid repetition of the same infant. In addition, because the group was often spread over 50-150 m, we conducted successive samples on individuals that were distantly located.

Data Analyses
We used descriptive statistics to quantify the following variables: nursing bout duration, percent of social interactions toward adult males that were agonistic, percent occurrence of different types of IMA, percent IMA according to male robustness grade. We also conducted a Chi-squared analysis to test whether adult males differed in number of IMAs received, according to their robustness level. Instantaneous observations within each infant focal sample are not independent; therefore, we treated each sample (rather than each observation) as an independent data point. The categorical activities "activity" and "NN" were converted to quantitative variables as proportion of intervals. The effect of infant sex on each activity and on NN was then analyzed with unpaired t-tests, with the p value set at $p < 0.05$. All tests were two-tailed.

Results

General context of IMAs in S. collinsi
We observed 99 cases of IMA during the three mating periods, and 17 cases of infants tolerating adult males that were nearby. We did not observe affiliative interactions between infants and adult males. This indicates that 85% of the 116 interactions between infants and adult males involved agonism. In 76% of the 116 observations, an adult female (likely the infant's mother) was within 5 m of the infant-male pair, forming a triad (infant, mother, adult male). In 44% of these 88 observations, we were able to determine that the male was, either, sexually pursuing the

Table 1. Ethogram of social behaviors of infant *Saimiri collinsi*.

Behavior	Definition
Approach	Infant comes within less than 0.5 m of another individual, with or without physical contact
Block	Infant positions itself behind mother (without intromission) usually to block copulation by adult male
Pursuit	Infant follows mother and/or adult male, attempting to maintain physical proximity
Displacement	Infant approaches another individual and takes its place
Threat	Infant vocalizes and lunges toward another individual
Chase	Infant runs after another individual for at least 2 m, usually with threatening vocalizations
Attack	Infant jumps on, bites or scratches another individual
Tolerance	Infant is neutral in the presence of another individual (possibly maintaining physical contact), with no agonism
Play	Infant jumps on, lightly bites or wrestles with another infant or juvenile

Table 2. Number of agonistic interactions between adult males and infant *Saimiri collinsi*, over three mating seasons (2011, 2012, 2013). The first column indicates interactions initiated by infants, second column indicates interactions initiated by adult males.

Behavior	Infant→ Adult male	Adult male→ Infant
Attack	3	0
Block	3	0
Threat	52	2
Chase	35	2
Displacement	2	0
Total	95	4

Figure 1. Effect of infant sex on its activity budget, during the 2013 mating period. N=56 focal samples. RE=rest; SO=social; LO=locomotion; FO=forage

Figure 2. Effect of infant sex on its NN (within 5 m), during the 2013 mating period. N=56 focal samples. AM=adult male; AF=adult female; JV=another juvenile or infant; AL=alone.

adult female, conducting genital inspections or mounting the female.

As shown in Table 2, adult males directed agonism toward infants only on four occasions. IMAs consisted of vocal threats, chases and, rarely, physical aggression in the form of biting. On nine occasions, we also observed infants moving toward and chasing males that were on a nearby branch (that is, not interacting directly with an adult female). We also observed two cases in which a resting male was approached by an infant who jumped on and bit the adult male, resulting in the adult male leaving the scene. Finally, we note three cases when the infant effectively "blocked" adult males from mounting their mothers; specifically, the infant mounted his mother, blocking access by the male.

*Occurrence of nursing within the mating period*

We observed nursing bouts during all three mating seasons. Over the three seasons, we recorded 25 nursing events, with a mean duration of 29 ± 4 seconds (N=7 timed bouts). In 12 cases, we could not identify the sex of the infant due to its nursing position. We identified the infant as male in five cases and as female in one case. In three cases, we observed nursing bouts during a time when an adult male was pursuing the infant's mother. In one of these cases, a male infant threatened the adult male and then immediately nursed. Qualitatively, we observed an increase in weaning conflicts between mother and infant after August 15 (females forcefully removing infants from the nipple, with infants vocalizing in distress).

Effect of infant sex on its activities and nearest neighbors
Infants of both sexes spent over 50% of their time foraging independently (Fig. 1). We did not observe an effect of sex on the infants' activity budget (FO: t_{54}=0.61, NS; RE: t_{54}=-0.69, NS; LO: t_{54}=0.54, NS; SO: t_{54}=0.70, NS). Infants of both sexes also spent over 50% of their time budget near other infants/juveniles (Fig. 2). There was no effect of infant sex on proportion time spent with adult males (t_{54}=-0.97, NS), adult females (t_{54}=0.43, NS), juveniles/infants (t_{54}=0.07, NS) or alone (t_{54}=-1.52, NS). In the 99 cases of IMAs, we were only able to determine the sex of
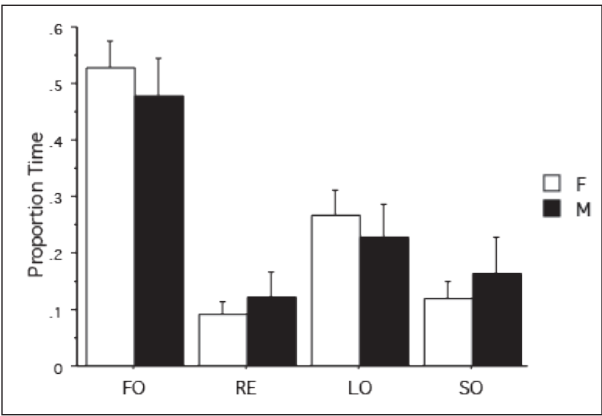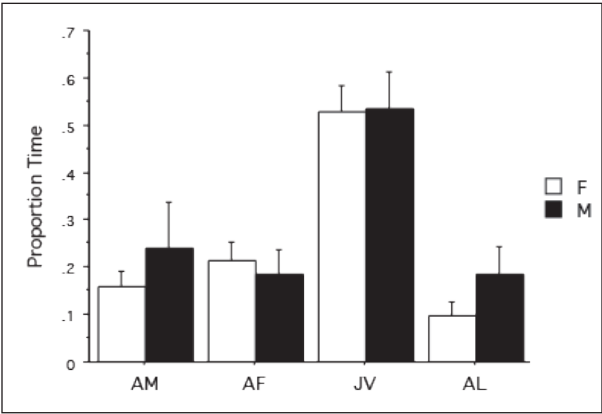
the infant in seven cases (five males and two females) because of the short duration of the IMA.

Effect of male grade on IMAs received
We were able to register male robustness level for in 18 IMAs (Table 3). The intermediate fat males received 44% of agonism cases, followed by the least fat males (39%) and the fattest males (17.6%) but this difference was not significant ($\chi2$=1.81, df=2, p=0.40). We also highlight that only Grade 2 and 3 males were tolerated by infants when in proximity to females (n=5 cases where male grade was identifiable).

Discussion

This study confirms prior qualitative observations of the occurrence of IMAs in *Saimiri collinsi* (Stone, 2014). However, this study is the first to quantify the occurrence of this behavior in the field, confirming that most of the interactions between infants and adult males during the mating season are agonistic, and that males do not retaliate against infants, often leaving the location. Most of the interactions consist of vocal threats and chases, but they may also reach

Table 3. Number of IMAs received by adult males according to their robustness levels.

Male grade	Observed values	Expected values
Grade 1 (n=2)	7	4
Grade 2 (n=4)	8	8
Grade 3 (n=3)	3	6
Total	18	18

physical aggression. We also confirm that IMAs occur predominantly within a context of sexual interference; that is, in most cases, the infant is near its mother when the adult male approaches her for copulation or genital inspection. In coatis (*Nasua nasua*), juvenile agonism toward adults is also observed commonly. Rather than reflecting social dominance, the interactions consist of tolerated juvenile aggression, particularly during feeding contexts, so that juveniles have better access to food sources during growth and development (Hirsch, 2007). The pattern that we observed in squirrel monkeys differs in that infant intolerance toward males occurs mostly within a socio-sexual context.

We observed overlap between the copulation period and the end of the nursing period. Specifically, we observed IMAs performed by infants who are not fully weaned. This observation supports the first hypothesis that the infant's interference is an attempt to prevent its mother's pregnancy. However, data from captivity and from the field indicate that lactating squirrel monkey females are still able to get pregnant (J. Ruiz, personal communication for *S. boliviensis*; L. Kauffman, personal communication for *S. sciureus*), indicating that these primates do not undergo lactational anovulation. Therefore, a more likely, non-physiological explanation for our results then is that, nursing infants could be engaging in IMAs to prevent their mothers from spending time in mating activities, which would detract from time invested in nursing bouts. Mating activities can occupy a significant portion of a female's day; consortship pairs are common, in which males pursue adult females for several hours while conducting genital inspections, branch inspections and vocalizing to her (Stone, 2014). As such, this would still be a case of classic weaning conflict (Trivers, 1974). Our study only covered the mating season (two months in each year); therefore, we cannot affirm that IMAs occur exclusively during this season. However, we do know that adult males remain at the periphery of the group at other times of the year (Stone, 2004), reducing the chances of social contact between infants/juveniles and adult males. This suggests that IMAs probably are restricted to the mating season, which also supports the weaning conflict hypothesis.

The second hypothesis we considered was that most IMAs would be initiated by female infants, in order to establish early social dominance over adult males, a pattern similar to seen in hyaenas (*Crocuta crocuta*). Infant females in this species are highly aggressive (Smale et al., 1995) because adult females are dominant to adult males (Frank, 1986). Against this hypothesis, we did not observe sex differences in the amount of time infants spend near adult males, suggesting that female infants do not have more chances to show agonism toward adult males. We were only able to determine the sex of the infant in seven IMAs, which makes it impossible at this time to further evaluate this hypothesis. However, the prevalence of IMAs in the mating season, rather than all year round (Stone, 2014), does not lend support to the dominance hypothesis.

Although we did not find that the fattest males were targeted less for IMAs, given the small number of observations in which male grade was reliably determined, this hypothesis should be re-evaluated with additional field observations. However, given that adult females themselves spend more time in proximity to fatter males (Stone, 2014), it is possible that infants also are more tolerant of more robust males. An additional hypothesis, not tested here, is that infants may be targeting strange males (males that do not share genes with them). Otherwise, it is possible that the more robust males were also the more robust in the previous breeding season, and thereby have a higher likelihood of siring the infants. This interesting hypothesis can be examined once we collect DNA samples from infants and adult males. We hope to be able to test this hypothesis with the continuation of our trapping program, initiated in 2012.

Are infants effective in blocking the adult males who approach their mothers? This question can be addressed at several levels. Our behavioral data show that, in most cases, the male submits to the infant's threats, leaving the vicinity of the infant and adult female. Thus the male loses immediate access to the female. In this way, the behavior of the infant and the male suggests that the infants are successful in disrupting mating efforts of adult males. However, we know that most females get fertilized during the mating season. In November 2013, 10 out of 11 captured females were pregnant (Stone et al., in press). From this numeric point of view, infants are not effective in ultimately blocking adult males. However, without knowing whether the infants target specific adult males (*e.g.*, subordinate males, unrelated males, less robust males) it is not possible to quantify their efficacy. For example, it is possible that the 10 females were fertilized by one or two dominant males, while the infants blocked attempts of the remaining males. Therefore, the question becomes: who are the adult males that the infants are targeting? This is an important question that merits future investigation. A final question is whether *S. collinsi* is unique in the existence of IMAs. We argue that this behavior likely occurs in other *Saimiri* species as well, but simply has not been investigated. All squirrel monkeys show highly seasonal breeding (Di Bitetti and Janson, 2000; Zimbler-DeLorenzo and Stone, 2011) and all show the "fatted male phenomenon" (Stone, 2014). Therefore,

we suggest that these two life history traits likely contribute to the occurrence of IMAs in all squirrel monkey species.

The data collected in this study indicate that: (1) most inter-actions between adult males and infants during the mating season consist of harassment in the context of sexual inter-ference and that they are mostly initiated by infants; (2) infants of both sexes avoid and harass adult males; (3) in-fants may be attempting to maintain maternal investment in the form of proximity and nursing, which is in conflict with time and energy expended in mating activities; (4) infant harassment may be an effective tactic in blocking approaches by specific, perhaps less robust adult males.

Acknowledgements

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