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Social Relationships Among Male *Alouatta pigra*

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Abstract We investigated male social relationships in 2 groups of black howlers (*Alouatta pigra*) in Palenque National Park, Mexico, over a 14-mo study characterized by frequent changes in male group membership. Both single males and pairs of males entered our focal groups. Single males tended to join groups, whereas pairs of males entering groups together successfully evicted resident males. The 19 male dyads across the 11 periods defined by changes in group membership were rarely in close proximity or interacting with one another. Nevertheless, 1 male formed significantly closer associations with resident females in 6 periods and achieved higher mating success during 4 of the periods when ≥1 female was sexually active. In the other 5 periods, no particular male maintained significantly closer associations with resident females, which may be a result of the rapid sequence of changes in male membership and corresponding social instability. Resident males participated frequently and consistently in mutual howling, but the resident male with the strongest female associations and highest mating success initiated howling bouts more frequently in all but 1 of the 6 socially stable periods. Though still preliminary, our findings suggest that variation in social relationships among male black howlers may be more related to their ability to establish strong relationships with females than to their relationships with one another.

Keywords *Alouatta pigra* · cooperation · howler monkey · male social behavior · male takeover

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Introduction

Male primate social relationships range from aggressive and competitive to affiliative and cooperative and vary across species, among populations of the same species, and over the course of an individual's lifetime (Kappeler 2000). The variation is generally explained by the tradeoff between intragroup and intergroup competition over access to limited resources (van Hooff 2000; van Hooff and van Schaik 1992, 1994). Male reproductive success is limited mainly by access to receptive females, and males will attempt to exclude each other from sexual interactions or, more strongly, from membership in heterosexual groups (van Hooff and van Schaik 1994). When intragroup competition is high, males may form 1-male groups by ousting all young natal males and preventing other males from joining them, e.g., geladas (Dunbar 1984), snub-nosed monkeys (Zhang *et al.* 2006), and some guenon species without male influxes (Cords 2000, 2002; MacLeod *et al.* 2002). When males cannot exclude other males, dominance relationships based on outcomes of agonistic and submissive interactions develop among resident males, with reproductive success usually skewed toward the dominant males (Hager 2003; van Hooff 2000). In addition, weak affiliative relationships may develop among resident males (Hill and van Hooff 1994; van Hooff and van Schaik 1992, 1994), e.g., olive baboons (Packer 1979) and black-crested macaques (Reed *et al.* 1997).

When intergroup competition is high, multiple males might win more often against 1-male groups by cooperating with one another. Intragroup competition might be relaxed as an incentive for subordinate males to stay in the group and aid in group defense (Vehrencamp 1983). Therefore, male-male social relationships should be less aggressive and more affiliative (van Hooff and van Schaik 1992, 1994), and reproductive success might be more evenly distributed among resident males (Hager 2003; van Hooff 2000). Because fertilization cannot be shared among males (van Hooff and van Schaik 1992), kinship and the benefits males accrue via inclusive fitness can explain high levels of male-male affiliation and cooperation (Silk 2006), e.g., mountain gorillas (Robbins 1995; Watts 2000), langurs (Sterck and van Hooff 2000), Costa Rican squirrel monkeys (Boinski 1994), muriquis (Strier 1994), and spider monkeys (Fedigan and Baxter 1984; Symington 1990). Yet, several researchers showed that relatedness is not a prerequisite for the formation of cooperative alliances among males (Avilés *et al.* 2002; Chapais 2006), e.g., macaques (Hill 1994; Silk 1994), baboons (Noë 1992; Noe and Sluijter 1995), and chimpanzees (Mitani *et al.* 2000, 2002).

Howlers (*Alouatta* spp.) are good subjects to test hypotheses about male-male social relationships because they show great variability in inter- and intraspecific social structure, which includes a mixture of 1-male and multimale bisexual groups in most populations (Di Fiore and Campbell 2007). The 2 most studied howler species, mantled howler (*Alouatta palliata*) and red howler (*Alouatta seniculus*), show striking differences in their grouping patterns and social behavior (Crockett and Eisenberg 1987; Pope 2000). Mantled howlers live in relatively large groups from 2 to *ca.* 40 members with an average of 3 adult males and 5 adult females (Di Fiore and Campbell 2007). Single mantled howler males can successfully take over established groups by achieving the dominant position, while deposed dominant males may remain in the group as subordinates (Clarke 1983;

Glander 1992). Researchers at La Pacifica, Costa Rica showed that mantled howler males display an age-reversed linear dominance hierarchy based on supplantations at feeding and resting sites (Glander 1980, 1992; Jones 1980). However, in 1 group of mantled howlers on Barro Colorado Island, Panama, Wang and Milton (2003) discerned no dominance ranks apart from a dominant male. Red howlers live in small groups of 2–17 individuals with an average of 2 adult males and 3 adult females (Di Fiore and Campbell 2007). Coalitions of 2–4 male red howlers are more successful at taking over groups, ousting resident males, and defending their new group against other males than single males are (Crockett and Sekulic 1984; Pope 1990, 2000). Single males very rarely take over groups successfully, and more typically join established groups as subordinates (Crockett and Pope 1993; Crockett and Sekulic 1984; Izawa 1997; Izawa and Lozano 1991; Kimura 1992; Pope 1990, 2000).

Black howlers (*Alouatta pigra*), which are endemic to southern Mexico, Belize, and northern Guatemala, form a sister clade with mantled howlers (Cortés-Ortiz *et al.* 2003; Ford 2006), yet, their grouping patterns and social system appear to be more similar to those of red howlers. Group size ranges from 2 to 12 individuals with an average of 2 adult males and 2 adult females (Van Belle and Estrada 2006). Both coalitions of 2–3 males and single males take over groups in Belize (Horwich *et al.* 2000), but it is not known whether coalitions of black howler males cooperate with one another to accrue similar advantages as red howler males do or whether single males successfully take over groups by establishing dominance ranks as mantled howler males do. Further, though all howlers engage in mutual howling during dawn choruses and intergroup encounters, participation in howling bouts by subordinate black howler males can be highly variable and may be a measure of the strength of the cooperative alliance among them (Kitchen 2004; Kitchen *et al.* 2004). In fact, very little is known about male cooperation in black howlers and the ways it may be reflected in their spatial and social relationships with one another or with females.

We provide data on patterns of changes in male group membership, on spatial and social relationships among males and their howling patterns, and on spatial relationships between males and females and male mating success during a 14-mo study characterized by frequent changes in male group membership. We predicted that pairs of black howler males cooperating with one another would be more successful at joining established groups, ousting resident males, and preventing other males from subsequently joining or taking over their groups than single males could. We also predicted that cooperating male dyads would exhibit strong spatial associations and engage in relatively frequent affiliative interactions and mutual howling, and that either one or both males in a cooperative alliance would have stronger associations with females and higher mating success than other males in their groups would.

Materials and Methods

Study Site and Subjects

Palenque National Park (PNP), in northeastern Chiapas, Mexico (17° 28′N, 99° 03′W; Fig. 1), encompasses 1771 ha of which 597 ha are covered by primary tall evergreen

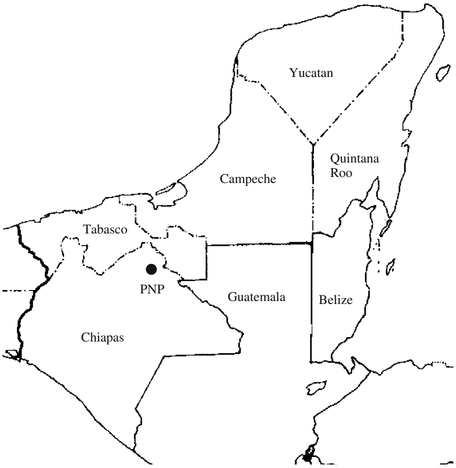

Fig. 1 Map of Southern Mexico, Belize, and Guatemala. Palenque National Park (PNP) is indicated by dot.

tropical rain forest, 300 ha contain forest vegetation in various stages of regeneration, and the remaining land consists of human-induced pasture lands (Díaz Gallegos 1996). Mean annual rainfall is 2200 mm with a dry season between January and April (mean monthly rainfall = 62±18 mm) and a wet season between May and December (mean monthly rainfall = 240±106 mm). Mean temperature is 26°C (range 22–29°C; Estrada *et al.* 2002). Population surveys in 2000 reported the presence of 128 monkeys in 19 groups and 8 solitary individuals in PNP (Estrada *et al.* 2002). Mean group size was 6.74 individuals, ranging from 2 to 12 individuals. Sixty percent of the groups were multimale, with an average of 2.05±0.91 adult and subadult males, 1.95±1.03 adult and subadult females, and 2.74±1.88 immatures. Estimated density for the howler population was 23 individuals/km^2.

We selected 2 multimale, multifemale black howler groups (Balam and Motiepa) for systematic observations based on their group composition and accessibility. The groups inhabited the same section of the primary tall forest, but their home ranges did not overlap. Balam had 1–3 adult males, 0–1 subadult male, 2–3 adult females, and 0–2 immatures. Motiepa had 1–2 adult males, 2 adult females, and 2–3 immatures. Both groups underwent changes in group membership (Table I). We recognized all individuals by permanent scars, broken fingers, genital pigmentation (especially females), or botfly marks.

Data Collection

From June 11, 2006 through July 24, 2007, we collected data during blocks of 8 consecutive days (0630 h–1730 h) separated by 1 day out of the field resulting in 306 data-collecting days in the field. During the 8-d blocks, we alternated observations on each focal group every 2 d. Because the study was part of a broader investigation of sexual behavior in black howlers, during periods of sexual activity in one of the focal groups, we spent more consecutive days with that group at the expense of the other, resulting in more observations on Balam than on Motiepa.

We used 60-min focal individual samples (Altmann 1974) to record the activity of adults and subadults of both sexes in each group. It was not feasible to follow a predetermined sampling sequence owing to the difficulties of locating a particular individual in a densely foliated tall forest. Instead, we conducted focal samples on all subjects in a group before beginning a new round of samples. When this was impossible, we separated focal samples on the same individual by ≥2 h. We also

Table I Events involving changes in group membership for the 2 focal groups

	Date	No. of males original	No. of males left prior	No. of males entered	No. of males ousted	No. of males remained	Male-male aggression
Balam group							
Event 1[a]	Jul 25, 06	3 (BA, RO, PA)	1 (BA)				
	Jul 26, 06			1 (BT)	0	2 (RO, PA)	Chase
Event 2	Aug 7, 06	3 (BT, RO, PA)	0	2 (PE, LO)	2 (RO, BT)	1 (PA)	Fight
Event 3	Aug 26, 06	3 (PE, LO, PA)	1 (PA)				
	Aug 28, 06			1 (BT)	0	2 (PE, LO)	No
Event 4[b]	Sep 24–25, 06	3 (PE, LO, BT)	0	1 (VI)	1 (BT)	2 (PE, LO)	No
Event 5[c]	Oct 28, 06	3 (PE, LO, VI)	2 (PE, LO)	____	0	1 (VI)	____
Event 6[d]	Nov 18–23, 06	1 (VI)	0	2 (DV, LF)	1 (VI)	0	?
Event 7[e]	Dec 18, 06– Jan 7, 07	2 (DV, LF)	0	2 (GZ, KR)	2 (DV, LF)	0	?
Motiepa group							
Event 8	Mar 14, 07	2 (JP, BO)	1 (BO)	0	0	1 (JP)	No
Event 9[f]	Apr 3, 07	1 (JP)	0	1 (HG)	0	1 (JP)	Possibly fight

No. of males original is the number of males during the last contact with the group before the event; No. of males left prior is the number of males that left the group without being ousted; No. of males entered is the number of males that joined one of the focal groups during the event; No. of males remained is the number of males that remained in the group throughout the event. Initials represent male identities.

[a] On July 25, the resident male BA fought with a solitary subadult male, incurred injuries, and subsequently disappeared. On July 26, a solitary adult male BT, not involved in the fight, joined the group.

[b] On September 24, an adult male VI entered the group. VI howled together with PE against BT, which resulted in his eviction on September 25.

[c] During the night of October 27–28 a storm passed over PNP. Even though no trees were damaged in the group's sleeping area, 2 males, PE and LO; 1 female, MI; and 2 immatures disappeared after the event. One male, VI, and 2 females, TE and LU, remained in the group.

[d] Event not observed. We last observed Balam on November 14 with 1 male, VI, and 2 females, TE and LU. On November 18 and 19, we observed 2 solitary adult males, DV and LF, in the home range of Balam. On November 23, we encountered Balam again, now with 2 new males. Presumably DV and LF took over the group, evicting VI.

[e] Event not observed. The event occurred during a period out of field between December 18, 2006 and January 7, 2007. Presumably, 2 solitary adult males, GZ and KR, took over the group, evicting DV and LF.

[f] A solitary male, HG, joined the group. On April 7, he had an open wound above his eye, but we do not know who inflicted the wound.

made weekly adjustments to ensure that all focal subjects' samples were evenly distributed throughout the day. When focal subjects were out of view for >15 min, we started the next focal individual sample and we discarded focal samples of <30 min (Wang and Milton 2003). We analyzed 1832 focal h (Balam: 1027 h; Motiepa: 805 h). During focal samples, we recorded continuously, to the nearest second, all activities and social interactions displayed, along with the identity of all participants and directionality of social interactions. We classified behaviors into the following general categories: resting, feeding, moving within and traveling between feeding or resting patches, vocalization, scent-marking, social behavior, and out of sight. We subdivided vocalizations into howling, i.e., roaring and barking, and nonhowling, i.e., all other types of vocalizations. Social behaviors included supplantations, agonistic interactions (pushes, chases, grabs, and fights), aggressive displays (branch breaking and branch shaking), affiliative interactions (playing, greeting, embracing, touching, and allogrooming), and sexual interactions (solicitations and copulations).

We conducted instantaneous scan samples (Altmann 1974) during the first 5 s of every 10-min interval throughout the focal individual samples to record the identity of all independent neighbors at 0 m, >0–1 m, and >1–5 m of the focal individual (Wang and Milton 2003). We included only scan samples for which we identified all neighbors, representing 11,117 scan samples (Balam: 6328 scan samples; Motiepa: 4789 scan samples). In addition, we recorded all occurrences of social and sexual behaviors observed *ad libitum* (Altmann 1974).

Data Analyses

The 14-mo study was characterized by 9 discrete changes in male group membership that occurred in the 2 focal groups (Table I). Therefore, we divided the observations into 11 periods based on the changes in male membership in the 2 groups (Fig. 2). We excluded focal samples and scan samples collected on days of actual group takeovers to avoid overlap in group membership between incoming males and evicted males.

Because focal subjects spent very little time in contact with neighbors (0.48% of total scan samples), we lumped their time spent in contact with their time spent at >0–1 m. We calculated the spatial relationships for each male-male dyad as the percentage of time that pairs of males were in proximity (0–1 m) and in each other's neighborhood (>1–5 m) during the scan samples for each period. We calculated male-female spatial relationships as the percentage of time that each male was in proximity and in the neighborhood of ≥1 female during the scan samples for each period.

We calculated male-male dyadic rates of social behavior as the number of bouts between pairs of males per observation hour for both males. We defined a social bout as ≥1 events of social behavior of the same category, i.e., agonistic interactions, affiliative interactions, and supplantations, between the same individuals separated by ≤5 min (Neville 1972).

To compare spatial and social patterns among males, we distinguished male-male dyads by whether pairs of males were present at the onset of the study or remained in the group together after a change in another male's membership, i.e., remaining male dyads; whether the males had entered the group together, i.e., entering male dyads;

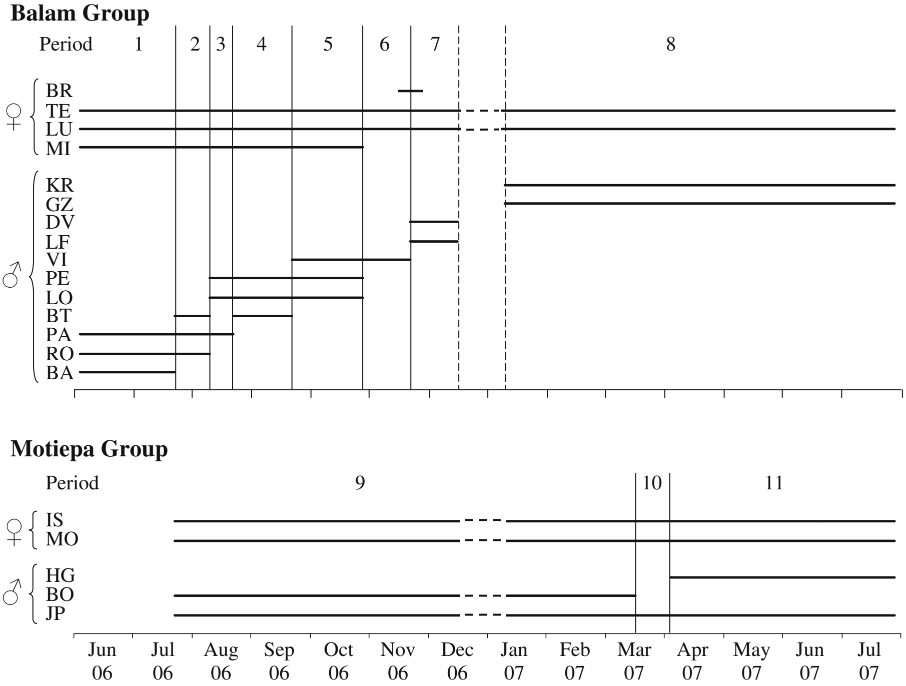

Fig. 2 Group membership changes for the 2 focal groups. Initials represent adult males and females in each group (PA and BR are subadults). Solid vertical lines represent events involving changes in group membership (Table I). Dotted vertical and horizontal lines represent a period out of the field. The numbers refer to the different periods based on the changing identities of adult males.

or whether dyads comprised an entering and a remaining male, i.e., entering-remaining male dyads.

In 4 of the 11 periods, ≥1 female was sexually active. Though mating success does not always coincide with reproductive success (Manson 2007), in the absence of paternity data, we tallied copulation frequencies for each male during the periods, and compared them with the percentage of time males spent in proximity with all females.

To examine male contributions to howling bouts, we calculated the hourly rate at which each male howled with ≥1 other group member, the hourly rate at which each male howled alone, the percentage that each male participated in howling bouts, and the percentage of howling bouts that each male initiated. We defined a howling bout as a sequence of continuous howling interrupted by ≤15 min of silence (Sekulic 1982a). To calculate the hourly rates of howling with group members, we first calculated rates of howling with group members per focal sample for each male, i.e., the sum of seconds the focal male howled with group members in a focal sample/duration of that focal sample in seconds. If we collected >1 focal sample for a male on any given day, we took their average rate. We then calculated hourly rates of howling with group members as the average of rates per day for each male across the 11 periods. We calculated hourly rates of howling alone for each male across the 11 periods in the same manner. We expressed each male's participation in howling bouts as the percentage of time he howled during all howling bouts recorded during focal samples for each period. We compared each male's contribution to howling bouts with the percentage of his time spent in proximity with females.

All statistical tests were nonparametric and 2-tailed, with $\alpha \leq 0.05$. We used Kruskal-Wallis tests when comparing the interactions between the 3 classes of male-male dyads, i.e., remaining male dyads, entering male dyads, and entering-remaining male dyads. We used χ^2 tests to compare the frequency of male proximity patterns with females, their frequency of participation in howling bouts, and the number of howling bouts they initiated in each period (Wang and Milton 2003), comparing observed values with expected values. We calculated the expected values under the null hypothesis that males associated equally with females and contributed equally in howling bouts. Results are means ± SD.

Results

Changes in Group Membership

The 9 discrete changes in male group membership involved 13 males (Balam: 7 changes involving 11 males; Motiepa: 2 changes involving 2 males; Table I). A 14th male was present in Motiepa throughout the study period. In 3 cases, the departure of 1 resident male was rapidly followed by the immigration of a new male into the group. In 1 case, an adult male joined the group and evicted 1 of the 3 resident males. In 3 cases, 2 solitary males jointly took over the group, evicting the resident adult males, and in 1 of these cases, the subadult disappeared 18 d after the takeover. The remaining case occurred when 5 individuals (2 adult males, 1 adult female, and 2 immatures) disappeared after a strong local overnight storm.

In 2 of the 5 observed cases in which male(s) entered our focal groups, resident males aggressively defended their positions in the group (Table I). It is possible that in a third case, the resident male JP of Motiepa injured the incoming male HG, but we did not observe this. Four days after HG had joined the group, he had an open wound above his left eye.

Based on the changing identities of adult males, we recognize 8 distinct periods in the history of Balam and 3 distinct periods in the history of Motiepa (Fig. 2). The number of males present in each period varied from 1 ($n=2$), to 2 ($n=4$), to 3 ($n=5$). Of the 16 different pairs of males, 2 persisted across 2–3 periods (Fig. 2). We examined the dyads in each period separately to evaluate whether their relationships changed over time, which resulted in a total of 19 male-male dyads across all 11 periods. Seven of the dyads were remaining male dyads, 3 were entering male dyads, and 9 were entering-remaining male dyads.

Male-male Spatial Patterns

Male-male dyads ($n=19$) spent on average 4.3±9.5% of their time in proximity (median = 0.3%, range = 0–30.7%), and 19.7±16.3% of their time in the neighborhood of one another (median = 13.1%, range = 1.0–60.0%). Owing to the low frequencies that males spent in proximity of each other, we combined the 2 spatial categories and compared the frequencies at which male-male dyads spent at

0–5 m. Spatial patterns do not differ significantly among remaining male dyads, entering male dyads, and entering-remaining male dyads (Fig. 3; Kruskal Wallis χ_2= 1.504, df=2, p=0.618).

Four dyads involving 2 different pairs of males maintained close association in 4 of the periods (Fig. 3). In period 2, RO and PA spent 48.8% of their time at 0–5 m of one another, which is significantly greater than in period 1, when they spent 5.8% of their time at 0–5 m (χ^2=37.9, df=1, p<0.0001). One can attribute their close association to the significantly closer associations among all group members during the period after the disappearance of one resident adult male and the entrance of a new adult male into the group (event 1 in Table I) than before the changes (period 2: mean = 27.34±14.27% vs. period 1: mean = 13.15±9.91%, Wilcoxon signed test: n=15 adult and subadult dyads of both sexes, Z=−2.442, p=0.015). The other pair of males, PE and LO, entered Balam together in period 3 and remained together in the group through periods 4 and 5. They maintained close association across all 3 periods (Fig. 3). PE and LO were significantly closer to each other than either PE or LO was to the third resident male during the 3 periods (n_1=3, n_2=6, U=0.0, p= 0.020). They were the only pair of males that displayed such a close and persistent spatial association spanning successive periods.

Male-male Social Interactions

Rates of social interactions among males were uniformly low (Fig. 4). During >1800 h of observation, only 4 bouts of male-male aggression (mean dyadic rate = 0.007± 0.018 bouts/h, range = 0.0–0.066 bouts/h), 11 bouts of male-male supplantation (mean

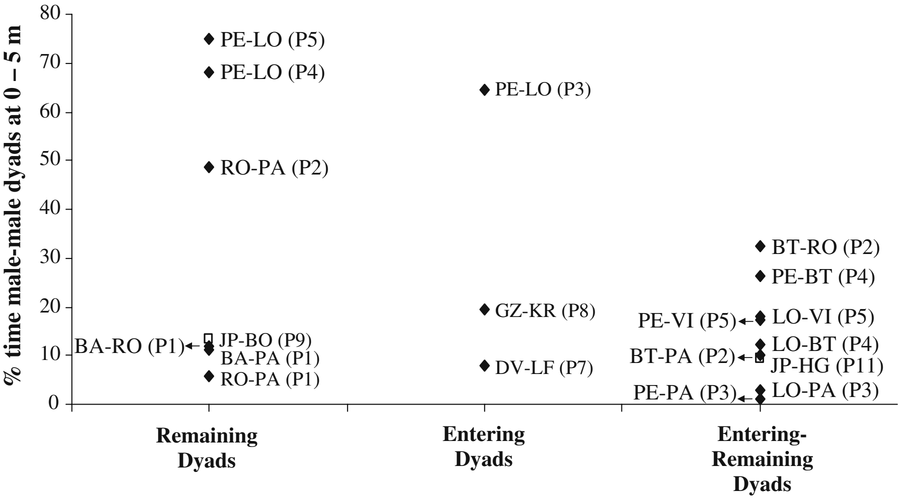

Fig. 3 Percentage of time male-male dyads spent at 0–5 m. Remaining Dyads are male-male dyads present at the beginning of the study or remaining in the group after a change in male group membership; Entering Dyads are male-male dyads entering a focal group together; and Entering-Remaining Dyads represent dyads between 1 male that recently entered the group and another male that remained in the group. For each dyad male identities and period (P#) are given, per Fig. 2. ♦ = dyads in Balam; □ = dyads in Motiepa.

dyadic rate = 0.009±0.017 bouts/h, range = 0.0–0.059 bouts/h), and 14 bouts of male-male affiliation (mean dyadic rate = 0.009±0.025 bouts/h, range = 0.0–0.100 bouts/h) occurred. Though the sample size is too small for reliable statistical analyses, both remaining and entering male dyads tended to engage in lower rates of agonism and higher rates of supplantation and affiliation than entering-remaining male dyads did (Fig. 4).

Male-female Spatial Patterns and Male Mating Success

Males spent an average of 4.3±3.6% of their time in proximity (median = 3.9%, range = 0.0–12.2%) and 23.6±12.0% of their time in the neighborhood of ≥1 female (median = 21.0%, range = 7.9–47.8%; *n*=25 males across 11 periods). We detected significant differences in male proximity with females in 6 of the 9 periods with multiple males present (Fig. 5). In 5 of these periods—periods 1, 7, 8, 9, and 11— 1 male spent significantly more time in proximity to ≥1 female than the other male(s) did (Fig. 5). In periods 1, 7, 8, and 11, ≥1 female was sexually active and in consortships that involved close proximity with the males. Excluding days with sexual activity did not alter the strength of associations between these males and females. The males with the strongest female associations copulated most often (Table II).

In period 4, the 2 males that associated closely with one another (PE and LO) both spent significantly more time in close proximity to females than the third male present did. In the other 3 periods with multiple males present—periods 2, 3, and 5— there was no evidence that a particular male spent significantly more time in close proximity to females (Fig. 5).

In 2 periods, only 1 male was present. In period 6 of Balam, VI was not in proximity to the 2 females remaining after the storm, which is similar to the previous

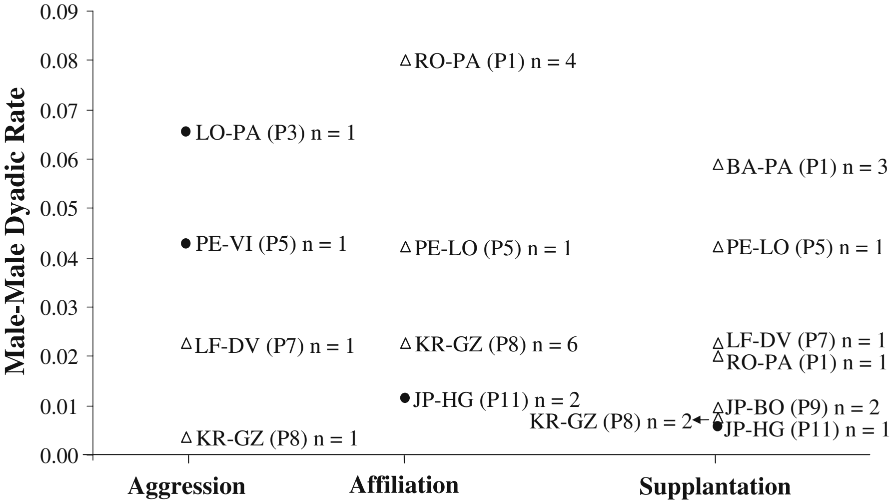

Fig. 4 Rates of aggression, affiliation, and supplantation bouts per observation hour between male-male dyads. We show only dyads engaging in social interactions. For each dyad, male identities, period (P#), and number of bouts are given. △ = remaining male dyads + entering male dyads. ● = entering-remaining male dyads.

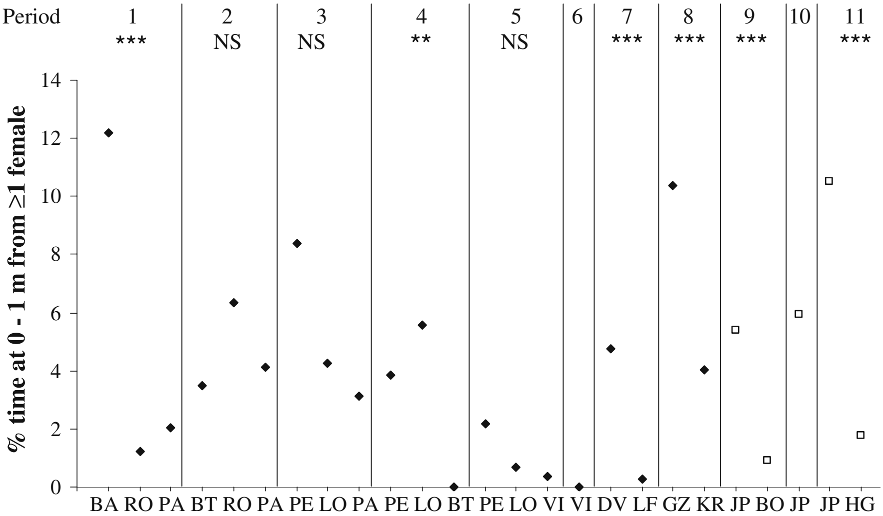

Fig. 5 Percentage of time males spent in proximity of ≥1 female across the different periods, per Fig. 2. Initials on the *x*-axis represent individual males. χ^2 tests compare males within the same period. For example, for period 1, BA spent significantly more time close to females than RO and PA did. *$p<0.05$, **$p<0.01$, ***$p<0.001$. ♦ = males in Balam; □ = males in Motiepa.

period when he also did not spend time in proximity to the 2 females. In period 10 of Motiepa, JP maintained his strong associations with females after the disappearance of the male with weak female associations (Fig. 5; $\chi^2=0.1$, df=1, $p=0.729$).

Howling Patterns Among Males

Hourly rates of howling with group members and of howling alone for each male per period are in Table III. In 6 of the 9 periods with multiple males present, >1 male howled alone and resident males tended to howl alone at similar rates. In period 1, the male with strong female associations (BA) was the only male to howl alone. In periods 4 and 5, only 1 male (PE in both periods) howled alone but sample sizes are too small to rule out that the other resident males did not howl alone. In 5 of the 9 periods with multiple males present, all resident males participated equally often in howling bouts, i.e., they often howled mutually (Table III). In the other 4 periods, 1 male participated in howling bouts significantly less while the other 2 resident males

Table II Distribution of copulations among resident males and females in 4 periods

	Male with strong female associations	Male(s) with weak female associations
Period 1	BA: 23	RO: 0; PA: 0
Period 7	DV: 2	LF: 0
Period 8	GZ: 30	KR: 3
Period 11	JP: 14	HG: 0
Sum of copulations	72	

Per period, male identity and number of observed copulations is given.

participated in howling bouts equally often, i.e., they often howled mutually and were seldom joined by the third male (Table III). In 3 of these periods, the same and only subadult male rarely participated in howling bouts.

Balam engaged in 268 howling bouts and Motiepa in 136 howling bouts, including 29 bouts and 16 bouts, respectively, during which 1 male howled alone. We established the initiator for 147 of the howling bouts (54.9%) in Balam and for

Table III Contribution of each male to howling bouts measured as hourly rates howling with group members, hourly rates howling alone, % participation in howling bouts, and the number of howling bouts initiated per period

		Hourly rate howling with group members	Hourly rate howling alone	% participation in howling bout			No. of howling bouts initiated	
Balam								
Period 1	BA	0.027 ± 0.076	0.008 ± 0.024	100.0	< 0.0001[a]	0.156[b]	36	< 0.0001
	RO	0.016 ± 0.050	0	81.0			2	
	PA	0.001 ± 0.003	0	5.3			0	
Period 2	BT	0.031 ± 0.057	0.036 ± 0.057	90.8	< 0.0001	0.114	6	____
	RO	0.081 ± 0.142	0.022 ± 0.039	70.4			3	
	PA	0	0	0.6			0	
Period 3	PE	0.122 ± 0.281	0.018 ± 0.042	98.4	< 0.0001	0.268	3	____
	LO	0.039 ± 0.096	0.003 ± 0.008	80.5			2	
	PA	0	0	0.0			0	
Period 4	PE	0.060 ± 0.113	0.004 ± 0.011	93.2	0.0003	0.762	3	____
	LO	0.013 ± 0.032	0	88.1			0	
	BT	0.006 ± 0.013	0	38.0			0	
Period 5	PE	0.003 ± 0.009	0.001 ± 0.001	100.0	0.998		1	____
	LO	0.005 ± 0.016	0	97.8			0	
	VI	0	0	98.2			3	
Period 6	VI	0	0.015 ± 0.034	100.0	____		5	____
Period 7	DV	0.060 ± 0.171	0.016 ± 0.031	93.0	0.583		9	0.035
	LF	0.009 ± 0.032	0.004 ± 0.016	85.6			2	
Period 8	GZ	0.050 ± 0.096	0.004 ± 0.015	93.0	0.236		9	< 0.0001
	KR	0.055 ± 0.091	0.009 ± 0.034	97.6			63	
Motiepa								
Period 9	JP	0.025 ± 0.079	0.006 ± 0.027	83.1	0.199		25	0.033
	BO	0.019 ± 0.048	0.005 ± 0.023	91.6			12	
Period 10	JP	0.002 ± 0.005	0.009 ± 0.022	100.0	____		6	____
Period 11	JP	0.029 ± 0.140	0.004 ± 0.022	95.0	0.881		17	0.002
	HG	0.044 ± 0.103	0.004 ± 0.018	96.5			3	

[a] *p* value of χ^2 tests comparing all resident males per period; χ^2 compared observed values with expected values calculated under the null hypothesis that males contributed equally to howling bouts.

[b] *p* value of χ^2 tests comparing 2 resident males if there was a significant difference among all resident males.

62 bouts (45.6%) in Motiepa. The males with the strongest female associations initiated significantly more howling bouts than the other resident males (67.6–94.7%) in 4 periods (Table III). In period 8, the male with the weakest female associations (KR) initiated significantly more howling bouts (87.3%) than the male with the strongest female associations did (Table III). Unfortunately, in the periods when no particular male had strong associations with females, howling bouts were too infrequent to detect any pattern among males.

Discussion

Both single males and pairs of males entered our focal groups, indicating that black howler males do not require an ally to enter an established group. However, single males tended to join groups, whereas pairs of males entering groups together successfully evicted all other adult, but not subadult, resident males. Nonetheless, pairs of resident males cooperatively defending their groups were not always successful at preventing single males or pairs of males from joining their groups or usurping them. Our findings are consistent with those on changes in male group membership in a population of black howlers in a fragmented forest at Community Baboon Sanctuary (CBS), Belize (Horwich *et al.* 2000). In addition, Horwich *et al.* (2000) observed a single male that successfully evicted resident males in 2 of 7 group takeovers. The patterns are similar to those of red howlers (Crockett and Pope 1993; Crockett and Sekulic 1984; Izawa 1997; Izawa and Lozano 1991; Kimura 1992; Sekulic 1983). Unique to our study is the rapid changes in male group membership over a relatively short period of time in Balam: 7 changes in 6 mo. Horwich *et al.* (2000) and Sekulic (1983) described disappearances of resident males in a group that perpetuated in changes in neighboring groups. The rapid sequence of changes in male membership in Balam could also be part of such cascading effects, but we were not familiar enough with the individuals of neighboring groups to confirm this.

Changes in male group membership by our subjects sometimes, but not always, involved overt male-male aggression, as was also the case in CBS (Horwich *et al.* 2000). When the interactions escalated to physical aggression, males could incur bloody and even lethal wounds. In all 4 observed changes in group memberships in red howler males, males incurred bloody wounds during fights and 1 male died from his injuries (Crockett and Pope 1988; Izawa 1997; Izawa and Lozano 1991; Sekulic 1983). Though data on changes in male membership in black howlers are still preliminary, resident black howler males might experience high levels of intergroup competition over access to receptive females, and males forming coalitions to usurp established groups jointly and to defend their group against other males might accrue higher benefits than males acting alone.

We predicted that males cooperatively taking over groups and defending their groups would maintain close associations and engage more frequently in affiliation than aggression relative to other males. Our results show that black howler males were rarely in close proximity or interacting with one another. The spatial relationships of remaining and entering male dyads were indistinguishable from those of entering-remaining male dyads. Only 1 of the 3 pairs of males that jointly took over a group maintained a close spatial association, and even this dyad did not succeed in preventing 2 additional males from joining their group in 2 successive periods. The situation differs from the close associations between resident adult and subadult red howler males, possibly fathers and sons, whose coalitions successfully ousted a third resident adult male on 2 of 3 occasions (Sekulic 1983).

Our results indicate a tendency for remaining and entering male dyads to engage in affiliation at higher rates and in aggression, excluding supplantations, at lower rates than entering-remaining males; but, the significance of the difference is difficult to assess because of the overall low rates at which interactions of any kind occurred. Nonetheless, instead of dominance hierarchies, relationships among black howler males seem to be based on tolerance and avoidance, and the history of joint actions between pairs of males against other males are not overtly reflected in either their spatial or social relationships. Low rates of social interactions are characteristic for howlers (Altmann 1959; Crockett and Eisenberg 1987; Kowalewski 2007; Sekulic 1983; Wang and Milton 2003; Zucker and Clarke 1986), yet in mantled howlers in groups with ≥3 adult males, a dominant male could be recognized (Dias *et al.* 2008; Jones 1980; Wang and Milton 2003). Further, affiliation among mantled howler males most frequently involved greeting behavior (Dias *et al.* 2008; Wang and Milton 2003). The ritualized embracing and mutually inspecting of their partner's genitals may serve to reaffirm social relationships among male coalitions (Colmenares 1991; Dias *et al.* 2008; Smuts and Watanabe 1990; Wang and Milton 2003). Though no comparable greeting behaviors occurred among male black howlers at PNP, researchers have observed them in black howler males in CBS, especially during howling bouts during group encounters (Kitchen 2004, *pers. comm.*; see also Sekulic 1982b). Like greetings in mantled howlers, greetings in black howler males could serve to reinforce their social relationships and their commitment to cooperative group defense. Though PNP focal males groomed, played, and touched one another in affiliative contexts, the rates of the interactions were too low to assess their contribution to male social relationships overall.

Despite the weak spatial relationships and low rates of interactions among most males in our study, male-female dynamics were highly skewed. One male formed significantly closer associations with resident females during 5 of the 9 periods with multiple resident males in the group, and achieved higher mating success during 4 of the periods when ≥1 resident female was sexually active. Also, in one period with only 1 resident male present, the male maintained his strong associations with the resident females after the departure of the other male. Similar patterns occurred in other howler populations, in which researchers used variation in male-female spatial relationships to distinguish dominant vs. subordinate males (Kitchen *et al.* 2004; Wang and Milton 2003). In red howlers, the resident male with the strongest association with resident females had priority access to receptive females (Sekulic 1983), and paternity studies have revealed that the dominant male sired most, if not all, offspring conceived during his tenure (Pope 1990). Likewise in mantled howlers, dominant males had more spatially central positions in the group, yet it did not necessarily lead to increased mating success because all resident males mated with receptive females (Jones 1982, 1985; Wang and Milton 2003). Further analyses of male-female social relationships and female mate choice are necessary to investigate the mechanisms responsible for the disproportionate success of socially central black howler males. As in mountain gorillas (*Gorilla beringei beringei*), wherein male-female relationships form the core of bisexual groups (Robbins 1996; Sicotte 1994), black howler males may attempt to form strong relationships with resident females instead of with one another. The 5 periods in which no particular male maintained significantly closer associations with resident females may have been too unstable for any of the males to establish strong associations with females because of the high rates of male membership changes. By contrast, the 6 periods in which we detected strong male-female associations might indicate greater social stability.

Because the male with the strongest female associations and highest mating success may have more to lose if ousted by incoming males, the relative benefits of defending his position by initiating howling bouts might be higher for him than for other males (Kitchen *et al.* 2004; Sekulic 1982b). Consistent with this prediction, the males with the strongest female associations initiated more howling bouts than other males did during 5 of 6 socially stable periods. However, in 1 period, the male with the weakest female associations and lowest mating success initiated the most howling bouts. Further, both males with strong and with weak female associations howled alone at similar rates and participated equally in mutual howling bouts. Our findings differ from those of Kitchen *et al.* (2004), wherein only the male with the strongest female associations howled alone and males with the weakest female associations and short-term associations with the other resident males varied in their participation in howling bouts. However, ≥2 of our resident males usually howled together regardless of their relationships: remaining and entering male dyads vs. remaining-entering male dyads. Their participation in mutual howling bouts implies a strong and consistent commitment to group defense and appears to be their most obvious expression of any cooperative alliances. Kitchen *et al.* (2004) suggested that black howler males with weak female associations were more likely to join in howling bouts with males with strong female associations if they were related. Similarly, in red howlers, dominant males had longer tenures when their coalitionary males were kin than nonkin resident males (Pope 1990). Thus, at least some of the male dyads that howled together during our study may have been related to one another. Studies of relatedness among black howler males are necessary to examine the variation among males in participation in howling bouts and social relationship more generally.

Our study was characterized by many changes in male group memberships in 1 of the 2 study groups (Balam), which might have caused an unusually extended period of social instability that affected our ability to evaluate the degree to which our focal subjects formed cooperative coalitions. Our findings suggest that black howler males experienced high intergroup competition over access to females. Though pairs of males were more successful at taking over established groups, males did not always have allies when they joined a group, and pairs of males did not always succeed in their efforts to keep other males from joining or usurping their group. Apart from the participation of resident males in mutual howling bouts, neither their spatial nor social relationships indicated strong cooperative relationships. Further, our findings suggest that variation in social relationships among black howler males, and group stability overall, may be influenced more by the ability of males to establish strong relationships with females than by the formation of cooperative alliances with one another *per se*.

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