SHORT COMMUNICATION

Coalitions and male–male behavior in *Alouatta palliata*

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Abstract Coalitions influence the establishment and maintenance of social relationships among males in primate species. In this study, we compare the social behavior of males between two groups of *Alouatta palliata*: a group that was recently taken over by a coalition of two males (Mt), and a group that had a stable composition for at least 9 months (Rh). We predicted that coalition partners would be more cooperative and less competitive than dyads formed by immigrant and long-term resident males, and dyads formed by long-term resident males. Additionally, we predicted that these dyadic trends should be reflected in more competition and less cooperation in the group that was taken over. As predicted, the coalition partners of Mt showed the highest levels of cooperation among all dyads and the second lowest rate of agonism. Cooperation was higher in the group that had a stable composition. Results from this study suggest that the social relationships of male mantled howlers vary as a function of familiarity between males and that in the context of coalitionary takeovers, coalitionary males are highly cooperative. Cooperation is lower in groups recently taken over and competition is more intense, perhaps as a consequence of the process of establishment and reorganization of power relationships within some dyads. In the future, we must determine the frequency of coalitionary takeovers in this population and assess its ultimate consequences for male–male social relationships.

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Introduction

The formation of male–male coalitions to takeover groups has been observed in many primate species (Harcourt and de Waal 1992). In general, these coalitions are expected to result in benefits for coalition partners, both in terms of increasing their probabilities of usurping resident males, and improving their fitness (van Schaik et al. 2004). Therefore, coalitions in the context of group takeovers are expected to influence the social relationships of males.

In howlers (genus *Alouatta*), immigrating males attain group membership by defeating dominant males (Pope 1990; Glander 1992; Van Belle et al. 2008). Takeovers are associated with intense fighting, which frequently results in injuries and sometimes in the death of males (Crockett and Pope 1988; Cristóbal-Azkarate et al. 2004; Van Belle et al. 2008). In mantled howlers (*Alouatta palliata*), males usually invade groups individually, and defeated males remain in the group (Glander 1992; Ryan et al. 2008). Infanticide is also common following takeovers (Crockett 2003), and dominant males have priority of access to receptive females (Jones 1995; Ryan et al. 2008). Therefore, in mantled howlers, male immigrations impose fitness costs to resident males.

In this study, we compared the social behavior of males between a group of mantled howlers that was recently invaded and a group with stable composition, and we analyzed the influence of familiarity on both dyadic and group-level male–male social behavior. In particular, we predicted that when males join groups in pairs, coalition partners would be more cooperative and less competitive than dyads formed by immigrant and long-term resident

males, and dyads formed by long-term resident males. Additionally, we predicted that these dyadic trends should reflect in more competition and less cooperation in the group that was taken over.

Methods

Study groups and subjects

Since the late 1990s, the Universidad Veracruzana and Universitat de Barcelona have carried out systematic studies on the demography, behavior, and ecology of *Alouatta palliata mexicana* in the northern tract of Los Tuxtlas, Mexico (Cristóbal-Azkarate et al. 2009). During our surveys, in December 2003, we observed two males invading a group of mantled howlers near the village of Montepío. This group (henceforth Mt; 18°38′29″N, 95°05′28″W) included two males, four females, a subadult, and four immatures. One of the resident males was attacked by the invading males during the takeover and subsequently died. Following the takeover, the adult composition of this group remained unchanged until the end of the study (i.e., three males and four females). In order to understand how familiarity and takeovers affect the behavior of males, we selected another group that lived near the first group (ca. 2.5 km), with similar size and composition but a stable composition (henceforth Rh; 18°37′13″N, 95°06′45″W). In February 2004, when our systematic observations began, Rh composition had remained unchanged at least since May 2003. This group comprised three males, three females, two subadults, and one infant.

Data collection

The behavior of males was observed for 732.5 h (Mt = 361.25 h; Rh = 371.25 h) distributed over 10 months (February to November 2004). We sampled each group for an average [± standard deviation (SD)] of 5 days each month (Mt = 5.4 ± 0.51 days; Rh = 5.5 ± 0.53 days) and an average of 6.72 h each observation day (Mt = 6.69 ± 0.64 h; Rh = 6.75 ± 0.63 h). All males were easily identifiable by their natural marks, such as physiognomy; blond hairs and skin pigmentation on the feet, hands and tail; scars; and broken fingers. We recorded all occurrences (Altmann 1974) of: (1) agonistic (threats, supplants, pushes, fights) and affiliative (greetings) interactions; (2) establishment of sexual consortships inside (copulations take place within the context of the group in view of other mature males) or outside (when a male leaves his group with a receptive female and copulates with her out of view and vocal contact with other group males) the groups (see Jones 1995), and the interference of other males in ongoing sexual activities; (3) number of males that participated in loud

calls, in other words, roaring and barking (hereafter howling; Whitehead 1987). To study proximity patterns, we used the focal animal sampling (1-h samples) with an instantaneous recording repeated at 15-min intervals (Altmann 1974). In each instantaneous recording, we noted the presence of all males ≤5 m from the focal. Focal observations were evenly distributed across all males in each group.

Data analyses

We used a Mann–Whitney test to compare the rates of social interactions per hour between groups, calculated for each observation day as the frequency of interactions observed in a particular day, divided by the number of observation hours performed in that day (Mt = 54 observation days, Rh = 55). With the same test, we compared the proportion of time spent in proximity per focal between groups, calculated per focal period as the percentage of instantaneous samplings in which the focal had another male at ≤5 m (Mt = 362 focals, Rh = 374). We determined the dominance hierarchy based on decided agonistic interactions (i.e., when one male displayed only submissive signals whereas the other displayed only aggressive signals, or when one male displayed submissive signals whereas the other male failed to respond; Silk et al. 2004). Dominance ranks of males were then calculated with David's score. This method provides a weighted measure of individual agonistic success, as it is based on the outcomes of decided agonistic interactions of individuals with other group members, while taking the relative strengths of their opponents into account (Gammell et al. 2003). We used the mean rank distance among males as a measure of the consistency of dominance relationships, calculated as the difference between the ranks of males in each dyad; small distances indicate undecided rank relationships and higher probabilities of engaging in aggression (de Waal 1991). We used χ^2 tests to compare among dyads within each group: (1) rates of affiliation and agonism; (2) time spent in proximity; (3) proportion mutual howling. We used the same test to compare between groups the proportions of: (1) consortships established outside the group; (2) number of males participating in howling. In both cases, we compared observations with expected values calculated on the premise that each dyad's and group's data set was independent and that no preferential association existed between dyads and groups, respectively. In these tests, degrees of freedom are shown as subscripts.

Results

The dyad formed by the coalition partners of Mt exchanged significantly more affiliation than the dyads formed by those

males and the male that resided in the group before the takeover ($\chi_2^2 = 14.00$, $P < 0.001$; Fig. 1a). In both groups, there were differences among dyads in the rates of agonism (Mt: $\chi_2^2 = 28.152$, $P < 0.001$; Rh: $\chi_2^2 = 17.538$, $P < 0.001$), which in Mt were due to less agonism exchanged between the coalition partners (Fig. 1b). The proportion of time dyads spent in proximity differed only in Mt due to the frequent proximity maintained by the coalition partners ($\chi_2^2 = 39.716$, $P < 0.001$; Fig. 1c). Finally, in Mt, there were differences among dyads in cooperation during howling, with the coalition partners howling together more frequently ($\chi_2^2 = 7.658$, $P < 0.02$, Fig. 1d).

Affiliative interactions were exchanged at the same rate (0.06/h) in both groups. However, the rates of agonism were significantly higher in Mt (Mt = 0.411/h, Rh = 0.210/h; Mann–Whitney $Z = 2.898$, $N1 = 55$, $N2 = 54$, $P < 0.01$). The most frequent agonistic interactions were threats and supplants, which accounted for 93.2% and 96.2% of all agonistic interactions among males in Mt and Rh, respectively. Agonistic interactions that involved physical contact occurred only in Mt, specifically fights, pushes, and bites. The mean rank distance was higher among males of the Rh group (Mt = 1.44, Rh = 3.25). Males were closer to each other more frequently in Mt (Mt = 6.09%, Rh = 3.57%; Mann–Whitney $Z = 3.107$, $N1 = 362$, $N2 = 374$, $P < 0.001$). In Mt, and in contrast with Rh, the majority of copulations occurred outside the group (Mt = 88.9%, Rh = 20%; $\chi_1^2 = 43.5.09$, $P < 0.001$). We never observed copulation interference between males, and only two males were observed to copulate with receptive females in each group. In Mt, those males were one of the invading males (the alpha) and the remaining resident male (beta), whereas in Rh, those were

the alpha and beta males. Howling was mostly performed by one or two males in Mt, whereas in Rh, all males tended to participate in howling. The proportion of howling in which two males participated was significantly higher in Mt (Mt = 37.5%, Rh = 15%; $\chi_1^2 = 9.91$, $P = 0.002$), whereas the opposite result was found for howling with three males (Mt = 27.6%, Rh = 55%; $\chi_1^2 = 9.09$, $P = 0.003$).

Discussion

Our results support the prediction that the social relationships of male mantled howlers are influenced by familiarity within dyads, and in particular, that coalitionary partners are highly affiliative with one another. Additionally, the observed dyadic patterns are reflected in several group-level measures of cooperation and competition and suggest that cooperation is lower and competition higher in the group recently taken over.

For males of Mt, the lack of previous interaction experience within some dyads may have led to the escalation of conflicts and inconsistencies in their rank relationships. Takeovers disrupt the existing organization (Mason 1993) and require that males establish a new dominance hierarchy (Glander 1992). Although immigrant mantled howlers have to defeat dominants to become group members (Glander 1992; Ryan et al. 2008), it is improbable that a dominance hierarchy is formed from the moment of takeover. Dominance relationships build on information gathering about the power of opponents, which is achieved through assessment (Kitchen et al. 2005). As a consequence of the high costs of aggression, such as the death of the male that was attacked by invading males, assessment is mostly based on behaviors that involve low physical risk (Preuschoft and van Schaik 2000). This may explain the predominance of low-intensity agonistic interactions and greetings in howlers' behavioral repertoire (Wang and Milton 2003; Dias et al. 2008; Van Belle et al. 2008), although in Mt, agonism sometimes escalated toward intense forms of aggression. In contrast, the higher group level cooperation among Rh males, especially in howling, could result from their extended coexistence in the group, as has been observed in both red and black howlers (*A. seniculus*: Kitchen 2004; *A. pigra*: Pope 1990).

This is the first report of the invasion of a group of mantled howlers by a coalition of males. Coalition formation has been reported in black (Horwich et al. 2000; Van Belle et al. 2008) and red (Pope 1990) howlers and seems to be associated with increased abilities to invade and defend groups. Additionally, in red howlers, coalitions formed by related males are more persistent and relate to longer tenure times (Pope 1990). In these species, reproduction is usually monopolized by a single dominant male, and for subordinates, the advantages of cooperating arise from inclusive fitness, group
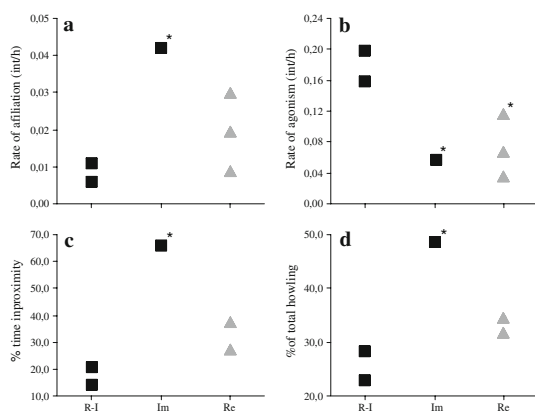

Fig. 1 Cooperation and competition among dyads: **a** rate of affiliation; **b** rate of agonism; **c** percentage of time spent in proximity; **d** percentage of cooperative howling. *R-I* are dyads composed by a long-term resident and an immigrant male; *Im* are dyads composed by immigrant males; *Re* are dyads composed by long-term residents in the group. *Filled squares* dyads in Mt; *filled triangles* dyads in Rh. *Asterisks* dyad contributing large proportion of nonrandomness

membership, and the prospects of becoming dominants (Pope 1990; Kitchen 2004). In contrast, mantled howler groups include more males that are usually not related (Glander 1992), and dominant males do not monopolize reproduction (Jones 1995; Wang and Milton 2003). For these reasons, cooperation in the form of coalitions is probably not so beneficial for mantled howler males. Among the coalition partners of Mt, only one of them copulated during our observations. Therefore, it remains to be assessed whether coalition formation is frequent in Los Tuxtlas. We are currently monitoring the occurrence of takeovers in this population to address this question.

In this fragmented landscape, mantled howlers live in forest patches with diverse environmental and demographic characteristics. Our study groups occupied patches with different population (Mt = 0.7 ind/ha; Rh = 0.1 ind/ha) and group (Mt = 0.08 group/ha; Rh = 0.02 group/ha) densities, which could lead to variation in intragroup (e.g., more agonism) and intergroup (e.g. more howling) competition. It may be hypothesized that these differences in demography explain why males in Mt form coalitions to takeover groups, and inclusively, why Rh's composition was stable for so long. When populations are near to carrying capacity or are already saturated, the ability of single males to invade groups decreases (Crockett and Janson 2000), and takeovers become more frequent (Sterck 1998). Additionally, the presence of groups with different numbers of males in the vicinity of the two study groups could also explain differences in howling patterns, as howlers' vocal responses to neighboring groups vary as a function of numeric odds and of the behavior of rivals (Sekulic 1982; Whitehead 1987; Kitchen 2004). Therefore, in the future, we will have to assess the relationship between these and other ecological and demographic characteristics and the cooperation and competition patterns of males in Los Tuxtlas.

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