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Insights into social relationships among female black howler monkeys

Alouatta pigra at Palenque National Park, Mexico

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Abstract We investigated the social relationships among adult females in two multimale-multifemale groups of black howler monkeys *Alouatta pigra* during a 14-month study in Palenque National Park, Mexico. Based on over 900 focal hours and over 5400 scan samples recording neighboring group members, we found that females very rarely engaged in agonistic interactions and no dominance hierarchy could be discerned. Relationships among resident females were primarily affiliative, but females of one study group spent a higher proportion of time in close proximity and engaged in affiliative interactions with one another at higher rates than females in the other study group. The strength of female relationships increased with the birth of an infant. Although no females immigrated during the study period, the temporary association of three extragroup females with our study groups implies that the social system of black howler monkeys is more dynamic than previously suggested. These findings suggest that female black howler monkeys behave more similarly to female red howler monkeys *A. seniculus* than to female mantled howler monkeys *A. palliate* [*Current Zoology* 57 (1): –, 2011].

Keywords Black howler monkey, *Alouatta pigra*, Affiliation, Agonism, Female dispersal

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Relationships among female primates are generally explained by the type and intensity of competition versus cooperation over access to resources essential for their reproductive success, and are reflected in their dispersal patterns (Isbell, 2004; Koenig, 2002; Sterck et al., 1997; van Schaik, 1989). Female dispersal has been reported in howler monkeys (black howler monkeys *Alouatta pigra*: Brockett et al., 2000; mantled howler monkeys *A. palliata*: Glander, 1980, 1992; Jones, 1980; Clarke and Glander, 2008, 2010; red howler monkeys *A. seniculus*: Crockett, 1984; Crockett and Pope, 1993; Pope, 1992; black-and-gold howler monkeys *A. caraya*: Calegario-Marques and Bicca-Marques, 1996; Guidice, 1997; brown howler monkeys *A. guariba*: Miranda and Passos, 2005; and red-handed howler monkeys *A. belzebul*: Bonvicino, 1989), yet female dispersal regimes, grouping patterns, and female social relationships show great variability among different species (Chapman and Pavelka, 2005; reviewed in Di Fiore and Campbell, 2007). For example, red howler monkeys live in small groups of two to 17 individuals with one to three adult males and one to four adult females (Di Fiore and Campbell, 2007). Resident red howler females form coalitions to aggressively prevent extragroup females from immigrating (Pope, 2000a), and extragroup females must form new social groups with other extragroup males and females to successfully establish membership in a social group (Crockett, 1984; Crockett and Pope, 1993). Females in recently established groups are generally unrelated, but they prefer female kin as future coalition partners (Pope, 2000a). Resident females compete to recruit their own daughters as additional breeding females, and the daughters of the other females are forcefully evicted as juveniles. Eventually, all female juveniles will be evicted once four adult females reside in the group. Groups with three to four adult females become increasingly more attractive targets to coalitions of extragroup males, which attempt to take over the group by evicting resident males, and may commit infanticide (Crockett and Janson, 2000).

Mantled howler monkeys, by contrast, live in relatively large groups of two to *ca.* 40 members with one to six adult males and one to 15 adult females (Di Fiore and Campbell, 2007). Resident

mantled howler females form an age-reversed hierarchy based on agonistic interactions and spatial supplantations (Jones, 1980; Zucker and Clarke, 1998). Virtually all juvenile females are forcefully evicted from their natal group (Glander, 1980, 1992; Clarke et al., 1998; Clarke and Glander, 2008), but may successfully immigrate into other social groups when they can overcome the aggressive resistance of resident females and gradually fight their way up the hierarchy (Glander, 1980, 1992; Jones, 1980). Establishing affiliative and sexual relationships with resident males seems to be an effective tactic for immigrating into an established group. Nonetheless, females who eventually fail to attain the dominant position will leave the group and will attempt immigrating into another established group (Glander, 1992).

Genetically, the black howler monkey forms a sister clade with the mantled howler monkey (Cortés-Ortiz et al., 2003), yet, its group size (two to 12 individuals) and composition (one to three adult males and one to three adult females) appear to be more similar to those of the more distantly related red howler monkey independent of local ecological conditions (Van Belle and Estrada, 2006). Thus, studying black howler monkeys is important to address evolutionary and ecological questions about the nature of the social diversity of howler monkeys. Intermittent monitoring over a 4-year span of the black howler population at the fragmented landscapes of Community Baboon Sanctuary (CBS), Belize has revealed that females disperse as juveniles ($n = 4$) and adults ($n = 2$) and that solitary females are usually prevented from immigrating into established groups by resident females (Brockett et al., 2000). However, adult females have been observed to emigrate and subsequently immigrate into social groups after their groups were translocated as entire units from the CBS forest fragments to the continuous forest of Cockscomb Basin Wildlife Sanctuary, Belize where they were previously extirpated (Ostro et al., 2001).

Because habitat fragmentation and translocation may disrupt the social organization of groups and alter dispersal patterns, it is unknown whether female black howler monkeys residing in continuous habitats are able to immigrate into established groups, similar to mantled howler

monkeys, or whether they are prevented from doing so by resident females, similar to red howler monkeys. In this paper, we present preliminary data on female dispersal and report data on agonistic and affiliative interactions and spatial associations among resident females from a 14-mo study of two multimale-multifemale black howler groups in Palenque National Park, Mexico.

1 Materials and Methods

1.1 Study site and subjects

Palenque National Park (PNP), Mexico ($17^{\circ} 28' N$, $92^{\circ} 03' W$) encompasses 1771 ha of which about 900 ha are covered by primary tall evergreen tropical rainforest and forest vegetation in various stages of regeneration. The remaining land consists of human-induced pasture lands (Díaz Gallegos, 1996). Detailed data on climate and the black howler population is provided in Estrada et al. (2002). During a 14-month period (June 2006–July 2007), we studied two multimale-multifemale black howler groups. The groups inhabited the same section of the primary tall forest, but their home ranges did not overlap. Individual group members were classified as infants (clinging ventrally or dorsally to mother), juveniles (independent of mother and $1/4$ – $1/2$ the size of adults), subadults ($3/4$ the size of adults), and adults (all large and robust individuals) following Balcells and Veà (2009). The Balam group varied in size from 4 to 9, with 1–3 adult males, 0–1 subadult male, 2–3 adult females, 0–2 juveniles, and 0–1 infants. The Motiepa group varied in size from 5 to 7 and had 1–2 adult males, 2 adult females, 1 juvenile male, and 1–2 infants. One female of the Balam group (MI) disappeared, together with two adult males and two juveniles, after a strong local storm the night of October 27, 2006. The two other females of the Balam group and the two females of the Motiepa group were present throughout the study period. Females could be recognized individually by crooked fingers and genital pigmentation.

1.2 Data collection

Behavioral data were collected on a total of 306 days (06:30 h–17:30 h) from June 11, 2006 through July 24, 2007, alternating observations between the two study groups every two days. Behavioral data were collected on all adult females in both groups during 60-min focal animal samples (Altmann, 1974). When focal subjects were out of view for more than 15 min, we started the next focal animal sample, and focal samples of less than 30 min were discarded (Wang and Milton, 2003; Van Belle et al., 2008). We analyzed a total of 916 focal hours of observations on adult females (Balam: 509 hours; Motiepa: 407 hours). During focal samples, we recorded continuously (to the nearest second) all activities and social behavior displayed, along with the identity of all participants and directionality of social interactions. Social behaviors included supplantations, agonistic interactions (lunging, pushing, chasing, grabbing, and fighting) and affiliative interactions (playing, greeting, embracing, touching, and allogrooming). Additionally, data on approaches to or by and retreats from or by the focal individual within 1 m of the focal subject were recorded during focal samples.

We carried out instantaneous scan samples (Altmann, 1974) at 10-min intervals throughout the focal animal samples to record the identity of all adult and subadult neighbors at 0–1 m of the focal individual (Wang and Milton, 2003; Van Belle et al., 2008, 2009a). To prevent biasing our results in favor of the most visible group members, we only included scan samples for which all neighbors were identified in the analyses, representing a total of 5436 scan samples on females (Balam: 3063 scan samples; Motiepa: 2373 scan samples). In addition, we recorded all occurrences of social interactions outside focal samples and all sightings of extragroup individuals *ad libitum* (Altmann, 1974).

1.3 Data analyses

We calculated percentages of spatial associations and rates of social interactions for all female-female dyads. For the Balam group, we calculated these measurements when the group had three versus two resident females separately. Dyadic spatial associations were calculated as the

percentage of time each pair of females was observed in close proximity (0–1 m) of each other during scan samples of both individuals. Dyadic rates of social interactions were calculated as the number of observed social bouts between female dyads divided by the total sum of focal hours on both individuals. We defined a social bout as one or more events of social behavior of the same category (i.e., agonistic or affiliative interactions) between the same individuals separated by ≤ 5 min (Neville, 1972; Van Belle et al., 2009a). The three females of the Balam group were not observed to engage in a social interaction simultaneously.

We used the Hinde's index (Hinde and Atkinson, 1970) to measure which member of each female-female dyad was responsible for maintaining close proximity. Following Hill (1990), we calculated the Hinde's index only for dyads with a total of 10 observations of approaches and retreats by both individuals.

Because of small sample size, we used Chi-square tests to compare the frequencies of spatial associations and social interactions among (1) the three female dyads of the Balam group when three females were present, (2) the female dyad (LU-TE) of the Balam group when three versus two females were present, and (3) the female dyads of the Balam group versus the Motiepa group when two females were present in each study group. Observed frequencies were compared against expected frequencies calculated based on the representation of each dyad during focal animal samples and scan samples, following Corewyn and Pavelka (2007). Statistical tests were two-tailed with $\alpha \leq 0.05$. Results of these Chi-square tests need to be interpreted with caution because of the potential interdependence of the data on dyadic social interactions and spatial associations.

2 Results

2.1 Female-Female Spatial Associations and Social Interactions

In the Balam group, the two dyads MI-LU and MI-TE each tended to spend slightly more time in close proximity than the other dyad LU-TE, however this was not statistically significant ($\chi^2 = 5.81$,

$df = 2$, $P = 0.055$, Table 1). MI was responsible for maintaining close proximity to both females (Hinde's index, MI-LU = 0.29, MI-TE = 0.31). Both of the Balam females, LU and TE, that were present in the group throughout the entire study spent equally little time in close proximity when they were the only resident females present compared with when MI was present as well ($\chi^2 = 0.01$, $df = 1$, $P = 0.907$, Table 1). LU and TE were mutually responsible for maintaining close proximity to one another (Hinde's index = 0.09) when they were the only resident females.

In the Motiepa group, the two females (MO and IS) spent significantly more time in close proximity of each other ($\chi^2 = 52.11$, $df = 1$, $P < 0.001$, Table 1) compared with the Balam females. Female MO gave birth on June 1, 2007, and female IS spent increasingly more time in close proximity to MO during the first four weeks after the parturition (Fig. 1). The Motiepa females were mutually responsible for maintaining close proximity to each other before the birth (Hinde's index = 0.06), but IS was largely responsible when MO had her newborn infant (Hinde's index = 0.58). Infrequent data collection on the Motiepa group in July 2010 did not allow for further evaluation of the females spatial association beyond four weeks after the parturition.

Only one bout of female agonism and seven supplantations were observed during over 900 focal hours of observations on both groups (Table 1). In addition, the Balam females seldom engaged in affiliative interactions, and low sample sizes preclude statistical analyses among dyads. The Motiepa females, however, affiliated at significantly higher rates than the Balam females ($\chi^2 = 10.55$, $df = 1$, $P = 0.001$, Table 1). Interestingly, MO initiated affiliative interactions with IS at a much higher rate (0.050 bouts/h) than IS did before MO gave birth (0.005 bouts/h; $\chi^2 = 12.67$, $df = 1$, $P < 0.001$). These females initiated affiliation with one another at equal rates after the birth of MO's infant (MO to IS: 0.128 bouts/h versus IS to MO: 0.097 bouts/h; $\chi^2 = 0.26$, $df = 1$, $P = 0.614$).

2.2 Female dispersal patterns

Extragroup females were sighted nine times in the home range of the Balam group and ten times in the home range of the Motiepa group during the 14-month study period. Extragroup females were

usually subadults ($n = 10$) or adults ($n = 7$), but three juveniles (*ca.* two years old) were also observed. Sixteen sightings involved extragroup females traveling alone, one involved two adult females forming a pair, one sighting involved one subadult female traveling with an adult male, and one was a juvenile female traveling with an adult male. Of the 17 extragroup females that encountered our study groups, nine were howled at by the group males or chased away by the group females; others were ignored by group members ($n = 8$). One extragroup female copulated with a male of the Motiepa group, but she was later aggressively chased away by one of the Motiepa females (IS).

One subadult female joined the Balam group for 14 days. She was first sighted with the group on November 13, 2006 when she and a resident female (LU) engaged in an aggressive display involving branch breaking, piloerection, and grunting. No such aggressive displays were observed on subsequent days, and the subadult female maintained a peripheral position in the group (i.e., > 5 m of other group members). She stayed with the Balam group through a male takeover event, but disappeared on November 27, 2006 and her fate is unknown. On a second occasion, coincidentally the next day (November 28, 2006), the Balam group encountered an extragroup adult male paired with a juvenile female. The male was chased away, but the juvenile female remained with the Balam group for three months. No agonistic interactions were directed toward her by either males or females, and she stayed with the group after a male takeover event. She was last seen with the group on March 8, 2007, but she had previously been absent during 10 of the 19 observation days on the Balam group during the previous month. Similarly, another juvenile female was observed in close association with the Motiepa group from June 15, 2007 through July 13, 2007. This female was occasionally chased away by resident adult and juvenile males and she remained peripheral to the group.

At the onset of the study, a subadult female was present in the Motiepa group. On July 20, 2006, this female was chased to the ground by unidentified group member(s), and disappeared soon after.

On July 22, 2006, this subadult female returned to the group and approached and rested in close proximity to both resident females and immatures without eliciting any aggression from the resident females. She was not observed on subsequent days.

3 Discussion

Black howler females very rarely supplanted each other or engaged in agonistic interactions in either of our study groups. In contrast, mantled howler females are reported to engage in agonism at an average rate of 0.38 interactions/hr (range = 0–1.44 bouts/hr) with dominant females engaging in more agonism than lower ranking females in order to maintain their high ranks (Zucker and Clarke, 1998). Based on the low rates of agonism and supplantation, along with the absence of submissive behavior, no female dominance ranks could be discerned in our study groups, and female social relationships were primarily affiliative or neutral. The two Motiepa females, however, spent more time close to each other and they engaged in affiliative interactions at higher rates than the Balam females, whose group membership was also less stable during this study (Van Belle et al., 2008). Female mountain gorillas coresiding with both related and unrelated females had stronger affiliative bonds with their kin than with nonkin (Watts, 1994, 2001). The stronger affiliative relationships of the Motiepa females might reflect their kinship compared to the Balam females, but genetic analyses are needed to evaluate this possibility. Furthermore, in three black howler groups at Monkey River, Belize, each composed of one adult male, two adult females, and immatures, adult females spent considerably more time (44%–69 %) in close proximity of each other compared to either Balam and Motiepa females (Corewyn and Pavelka, 2007). Although the differences in proximity classes used by the two studies (1 m versus 2 m) might partially explain the differences in female spatial associations, it is also possible that the strength of social relationships among female black howler monkeys may vary greatly. More studies are needed to assess the demographic, social, genetic, and ecological factors that may influence female relationships in this primate.

It is unclear why social interactions between the Motiepa females was asymmetrical, but this disappeared with the birth of MO's infant, when IS increased her interactions with MO. Interest in neonates by females other than the mother has been observed in many primate species, including several species of howler monkeys (reviewed in Clarke et al., 1998). In mantled howler monkeys, nonmothers interacted both affiliatively and aggressively with neonates, with new mothers invariably responding negatively and sometimes separating themselves from their group for several days after giving birth to avoid these interactions (Clarke et al., 1998).

During our study, female group membership was relatively stable, while male group membership changed frequently as a result of male group takeovers and immigrations (Van Belle et al., 2008). The stability in female membership suggests that resident females form the core of black howler social groups in continuous forest, just as in fragmented landscapes (Brockett et al., 2000). Nevertheless, we observed what appeared to be an eviction of one subadult female from the Motiepa group at the onset of the study. Furthermore, no females permanently immigrated into our study groups, and ten of 19 solitary females were aggressively chased away by resident females upon encounters. Interestingly, we observed one subadult female and one juvenile female that temporarily joined the Balam group without eliciting overt aggression among females. The neutral behavior toward females temporarily joining a social group might reflect a form of nepotism if the visiting females were returning daughters. It is not clear why these females ultimately left the social group, but it might reflect failure to establish affiliative relationships with either males, females, or both, similar to dispersing mantled howler females failing to attain the dominant female position in the group. One extragroup black howler female was observed to copulate with a resident male, which might be a tactic to establish an affiliative and sexual relationship with resident males that could facilitate successful immigration, as is the case in mantled howler monkeys (Glander, 1992). Affiliative interactions and copulations between extragroup females and resident males have also been observed in red howler monkeys, yet these relationships did not enable to extragroup

females to overcome the persistent aggression received from resident females (Sekulic, 1982; Pope, 2000b). Similarly, in our study, the extragroup black howler female who copulated with a resident male was nonetheless aggressively chased away by one of the resident females.

The results presented here provide some preliminary insights into female social relationship in this primate species. Our findings suggest that in their grouping patterns and social relationships, but perhaps not in their dispersal patterns, black howler females behave more similarly to red howler females compared to mantled howler females, and that they form neutral to affiliative coalitions with one another to attempt preventing extragroup females from immigrating into social groups. In addition, our data suggests that the social interactions and dispersal patterns of females in continuous forest are similar to those observed in fragmented forests. Future studies that include long-term observation on more groups and information on genetic relatedness are needed to further examine female dispersal patterns and differences in the strength of relationships and the effect of kinship among resident female black howler monkeys. Additional studies in other howler monkeys are needed to improve our comparative power and to advance our understanding of the variance in social organization among different howler monkey species.

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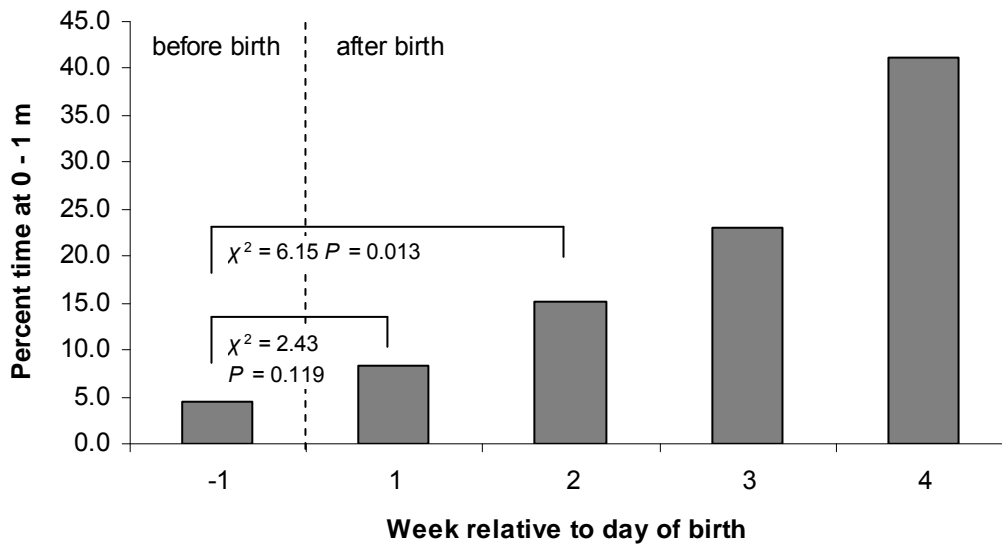
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Table 1 Percentages of spatial associations and hourly rates of affiliative and agonistic interactions and supplantations for each female-female dyad of the two study groups

	Female Dyads	Percent 0 – 1 m	Affiliation		Agonism		Supplantation	
			Rate	n	Rate	n	Rate	n
Balam group								
11 Jun 06 – 27 Oct 06 (3 ♀) (199 focal hours)	LU-TE	0.82	0	0	0	0	0	0
	MI-LU	2.19	0.0075	1	0	0	0.0075	1
	MI-TE	2.34	0.0151	2	0	0	0	0
28 Oct 06 – 20 Jul 07 (2 ♀) (310 focal hours)	LU-TE	0.86	0.0226	7	0.0032	1	0.0065	2
Motiepa group								
(407 focal hours)	IS-MO	8.85	0.0792	32	0	0	0.0098	4

For the Balam group, measures were calculated separately before and after the disappearance of MI on 27 Oct 06. Numbers of affiliative, agonistic, and supplantation bouts recorded during focal samples are shown.

Fig. 1 Percentages of time the two Motiepa females spent in close proximity to each other one week before up to four weeks after the birth of MO's infant



Females spent significantly more time close to each other after the birth by the second week onward compared to the week before the parturition.