# Seasonal Changes in Male Associative Behavior and Subgrouping of *Alouatta palliata* on an Island

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Received March 10, 2005; revision July 6, 2005; accepted October 19, 2005; Published Online December 5, 2006

Howler groups are usually spatially cohesive and stable in composition; however, more flexible grouping patterns occur in some social groups. We analyzed the associative and subgrouping patterns of males living in a group with fission-fusion social organization. Based on information from previous studies on Alouatta palliata and other primates and in the current socioecological models, we established initial predictions on the variations in male behavior according to several socioecological factors. We studied associative behavior via scan sampling at 15-min intervals to register the identity of males in the subgroups and the presence and number of receptive females. We calculated an association index that was then transformed into a measure of association strength. We found individual association trends, as well as important seasonal differences in the subgrouping patterns of males. During the dry season the presence of many receptive females resulted in reduced levels of association, and therefore fewer males per subgroup. The scenario changed during the wet season, when males grouped together significantly more and kinship relationships were a major determinant for individual association preferences.

**KEY WORDS:** *Alouatta palliata*; grouping patterns; interindividual association; male behavior; seasonality.

## INTRODUCTION

A basic assumption of current socioecological models is that the distribution of males and their social relationships are determined mainly

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by access to reproductive females, and by the degree to which fertilizations can be monopolized (van Hooff and van Schaik, 1994). *Alouatta palliata* are nonseasonal breeders (Di Bitetti and Janson, 2000), but researchers have reported contrasting results on the relationship between social status and reproductive monopolization. Jones (1985) found that dominants were more often solicited by receptive females and had exclusive access to them at peak estrus, whereas Wang and Milton (2003) found that all males had access to females; in addition, in the latter study some data suggest that multiple males may copulate with the same female at peak estrus. Two opposite relationship systems are defined in the studies: contest polylyny (Jones, 1985) and scramble polygynandry (Wang and Milton, 2003).

The latter competition system is expected in mantled howlers with a fission-fission social organization because the spatial dispersion of females will further obfuscate the monopolization of sexual activities by a single male, even when estrus are asynchronous. Groups of Alouatta palliata are usually spatially cohesive and stable in terms of composition (Crockett and Eisenberg, 1987), several authors have described group division (Bezanson et al., 2002; Carpenter, 1964; Chapman, 1988; Chivers, 1969; Goldsmith and Winkler, 1999; Jones, 1995a; Leighton and Leighton, 1982; Mittermeier, 1973; Stevenson et al., 1998; Winkler, 2000). They associated the emergence of the fission-fusion social organization was related with responses to spatial coordination and social regulation requirements in large groups, demographic control strategies in saturated habitats, and mechanisms to improve foraging efficiency. In addition, several reports document the influences of fission-fusion in different behavioral aspects, such as social hierarchies (Goldsmith and Winkler, 1999), subgrouping patterns (Winkler, 2000), and individual association and affiliation preferences (Bezanson *et al.*, 2002).

Despite significant contributions, the majority of reports focused exclusively on the identification of the factors that lead to this type of grouping organization; researchers have not attempted to integrate information on the behavior of mantled howlers in fission-fusion societies with specific social strategies.

We investigated male associative patterns in a group of *Alouatta palliata* with fission-fusion social organization. In fission-fusion societies individuals can successively reiterate associative choices and their timing. Therefore, we explored interindividual differences in associative trends and related them with both variations on the availability of resources and specific characteristics of the social relationships of males.

On the basis of demographic data, there may be an important degree of breeding seasonality in our group. A birth peak occurs in

September–November—the wet season—which accounts for almost half of all births at the site (Dias and Rodríguez-Luna, unpublished data). Therefore, there is a temporal concentration of mating opportunities during the dry season. Conversely, at Agaltepec high-quality food resources vary seasonally (Rodríguez-Luna, 2000; Serio-Silva, 1992); therefore, it is reasonable to consider that, as in other species (e.g., *Ateles belzebuth*: Shimooka, 2003), females are more spatially dispersed during periods of scarcity. Because the sociosexual strategies of males depend primarily on the spatial dispersion of females and temporal distribution of reproductive opportunities, we predicted that male-male associative behavior and subgrouping patterns should vary seasonally as a response to the temporal variations in both factors. Specifically, because in the dry season there are more reproductive opportunities, and females are supposedly more dispersed, we expected males to associate less and to find a smaller number of males in the subgroups.

However, if associative behavior of males living in fission-fusion societies reflects individual strategic decisions (Newton-Fisher, 1999), it should differ between males and between dyads because it must be influenced by intrinsic characteristics of individuals and of the social relationships that they maintain with other group members. In view of this reasoning, we also investigated the effects of age and kinship on the associative patterns of males.

In mantled howlers, dominance relationships are age-graded (Jones, 1980): younger individuals have higher ranks, and competitive capabilities seem to decrease as they grow older (Jones, 1995b; Wang and Milton, 2003; Zucker and Clarke, 1998). In a study on reproductive behaviors of mantled howlers, Jones (1995b) found that young dominant males had the most successful mating strategies, while middle-aged and old males employed a series of suboptimal tactics. If the resource-holding potential of males is maximum when they are younger, then older individuals must show more flexible behavioral strategies to maximize their access to resources. We therefore predicted that the associative patterns of males should vary according to their age. Older adult males should associate less with other males, especially young adults, and spend more time without other males. Moreover, when receptive females are present, the males should try to associate alone with them to reduce interference from younger, presumably dominant, males (Jones, 1995b).

At Agaltepec, adolescent males remain solitary until sexual maturity, but, and contrasting with results among other populations (Glander, 1992), they always rejoin their natal group. Though in mantled howlers kinship does not seem to be a necessary condition for cooperation among males (Wang and Milton, 2003), when related and unrelated individuals live in the

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Social and demographic characteristics	Other sites (continuous habitat and fragments)	Agaltepec (Island)
Group size	9.12 <sup>a</sup>	59
Population density	0.23 individuals/ha <sup>a</sup>	7.11 individuals/ha
Sex ratios	$1.37^{a}$	0.52
Number of males per group	3 <sup>a</sup>	13
Home ranges	60 ha <sup>a</sup>	8.3 ha
Dispersal patterns	Usually both sexes leave their natal groups. <sup>b</sup>	Males emigrate, but rejoin the natal group.
Presence of kin related animals in groups	Infrequent	All animals have relatives in the group.
Grouping patterns	Cohesive unimale or multimale groups <sup>b</sup>	Fission-fusion

**Table I.** Comparison of social and demographic characteristics of *Alouatta palliata* populations between the Agaltepec Island and other locations in Los Tuxtlas

<sup>a</sup>Estrada (1982), mean values for continuous habitat in Los Tuxtlas.

<sup>b</sup>Dias (*pers. obs.*), fragmented habitat.

same group, differences in bonding may emerge. In some primate species, when scramble polygynandry is combined with male philopatry, kinship among males may play an important role in structuring their social relationships (e.g., *Brachyteles arachnoides*: Strier, 1994 and *Pan troglodytes*: Morin *et al.*, 1994). Thus, we predicted that dyadic association and subgrouping patterns should vary according to the degree of relatedness of males.

Finally, though the Agaltepec group has several socioecological characteristics that diverge from those of the species at other locations (Table I), in some aspects it resembles the conditions faced by mantled howlers in some forest fragments: in Agaltepec there is only 1 group; the available habitat is reduced and completely isolated; predators are absent; and the dispersal patterns are altered. Therefore, this population is an interesting subject for the analysis of behavioral adaptive processes of howlers living in disturbed conditions.

#### METHODS

#### **Study Site**

The Agaltepec Island (18°24', 18°25'N and 95°05', 95°06'W; Veracruz, Mexico) is the largest of four volcanic islands in Lake Catemaco. The climatic conditions at the site are warm-wet [Am(e)gw], with mean annual temperature of 24°C (min 12.9°C, max 36.7°C), and mean annual rainfall of 1980.1 1 mm (González-Capistrán, 1991). Two seasons are distinguished: a dry season, February–May, and a wet season, June–January.

With a total area of 8.3 ha, four main types of vegetation occur on the island (López-Galindo and Acosta-Pérez, 1998): semi-evergreen rain forest (*ca.* 65% of total area); riparian vegetation (20%); areas of secondary forest growth (10%); and pasture areas (5%).

#### **Subjects**

From November 1998 to October 1999 we studied all 13 adult males of the group (78 dyads), which comprised 59 howlers (13 adult males, 21 adult females, 10 subadults, nine juveniles, and six infants). We reliably identified all males by the distinguishing color patterns on their feet and tails, and named each via a 2-letter identification code (Pr, Nc, St, Cu, Pt, Nk, Pc, Vn, Nn, Sb, Ro, Pn, Ca). All subjects were born during the multiple studies at the site; therefore, their ages are known, varying between 10 yr and 10 mo (Pr, oldest male) and 5 yr and 5 mo (Ca, youngest male). We classified each adult male in different age classes according to Jones (1985): late middle-aged males (10–15 yr), early middle-aged males (7–10 yr), and young adult males (5–7 yr).

The translocation program that resulted in the release of mantled howlers in Agaltepec initiated in 1987, with the capture of 2 groups that inhabited two highly degraded forest fragments. Both groups lived separately in captivity during a quarantine period. In October 1988 we released the first group of one male and four females in Agaltepec. The male (M1) died a few days after the release, and 1 wk later a male infant was born (Pr, October 31, 1988). We released the second group, with the same composition (one male, M2, and four females), in April 1989, and the individuals joined the 4 females and the infant that were already at the island forming a single group (Rodríguez-Luna, 2000). After the birth of Pr, the next parturition at Agaltepec occurred in October 28, 1989-a male infant that died 1 wk later. Considering that the mean gestation period in Alouatta palliata is 186 d (Glander, 1980), the infant was conceived *ca*. 6 mo after the death of M1. Thus, all infants born in Agaltepec until Pr reached sexual maturity were sired by M2. In mantled howlers, males are sexually mature at 3.5 yr (Glander, 1980); therefore, Pr could have been reproducing in 1992. According to Glander (1980) sexual activity of male Alouatta palliata may be physiologically possible by the time they are 3 yr old; hence, conservatively, we consider that individuals born after April 1992 could have been sired by either M2 or Pr.

Therefore, the continuous observation of the population, and consequent knowledge of individual life histories, allowed us to deduce kinship relationships. We classified known kin relationships between males according to different categories: brothers (same mother and father), maternal half-brothers, paternal half-brothers, and unrelated. We did not consider the 11 dyads with unknown kinship relationships in the analysis.

#### **Data Collection**

A subgroup comprised an aggregation of individuals that concentrated in an area at a certain moment and that we could conspicuously differentiate from other grouping units. Because howlers usually show high activity coordination, and observational conditions ensured a significant control of all individuals that joined, left, and were present in these social units, a spatial definition of subgroup was not necessary.

Each day we walked through the island until we located a subgroup and checked it for the presence of males. To record the number of males in subgroups we used the scan sampling method (Altmann, 1974) at 15-min intervals with an instantaneous recording. During each scan we registered the identity of all males present in the subgroup and, when it was the case, the presence and number of receptive females (RF) based on the occurrence of proceptive or other sexual behaviors.

#### **Data Analysis**

For the total data set (1935 scans), and to ensure sample representativeness, we matched the number of scans by male (126 scans/male) and by season (819 scans/season, 63 scans/male per season), considering therefore only 84% of all scans. We made the selection randomly.

We analyzed association data by season via the twice-weight index (Cairns and Schwager, 1987):  $I_{AB} = \text{no. AB}/(\text{no. A} + \text{no. B} - \text{no. AB})$ .  $I_{AB}$  is the dyadic association index of the dyad AB, no. AB is the number of scans with both individuals present, no. A is the number of scans in which A was present without B, and no. B is the number of scans in which B was observed without A. This index has the advantage of reducing possible overestimations of association frequencies between dyads because both the number of occasions that individuals are together and separated are analyzed.

We then transformed the dyadic indexes into a relative measure of association, as Newton-Fisher (1999) suggested:  $Z_{AB} = (I_{AB} - I)/s$ . *I* is the mean association index across all dyads, and *s* is the sample's standard deviation. The measure expresses dyadic association strength as its deviation from the indexes of all dyads because values are outweighed by mean association levels across all dyads. We used several nonparametric tests for data analysis: Wilcoxon; Friedman ANOVA; Kruskal-Wallis ANOVA; one-way ANOVA with the Duncan *post hoc* test; Mann-Whitney; and Spearman *r*. All tests are 2-tailed, and the statistical threshold for all analysis is p = 0.05. In addition, we organized association data by season in square matrixes that we analyzed via a cluster analysis. We then used the Mann-Whitney and Kruskal-Wallis tests to compare the clusters. We calculated all analyses with Statistica (StatSoft, Inc.).

### RESULTS

#### **Association Patterns**

Association between the males varies seasonally, and dyadic association strength is significantly higher during the wet season (Wilcoxon Z = 2.394, p < .01; Fig. 1).

In both seasons, there are no differences in dyadic association depending on the age of males [dry season: Kruskal-Wallis H(5, 78) = 8.613, p = .072; wet season: H(5,78) = 4.26, p = .372]. However, though association strength does not vary according to the kinship relationships in the dry season [Kruskal-Wallis H(3, 65) = 2.117, p = .549], during the wet season



Fig. 1. Mean association strength in the dry and wet seasons. In the wet season the males associated significantly more than in the dry season.

related males associate more frequently [Kruskal-Wallis H(3, 65) = 7.936, p < 0.05] (Fig. 2a, b).

During the dry season the mean percentage of time spent alone, with or without females, across all males is significantly higher than in the wet season (Wilcoxon Z = 2.061, N = 13, p = .032, dry season: 37.1%; wet season: 18.7%). In addition, significant differences between individuals occur in both seasons [dry season: Friedman ANOVA = 125.489, df = 12, p < .001; wet season: Friedman ANOVA = 132.346, df = 12, p < .001] and are not related with the males' ages [dry season: Kruskal-Wallis H(2, 13) = 1.032, p = .597; wet season: Kruskal-Wallis H(2, 13) = 2.874, p = .238].

Cluster analysis of mean association indexes per male allows one to distinguish individual trends, which vary significantly during the dry season (Friedman ANOVA = 34.212, df = 12, p < .001; Fig. 3a). Two clusters are differentiated, one including two males (Pr an Sb) with lower levels of association, and a second one comprising the remaining males (clusters A and B, respectively). The differences between these two groups are significant (Mann-Whitney Z = 2.171, p < .05).

Differences in mean association indexes per individual are not significant during the wet season (Friedman ANOVA = 13.238, df = 12, p = .183). Nonetheless, cluster analysis separated males into three main clusters, suggesting that there was a differentiation in associative tendencies among certain males. Sb and Ro (cluster A, Fig. 3b) associated less in this season, while the remaining males associated more (cluster B and C). The differences between the clusters are significant [Kruskal-Wallis H(2, 13) = 7.849, p < .01].

#### Subgrouping

Usually only a few males gathered simultaneously in subgroups because in almost half of the scans (48.7%) we observed only 2–4 males together (median = 4). The number of males in subgroups varied between seasons (Wilcoxon Z = 9.433, N = 819, p < .001), and both the median and the maximum number of males per subgroup are lower during the dry season (medians: dry = 3, wet = 4; minimum: dry = 1, wet = 1; maximum: dry = 8, wet = 12; Fig. 4).

The number of males with which each individual associated in the subgroups does not differ across age classes in both seasons [dry season: Kruskal-Wallis H(2, 2077) = .916, p = .662; wet season: Kruskal-Wallis H(2, 3193) = 1.716, p = .327]. However, during the wet season kin-related dyads were usually together in subgroups including fewer males [Kruskal-Wallis H(3, 67) = 8.697, p = .032], while no difference occured in the dry



Fig. 2. Variations in dyadic association strength according to the kinship relationships among males. In the dry season (a) there is no significant difference between kin and nonkin, but during the wet season males preferred to associate with kin (b).



**Fig. 3.** (a) Dendogram showing the results of the cluster analysis of mean association indexes per individual during the dry season. Two main groups are distinguished: males that rarely associated with other males (A), and more associative males (B). (b) Cluster analysis of mean association indexes per individual during wet season. Three groups are distinguished: males that rarely associated (A), more gregarious males (B), and highly associative males (C).

season between related and unrelated dyads [Kruskal-Wallis H(3, 67) = 5.489, p = .139].

In the wet season the association strength of dyads correlates negatively with the number of males in subgroups ( $r_s = -0.72$ , p < .001), suggesting that dyads that associated more were usually together in subgroups with fewer males, and vice versa.



Fig. 4. Number of males in the subgroups expressed as percentage of scans for each season.

#### **Presence of Receptive Females**

There were seasonal differences in the presence of RF in the subgroups (Wilcoxon Z = 11.242, N = 819, p < .001). During the dry season there was  $\geq 1$  RF in 23.1% of all scans, while in the wet season the proportion decreased to 2.6%. Though in both seasons males usually associated with each other when RF were present (61.4% of all scans with RF), in the wet season there were significantly fewer males in subgroups with RF (Mann-Whitney Z = 5.668, N = 1638, p < .001).

To examine the effects of the presence of RF in the subgrouping patterns of males, we analyzed the variations in the number of males per subgroup according to the seasonal occurrence and number of RF, and found significant differences (ANOVA F = 60.189, df = 4, p < .001; Fig. 5). Though during the dry season males usually grouped with more males when two RF were present (median = 4), the number of males in the subgroups was similar with one or with no RF (Duncan *post hoc* test, p = .179; with one RF and without RF: median = 2). In the wet season the presence of one RF (we never observed > 1 RF in subgroups during this season) resulted in fewer males per subgroup (with RF: median = 1; without RF: median = 4).

Age did not determine whether a male grouped alone or with other males when RF were present in either season [dry season: Kruskal-Wallis H(2, 189) = 0.529, p = .721; wet season: H(2, 21) = 0.925, p = .165].



Number of Receptive Females

Fig. 5. Variations in mean male subgroup size according to seasonal variations on the number of receptive females in the subgroups.

Males with higher association levels usually remained with other males in subgroups including RF ( $r_s = 0.58$ , p < .05), and associated less with RF outside the subgroups ( $r_s = -0.60$ , p < .05). However, during the dry season males that spent more time alone associated more with RF without other males ( $r_s = 0.78$ , p < .05).

#### DISCUSSION

Male howlers in Agaltepec show nonrandom associative and subgrouping patterns. Though some individual trends occurred, there were differences in male behavior in relation to the season of the year, the presence and number of RF in subgroups, and kinship relationships.

We expected that associative and grouping patterns of males were influenced by age. Mantled howler males disperse during adolescence from their natal groups and live solitarily for a variable time (Glander, 1992). They then fight their way into a new group (Cristóbal-Azkarate *et al.*, 2004; Glander, 1992) and group membership only attained if challengers become dominant. Therefore, in an established group with several males, there is usually an age-reversed dominance hierarchy (Jones, 1980). The lack of any relationship between age and associative behavior in the Agaltepec population could be due to two main reasons. On one hand, Agaltepec males rejoin the natal group pacifically (Dias, *pers. obs.*) and age does not seem to assume the structuring function found at other sites. On the other hand, no male is > 15 yr; therefore, it is possible that age-dependent social strategies currently cannot be detected owing to the small age differences among adult males.

As predicted, there were variations in association between males depending on their kinship relationships. In the wet season, related males spent more time together and gathered in subgroups with fewer males, a possible indicator of higher social tolerance. The emergence of a nepotistic associative pattern may result from a relaxation in reproductive competition, under such circumstances male bonding is more probable. For instance, in Costa Rican squirrel monkeys male-male contest interactions are frequent during the brief breeding season, whereas relationships are mostly egalitarian throughout the rest of the year (Boinski, 1994). As in other primate species (e.g., Brachyteles arachnoides: Strier, 1994 and Saimiri oerstedi: Boinski and Mitchell, 1994), relatedness may be important for the expression of individual preferences of association among males in this group. Alternatively, the decrease in reproductive opportunities during the wet season in Agaltepec could have promoted the establishment of coalitions between related males. Pope (1990, 1998) found that in red howlers (Alouatta seniculus) cooperation among kin was a prerequisite for maintaining breeding tenure in groups in saturated habitats. Cooperation between related males could enhance the probabilities of successfully defending access to the few females that are receptive during the wet season, and the reproductive benefits to coalition members would arise through either direct or inclusive fitness. Contrary to the hypothesis is the fact that on the few occasions that we observed a cycling female during the wet season she usually remained alone with only one male, not with a coalition of males; however, Ro, the male that associated more with RF then, had no known male relative in the group. Finally, the effect of kinship could result from independent attraction of males toward their mothers, a bias in several macaque species (Chapais, 2001). However, because paternal half brothers had higher association levels than unrelated males, the possibility seems unlikely.

We consider that the temporal changes in associative and subgrouping behavior of Agaltepec males are related primarily with an important degree of reproductive seasonality. In the dry season, the period during which we observed more RF, males associated less, spent more time without other males, and there were fewer males in the subgroups. In this period, the presence of cycling females was associated with increases in the number of males per subgroup, an effect of attractiveness similar to that in *Pan troglodytes*  (Hashimoto *et al.*, 2001; Wrangham, 2000). Nevertheless, different threshold levels seem to exist with respect to the maximum number of males in subgroups according to the number of RF: with one RF usually only two males remain in the same subgroup; with > 1 RF there is a two fold increase in the number, to four males. These results are analogous to those of Newton-Fisher (1999) among chimpanzees in the Budongo Forest.

Though we do not present data on mating success of males using different reproductive tactics, in mantled howlers the establishment of sexual consortiums within the context of the group is associated with both higher rank and higher copulation frequencies (Jones, 1995b). Therefore, the fact that during the dry season males spent more time with no other male were the ones that usually grouped alone with RF, may be a consequence of individual inabilities to evade interventions from other males. Individual association trends could be a reliable indicator of the reproductive tactics of males if mating success proved to be associated directly with specific associative strategies. Additional data on copulation frequency are necessary to assess this relationship.

During the dry season Pr and Sb associated less with other males. Sb is probably a socially peripheral male because, in contrast with Pr in the dry season and Ro in the wet season that showed varying association patterns throughout the study, he was among the less associative males in both seasons. Regarding the two other males, though age differences did not account for variations in association, Pr was the oldest male in the group. Pr may have lost some competitive capabilities and could be displaying during the dry season a confrontation avoidance strategy. During the wet season, male associative patterns changed significantly in comparison with the previous season: association levels increased, time spent alone diminished, and subgroups included more males. Cluster analysis isolated two males that associated less, Sb and Ro, during the wet period Sb maintained a peripheral situation throughout the entire study period. Ro associated more with RF in the dry season, and he usually did it outside the subgroups; this tendency must have influenced his lower levels of association.

Two main associative trends occur among males in the group: spatial dispersion in the dry season related with the presence of more RF, and spatial concentration during the wet season, possibly associated with a relaxation in reproductive competition. In the latter period kinship relationships seem to play an important role in individual association preferences.

Our results fit previous findings about male-male social dynamics in mantled howlers. Intense conflicts may occur in this species (Cristóbal-Azkarate *et al.*, 2004; DeGusta and Milton, 1998), but male-male relationships are for the most part maintained through the use of indirect forms of interaction, such as vocal displays, distance relationships, or ritualized behavior (Baldwin and Baldwin, 1976; Jones, 1980; Wang and Milton, 2003; Zucker and Clarke, 1998). Facing energetic restrictions associated with a highly folivorous diet (Milton, 1980), adoption of conditional associative strategies by male howlers in fission-fusion societies may be an additional mechanism for the establishment and maintenance of howler social relationships.

It is important to emphasize that the Agaltepec howlers are extremely different, especially demographically, from other populations studied elsewhere. It would be inappropriate to extrapolate our conclusions to other populations (and it is not our intension to do so), but Agaltepec is undeniably an important case study for the evaluation of adaptive processes that develop in saturated habitats.

#### ACKNOWLEDGMENTS

The Fundação para a Ciência e a Tecnologia, Ministério da Ciência e Tecnologia of the Portuguese Government provided financial support (BM/15/2000). The Parque de la Flora y Fauna Silvestre Tropical of the Universidad Veracruzana, Mexico, provided help with logistics. The suggestions of Jurgi Cristóbal Azkarate and 3 anonymous reviewers significantly improved the article.

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