

RESEARCH ARTICLE

Mating Promiscuity and Reproductive Tactics in Female Black and Gold Howler Monkeys (*Alouatta caraya*) Inhabiting an Island on the Parana River, ArgentinaMARTIN M. KOWALEWSKI^{1,2*} AND PAUL A. GARBER²¹Estación Biológica de Usos Múltiples de Corrientes (EBCo), Museo Argentino de Ciencias Naturales-CONICET, Argentina²Department of Anthropology, University of Illinois, Urbana-Champaign, Illinois

In several primate species, females mate promiscuously and several adult males peacefully co-reside in the same social group. We investigated female mating behavior in two neighboring multimale–multifemale groups of *Alouatta caraya* in northern Argentina (27°20'S–58°40'W). All adult individuals in each group were marked with identification anklets and ear tags, and followed for five consecutive full days per month during 20 consecutive months. We recorded 219 copulations for eight resident females in these two groups. Thirty-two percent of matings involved extra-group copulations and 68% were with resident males. During periods when females were likely to conceive and during periods when females were nonfertile (pregnancy and lactation), there were no significant differences in the average number of resident and nonresident males with which they copulated (G -test: $G_{adj} = 0.1$, $df = 3$, $P > 0.05$). In both of our study groups, adult males were tolerant of the mating activities between resident males and resident females, but acted aggressively and collectively (howling, border vigilance, and fighting) when extragroup males attempted to enter the group and mate with resident females. Given the frequency of extragroup matings, we examined the distance females traveled to engage in these copulations, time engaged in pre- and postcopulatory behavior, and the risk of injury during extragroup copulations. These costs were found to be relatively small. We suggest that female promiscuity is the prime driver or constraint on male reproductive opportunities in this species. Female promiscuity in *A. caraya* appears to represent a mixed mating strategy that may serve to increase opportunities for genetic diversity between a female's successive offspring as well as minimize the risk of infanticide by spreading paternity estimates across a larger number of adult males. *Am. J. Primatol.* 72:734–748, 2010. © 2010 Wiley-Liss, Inc.

Key words: female promiscuity; intersexual conflict; *Alouatta*; Argentina; mating strategies

INTRODUCTION

Sexual selection theory predicts that given differences in the costs of reproduction, male and female primates are expected to develop a set of alternative behavioral tactics and strategies for obtaining access to mates and increasing individual reproductive success [Brockman, 2001; Clarke et al., 2009; Hrdy, 1977; Manson, 2007; Smuts & Smuts, 1993; Trivers, 1972]. Under conditions in which male and female reproductive strategies conflict, for example, when there are advantages to females of mating with multiple males and advantages to individual males of restricting female mating behavior, intersexual conflict can result in dominant males attempting to control female reproductive options through coercion, aggression, or infanticidal behavior [Boyko & Marshall, 2009; Clarke et al., 2009; Henzi & Barrett, 2003; Kitchen et al., 2009; Pradhan & van Schaik, 2008]. Several recent models of primate sociality argue that intersexual conflict is a primary driver of male–female mating behavior and social relationships, and that in populations in

which the threat of infanticide by adult males is severe and correlated with paternity estimates, the benefits to females of promiscuous matings are largely dependent on whether changes in male dominance relationships are the result of new males entering the group from the outside or a powershift among males currently residing in the group [Clarke et al., 2009; Henzi & Barrett, 2003; Pradhan & van Schaik, 2008]. Pradhan and van Schaik [2008: 255] predict that when changes in male leadership occur

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*Correspondence to: Martin M. Kowalewski, Estación Biológica de Corrientes (Museo Argentino de Ciencias Naturales), División Mastozoología, Av. Angel Gallardo 470, 1405 Ciudad A. de Buenos Aires, Argentina. E-mail: mkowalew@illinois.edu

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from within the group, a female is expected to minimize risk to her young infant by allocating “enough paternity to the dominant male so that he protects the infant, but also sufficient paternity to subordinate males to prevent them from attacking the infant when their dominance prospects improve...”. Alternatively, when the breeding tenure of the dominant male is relatively long (exceeds the period from conception through infant weaning) and male takeovers occur from outside the group, a receptive female is expected to exhibit mate fidelity by restricting copulations to fertile periods, and concentrating paternity in the dominant male to insure that he protects her infant during its vulnerable period [Clarke et al., 2009; Pradhan & van Schaik, 2008]. Finally, under conditions in which the breeding male is frequently challenged by solitary males or coalitions of extragroup males, females may be expected to mate with both resident and nonresident males as a strategy to avoid injury or infanticide [van Schaik, 2000; van Schaik et al., 2004]. Thus, depending on the proximate conditions of the social environment and constraints imposed by male coercion, female primates may be expected to adopt a mixed mating strategy in which they mate promiscuously to confuse paternity or promote sperm competition or mate selectively and restrict copulations to a single or small set of preferred males.

Several other factors may also constrain female mating activities. It has been suggested that copulating is a potentially costly activity in terms of: (i) a reduction in future reproductive success if time and energy spent pregnant or lactating does not result in offspring that survive to reproductive age [Clutton-Brock et al., 1989; Roulin, 2002], (ii) risk of contracting a sexually transmitted disease [Nunn, 2003], (iii) increased susceptibility to predation, and (iv) the possibility of injury from males or females associated with reproductive competition [Lessells, 2005]. However, field observations indicate that in several species of primates, females copulate with multiple males including both resident and extragroup males, as well as engage in nonprocreative mating [Clarke et al., 2009; Garber, 1997; Guo et al., 2009; Jones, 1980; Reichard, 1995; Robbins, 1999; Strier, 1997; Stumpf & Boesch, 2006].

Although the potential costs of promiscuity may be high, there exists a growing body of data that in addition to paternity confusion associated with decreased infanticide risk [van Schaik, 2000], there are significant benefits linked to female promiscuity including: (1) insuring high-quality genes for their offspring by promoting direct male–male competition and/or sperm competition [Jennions & Petrie, 1997; Zeh & Zeh, 2001]; (2) insuring fertilization [Small, 1993]; (3) mating with novel males and thereby increasing the likelihood that successive offspring are sired by different males (increase offspring genetic variability) [Pusey & Wolfe, 1996]; and (4)

reinforcing affiliative social bonds between mating partners [Lemasson et al., 2008; Smuts, 1985]. Given a range of mating options, female primates may be expected to have multiple and nonexclusive reasons for mating both promiscuously and selectively.

In this study we present data collected over a 20-month period on female mating behavior in two multimale–multifemale groups of black and gold howler monkeys (*Alouatta caraya*) inhabiting Isla Brasilera in northern Argentina. Based on the reports from several species, there is evidence that howler females may mate with multiple adult males [*Alouatta palliata*, Wang & Milton, 2003; *A. seniculus*, Agoramorthy & Hsu, 2000; *A. pigra*, Van Belle et al., 2009; *A. guariba*, Fialho & Setz, 2007], females mate during all phases of their reproductive cycle [van Belle et al., 2009, *A. pigra*], increased risks of infanticide may occur in groups containing three or more adult females [Crockett & Janson, 2000, *A. seniculus*, but not in *A. palliata*, Bezanson et al., 2008], and male takeovers can occur from outside the group as well as from shifts in male dominance within the group [Kowalewski, 2007, *A. caraya*]. Our goals are to document and describe patterns of within-group and between-group mating in black and gold howler monkeys and to test a series of predictions concerning the potential costs and benefits to females of selective and promiscuous matings.

First, if females use within-group promiscuous mating to promote social relationships with male partners and to distribute paternity estimates among multiple resident males (females benefit by promoting collective male mate and group defense and thereby increasing the length of male tenure in the group), then we expect females to mate relatively equally with all or most resident males during both fertile and nonfertile periods, and rarely to engage in extragroup mating. Second, if a female’s mating choices are aimed at maximizing her chances of conceiving offspring with the group’s dominant resident male (females benefit by increased access to resources by developing a bond or friendship with the dominant male and protection for her infant), then females are expected to mate principally or exclusively with that male during her fertile period and either avoid mating with subordinate resident males and nonresident males, or only mating with these other males during nonconceptive periods. A corollary to this is if females’ preferentially solicit sexual partners that exhibit traits associated with male dominance (increased body mass, priority access to resources, frequent howling), then females are expected to mate principally with the central male of her resident group as well as with the central male of neighboring groups, especially during fertile periods (females benefit by insuring high-quality genes for their offspring). Third, if females’ mating choices are affected by expectations that a shift in male dominance from within the group will likely

result in the replacement of the central male and possible infanticide, females are expected to increase their relative frequency of mating with the second highest ranking male or other resident males, reduce their frequency of mating with the central male, and rarely mate with extragroup males during both fertile and nonfertile periods. Fourth, if females' mating choices are affected by expectations that a successful male takeover from outside the group will increase her risk of infanticide, then females are expected to increase their frequency of mating with extragroup males (and decrease their frequency of mating with resident males) during both fertile and nonfertile periods. Fifth, if females use promiscuous matings to increase the likelihood that successive offspring are sired by different males and to indirectly select among males via sperm competition, then they are expected to mate with multiple resident males and multiple extragroup males, principally during fertile periods. In all cases, mating frequency and mating patterns are constrained by the costs of mating, which include time or duration of copulatory events, distance traveled to encounter a sexual partner, and risk of attack by adult males or adult females during mating. We recognize that our predictions are not mutually exclusive. However, we offer them as a framework from which to begin to evaluate mating behavior in female black and gold howlers, as well as to highlight the possibility that within a given primate species, patterns of selective mating and patterns of promiscuous mating may represent a mixed mating strategy used by females in response to proximate changes in the size, composition, and social hierarchy of their resident group and changes in their interactions with members of neighboring groups.

METHODS

Study Site

The field site is located on Isla Brasilera near the confluence of the Paraná and Paraguay rivers in northern Argentina (27°20'S–58°40'W) (Fig. 1). The island covers an area of 292 ha without permanent human settlements, and is characterized by a continuously flooded forest and temporary lagoons. At least 35 groups of black and gold howler monkeys (*Alouatta caraya*) naturally inhabit the island. The climate is subtropical with an average annual temperature of 21.6°C and an average annual rainfall of 1,200 mm. A more complete description of the site is provided elsewhere [Kowalewski, 2007; Kowalewski & Zunino, 2004].

Study Subjects and Study Groups

Alouatta caraya is a sexually dichromatic howler species that occupies the southernmost distribution of all neotropical primates. Black and gold howlers

live in social groups composed of an average of 1.7 adult males (range 1–6), 2.7 adult females (range 1–6), 1.3 juveniles (range 1–2), and 1.9 infants (range 1–3) [Kowalewski, 2007]. We focused our study on two neighboring howler social groups. Group X contained 9 members including 3–4 adult males and 3–4 adult females (group size changed during the study). Group G contained 11–12 individuals including 4 adult males and 4 adult females. All adults in our study groups were marked with anklets and ear tags to insure accurate identification. We recorded the social interactions (including grooming, sexual solicitations, and copulations, see definitions below) between individuals in our two study groups, as well as their interactions with individuals in three neighboring groups (Group E, Group M, and Group LR) and one solitary male who had emigrated from Group G in 2002 [Oklander, 2007] (Fig. 1). Seventy-seven percent of the 5.9 ha home range of Group X overlapped with neighboring groups (Group E, Group M, and Group G) and 66% of the 6 ha home range of Group G overlapped with neighboring groups (Group X, Group M, and Group LR). The number of adult males in these neighboring groups ranged from 1 to 5, and the number of adult females in neighboring groups ranged from 2 to 6. The population density of howlers on Isla Brasilera is 348 ind/km². This value is considerably higher than the density (104 ind/km²) reported for populations living in nearby anthropogenically altered mainland forests [Kowalewski & Zunino, 2004; Zunino et al., 2007].

Behavioral Data

Behavioral and ecological data were collected from March 2003 through November 2004 (20 months) using a scan sampling technique [Altmann, 1974] in which we recorded the activities and interactions of all adult individuals in our two howler study groups. Each study group was followed from sunrise to dusk during five consecutive days per month (total of 2,390 hr of quantitative behavioral data with approximately 1,195 hr collected per group). During all observation periods, three trained researchers followed and tracked all individuals in the target study group. All field researchers trained together for a period of 10–15 days before data collection in order to maximize accuracy and inter-observer reliability.

Scan sampling data were collected by dividing each hour of the day into six 10 min periods. During the first 2 min of each 10-min period we systematically recorded the behavior, location, diet, activity, and distance to its nearest neighbor of each group member. Thus, we obtained six data points per group member per hour or a total of 35,160 individual activity records for Group X and 39,555 individual activity records for Group G (December 2003 to

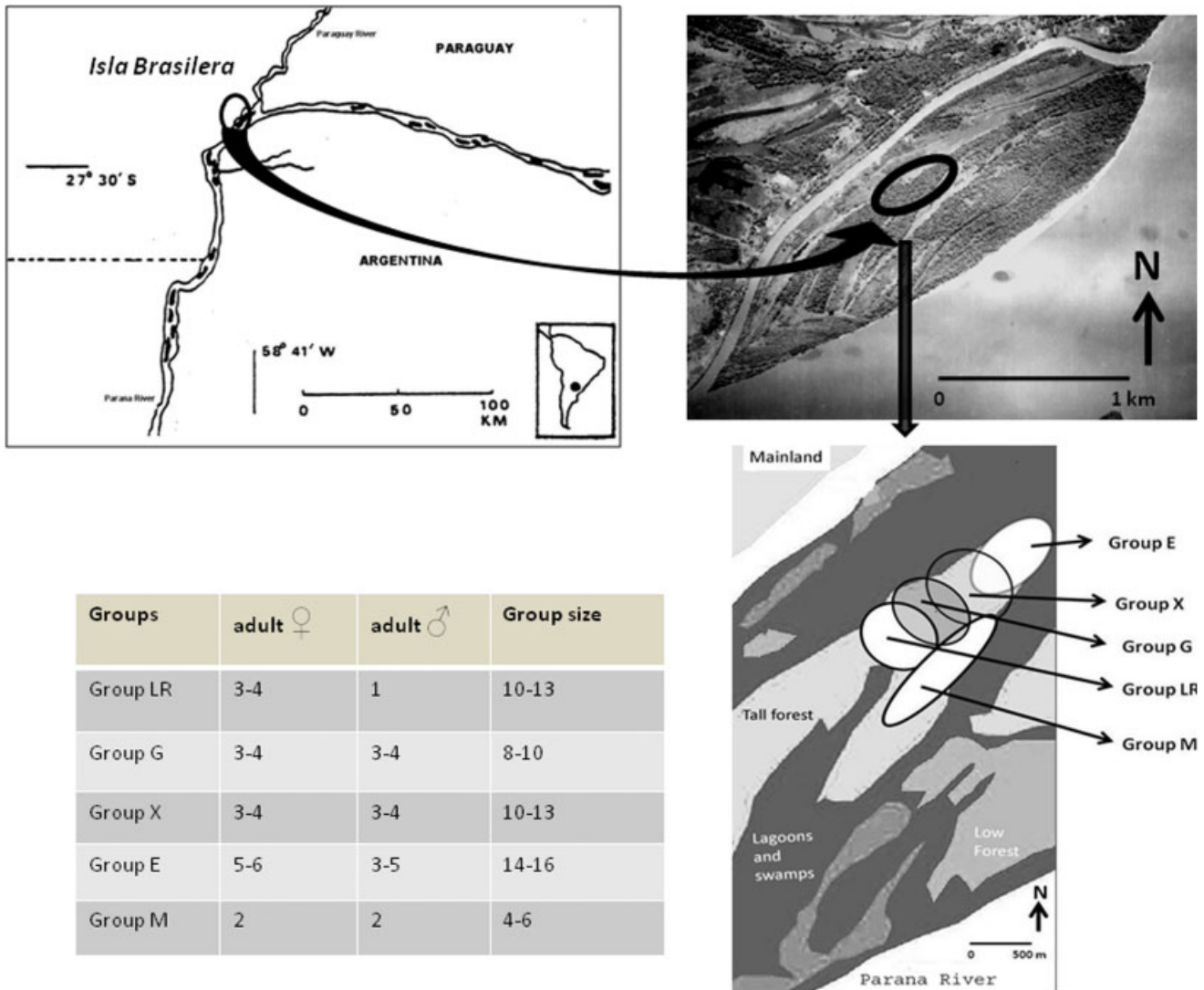


Fig. 1. Map of the study site in northern Argentina and the area on Isla Brasilera occupied by our study groups (X and G) and three neighboring groups (LR, M, E). Home range sizes of howler groups varied from 4 to 6 ha. Group size and composition are indicated in the table.

November 2004). Our goal was to obtain information on all group members throughout the day, and track the coordinated activities and social interactions of the entire group [Altmann, 1974; Martin & Bateson, 1986]. We were able to accomplish this because the structure of the forest, mainly low and relatively open, offered excellent visibility to observe our habituated study groups. In addition, given that the black and gold howlers rested 59% of the day and were characterized by a daily path length of only 684 ± 225 m, the behavior of all group members could be recorded reliably during each scan. Finally, in waiting 8 min between sample intervals (2 min scan plus 8 min wait = 10 min), we attempted to increase the likelihood that activities recorded in successive scans were independent. On those occasions when an adult left the vicinity of the group, one observer was assigned to follow that individual and record its

behavior until the individual returned. If that individual was observed to engage in sexual behavior or bouts of grooming, these data were recorded *ad libitum* and the event was timed to the nearest second. During 7 additional days per group per month, we conducted group counts and monitored changes in group composition (births, deaths or emigrations, and immigrations). Using this set of data-collecting techniques, we are confident that we obtained an accurate and representative sample of social interactions between individuals in each study group and between residents and individuals from neighboring groups.

Mating Behavior

The identity and activity of all individuals involved in precopulatory, copulatory, and postcopulatory

sociosexual behavior (solicitation, copulation, grooming) were recorded from May 2003 to November 2004 (20 months of observations). We considered sexual solicitation or female mate choice to have occurred when a female actively pursued a particular male by grooming, touching, and following him (to within a distance of 2 m), and by displaying a characteristic proceptive posture in which the female faced away from the male exposing her thighs, and then turned her head towards the male. A copulation was scored when we observed a mounting, intromission, and a thrusting sequence [Jones, 1985; Strier, 1997]. Serial copulations were scored as a single copulatory bout if they occurred in rapid sequence or during the same resting period (we defined a resting period as a group-based activity during which all or virtually all adult group members were inactive and remained quiet for at a period of at least 30 min). Typically, there were three resting periods during the day. Female sexual receptivity was determined by their sexual activity. A female was considered sexually active on a given day if she was observed copulating. Data from other studies indicate that black and gold howler females conceive during a 3–4 day ovulatory period [Di Fiore & Campbell, 2007]. At present it remains unclear whether male howlers are able to use visual or olfactory cues to distinguish ovulatory stages in females. From the perspective of the observer, female *A. caraya* do not exhibit a conspicuous genital swelling during ovulation. It is possible, however, to detect a slight vaginal tumescence and color change associated with mating receptivity. Data collected under more controlled conditions are required to determine the degree to which vaginal tumescence is an honest signal and remains constant during the 3–4 day ovulatory period or changes during the time of maximum likelihood of conception.

We identified the date of birth to within 7 days of 10 infants born into our study groups. This was based on direct observations of three births, and 7 estimated dates of birth based on sightings of newborns during the 12 days per month (5 days data collection and 7 days censusing) that each study group was monitored.

A female was categorized as conceptive if she gave birth within 187 ± 7 days after copulation. This number is consistent with the gestation lengths reported in other howler studies [*A. caraya*: Colillas & Coppo, 1978; Kowalewski & Zunino, 2004; Shoemaker, 1979, but see Calegario-Marques & Bicca-Marques, 1993; *A. palliata*: Glander, 1980; *A. seniculus*: Crockett & Sekulic, 1982; *A. pigra*: van Belle et al., 2009]. Using this value, we were able to count back to identify the likely period of conception and pregnancy for individual females.

We considered a female to be ovulating and have conceived (CON = conception period) during a given monthly study period if she was observed to copulate and then gave birth within the next 180–194 days.

The term potentially fertile (PFP) is used to describe the period during which a female was neither pregnant nor lactating, engaged in copulations, but did not give birth during the next 180–194 days. We consider her potentially fertile because it is possible that she ovulated, conceived, and aborted or miscarried. It is also possible that she was fertile but did not conceive. We considered a female to be nonfertile (NF) during periods when she was pregnant (PREG) or lactating (LACT). Given that we used behavioral measures to assess fertility rather than endocrine profiles, we are likely to have misclassified some periods during which sexually active nonpregnant, nonlactating females were not ovulating (NF) as potentially fertile (PFP).

Rates of agonistic interactions among resident male black and gold howlers are extremely low [0.005/indiv/hr; Kowalewski, 2007]. Therefore, we used other behavioral measures to assess dominance. The dominant or central male of each group was identified based on priority access to females (only the central male engaged in mate guarding), visibly larger body size, and the initiation of howling vocalizations followed by travel to confront neighboring groups during intergroup encounters [Kowalewski, 2007]. Similar measures have been used to identify the α or central male in other howler species [*A. palliata*; Wang & Milton, 2003; *A. pigra*; Van Belle & Estrada, 2008].

Statistical Analyses

Differences in the frequency, duration, and distance that females traveled to engage in intragroup and extragroup copulations were compared using Mann–Whitney *U* tests. We used the number of individual males and/or females engaged in copulations (not the number of copulations) to determine sample size. We ran a *G*-test of independence and χ^2 test to explore and compare differences in female behavior during different reproductive states. We considered a criterion for significance for all statistical tests at $P < 0.05$. This research was part of larger populational study of behavior and affiliative relationships in *A. caraya* on Isla Brasilera and complied with the *American Journal of Primatology* principles for the ethical treatment of nonhuman primates, the University of Illinois, Urbana guidelines for animal research, and the laws of Argentina (IACUC protocol #01071).

RESULTS

Characteristics of Copulatory Bouts

We recorded 219 copulatory bouts involving 8 resident adult females in our two study groups. Overall, 68% ($N = 149$) of copulations were within-group (58% with the central male and 10.5% with the other resident males) and 32% ($N = 70$) were

extragroup. Adult females were observed to solicit copulations with males during 90.8% (199/219) of all matings. During extragroup copulations, females solicited nonresident males 95.7% of the time and in the case of within-group copulations females solicited resident males 88.6% of the time. Approximately 6% of copulatory events were solicited by males, and for the remaining 3.2% of copulations it was not possible to unambiguously identify the solicitor. Over the 20-month period (Table I) each resident female was observed to copulate, on average, 1.37 ± 0.5 times per 5-day sample period.

On average, the 219 copulations lasted 47.8 ± 16.6 sec and included 1–3 intromissions. Although virtually all copulatory events were terminated in less than 1 min, there was evidence of a slight but statistically significant difference in the duration of copulatory bouts engaged by resident males and extragroup males (resident males: range 18–140 sec, median = 44.5 sec; extragroup males: range 13–68 sec, median = 49.4 s, Mann–Whitney *U* test: $Z = -2.1$, $N = 8, 8$, $P = 0.036$). Similarly, courtship associated with precopulatory grooming was more frequent during intragroup (65%) than during extragroup copulations (35%) ($G = 96.7$, $df = 1$, $P < 0.001$). During extragroup copulations, the duration of precopulatory grooming bouts ranged from 15 to 150 sec (median = 62 sec). This was significantly shorter than the duration of precopulatory grooming bouts engaged in by adult females with males of their resident group (range 56–900 sec, median = 292 sec;

Mann–Whitney *U* test: $Z = -3.4$, $N = 8, 8$, $P < 0.001$). When resident and nonresident central males were compared with subordinate males, we found no differences in the duration of copulations (range for subordinate males was 18–105 sec, range for central males was 18–140 sec; Mann–Whitney *U* test: $Z = -0.3$, $N = 3, 4$, $P = 0.76$). We did find, however, that subordinate males engaged in shorter periods of precopulatory grooming than did central males (range subordinate males 56–450 sec, range central males 60–900 sec; Mann–Whitney *U* test: $Z = -4.24$, $N = 3, 4$, $P < 0.001$). The exact implications of this difference remain unclear.

Pattern of Within-Group Copulations

Matings between a resident female and her group's central male and other resident males occurred in full view of group members. All resident adult males were observed to copulate. During this study, we never observed a resident female to be attacked or threatened by other resident males or other resident females while engaging in precopulatory, copulatory, or postcopulatory behavior. However, the central male in each group was observed to engage in mate guarding. In *A. caraya*, male mate guarding is characterized by persistent following of a female at close range for 2–3 days. During this period, central males spent 64% of their day within 2 m of the mate-guarded female. Central males in each group were responsible for 100% of the mate

TABLE I. Number of Copulations per Female per Sample Period During Each Month of Study from April 2003 to December 2004

Year	Month	Female							
		Ana	Chiqui	Josefa	Gorda	Lola	Monga	Orejas	Tamara
2003	April					4			
2003	May	1			1				4
2003	June					2			2
2003	July	4		3					1
2003	August	5		2				1	2
2003	September	6	1	1			1	1	7
2003	October	4	1	10	3		1	1	2
2003	November			3	2		5		
2003	December	1			3		1	3	1
2004	January		2		11		1		1
2004	February	2			3			1	1
2004	March				5				1
2004	April	3	1	1	5		4	3	3
2004	May		5		3	2		1	
2004	June		1			2			
2004	July		3		1	6	1		
2004	August		8		2	2			
2004	September		1			9			
2004	October	7	7	4	2	2		1	
2004	November	2	6	1	1		1		
	Total	35	36	25	42	29	15	12	25

guarding events ($N = 95$), and were never challenged by the other resident males. During periods when females were fertile or potentially fertile (PFP), mate guarding resulted in the central male in Group X accounting for 77.8% of copulations and the central male in Group G accounting for 55 and 75% of copulations (in Group G adult males Jose and Hermoso each held the central position during part of the study; Table II, part A). Central males were never observed to engage in mate guarding during a resident female's nonfertile period. Despite male mate guarding, mate-guarded females were observed to successfully copulate with other resident males and extragroup males. Copulations with extragroup males occurred during intergroup encounters when the central male was engaged in howling and other forms of group defense, and during extended periods when the central male was resting. Copulations between resident females and resident males also tended to occur during periods of the day when the group was relatively inactive. In these cases, females did not travel away from the group to mate, and the copulations occurred within the crown of a tree jointly occupied by several group members. Given the proximity of the central male to the copulating pair (<10 m), and the fact that neither the subordinate resident male nor the resident female made any attempt to conceal their behavior, we conclude that the central male was tolerant of the mating activities between resident females and resident males.

During the 2–3 day period in which the central male was involved in mate guarding, the mate guarded female was observed to copulate with an average 0.62 ± 0.67 other resident males and 0.96 ± 1.1 extragroup males. Overall, 59.5% of resident subordinate male-resident female copulations (range per male from 50 to 67%) occurred during CON and PF periods and 40.5% during NF periods (range per male from 33 to 50%) (Table II, part A). Thus, based on their mating histories, the central male engaged in a greater number of copulations with resident females during likely fertile periods than did either neighboring males or other resident males. However, several other males also mated with the same female during likely fertile periods and therefore had positive paternity estimates.

Pattern of Extragroup Copulations

Extragroup copulations occurred in two main contexts; intergroup conflicts or during resting periods when a female left her group and traveled to a neighboring group. Given that extragroup copulations could potentially result in considerable costs to a female in travel time, predation risk, and attack from conspecifics, we attempted to evaluate these costs. Fifty-four percent (38 of 70 extragroup copulations involving 8 females) of extragroup

copulations occurred when neighboring groups were engaged in an intergroup conflict and most resident males were howling or tracking the activities of neighboring males. In these cases, a male and female from different groups were observed to hide or conceal themselves in dense vegetation at a mean distance of 26 ± 16 m from their resident groups and mate. In the remaining 32 extragroup copulations, a female ($N = 8$) traveled 86 ± 30 m from her resident group to encounter a neighboring male (Mann–Whitney U test: $Z = -3.2$, $N = 8$, $P < 0.01$). These mating excursions averaged 8 ± 1.9 min from the time the female left her group until the time she returned, and accounted for 0.28% of a female's total time budget during that day. The average round trip distance traveled by a female (172 m) represented 25% of the daily path length of each group (Day range = 699 ± 215 m in Group G and 670 ± 237 m in Group X—these data are based on detailed maps constructed for the 12-month period between December 2003 and November 2004).

In both contexts, extragroup copulations occurred outside of visual contact of a female's resident group. During these extragroup copulations, females were rarely attacked or threatened by males or females of the neighboring group. On 2 occasions, however, extra-group copulations were observed by a resident adult male during an intergroup conflict, and in both cases the male aggressively interrupted the mating event by rapidly approaching and threatening the consorting pair. In each case, the pair separated, and there was no physical contact among any of the participants. On one other occasion, two of four males from Group G copulated with an adult female from Group LR in view of the only resident male of her group. This male did not interrupt the copulations, suggesting that numeric odds may play a role in a male's assessment of the benefits and risks of mate defense [See Kitchen, 2004].

Finally, when females returned to their group after an extragroup copulation, they were not subjected to aggressive behavior from either resident females or resident males. Based on these observations, female promiscuity in black and gold howlers appears to represent a relatively low-cost activity in terms of time (greater cost in terms of travel distance), and was associated with minimal risk of injury. The potential cost of sexually transmitted diseases resulting from within-group or extragroup copulatory behavior in *A. caraya* remains unknown.

Distribution of Copulations

In Figure 2 we present a distribution of the number of extragroup and within-group copulatory events engaged in by female black and gold howlers, controlling for changes in the number of pregnant, lactating, fertile, and potentially fertile females

TABLE II. Continued

Females	Reproductive state	Number of fertile and nonfertile periods	Extragroup males										
			Resident males					Ova					
			HERMOSO Group G	JOSE Group G	Rocky Group G	MARLEY Group M	Mukenio Group M	PETE Group E	adm2 Group E	HERMOSO Group G	JOSE Group G	Ova Group G	Rocky Group G
Group G	Orejias	Fertile 4 Nonfertile 17	HERMOSO 2 JOSE 3	Ova 1	Rocky 1	MARLEY 0	Mukenio 0	PETE 0	adm2 0	HERMOSO 1	JOSE 2	Ova 1	Rocky 1
	Lola	Fertile 7 Nonfertile 14	HERMOSO 13 JOSE 1	Ova 1	Rocky 1	MARLEY 0	Mukenio 0	PETE 0	adm2 0	HERMOSO 6	JOSE 1	Ova 2	Rocky 0
	Monga	Fertile 16 Nonfertile 5	HERMOSO 4 JOSE 3	Ova 2	Rocky 0	MARLEY 0	Mukenio 0	PETE 0	adm2 0	HERMOSO 1	JOSE 4	Ova 2	Rocky 1
	Tamara	Fertile 21 Nonfertile 0	HERMOSO 6 JOSE 5	Ova 2	Rocky 0	MARLEY 0	Mukenio 0	PETE 0	adm2 0	HERMOSO 2	JOSE 0	Ova 0	Rocky 0

The central male of each group is indicated in capital letters. In group G Jose and Hermoso each occupied the central position during different times. Note that Massi was the only adult male in Group LR. Tobi left Group G in April 2004.

across months. Combining data for both study groups, resident females did not copulate with a significantly greater number of different males during fertile (CON = average number of different males = 3 including 1.3 resident males and 1.7 extragroup males) or potentially fertile periods (PFP = average number of different males = 4.9 including 2.3 resident and 2.6 extragroup males) than during nonfertile periods (PREG = average number of different males = 2.8 including 1.5 resident and 1.3 extragroup males; LACT = average number of different males = 4.8 including 3 resident males and 1.8 extragroup males) ($\chi^2 = 0.62$, $df = 3$, $P = 0.9$). In addition, there were no differences in the average number of resident males or extragroup males that females copulated with during each of these periods (G -test: $G_{adj} = 0.2$, $df = 3$, $P = 0.98$).

During CON and PFP, 70% of copulations engaged in by resident females were with resident males and 30% of copulations involved extragroup males. During NF periods (gestation and lactation) females were also observed to engage in more frequent copulations with resident males than with extragroup males. For example, 60% of copulations during lactation were with resident males and 40% were with extragroup males. During gestation, 58% of copulations were with resident males and 42% with extragroup males. Although there was a tendency for females to mate with extragroup males more than resident males during nonfertile periods, this difference was not significant ($\chi^2 = 6.97$, $df = 3$, $P = 0.073$) and may be explained by the fact that in response to mate guarding by the central male, the movement of females during their fertile period was restricted. Overall, 16% of copulations occurred during CON periods, 57% during PF periods, and 27% of copulations occurred during a female's NF period.

Data presented in Table II, part B indicate that some females copulated more frequently with extragroup males than others, and that a given female appeared to exhibit a preference to copulate with a particular extragroup male. For example, in Group X, Gorda copulated a total of 24 times with 6 extragroup males during CON and PF periods, whereas Chiqui copulated with 5 extragroup males one time each during CON and PF periods. Gorda copulated with one male in Group M on seven occasions and the other male of Group M on three occasions. Similarly, the frequency with which Gorda copulated with each of the four adult males in Group G varied from 0 to 6 times (Table II, part B). Finally, during extragroup copulations females did not consistently copulate more frequently with the central male of a neighboring group than with subordinate males of that group (Table II, part A). We recorded 23 extragroup copulations in which resident females (6 females) copulated with the central male of a neighboring group and 38 copulations (8 females)

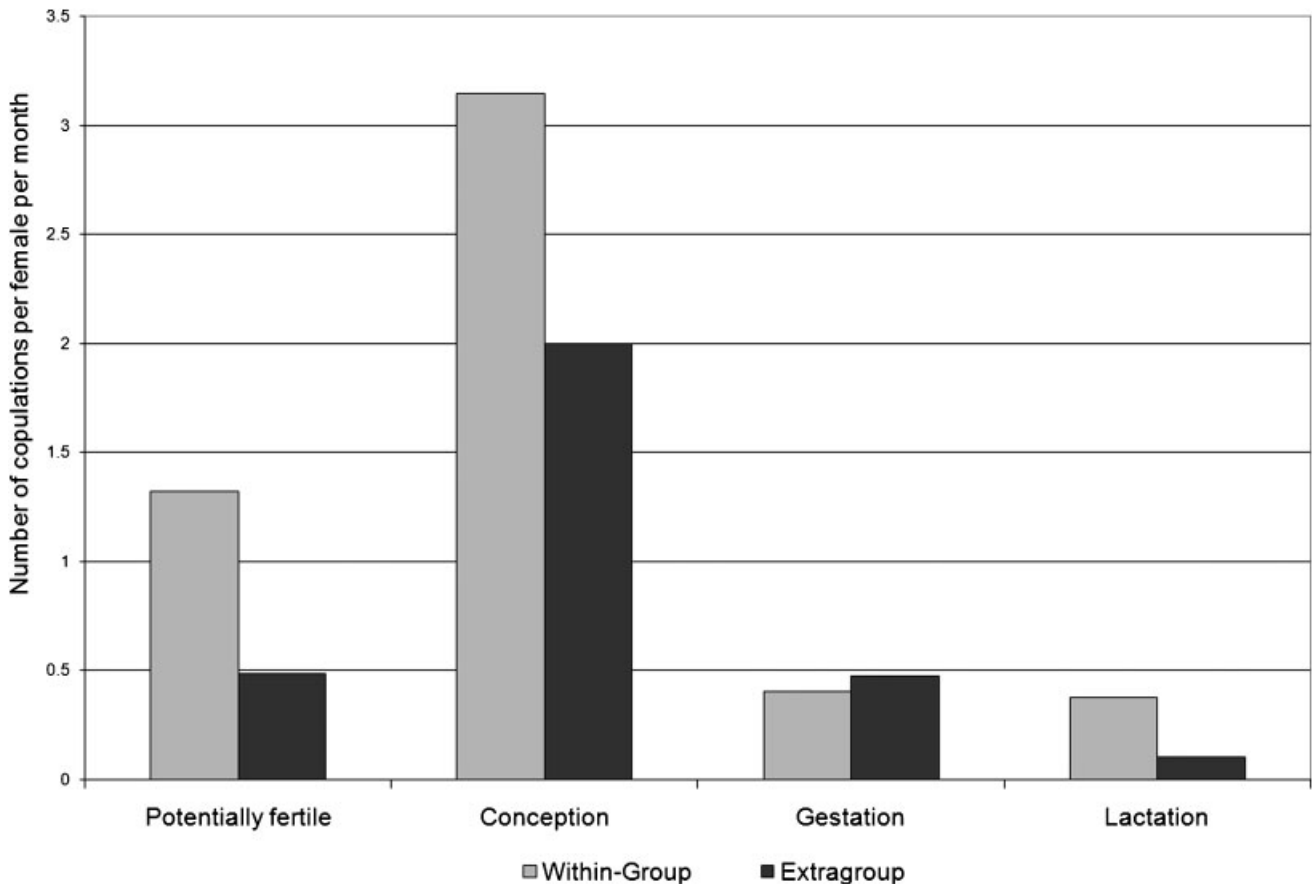


Fig. 2. Number of copulations engaged in by resident females with resident males and with extragroup males controlling for the number of females in each reproductive state per month. Potentially fertile includes periods in which the female was receptive and likely ovulating but did not conceive.

with subordinate males from these groups (Table II, part A).

DISCUSSION

In this study, we examined patterns of mating in two wild groups of *Alouatta caraya* during a 20 months field investigation in Argentina. In this population, female howlers were observed to mate with resident males and extragroup males during both fertile and nonfertile periods. Three of the four resident adult females in each of our two study groups copulated with all four resident adult male group members, and the remaining adult female in each group copulated with three resident males. These females also copulated with 2–6 extragroup males. Although the majority of intragroup and extragroup copulations occurred during periods in which females conceived or were likely fertile, 15% of copulations occurred during gestation and 13% occurred during lactation. Overall, we found that in *A. caraya* adult females (1) solicited copulations from both resident males and males living in neighboring social groups, (2) mated with a similar number of males during fertile periods ($CON = 3 \pm 1.74$;

$PF = 4.9 \pm 2.9$) and nonfertile periods ($GEST = 2.1 \pm 1.6$; $LACT = 3.9 \pm 3.2$), (3) copulated more frequently with the central male (46% of all copulations) than with other resident males (18%) or extragroup males (36%), and (4) the costs in time engaged in extragroup copulations (approximately 8 min or 0.28% of daily activity budget) and risk of injury to a female of copulating with either resident or extragroup males were small. However, females did travel an additional 172 m/day to encounter an extragroup male and return to her group. We also note that the length of precopulatory grooming bouts was significantly shorter between resident females and extragroup males than between resident females and resident males. It is possible that in an attempt to avoid detection by resident males, females reduce time devoted to courtship and engage extragroup males via direct solicitation.

Female promiscuity and extragroup copulations have been observed in several howler species [*A. seniculus*, Agoramoorthy & Hsu, 2000; *A. pigra*, van Belle et al., 2009; *A. guariba*, Fialho & Setz, 2007; *A. palliata*, Wang & Milton, 2003], as well as in other genera of the subfamily atelinae [Di Fiore, 1998; Di Fiore & Campbell, 2007; Strier, 1994]. For

example in *Brachyteles*, *Ateles*, and *Lagothrix* females mate during both fertile and nonfertile periods, and resident males are reported to be tolerant of each others mating activities (although in *Ateles geoffroyi*, Campbell [2006] reported that copulating partners hide from other resident males). In a 60-month study by Strier [1997], female muriquis (*Brachyteles hypoxanthus*) were reported to mate with an average of eight different sexual partners, and extragroup matings accounted for up to 13% of all adult female copulations. Campbell [2006] observed 18 copulations over a period of 17 months in a group of 10 adult and subadult female spider monkeys (*Ateles geoffroyi*). Almost 93% of these copulations occurred when females were cycling, with the remainder during their nonperiovulatory period. Female spider monkeys were observed to copulate with as many as four different males from their community [Campbell, 2006]. Finally, Di Fiore and Fleischer [2005] reported 44 copulatory events in woolly monkeys (*Lagothrix l. poeppigii*) in Ecuador. These authors note that copulations frequently occurred in full view of other adult male group members (no rate presented), females copulated with multiple males in their group, and males were highly tolerant of intragroup matings. In all ateline genera, females are reported to solicit copulations from males, and in several species, including *A. caraya*, resident males act jointly or cooperatively during intergroup encounters to exclude nonresident males from entering the group [Di Fiore & Campbell, 2007; Kowalewski, 2007; Strier, 1994].

We examined several factors that are likely to affect the costs and benefits to female black and gold howlers of within and between-group mating behavior. In species in which females solicit male mating partners and male aggression is rarely directed towards females, individual females may be expected to adopt a "mixed mating strategy" characterized by periods of selective mating and periods of promiscuous mating depending on proximate social and ecological conditions. Here we explore several possibilities. Under conditions in which distributing paternity estimates across multiple resident males offer females advantages associated with promoting collective male mate and group defense and possibly increasing the length of male tenure in the group, females are expected to mate with all or most resident males during fertile and nonfertile periods, and to rarely engage in extragroup matings. In support of this expectation, female black and gold howlers mated with both central and subordinate adult male group members during fertile and nonfertile periods (Group X = Central male: 42 copulations during PFP and 16 copulations during NFP; Subordinate males: 16 copulations during PFP and 8 during NFP; Group G = Central male: 35 copulations during FP and 19 during NFP;

Subordinate males: 9 copulations during FP and 2 during NFP; Table II, part A). Moreover, male tenure in established groups was 4–6 years and males collectively engaged in mate and group defense on average twice each day [Kowalewski, 2007]. However, female black and gold howlers also mated with extragroup males during fertile and nonfertile periods (30% of copulations during fertile periods were with extragroup males and approximately 40% of copulations during nonfertile periods were with extragroup male), which is not consistent with these expectations.

If female mate choice is directed principally to maximizing the likelihood that her offspring are sired by a dominant male, then females are expected either to mate exclusively with the central male, or to mate with subordinate resident males during non-conceptive periods and to mate with her group's central male principally during fertile periods. A corollary to this is that if females preferentially solicit males exhibiting behavioral and anatomical traits associated with high rank, then they are expected to mate with central males from neighboring groups more frequently than with subordinate males from neighboring groups. These expectations were only partially supported. Although resident females mated more frequently with the central male of their group than with other resident males (total for both groups is 81 copulations with central males vs. 25 with subordinate resident males = 76.4%, Table II, part A), the majority of copulations with subordinate resident males also occurred during fertile periods (Table II, part A, total for both groups = 35 copulations PFP and 17 copulations during NFP). In this population, despite evidence of sexual coercion in the form of mate guarding, the central male was unable to maintain exclusive access to a receptive female during her 3–4 day ovulatory period. Moreover, the majority of extragroup copulations by resident females occurred during fertile periods (Group X = 45 during PFP and 9 during NFP; Group G = 15 during PFP and 1 during NFP; Table II, part B), and females were as likely to mate with subordinate males from neighboring groups as they were with the central male of a neighboring group (total for both groups is 28 copulations with central males vs. 31 with subordinate males, Table II, part B). Thus, there was no evidence that females solicited extragroup males based on qualities that influenced male dominance status.

Our third expectation is that under conditions in which a change in male dominance from within the group results in the replacement of the central male and possibly increased risk of infanticide, females are expected to reduce their frequency of mating with the central male, and increase their frequency of mating with other resident males consistent with their rank. This shift in mating preference should occur during both fertile and nonfertile periods, and females are not expected to mate with extragroup

males. Our data do not fully support these expectations. For example, in Group G, resident male Hermoso replaced resident male Jose as the central male. Although this coincided with a gradual increase in the number of matings engaged in by Hermoso, females continued to copulate with other resident and nonresident males. A fourth expectation is that if female mating choices are affected by expectations of frequent male takeovers from outside the group and an increased risk of infanticide, then females are expected to increase their frequency of mating with extragroup males and decrease their frequency of mating with resident males during both fertile and nonfertile periods. Our data do not support these expectations.

Finally, under conditions in which females benefit via sperm competition and increasing the likelihood that successive offspring are sired by different males, females are expected to mate with multiple resident males as well as with multiple extragroup males during fertile periods. This expectation is generally supported. As indicated in Table II, in our two study groups, 70.1% (106/151) of copulations with resident males and 85.7% (60/70) of copulations with extragroup males occurred during a female's potentially fertile period. It has been argued that under conditions of environmental instability, increased genetic variability among successive offspring enhances the likelihood that some set of individuals in the population can successfully colonize and exploit new and ephemeral habitats [Crockett & Eisenberg, 1987; Dietz, 2004; Gangestad & Thornhill, 2004]. In this regard, black and gold howlers inhabit the southernmost distribution of any extant neotropical primate. This area includes northern Argentina, southern Brazil, eastern Bolivia, and Paraguay and is characterized by an extreme range of forest types such as gallery forests, flooded forests, subtropical forests, seasonal semideciduous fragmented forests, and less seasonal forests on island ecosystems that experience extensive periodic flooding of the Parana and Paraguay Rivers [Bravo & Sallenave, 2003; Kowalewski & Zunino, 2004]. The three most severe environmental challenges that howlers at such high latitudes face are cyclical floods resulting in catastrophic habitat change (see Pavelka and Chapman [2006] for a discussion of the effects of Hurricane Iris on black howler populations in Belize), low daytime and nighttime temperatures during the winter months (0–10°C), and limited diversity, availability, and productivity of food resources [Zunino et al., 2001]. Given that both male and female howlers disperse from their natal group, increased genetic variability may play an important role in offspring survivorship and reproductive success. Thus, it is possible that black and gold howler females mate with many different males to increase the probability of conception and/or the likelihood that successive infants are sired by

different males [Constable et al., 2001; Pusey & Wolfe, 1996].

A final point relates to the possibility that female black and gold howlers engage in promiscuity primarily as a mating strategy to decrease infanticidal risk from both resident and nonresident males via paternity confusion, as suggested in expectations three and four. Although we cannot exclude this possibility, we feel that it is not strongly supported by our observations. The black and gold howler population on Isla Brasilera (currently some 35 groups and almost 250 animals [Pave, pers. comm.]) has been under systematic observation for the past 7 years. During this period we have no direct observations of infanticide or instances of putative infanticide in this population [Kowalewski, 2007] despite observations of changes in male dominance from within the group (e.g. during the course of this study resident male Jose replaced resident male Hermoso as the central male in Group G), and from outside the group (e.g. from 2003 to 2006 at least four adult males are known to have successfully entered established groups containing infants and none of these events were associated with infant deaths or infant disappearances) [Kowalewski, 2007; Peker, pers. comm.]. Adult male tenure in established howler groups on Isla Brasilera generally ranges from 4 to 6 years [Kowalewski, 2007]. In this howler population, as has been suggested for certain other howler populations [Bezanson et al., 2008; Chapman & Pavelka, 2005; Estrada, pers. comm.], the risk of infant killing by adult males appears to be extremely low and offers only a limited explanation for the benefits of female promiscuity. Therefore, although we recognize that aspects of female mating patterns in black and gold howlers may represent a counter strategy to discourage infanticide, based on observations in our study population there may exist several factors that also contribute importantly to female reproductive success.

In conclusion, females in many primate species mate with multiple adult males during fertile and nonfertile periods. This is consistent with "a mixed mating strategy, incorporating elements of both selectivity and promiscuity" [Manson, 2007: 457]. Although in some primate populations the costs to females of mating promiscuity may be high, especially under conditions of intense male intersexual coercion [Smuts & Smuts, 1993] or increased levels of female reproductive competition [Jones, 2003], in our *A. caraya* study population the costs to females of mating with multiple resident males and extragroup males appear to be relatively low. Several theories have been proposed to explain the advantages to primate females of mate choice and mating promiscuity [Manson, 2007]. These include paternity confusion associated with decreased infanticide risk [van Schaik, 2000], insuring high-quality genes for their offspring [Zeh & Zeh, 2001], mating with novel males in order to promote genetic diversity between

successive offspring [Pusey & Wolfe, 1996], and reinforcing affiliative social bonds between individual mating partners [Smuts, 1985]. In many cases, the predictions offered by these theories are not mutually exclusive (i.e. mate with extragroup males to decrease infanticide risk vs. mate with extragroup males to promote genetic diversity of successive offspring) and therefore no single explanation may best predict the mating behavior of female howlers across species and populations. However, given that black and gold howlers inhabit the extreme southern distribution of all howler species and exploit habitats subject to strong seasonal variation in temperature and food availability, we offer the possibility that in conjunction with other factors, mating promiscuity in *A. caraya* represents a behavioral pattern favoring offspring genetic variability [but see Jack & Fedigan, 2006], and has the potential to result in a high degree of phenotypic variation within the population. In *Alouatta caraya*, female mate choice (for example, Gorda copulated with the same extragroup male on seven different occasions) as well as female mating promiscuity have the opportunity to influence male social relationships, male–female friendships, male reproductive strategies, and the benefits to males of collective group action and mate defense [Nunn, 2000] by manipulating male perceptions of paternity and males' common social attachments to the same females. We conclude that factors that promote and constrain female promiscuity offer an important perspective from which to evaluate mating tactics and social bonds among male and female primates.

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