# **RESEARCH ARTICLE**

# The Functions of the "Greeting Ceremony" Among Male Mantled Howlers (*Alouatta palliata*) on Agaltepec Island, Mexico

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Nonhuman primates use greeting behaviors as nonaggressive communicatory signals in multiple social contexts. Adult male mantled howlers (*Alouatta palliata*) perform a ritual greeting that has been associated with bond-strengthening functions. The aim of this study is to explore the greeting patterns of male howlers living on Agaltepec Island, Mexico. Specifically, we analyzed the relationships between greetings and several individual, relational, and contextual variables, such as the expression of affiliation and agonism, dominance rank, age, kinship relationships, spatial organization, activity patterns, and subgrouping patterns. Greetings were more frequent between males with closer dominance ranks. Among those dyads that greeted at least once, dominant males initiated greetings more frequently than less-dominant males. On the other hand, more greetings were observed when one of the participants had recently returned to a subgroup and during locomotion. On the basis of these results, we propose that on Agaltepec greetings are a conflict management mechanism used between males of similar ranks. The fission-fusion social system of this group of howlers allows males with conflicting interests to remain separated, and greetings may reduce tension during fusion events. Am. J. Primatol. 70:621–628, 2008. © 2008 Wiley-Liss, Inc.

#### Key words: social behavior; conflict management; dominance rank; fission-fusion

#### **INTRODUCTION**

Greeting displays have been observed in several nonhuman primate species [e.g., *Ateles geoffroyi*: Aureli & Schaffner, 2007; *Papio* spp.: Colmenares, 1991; *Pan* spp.: Hohmann & Fruth, 2000; Kummer et al., 1974; *Colobus guereza*: Kutsukake et al., 2006; *Cebus* spp.: Perry et al., 2003; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003].

Although a number of functions have been proposed for these behaviors, in several primate and nonprimate species greetings seem to be associated with conflict management strategies. In this context, greetings may be particularly important during tense situations, such as meetings between strangers [Preuschoft & van Schaik, 2000], reunions between familiar individuals that have been separated for some time [Aureli & Schaffner, 2007; Moss & Poole, 1983; Osborne, 1986], or competition for valued resources [Colmenares, 1991]. Accordingly, greetings have been functionally associated with reassurance and reconciliation [e.g., Macaca arctoides: de Waal & Ren, 1988; Papio hamadryas: Kummer et al., 1974; Crocuta crocuta: Wahaj et al., 2001], appeasement [e.g., Papio spp.: Hausfater & Takacs, 1987; Peláez, 1982; Sugawara, 1979], or assessment [e.g., Papio spp.: Colmenares, 1990, 1991; C. crocuta: East et al., 1993; Pan troglodytes: Nishida, 1970; Cebus capucinus: Perry et al., 2003; Smuts, 2002; Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003].

The "greeting ceremony" [Glander, 1975, 1980; greeting henceforth] is a ritual behavior that occurs among mantled howlers (*Alouatta palliata*). A typical greeting sequence between males consists of four stages. In the first stage, one of the participants—or both—approaches its partner, and both males start emitting vocalizations that are specific to this behavior [mostly throat rumbling and clucking; Wang & Milton, 2003]. If one of the males is sitting, he adopts a quadruped posture and waits until body contact is established. In the second stage, while standing in a face-to-face posture, males grab each other's shoulders with one hand, while sniffing the opposite armpit. Throughout this stage males keep

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producing the same vocalizations. In stage three, males proceed to a mutual rump-to-face position and sniff each other's genitals. Finally, in stage four, males either move away from each other or engage in other social interactions. On Agaltepec, as well as in several observed groups in the Los Tuxtlas region (Veracruz, Mexico), male greetings are always reciprocated, i.e., both males greet simultaneously [Dias, 2007].

Currently, only two studies have addressed the possible functions of greetings displayed by male mantled howlers. Both converge in the interpretation of greetings as a possible mechanism of bond strengthening, as this is usually the only affiliative behavior exchanged in between males [Wang & Milton, 2003; Zucker & Clarke, 1986].

In this study we analyzed the greeting behaviors of male mantled howlers that live on Agaltepec Island, Mexico. The extremely high population density observed at this site has been related to the adoption of a fission-fusion group structure [Dias & Rodríguez-Luna, 2006] and changes in foraging patterns [Asensio et al., 2007; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Rodríguez-Luna et al., 2003]. Previous research concerning the influences of the fission-fusion system on male behavior revealed that higher ranking males usually remain in subgroups including fewer males, fewer males gather in subgroups during periods of increased reproductive competition, related males associate preferentially when reproductive competition is relaxed, and that dyads composed of males of similar social rank associate less frequently and usually only gather in subgroups that contain several males [Dias & Rodríguez-Luna, 2003, 2005, 2006]. Similar trends have not been reported for other mantled howler populations.

The objective of this paper is to study the functions of the greeting ceremony among male howlers living in fission-fusion social groups. Specifically, three main analyses were conducted: (1) we analyzed the relationships between individual participation in greetings and factors such as age, dominance rank, participation in other social interactions (affiliation and agonism), and male spatial relationships; (2) we conducted an analysis of these same behaviors between male dyads; and finally (3) we analyzed temporal changes in male behavior before and after greetings, during changes in subgroup composition, and during different activities such as feeding, resting, and moving.

# **METHODS**

### **Study Site and Population**

We studied male howlers that inhabit Agaltepec Island (18°24'N and 95°05'W), a volcanic island located in Lake Catemaco, Veracruz, Mexico. This island has an area of 8.3 ha, and the predominant

vegetation types are semievergreen rain forest and riparian vegetation [López-Galindo & Acosta-Pérez, 1998].

The study group was released on this island as part of a translocation program [Rodríguez-Luna et al., 1993, 2003] and has been regularly observed since 1988. Individual age, matrilineal relationships, and patrilineal kinship for 69 of the 78 male dyads on the island are known. All individuals are easily identifiable by their natural marks, such as blond hairs on the feet and tails, skin pigmentation on the hands and feet, scars, broken fingers, and genital morphology [Asensio et al., 2007; Dias & Rodríguez-Luna, 2005, 2006]. During this study, the group comprised 59 individuals, including 13 adult males, 21 adult females, and their immature offspring.

## **Behavioral Observations**

Between November 1998 and October 1999, we used focal animal sampling [5-hr samples; Altmann, 1974] to record social interactions exchanged between the 13 adult males. Focal animals were selected on a pseudorandom basis, with priority given to those males that had been sampled infrequently. In addition to greetings, we noted all occurrences of affiliative (touching, playing, smelling) and agonistic (displacements, threats, fights) interactions. For each observed interaction, we recorded the time, the identity of both interacting males, and the context, defined as the activity (feed, rest, or move) performed by the focal animal immediately before the interaction. From these data, we calculated individual and dyadic frequencies of affiliative and agonistic interactions. We also collected data on the presence of receptive females, based on the occurrence of proceptive or other sexual behaviors such as genital presentations, tongue flicking, and copulations. Males were sampled at similar rates, with a mean  $(\pm SD)$  observation time per male of 35.2 hr + 5.10.

We used agonistic interactions with a clear winner and a clear loser to determine hierarchical relationships; these interactions included cases when one male displayed only submissive signals while the other displayed only aggressive signals (N = 100), or when one male displayed submissive signals while the other male failed to respond [N = 57; Silk et al., 2004]. The dominance rank of males was calculated with David's score, a method that provides a weighted measure of individual agonistic success [Gammell et al., 2003; Hemelrijk et al., 2005]. For each dyad (N = 78), the distance in rank was calculated as the difference between both males' rankings.

# **Proximity and Associative Behavior**

To study proximity among males, we recorded the presence of other males  $\leq 5 \text{ m}$  from the focal

male through instantaneous recordings at 15-min intervals [Altmann, 1974]. For each sample we additionally recorded the identity of all males present in the subgroup, as well as the predominant activity in the subgroup, defined as the activity (feed, rest, or move) of >50% of the individuals. Individuals were included in the same subgroup when they were in the same tree crown or in adjacent trees, could maintain visual contact, and/or coordinated their activities.

Howlers spend up to 80% of the day resting and sometimes occupy the same relative spatial positions within their subgroup for periods >15 min. To determine whether successive samples taken at 15-min intervals are independent from each other, we examined our database and checked whether from one instantaneous recording to the following instantaneous recording a change in the subgroup composition had occurred. We found similar proportions of recordings with and without composition changes, although in a majority of recordings (54.1%) subgroup composition changed. Therefore, in the following analyses we consider instantaneous recordings at 15-min intervals to be independent.

Dyadic proximity was defined as the frequency that both males were  $< 5 \,\mathrm{m}$  from each other. We used the data on the subgroups' compositions to quantify dyadic association. First, we calculated the "twice weight" index [Cairns & Schwager, 1987]:  $I_{AB} = AB/$ (A+B-AB).  $I_{AB}$  is the dyadic association index of the dyad AB; AB is the number of samples where individuals A and B were together in the same subgroup; A is the number of samples where A was observed without B; B is the number of samples where *B* was observed without *A*. These indexes were then transformed into a relative measure of association:  $Z_{AB} = (I_{AB} - I)/s$ . I is the mean association index across all dyads, and s is the sample's standard deviation [Newton-Fisher, 1999]; this measure of association will be referred in the text as Z. As an additional measure of spatial affinity, we calculated the mean number of males (MNM) with which each individual and dyad gathered in subgroups.

#### **Data Analysis**

As data were nonnormally distributed (based on the Kolmogorov–Smirnov test), we used nonparametric tests and generalized linear models; the latter allow controlling for the specific distribution of the data.

Nonparametric Spearman correlations were used to relate the frequency of greetings with the frequency of participation in social interactions (affiliation and agonism), dominance rank, age (in months), and variables of spatial proximity and organization variables (proximity, Z, and MNM) for each adult male (N = 13).

To analyze the patterns of greeting at a group level, we performed a series of partial correlation tests [ $\tau_{\rm Kr}$ ; Hemelrijk, 1990]. We constructed  $13 \times 13$ matrices for each of the variables referred to above and related them with a matrix representing greetings among all males. To identify which variables predict the probability of greeting exchanges between males, we ran a logistic regression analysis with a fixed binomial error by using generalized linear models [Crawley, 2002]. We first used Akaike's information criterion to select the most parsimonious model, that is, the combination of variables that best explained the probability of greeting among dyads [Motulsky & Christopoulos, 2003]. The effect of these variables on greeting occurrence/nonoccurrence was then analyzed with the regression model. Following the same procedures, we also examined which variables best explained differences in greeting frequencies among males that greeted at least once (N = 44). For this analysis we selected a Poisson distribution (to a count variable) with a log-link function [Crawley, 2002]. We used a Wilcoxon-signed rank test to compare the frequency of greetings initiated by the dominant and by the subordinate male in each dyad. With a Kruskal-Wallis test we analyzed differences in the frequency of greeting exchanges according to the kinship relationships of males. Males in each dyad were classified as full brothers (N = 2), maternal half brothers (N = 9), paternal half brothers (N = 13), unrelated (N = 43), or as males with unknown kinship relationships [N = 11; see Dias & Rodríguez-Luna, 2006 for a full description of kinship relationships in this group].

To examine the function of greetings we compared data on the frequency of affiliative and agonistic interactions in the 15-min period earlier to and after a greeting event. Specifically we compared (1) the frequency of greetings that occurred after affiliation with the frequency of greetings that did not follow affiliation; (2) the frequency of greetings that occurred after agonism with the frequency of greetings that did not follow agonism; (3) the frequency of greetings that occurred before affiliation with the frequency of greetings that were not followed by affiliation; and (4) the frequency of greetings that occurred before agonism with the frequency of greetings that were not followed by agonism. Additionally, we compared the frequency of greetings associated with the arrival of one of the participants into the subgroup during the 15-min period earlier to greeting with that of greetings that occurred when both males were in the same subgroup for  $\geq 15$  min. For these analyses we used Wilcoxon Rank tests. Two greetings were removed from the tests that analyzed interactions occurring after greetings and temporal association of greetings with changes in subgroup composition because focal observations terminated before 15 min passed since that greeting. We also analyzed

differences in greeting frequencies according to the activity of males (feed, rest, and move). As expected frequencies depend on the total time dedicated to each activity, we used the number of instantaneous samples where each activity was the predominant activity of the subgroup as a proxy for the proportion of time spent in each activity. These proportions were then used to correct the expected frequencies in a  $\chi^2$  test.

All statistical analyses (with the exception of  $\tau_{\rm Kr}$  correlations) were carried out with Statistica 6.0 [StatSoft, Inc., Tulsa, OK].

#### RESULTS

#### **Greetings and Individual Characteristics**

Eighty-nine greetings were recorded during 419 focal hours. All males were observed to participate in greetings, and on average  $(\pm SD)$  they were involved, either as actors or recipients, in  $13.69 \pm 4.35$  greetings (range = 7–22).

The frequency of greetings initiated by males was not related to the initiation of affiliative (N = 13,  $r_{\rm s} = 0.08$ , P > 0.05) or agonistic behaviors ( $r_{\rm s} = 0.32$ , P > 0.05). Similarly, there was no relationship between the frequency of received greetings and received affiliative behavior ( $r_{\rm s} = 0.27$ , P > 0.05) or agonistic behaviors ( $r_{\rm s} = -0.20$ , P > 0.05).

No correlation (P > 0.05) was found between the frequency of greetings in which each male participated and the frequency of social interactions (affiliation and agonism), dominance rank, age, and variables of spatial proximity and spatial distribution (proximity, Z, and MNM ).

#### Greetings and Dyadic Relationship Characteristics

The average ( $\pm$ SD) frequency of greetings across all dyads was  $1.14\pm1.33$  (range = 0–5). The only variable that correlated with the frequency of greetings within dyads was the distance in dominance ranks (N = 78,  $\tau_{\rm Kr} = -0.58$ , P = 0.001). Specifically, males that were closer in rank greeted each other more often (Fig. 1).

Only 56.4% of the dyads greeted at least once; for these, the average ( $\pm$ SD) number of greetings exchanged was  $2.02\pm1.15$ . Akaike's criterion determined that the combination of variables that best explained the occurrence/nonoccurrence of greetings was rank proximity and Z. The logistic regression model analyzing the relationships between greetings and these variables suggests that the probability of greeting increased among males closer in rank (Wald's  $\chi^2 = 18.69$ , P < 0.001) and among dyads that associated less (Wald's  $\chi^2 = 4.19$ , P = 0.04; Table I). For those dyads that greeted at least once, dominant males were more likely than subordinates to initiate greetings (Wilcoxon Z = 3.511, P < 0.001; Fig. 2). The



Fig. 1. The number of greetings exchanged within dyads as a function of their distance in dominance ranks ( $\tau_{\rm Kr} = -0.58$ , P = 0.001).

TABLE I. VariablesThatBestExplaintheOccurrence/Nonoccurrence of GreetingsBetween allDyads (a) and the Frequency of GreetingsBetweenDyads That Greeted at Least Once (b)

	Parameter	SE	$\chi 2$	P
a				
Distance in rank	-2.064	0.477	18.699	0.000
Ζ	-0.893	0.437	4.187	0.040
Intercept	-5.342	1.254	18.154	0.000
b				
Proximity	-0.033	0.016	4.386	0.036
Intercept	0.944	0.146	41.714	0.000



Fig. 2. Median number of greetings initiated by the dominant and the subordinate male among dyads that greeted at least once (Z = 3.511, P < 0.001).

most parsimonious model for explaining differences among dyads according to the frequency of greetings exchanged, included only one variable, proximity, suggesting that the frequency of greetings decreased



Fig. 3. The number of greetings observed in relation to different contextual events: interactions occurring before (a) and after (b) greetings; (c) greetings temporarily associated with the arrival of one of the males to the subgroup, compared with those occurring when subgroup composition was stable; (d) frequencies of greetings associated with different activities (solid lines represent expected frequencies). \*Activity contributing large proportion of nonrandomness.

with increasing proximity between the males (Wald's  $\chi^2 = 4.39$ , P = 0.036; Table I).

Differences in the frequency of greetings were not related to kinship. This was true among all dyads (K–W  $H_{4,78} = 6.01, P = 0.198$ ), and among dyads that greeted at least once (K–W  $H_{3,44} = 4.66, P = 0.199$ ).

#### **Contexts of Greeting**

Only 11.2 and 4.5% of all greetings were preceded by affiliation (Wilcoxon Z = 6.35, P < 0.001; Fig. 3a) or agonism (Wilcoxon Z = 7.46, P < 0.001), respectively, and 27 and 24.7% were followed by affiliation (Wilcoxon Z = 3.77, P < 0.001; Fig. 3b) or agonism (Wilcoxon Z = 4.14, P < 0.001), respectively. Therefore, a majority of greetings were not temporarily associated with the occurrence of other social interactions.

On most occasions a change in subgroup composition did not result in greeting (87.6%). However, a majority of greetings occurred when one of the males had recently arrived into a subgroup (Wilcoxon Z = 2.49, P < 0.001; Fig. 3c) and during periods of locomotion ( $\chi_2^2 = 19.65$ , P < 0.001; Fig. 3d). Males never greeted when receptive females were present in a subgroup.

#### DISCUSSION

In contrast with previous reports, in which mantled howler greetings were interpreted as a mechanism of bond strengthening [Wang & Milton, 2003; Zucker & Clarke, 1986], in our study group there was no significant relationship between the frequency and context of greeting among adult male dyads and the frequency of affiliative or agonistic interactions or spatial proximity. In this group, greeting exchanges related negatively with distance in dominance ranks, depended on the relative status of males within dyads, and occurred more often when males returned to subgroups and during locomotion.

These patterns suggest that males may be using this behavior to reduce tension during fusion events to prevent the escalation of conflicts. Symmetries in power have been associated with reduced predictability about the outcome of confrontations [Maynard Smith & Parker, 1976; Preuschoft & van Schaik, 2000] and higher probabilities of conflict escalation [Enquist & Leimar, 1983; Vehrencamp, 2000]. For instance, greetings are more frequent between male baboons with unclear dominance relationships or matched fighting power than in unmatched dyads [Colmenares, 1990, 1991]. Direct confrontations between males are extremely infrequent among resident male howlers, and social cohesion is mainly maintained through vocal communication, tolerance, and spacing mechanisms [Whitehead, 1987]. This has been associated with the energetic constraints imposed by a primarily folivorous diet [Crockett & Eisenberg, 1987; Milton, 1980]. Nevertheless, fighting potential, as attested by canine size [Kay et al., 1988], is high, and it has been demonstrated that in howlers confrontations

between adult males can be associated with physical injuring and death [Cristóbal-Azkarate et al., 2004; Crockett & Pope, 1988; DeGusta & Milton, 1998]. Although intense fighting usually involves resident and extragroup males, the costs of conflict escalation between coresident males can be hypothesized to be similarly high.

On Agaltepec Island, rank proximity—probably allied with a nonlinear dominance hierarchy: Landau's index h = 0.3 [Dias & Rodríguez-Luna, 2005] could result in greater uncertainty in male rank and increase the probabilities of confrontation. An indirect mechanism to avoid such conflicts is the strategic regulation of associative patterns, as males with closer ranks associate less [Dias & Rodríguez-Luna, 2005, 2006]. However, all males joined at some point in the same subgroup, and in several fission– fusion societies meetings between individuals that are usually separated have been interpreted as tension-eliciting contexts [e.g., A. geoffroyi: Aureli & Schaffner, 2007; Loxodonta africana: Moss & Poole, 1983].

Within dyads that were closely matched, differences in the costs of conflict escalation could explain the higher frequency of greeting initiation by dominants because for them a defeat could result in a drop in status. By exchanging greetings with subordinates ranking below them, dominants may assess the probabilities of being challenged and, if greetings function as a social convention for peaceful interactions, avoid immediate challenges. Finally, and assuming that the frequency of greetings could also be associated with conflict prevention, under conditions in which the probabilities of conflict were higher, males usually remained more distant. Therefore, the use of greetings to assess physical, behavioral, and motivational traits may serve as a conflict management mechanism for male howlers living in fission-fusion societies.

It is important to remark that males never greeted when receptive females were present, a circumstance in which more conflicts could be expected to arise. In this group, however, fewer males gather in subgroups when females are cycling, and some males systematically establish consorts with females outside subgroups [Dias & Rodríguez-Luna, 2006]. Therefore, in the context of direct reproductive competition, conflict avoidance is mainly achieved by spatial regulation mechanisms.

Male interaction patterns observed in our howler study group could relate to several distinctive features of this population. The spatial isolation and history of the group have resulted in several demographic and socioecological differences between Agaltepec and other howler locations [Dias & Rodríguez-Luna, 2006]. For instance, population density on Agaltepec (9.5 individuals/ha) is more than ten times higher than on Barro Colorado Island [0.81 individuals/ha; Milton, 1982] and Hacienda La Pacifica [0.77 individuals/ha: Clarke et al., 1986], and the number of males in a single group (13) is also higher than on Barro Colorado Island [6; Wang & Milton, 2003] and La Pacifica [4; Zucker & Clarke, 1986]. Additionally, howlers living on Agaltepec are characterized by a remarkably different foraging strategy. For example, in contrast with reports from La Pacifica and Barro Colorado Island [Glander, 1978; Milton, 1980], on Agaltepec howlers include in their diet large proportions of lianas, vines, shrubs, and herbs (up to 33% of feeding time), and they frequently feed on the ground [Asensio et al., 2007; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Rodríguez-Luna et al., 2003]. In spite of these differences, the rate of greetings per individual observed in our study (0.0163/h/ind) are within the range reported in previous studies on male mantled howlers' behavior [0.0037/h/ind: Wang & Milton, 2003; 0.0246/h/ind: Zucker & Clarke, 1986]. This suggests that howlers living on Agaltepec may be adapting their social behavior to cope with habitat saturation without modifying the basic structure of social interactions, i.e., frequencies of behavior.

Finally, we plan to conduct research comparing the behavioral patterns observed among howlers on Agaltepec with those of groups living under different socioecological conditions. Only then will we be able to appreciate the social consequences of habitat saturation on Agaltepec and understand the ability of these primates to flexibly alter their behavior under new conditions.

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