

RESEARCH ARTICLE

Mated Pairs of Owl Monkeys (*Aotus nancymaae*) Exhibit Sex Differences in Response to Unfamiliar Male and Female ConspecificsCHRISTY K. WOLOVICH¹, SIAN EVANS², AND STEVEN M. GREEN^{1,2*}¹Department of Biology, University of Miami, Coral Gables, Florida²The DuMond Conservancy for Primates and Tropical Forests, Inc., Miami, Florida

In socially monogamous species, mate-guarding could be a reproductive strategy that benefits both males and females, especially when males contribute to parental care. By actively guarding mates, males may reduce their chances of being cuckolded, whereas females that mate-guard may reduce the likelihood that their mates will desert them or acquire additional mates, and hence limit or reduce paternal care of offspring. Owl monkeys (*Aotus* spp.) are socially monogamous with biparental care of young and, hence, potential beneficiaries of mate-guarding. We presented mated pairs of captive owl monkeys (*A. nancymaae*) with unfamiliar male and female conspecifics, to determine if either member of the pair exhibits intraspecific aggression toward an intruder or stays close to its mate, behaviors indicative of mate-guarding. Male mates were more responsible for the maintenance of close proximity between mates than females. Male mates also exhibited elevated levels of behavior that signify arousal when presented with a male conspecific. These responses by mated male owl monkeys are consistent with patterns that may help prevent cuckoldry. *Am. J. Primatol.* 72:942–950, 2010. © 2010 Wiley-Liss, Inc.

Key words: intrasexual aggression; intruder; mate-guard; monogamy; pair-bond

INTRODUCTION

Mate-guarding is a behavioral strategy that acts to preserve access to a mate while preventing same-sex potential rivals from gaining access [Buss, 2002]; it may include such behaviors as intrasexual aggression and maintaining close proximity to one's mate [Birkhead & Moller, 1992]. In species residing in large multimale multifemale groups, there can be intense intrasexual competition among males resulting in limited mating opportunities. In many of those species, mate-guarding by males is prevalent [*Papio cynocephalus*, Alberts et al., 2006; *Papio hamadryas ursinus*, Weingrill et al., 2003; *Mandrillus sphinx*, Setchell et al., 2005; *Pan troglodytes*, Watts, 1998; Boesch et al., 2006; *Lophocebus albigena*, Arlet et al., 2008].

Social monogamy is characterized by individuals spending the majority of their time close to and engaging in affiliative interactions with a single mate (a pair-bond) [Anzenberger, 1992; Fuentes, 2002]. Mate-guarding may be especially important for males in socially monogamous species that invest in parental care because the cost of cuckoldry is great. Recent behavioral evidence in nonhuman primates suggests that pair-bonded males and females may engage in extra-pair copulations [white-handed gibbons, *Hylobates lar*, siamangs, *H. syndactylus*,

Palombit, 1994; *H. lar*, Reichard, 1995]. Genetic evidence has verified the occurrence of extra-pair paternity in socially monogamous and pair-living prosimians [fat-tailed dwarf lemur, *Cheirogaleus medius*, Fietz et al., 2000; fork-crowned lemur, *Phaner furcifer*, Schulke et al., 2004]. Whenever extra-pair copulations are a real possibility as a consequence of the opportunities presented by ranging patterns and population density, mate-guarding by the paired males is expected. The affiliative behaviors that help define a pair-bond may serve as a form of mate-guarding, by virtue of the proximity maintained between the members of the pair. Mate-guarding by males has even been suggested as a potential driving force in the evolution and maintenance of pair bonds in hylobatids [Palombit, 1999].

In pair-bonded species, scent marking may function in intrasexual competition, if it is elevated

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when same-sex conspecifics are present and if the scent marks can be distinguished individually [Heymann, 2006]. Scent marking may play a role in mate-guarding, in particular if males overmark the scent marks deposited by their mates [klipspringer, *Oreotragus oreotragus*, Roberts & Dunbar, 2000], thereby reducing the possibility that their mates' scents attract additional males [Gosling, 1990; aardwolves, *Proteles cristatus*, Sliwa & Richardson, 1998; Verreaux's sifaka, *Propithecus v. verreauxi*, Lewis, 2005]. Females may not resist these guarding attempts if it is costly for them to have additional males in their territory [van Schaik & Kappeler, 2003].

Females as well as males of socially monogamous species with paternal care also benefit by guarding their mates [pipefish, *Corythoichthys haematopterus*, Matsumoto & Yanagisawa, 2001; *Homo sapiens*, Buss, 2002]. If a female's mate pairs with another female, thereby becoming polygynous or deserting her entirely, the overall care given to her offspring is likely to be reduced. If paired females exhibit high levels of intrasexual aggression, monopolization of their mates' caregiving activities may be facilitated [Sussman & Garber, 1987]. High levels of female intrasexual aggression have been noted to occur in pair-bonded primate species [common marmosets, *Callithrix jacchus jacchus*, Evans, 1983; titi monkeys, *Callicebus moloch*, Mendoza & Mason, 1986].

Owl monkeys (*Aotus* spp.) are socially monogamous nocturnal primates with biparental care of offspring [Wright, 1984], and hence both males and females might benefit from mate-guarding. Males carry infants up to 5 months old [Rotundo et al., 2005] and transfer food to them [Wolovich et al., 2006, 2008; Wright, 1984]. Male intrasexual aggression has been reported in captivity [Hunter & Dixon, 1983] and female-female aggression has been observed in the wild [Fernandez-Duque & Rotundo, 2003]. Encounters between neighboring pairs include visual, vocal, and physical interactions. During these encounters, owl monkeys arch their backs, emit "resonant whoops," chase one another, and wrestle [Fernandez-Duque, 2007; Moynihan, 1964; Wright, 1978; ckw, personal observation]. These preliminary field reports suggest that socially monogamous owl monkeys may mate-guard, but only an experimental study that controls for territorial quality and access to other resources (e.g. food, shelter) could isolate whether these behaviors may be primarily indicative of a reproductive strategy rather than guarding a resource other than mates.

We experimentally determined whether captive male and female owl monkeys alter their behavior in the presence of introduced unfamiliar adult conspecifics by examining whether subjects increase the maintenance of close proximity to their mates, if they engage in more frequent mating behavior, and if they display arousal as an indicator of potential

intrasexual aggression toward the experimentally introduced stranger.

METHODS

Subjects and Housing

Captive owl monkeys (*A. nancymae*) are housed in outdoor enclosures in the naturally forested area of the DuMond Conservancy for Primates and Tropical Forests, Inc. (Miami, FL). The owl monkeys are housed as male-female adult pairs with their offspring that have not sexually matured. Adult pairs without offspring are maintained in 2.4 m diameter \times 2.4 m height cylindrical wire mesh enclosures. Adult pairs with offspring are housed in 3 m \times 3 m cylindrical wire mesh enclosures. Each enclosure contains a wooden nest box and a variety of perches and platforms. The enclosures are visually separated from one another by dense foliage, but the owl monkeys hear vocalizations and can potentially detect chemical cues from nearby owl monkeys.

Ten male and ten female owl monkeys were the subjects of this study. Each was a member of ten male and female mated pairs that had resided together for at least 6 months and had been observed to copulate. Two older males and an older female had been wild-caught; the other 17 were born in captivity. Eight of the ten pairs had no offspring present, whereas two of the pairs had an infant present.

Stimulus Animals and Control Stimuli

Eight unpaired male (four captive-bred; four imported from Peru, at least two of which were wild caught) and six unpaired female (four captive-bred, two imported from Peru, of which at least one was wild caught) owl monkeys (*A. nancymae*) were used as experimentally introduced stimulus animals. All were sexually mature, with males aged from 28 months to more than 19 years and females from 32 months to more than 10 years. The youngest male and female captive-bred stimulus animals had been recently removed from their natal groups in advance of being paired with a mate; no monkeys were separated from their family group solely for the purpose of this study. Stimulus animals were removed from their normal enclosure and temporarily housed overnight in a smaller wire mesh cage (1 m \times 0.5 m \times 0.5 m) with food and water. This cage was used to transport each stimulus animal and to present it to the test subjects. The same cage without any monkey inside was used as the stimulus for control trials. The cage was thoroughly cleaned with bleach and water (1:20 dilution) between trials.

Experimental Design

Five pairs of male and female subjects were presented with an unfamiliar male and an unfamiliar

female stimulus animal in two separate trials. Four other pairs of subjects were presented only with an unfamiliar male stimulus animal and one additional pair was presented only with an unfamiliar female stimulus animal. With one male exception, each stimulus animal was presented to only one pair of subjects to avoid pseudoreplication; assignment of stimulus animals to trials was random. Each pair of subjects was also presented with a control (“empty-cage” trial) separately for each trial with a stimulus animal. In an attempt to minimize the effects of a female subject’s reproductive state and potential lunar illumination effects on the behavior within each pair of subjects, these temporally matched control and stimulus trials were run on consecutive evenings while systematically altering the order of presentation of the empty cage and the stimulus animal for each pair of subjects. For the five pairs of subjects presented with both male and female stimulus animals, at least 12 weeks separated the trials.

Procedures

Each trial began in the evening just after sunset and before the subjects were given their normal feeding. The stimulus animal or empty cage was introduced to the mated pair of subjects by placing the cage on a 1.5 m high stand (1.2 m × 0.75 m) close to the subjects’ enclosure (0.5 m from the perimeter). Observations began immediately after the introduction of the stimulus animal or empty cage. Using a checklist, all instances of social behavior [see Wolovich & Evans, 2007] by the male and female subjects, separately scored, were recorded for 20 min. Every approach of a subject monkey to its mate (to within arms’ reach) and every withdrawal from its mate (increasing the distance to beyond arms’ reach) were scored. Some of the behaviors that typically indicate arousal in owl monkeys were also scored, namely arching [each occurrence of the back being raised and strongly curved; Moynihan, 1964], chirping [each bout separated by at least 5 sec from another bout of a series of moderately pitched tonal notes each with sharp ascending and descending frequencies; Herrera et al., 2009], and piloerecting [if there was any time during which hair on tail and/or body was conspicuously raised and stood out; Wright, 1978]. These behaviors are given in the wild by agitated animals toward extra group members or in the presence of kinkajous, and have been interpreted as components of threat displays [Moynihan, 1964; Wright, 1978; ckw, personal observation].

A second observer recorded the behavior of the stimulus animal, noting for that trial whether or not it ate, vocalized, or engaged in those behaviors indicative of arousal. Autogrooming (manipulation of hair or skin with its hands or mouth) and back-flipping (repeatedly leaping from a substrate to an

overhead surface and, subsequently, leaping back to the same position on the original substrate) were also recorded, as these are typical indicators of stress [Maestripieri et al., 1992; Mason, 1991].

All procedures were approved by the DuMond Conservancy’s Animal Care and Use Committee (#2004-02) and were in compliance with the American Society of Primatologists’ Principles for the Ethical Treatment of Non-Human Primates. The DuMond Conservancy meets all standards set by the USDA.

Statistical Analyses

We first examine the approaches to each other by male and female subjects within each pair, separately for the male and female stimulus presentation trials and empty-cage control trials using a Wilcoxon Matched Pairs Signed Ranks (MPSR) test. But approaches by themselves do not account for the maintenance of proximity because they can be influenced solely by overall activity levels; withdrawals must also be considered.

Hinde’s Index of Association is used as a measure of the maintenance of close proximity between mates, and was calculated using the number of approaches and withdrawals by the male and female for each pair of subjects for each trial [Hinde & Spencer-Booth, 1967]. The resulting values can range between -1 and $+1$, with more negative values indicative of males being more responsible for the maintenance of close proximity and with more positive values indicative of females being more responsible. A value of zero indicates that neither sex was more responsible for the maintenance of close proximity. The MPSR test was used to examine whether the overall pattern across all subjects of the Hinde’s Index of Association values differed between stimulus and control trials. Male and female stimulus trials were not compared with one another for the five pairs of subjects that received both treatments. We did not do so because the interval between these male and female stimulus treatments introduced uncontrolled confounding variables (female reproductive state, lunar phase, and seasonal differences) that were likely to affect the monkeys’ behavior. All other statistical tests comparing treatment with control trials were performed separately for male and female stimulus trials. The median rates of behavior indicating arousal (the sum of arches, chirps, and occurrence of piloerection) for both male and female subjects were compared between stimulus and control trials using Wilcoxon’s MPSR tests. We statistically determined that there were no order effects of the presentation of control and stimulus animals to subjects by comparing the behavioral responses of subjects that received controls first and with subjects that received controls second.

For both male and female subjects, the frequencies of only the most common social behaviors during

stimulus and control trials were compared using Wilcoxon's MPSR tests. These behaviors are anogenital sniff, lip smack, partner mark, subcaudal scent mark, touch, urinate, and urine wash [Moynihan, 1964; Wolovich & Evans, 2007]. Behaviors that, by definition, included both members of the pair were also compared (nose sniff and mate). Bonferroni corrections to adjust the Type I error rate for the number of statistical tests used in the absence of an a priori hypothesis, regarding any one of the ten variables examined, proved to be irrelevant as no result from these tests approached $P = 0.05$. To determine if there was a difference between the responses of male and female subjects to stimulus animals, the rates of behaviors during stimulus trials and control trials were compared using Wilcoxon's MPSR tests; the same Bonferroni adjustments for multiple tests are appropriate, but such corrections were not necessary to apply because no result approached statistical significance.

In order to gauge if there was a difference in proportion of trials in which male compared with female stimulus animals ate (indicating low stress) or exhibited behaviors indicating arousal, we employed Fisher's Exact Test. To determine whether attributes of the stimulus animal were associated with the maintenance of proximity, as gauged by Hinde's Index, those same two behavioral attributes as well as age of the stimulus animal were each examined using a Mann-Whitney U test and calculating the Spearman correlation coefficient, respectively. All tests were performed using Systat (version 13) with its exact probability add-on module used to calculate probabilities for the Wilcoxon MPSR tests. For all results, only the two-tailed probability is reported.

RESULTS

There were no differences detected in the general behavior of subjects compared with those without offspring present toward their mates or stimulus animals.

Maintenance of Close Proximity

At the beginning of every stimulus animal trial, male and female subjects moved to an area of their enclosure closest to the stimulus animal and oriented their faces in the direction of the unfamiliar monkey. At the beginning of the control trials, on the other hand, the subject animals only briefly (<3 sec) oriented their faces in the direction of the empty cage and they did not move toward it. When pairs of subjects were presented with a male stimulus animal, subject males did not approach their female mates more often than they did during empty-cage control trials (median = 12.0 approaches/male stimulus trial, range = 3–44; median = 10.0 approaches/control trial, range = 3–27; $W = 8.5$, $N = 9$, $P = 0.875$)

nor more often than subject females approached their male mates (median = 8.0 approaches/male stimulus trial, range = 1–13; $W = 15.0$, $N = 9$, $P = 0.438$). Taking account of mates withdrawing from each other, however, male subjects were more responsible for the maintenance of proximity between mates during male stimulus trials (median Hinde's Index of Association = -0.241) than during control trials (median Hinde's Index of Association = 0.00) ($W = 42.0$, $N = 9$, $P = 0.020$) (Fig. 1).

When pairs of subjects were presented with a female stimulus animal, subject females approached their male mates about as often as they did during empty-cage control trials (median = 6.0 approaches/female stimulus trial, range = 1–14; median = 7.0 approaches/control trial, range = 0–10; $W = 10.5$, $N = 6$, $P = 0.500$) and also not different from subject males approaching their female mates (median = 8.0 approaches/female stimulus trial, range = 0–19; $W = 6.5$, $N = 6$, $P = 0.875$). When also taking account of withdrawals from each other, there is no statistically significant difference in the maintenance of proximity between mates, when pairs of subjects were presented with a female stimulus animal (median Hinde's Index of Association = -0.241) compared with presentation of an empty cage during control trials (median Hinde's Index of Association = -0.264) ($W = 5.0$, $N = 6$, $P = 0.625$) (Fig. 2).

There were no statistically significant differences in Hinde's Index when comparing its values between the sets of trials in which the stimulus animals (a) were known to be captive born or not, (b)

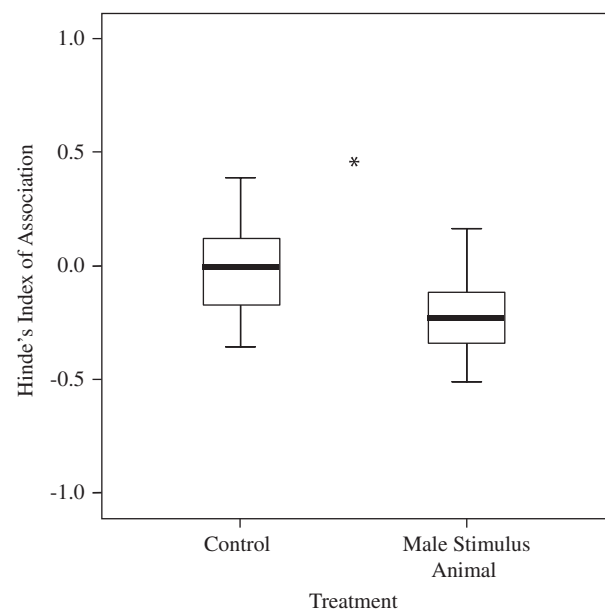


Fig. 1. The effect of a male stimulus animal on the maintenance of close proximity between a mated pair of male and female subjects ($N = 9$ pairs). Horizontal lines within box plots represent median values and box edges represent interquartile ranges. Whiskers are 1.5 times the interquartile range. * = indicates statistical significance ($P < \alpha = 0.05$).

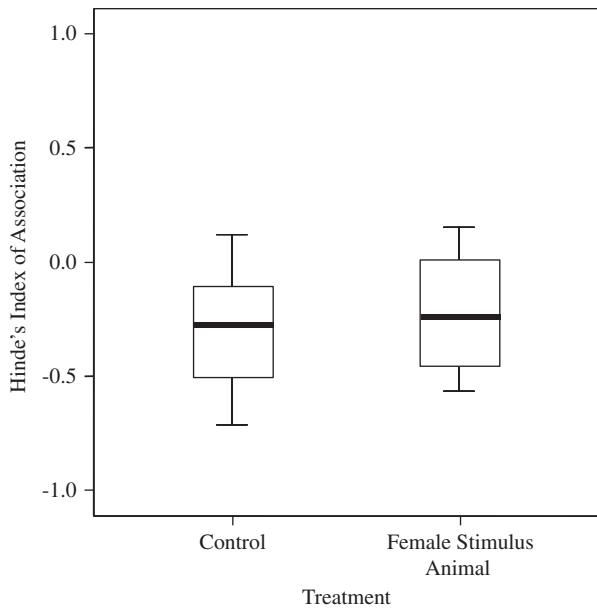


Fig. 2. The effect of a female stimulus animal on the maintenance of close proximity between a mated pair of male and female subjects ($N = 6$ pairs). Horizontal lines within box plots represent median values and box edges represent interquartile ranges. Whiskers are 1.5 times the interquartile range. The difference shown is not significant ($P > \alpha = 0.05$).

ate or did not, and (c) exhibited behaviors indicative of arousal or not. Each such comparison of subject responses (Hinde's Index) was performed for male and female stimulus animals separately and with both sexes combined. There were also no statistically significant correlations of age of stimulus animal with Hinde's Index, again examined for male and female stimulus animals separately and combined.

Mating Behavior

Two pairs (both without offspring) mated in the presence of a male stimulus animal but not during the control trial. There were no obvious similarities in the attributes or the behavior of the male stimulus animals for these two trials. One pair (also without offspring) mated during a female stimulus animal trial, but that same pair also mated during the control trial. No other social behavior between mates (affiliative, agonistic, or subcaudal scent marking) was affected by the presence of either a male or female stimulus animal (Tables I and II).

Arousal

Male subjects exhibited behavior indicating arousal (arching, chirping, or piloerecting) more frequently in the presence of a male stimulus animal (median = 18.0 per hour, range = 3–33) than an empty cage (median = 0 per hour, range = 0–24) ($W = 45.0, N = 9, P = 0.004$), but they did not engage in behavior indicating an aroused state more frequently in the presence of a female stimulus

TABLE I. The Behavior of Male Subjects ($N = 9$) and Female Subjects ($N = 9$) Presented With Male Stimulus Animals and Matched Empty-Cage Controls

Behavior	Control	Male stimulus	<i>P</i>
<i>Median number per hour (range)</i>			
Nose sniff	3.0	3.0	0.334
Mate	None	0 (0–3)	0.157
<i>Female subject</i>			
Ano-genital sniff	0 (0–3)	None	^
Lipsmack	0 (0–6)	0 (0–9)	1.0
Subcaudal scent mark	3.0	3.0	0.750
Touch	0 (0–6)	0 (0–6)	0.589
Urinate	3.0	3.0	0.915
Urine wash	0 (0–6)	None	^
<i>Male subject</i>			
Ano-genital sniff	3.0	3.0	0.194
Lipsmack	None	None	^
Partner mark	0 (0–6)	0 (0–39)	1.0
Subcaudal scent mark	3.0	9.0	0.153
Touch	0 (0–18)	0 (0–15)	0.916
Urinate	0 (0–18)	3.0	1.0
Urine drink	0 (0–3)	0 (0–3)	0.317
Urine wash	0 (0–3)	0 (0–6)	0.414

^ = indicates that because comparisons were not made owing to the lack of the behavior in one or both treatments; *P* is not listed. Values represent median rate (reported as instances per hour). When medians = zero, ranges are listed in parentheses. exact probabilities calculated by Wilcoxon's matched pairs signed ranks tests are given.

TABLE II. The Behaviors of Male Subjects ($N = 6$) and Female Subjects ($N = 6$) Presented With Female Stimulus Animals and Matched Empty-Cage Controls

Behavior	Control	Female stimulus	<i>P</i>
<i>Median number per hour (range)</i>			
Nose sniff	0 (0–6)	3.0	0.096
Mate	0 (0–3)	0 (0–3)	1.0
<i>Female subject</i>			
Ano-genital sniff	None	0 (0–3)	0.317
Lipsmack	0 (0–3)	0 (0–6)	0.276
Subcaudal scent mark	0 (0–3)	0 (0–12)	0.705
Touch	0 (0–6)	0 (0–12)	1.0
Urinate	0 (0–9)	0 (0–12)	0.593
Urine wash	0 (0–15)	0 (0–18)	1.0
<i>Male subject</i>			
Ano-genital sniff	6.0	3.0	0.157
Lipsmack	0 (0–3)	0 (0–3)	1.0
Partner mark	0 (0–3)	None	^
Subcaudal scent mark	4.5	4.5	0.786
Touch	6.0	7.5	0.336
Urinate	3.0	3.0	0.496
Urine drink	0 (0–3)	0 (0–3)	1.0
Urine wash	0 (0–3)	None	^

Values represent median rates (reported as instances per hour). When medians = zero, ranges are listed in parentheses. exact probabilities calculated by Wilcoxon's matched pairs signed ranks tests are given.

animal (median = 7.5 per hour, range = 0–15) than in the presence of an empty cage (median = 9.0 per hour, range = 3–24) ($W = 6.5, N = 6, P = 0.531$).

Female subjects did not differ in their rate of behavior indicating arousal when presented with male stimulus animals (median = 12.0 per hour, range = 0–60) compared with empty cage presentation (median = 18.0 per hour, range = 0–30) ($W = 15.0$, $N = 9$, $P = 0.937$), or when presented with a female stimulus animal (median = 27.0 per hour, range = 3–75) compared with empty cage presentation (median = 13.5 per hour, range = 3–72) ($W = 16.0$, $N = 6$, $P = 0.313$).

Because differences in the behavior of male and female subjects could potentially be consequences of a difference in the behavior of male and female stimulus animals, the behavioral patterns of the stimulus animals were also examined.

Behavior of Stimulus Animals

No stimulus animal exhibited any sign typical of stress during the experiments. No stimulus animal back-flipped or autogroomed during trials. Eating by a stimulus animal during a trial was more likely to occur when it was a female than a male (six of six trials with females, four of nine with males; Fisher's Exact Test $P = 0.044$). The number of trials in which a stimulus animal exhibited behaviors indicative of arousal is not associated with its sex (one of six trials with females, five of nine with males; Fisher's Exact Test $P = 0.287$).

DISCUSSION

Male owl monkeys behaved differently in the presence of male conspecific stimulus animals in contrast with empty-cage control trials and also in contrast to how the male subjects behaved in the presence of female stimulus animals compared with their empty-cage control trials. No such differences occurred with the female subjects. Behaviors by male subjects indicative of arousal, such as chirping, arching, and piloerecting [Moynihan, 1964; Wright, 1978; ckw, personal observation], were elevated when male stimulus animals were present. In addition, male subjects also became more responsible for the maintenance of close proximity between mates. This type of behavior is consistently described as a form of mate-guarding in birds as well as in other mammals [Birkhead & Moller, 1992; Hall & Magrath, 2000] and it, therefore, suggests that male owl monkeys actively guard females. The possibility that male owl monkeys may use mating itself as a form of mate-guarding cannot be ruled out at this time, because two of the nine pairs mated only in the presence of male stimulus animals. This behavior could play a role in sperm competition if the timing of insemination is important in ensuring successful fertilization [Birkhead, 1998]. Sperm competition is common in socially monogamous birds [Birkhead, 1998] and has also been suggested to occur in pair-living *P. fuscifer* [Schulke et al., 2004]

and cooperatively rearing *C. penicillata* [Decanini & Macedo, 2008].

There were no other significant changes in the overall patterns of behavior of the subjects, but some individual monkeys exhibited quite dramatic responses to the presence of male stimulus animals. One particular male subject elevated his rate of subcaudal scent marking and partner marking substantially and a female subject resonant whooped. When owl monkey pairs encounter each other in the wild, they frequently mark branches and their mates using their subcaudal glands (ckw, personal observation), and they may also emit resonant whoops [Wright, 1978, 1985; ckw, personal observation].

Pairs of owl monkeys had a less pronounced response to female conspecifics than to male conspecifics. Females did not become more responsible for the maintenance of close proximity to their mates in the presence of other females. It seems unlikely that females are soliciting copulations as a form of mate-guarding, as suggested in birds [Eens & Pinxten, 1995; Petrie, 1992], because none of the pairs mated only in the presence of female stimulus animals. It remains possible that female owl monkeys guard their mates, however, if females adjust their levels of guarding in correspondence with their reproductive state. Females would be expected to guard males more often when they are pregnant or lactating and when their female rivals are ovulating than at other times. Additional studies with females at known stages of their reproductive cycles would be necessary to test this prediction adequately.

Mate-guarding is predicted to offer benefits to males when females are widely dispersed. Rather than expending time and energy defending a large group of females from competitors, males may choose to remain with a single female and give up opportunities to gain additional mates. If a male cannot detect when females are fertile (e.g. a species in which females do not exhibit sexual swellings) and/or other females are not easily accessible, he may benefit by remaining with a single female and ensuring that she bears his offspring. Otherwise, a male might risk not only failing to find another fertile female, but also his original mate being fertilized by another male while he is away. Therefore, the cost of cuckoldry is high for socially monogamous males. Mate-guarding by male owl monkeys may reduce their risk of cuckoldry, given that female owl monkeys are widely dispersed [Aquino & Encarnacion, 1986; Fernandez-Duque et al., 2008; Wright, 1985], rendering any olfactory cues about changes in their reproductive condition not immediately accessible to their mates if they are not nearby and females display no visible signs of ovulation [Dixson, 1983]. Also, given that visibility is one of the main factors that determines the monopolizability of females [Schulke, 2002] and that owl monkeys are nocturnal, it is reasonable to suggest

that male owl monkeys would be more prone to maintain close proximity to their mates than diurnal species.

Earlier studies of pair-bonded Neotropical primates reveal various levels of intrasexual aggression by pair-bonded individuals to “intruders.” Both male and female common marmosets (*C. jacchus*) display and initiate attacks when they are in visual contact with unfamiliar conspecifics [Evans, 1983]. In cotton-top tamarins (*Saguinus oedipus*), intrasexual aggression is higher for males than for females when stimulus animals are introduced to resident pairs [French & Snowdon, 1981]. Captive titi monkeys (*Callicebus*) seem to rely less on intrasexual aggression and more on intersexual attraction, and pairs respond to stimulus animals with intrasexual displays and males exhibit a greater degree of sexual interest in potential mates than do females [*C. moloch*, Anzenberger, 1988; Mendoza & Mason, 1986]. In the wild, masked titi monkeys (*C. personatus personatus*) rarely engage in intergroup encounters and those that do occur are reported to be exclusively vocal [Price & Piedade, 2001].

The relatively subtle behavioral responses given by male and female owl monkeys in this study is nonetheless surprising, given that high levels of intrasexual aggression have been reported for *Aotus* [Fernandez-Duque, 2004; Hunter & Dixson, 1983; Wright, 1985]. By placing the stimulus animals in cages just outside the subjects’ enclosures, the owl monkeys may not have perceived the stimulus animals as being territorial intruders or as competitors for mating opportunities. But introducing stimulus animals directly into the subjects’ enclosures was deemed too likely to induce an injurious fight. Another factor that may have muted aggressive responses is that olfactory or acoustic cues from stimulus animals may have been familiar to the subjects, even though the animals were unfamiliar by sight, because some of them resided in the same colony before the experiments. Despite the fact that subjects may not have perceived the stimulus animals as threats or that some of the stimulus animals may have been familiar, male subjects nevertheless actively guarded females. This finding indicates that the experimental presentation of an intruder did elicit behavioral responses potentially important for preventing cuckoldry in monogamous owl monkeys.

Intergroup encounters in wild owl monkeys often consist of resonant whooping and arching [Wright, 1978, 1985; ckw, personal observation] that sometimes escalate into chasing and wrestling. Not all intergroup interactions are agonistic. Two neighboring groups of *A. azarai* in the same tree were observed without members of either group vocalizing or behaving aggressively toward the other (ckw, personal observation). Such variability in intergroup

tolerance also occurs in wild white-handed gibbons, another socially monogamous primate [Reichard & Sommer, 1997]. The costs associated with agonistic encounters (e.g., physical injury, conspicuousness to predators) may make it worthwhile for individuals to risk such costs only when substantial benefits can be gained. These benefits may vary among individuals (depending on territory quality), and for any given individual they may fluctuate in time (e.g., female reproductive status and seasonality of fruit availability). Limited food resources, fertile females, and high-quality territories would be most valuable and worth taking such risks for gaining or maintaining access. When females are fertile, mate-guarding behavior in wild owl monkeys is likely to be even more pronounced than male subjects responding to male intruders by maintaining proximity to females as we found in this study that was not restricted to periods of female fertility.

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