

Primate Rituals: The Function of Greetings between Male Guinea Baboons

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Abstract

The bond-testing hypothesis suggests that social animals can obtain honest information about the quality of their dyadic relationships by exchanging costly, high-risk signals (Zahavi & Zahavi 1997). We evaluated this hypothesis by investigating whether adult male baboons use intense greeting interactions to test the quality and strength of their social bonds. Intense greetings involve intimate and risky behaviors such as embracing and the diddling of the penis and/or scrotum. Data were collected on a colony of 40 Guinea baboons (*Papio papio*) at the Brookfield Zoo in Chicago. Fifteen adult male baboons were focally observed for 30-min sessions over a 6-mo period, resulting in 195 h of observation. We assessed the quality of male–male relationships using measures of affiliation, aggression, and social tolerance. As predicted by the bond-testing hypothesis, dyads with strong social bonds exchanged a higher frequency of intense greetings than did pairs with poor relationships. We found no support for the competing hypotheses, that suggest that greetings have an aggressive or submissive function or are used as a form of post-conflict reconciliatory behavior. Neither dominance relationships nor contextual variables were predictive of intense greeting patterns. We suggest that by imposing on his partner, a male baboon is able to obtain reliable information about this individual's current willingness to cooperate and invest in the relationship.

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Introduction

One relatively well-accepted view in the field of animal communication is that costly signals are more difficult to fake than cheap signals, and therefore more likely to convey honest information about the sender (Zahavi 1975, 1977a; Grafen 1990; Johnstone & Grafen 1993; Hauser 1996). Consistent with this view, it has been argued that social animals may engage in risky interactions (i.e., interactions

that carry substantial costs) with their conspecifics to exchange honest information about the quality of their relationships or to test the strength of their bonds (Zahavi 1977b; Zahavi & Zahavi 1997). The idea behind this 'bond-testing hypothesis' is that producing an aversive signal that has the potential to provoke an aggressive response allows the sender to reliably express its 'trust' in the recipient. Furthermore, the toleration of this imposition is assumed to be indicative of the recipient's current willingness to invest in this relationship. By gradually escalating the imposition and determining the point at which the recipient terminates the interaction, precise information can be obtained about a partner's motivational state and commitment to the relationship (Zahavi & Zahavi 1997).

Greeting interactions between male baboons are one potential example of honest communicative exchanges aimed at testing the quality of dyadic relationships (Kummer 1968; Saayman 1971; Sugawara 1979; Pelaez 1982; Smuts 1985; Manzollilo 1986; Hausfater & Takacs 1987; Colmenares 1990, 1991a,b; Smuts & Watanabe 1990). In baboons, a typical greeting sequence involves one male approaching another while producing affiliative facial expressions and gestures (e.g., lipsmacking, pinning the ears back, and crouching), followed by rump presentation, rump grasping, mounting, embracing, genital presentation, and/or the 'diddling' of the penis and/or scrotum. The fondling of the genitalia is a particularly intimate and risky interaction considering that male baboons have a high potential for aggression and that hitting or biting a male's genitalia could effectively end his future mating success. Some of these interactions (e.g., rump presentation and grasping) have also been described in other primate species (e.g., macaques; Maestripieri 1997) but the highly ritualized fondling of the genitalia observed in baboons has not been reported in other species.

It has been hypothesized that greetings may function to facilitate coordination of travel (in hamadryas baboons, *Papio hamadryas*; Kummer 1968), to appease dominant individuals in tense situations (e.g., Sugawara 1979; Pelaez 1982; Hausfater & Takacs 1987), to re-establish social bonds after agonistic conflicts (i.e., reconciliation; Kummer et al. 1974), or to assess the aggressive tendencies of male rivals and attempt to settle conflicts of interest without using aggression (Strum 1982; Smuts 1985; Colmenares 1991a,b; Colmenares & Lazaro-Perea 1994). The bond-testing hypothesis has been recently discussed in the context of greetings by Smuts (2002), who suggested that by engaging in potentially risky interactions such as fondling each other's genitalia, male baboons exchange honest information about their willingness to tolerate other males and cooperate with them. This hypothesis, however, has not yet been empirically tested and contrasted with competing hypotheses.

In the present study, we investigated male-male greetings in a species of baboon, the Guinea baboon (*Papio papio*), in which these interactions have not yet been studied. To test the hypothesis that greetings serve an aggressive or submissive function, we investigated whether dominance rank and involvement in aggression predicted interindividual variation in participation in

greetings, whether the exchange of greetings within male–male dyads was predicted by the distance in rank between the males, and whether the initiation of greetings within dyads was predicted by the relative ranks of the two males.

Specifically, if greetings serve an aggressive function, we predicted that they should be mostly initiated by high-ranking or highly aggressive individuals, and in particular by the dominant member of each male–male dyad. Conversely, if greetings serve a submissive function, we predicted that they should be mostly initiated by low-ranking individuals, especially during interactions with the high-ranking males in the group.

The hypothesis that greetings are functionally related to aggression or submission also leads to the prediction that they may be contextually and/or temporally associated with episodes of aggression or other potentially competitive situations (e.g., mating or feeding). For example, if greetings serve an appeasement function, they should be performed by low-ranking males shortly after receiving aggression or being displaced by dominants. If greetings are a form of reconciliation, they should occur shortly after conflicts between two individuals but they could be initiated by either the aggressor or the victim.

To test the hypothesis that greetings are used by male baboons to exchange honest information about the strength of their social bonds, we investigated whether the general quality of dyadic relationships was predictive of the frequency of greetings exchanged among pairs. Specifically, we predicted that pairs of males with high levels of affiliation and social tolerance would be more likely to exchange greetings than pairs of males with poor social relationships. As the bond-testing hypothesis is based upon the assumption that greetings are potentially costly interactions, we expected its predictions to be supported especially by data involving 'intense' greetings, i.e., greetings involving the most intimate forms of contact such as embracing and fondling of the genitalia.

Methods

Subjects and Housing

This study was conducted with a group of 40 Guinea baboons at the Brookfield Zoo in Chicago, Illinois. The group consisted of 15 adult males and 25 adult females. The males ranged from 9 to 22 yr of age ($\bar{x} = 14.0$, $SD = 4.16$) and the females from 11 to 21 yr ($\bar{x} = 14.36$, $SD = 2.89$). There are no infants, juveniles, or subadults in this population. All adult males are currently vasectomized (one is castrated) while all females except one are intact and cycling.

The group is housed in an outdoor, multi-level, grotto comprised of artificial rocks and measuring 57.3 m \times 47.2 m. The animals also have access to an indoor holding and feeding facility, in which the baboons are given an unlimited supply of water and monkey chow. At approx. 11.00 h each day, the group is fed a combination of various fruit and vegetables.

Procedure

Data were collected over a 6-mo period during the summer and fall of 2001. The 15 males were observed in 30-min sessions and their behavior was recorded using the focal sampling technique (Altmann 1974). Each male was observed for 13 h, resulting in a total of 195 h of observation. The order in which subjects were observed on a given day was randomized. Data were collected using a palmtop computer on which the Observer 3.0 software (Noldus, Sterling, VA, USA) was installed.

A number of social and non-social behaviors were recorded. In this study, the main variables of interest include the frequency of male–male greeting interactions, the number and duration of male–male grooming bouts, and the frequency of male–male aggressive bouts. A greeting was scored when at least one of the following behaviors was performed: diddling, embracing, rump presentation, genital presentation, hip-clasping, and/or hip-touching. For a greeting interaction to be scored as intense at least one diddle and/or embrace had to be exchanged. The approaching animal was considered to be the initiator of the greeting. Greetings occurred too quickly (2–3 s) to be recorded in terms of duration and they typically involved only one brief contact between the males. Grooming was scored when one animal manipulated the fur or skin of another. Both the number of bouts and the total duration of grooming were recorded. A bout of aggression was scored when one animal directed a threat, chase, or contact aggression (biting, hitting, or slapping) toward another. Agonistic support was defined as a third-party male intervening in a bout of aggression between two individuals and siding with either party.

The scan sampling technique was used to collect data on nearest neighbor proximity (Altmann 1974). Every minute, the focal animal's nearest male neighbor was categorized as being: in contact, in close proximity (< 1.5 m), or in distant proximity (1.5–3.0 m). If no other males were within 3.0 m of the focal animal, the scan was scored as no nearest neighbor.

During the focal observations, instances of aggression and submission between males (bared-teeth displays, presentations, and spatial displacements) were recorded ad libitum. These observations were used, along with the focal data, to construct a dominance hierarchy. If the dominance relationships between two or more males could not be determined unequivocally, these individuals were assigned an average ranking (e.g., the top four males were all ranked as 2.5). For each possible dyad of males, the distance in rank between the members was determined by calculating the difference between their individual rankings.

Relationship quality for all male–male pairs was assessed using the number of grooming and aggression bouts occurring within the dyad, the average proportion of scans the members of a dyad spent in contact or proximity, and a measure of social tolerance, calculated as the rate of aggression within a dyad, controlling for the time spent in contact or proximity.

Correlations between dominance rank and individual rates of behavior (e.g., greeting, aggression, and grooming) and between different individual behaviors (e.g., greetings and aggression) were calculated using the Spearman rank

correlation coefficient test. Correlations between behavioral characteristics at the dyadic level (e.g., between aggression and greetings exchanged within dyads) were calculated using the Mantel test (Mantel 1967) to take into account the non-independence of dyads. This method involves creating an interaction matrix for each behavioral variable (in which each individual's interactions with all the others are represented), and then assessing correlations between different behavioral matrices. We used the simple Mantel test in cases in which only two behavioral variables were considered. In cases in which a third variable was held constant, we used the partial Mantel test. Wilcoxon matched-pairs tests were also used for dyadic data analysis. All tests were two-tailed ($\alpha = 0.05$).

Results

Greetings, Affiliation, and Dominance Rank

Over the course of the study, 332 greetings were exchanged between males (range for participation in greetings by individual males = 18–78). Of these, 128 were considered intense greeting interactions (contained an embrace and/or at least one diddle). The focal males spent 18.9% of their scans either in contact or close proximity to another male (3.5% in contact, 15.4% in proximity), and all but one of the subjects were observed to engage in male–male grooming. Focal males spent 2.5% of their time grooming or being groomed by another male (range = 0–9.2%).

A significant positive correlation was found between an individual's rank and the number of intense greeting behaviors exchanged with other males in the group. Low-ranking males were more likely to be involved, as actor or recipient, in intense greeting interactions than were dominant males ($n = 15$, $r_s = 0.65$, $p = 0.009$). Specifically, low-ranking males received significantly more intense greetings than high-ranking males ($r_s = 0.63$, $p = 0.013$; Fig. 1b) while there was no significant correlation between rank and initiation of intense greetings ($r_s = 0.39$, $p = 0.15$; Fig. 1a). No relationship was found between the frequency of aggressive bouts initiated or received and the number of intense greetings in which a male was involved. Agonistic support occurred too infrequently to be analyzed quantitatively in relation to greetings. Finally, there was no correlation between an individual's rank and the likelihood of participating in less intense forms of greeting ($r_s = -0.009$, $p = 0.97$).

Low-ranking males were more likely to be involved in grooming than high-ranking males ($r_s = 0.71$, $p = 0.003$). Specifically, these individuals received more grooming, both in terms of total duration ($r_s = 0.62$, $p = 0.01$) and the frequency of bouts ($r_s = 0.71$, $p = 0.003$). Low-ranking males also performed grooming for a longer duration than high-ranking males ($r_s = 0.51$, $p = 0.05$).

Greetings, Relative Rank, and Relationship Quality in Male–Male Dyads

Over the course of the study, 53 of the 105 dyads exchanged at least one intense greeting interaction. On average, dyads exchanged 2.42 ± 1.78 intense

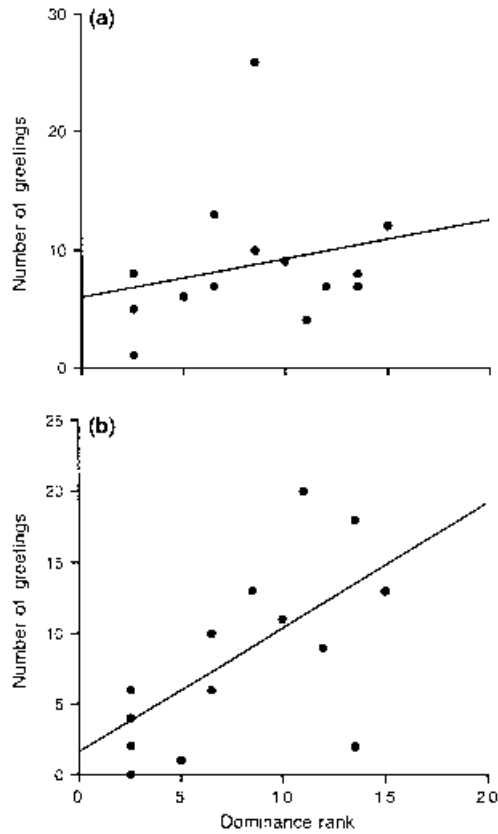


Fig. 1: (a) Relationship between dominance rank and the number of intense greetings initiated by individual males. (b) Relationship between dominance rank and the number of intense greetings received by individual males

greetings (range = 1–8). Of the males that participated in male–male grooming, most (85.7%) had two to three different partners. However, only 20 of all possible male–male dyads exchanged grooming.

There was no correlation between the distance in rank between members of a dyad and the number of intense greetings exchanged (simple Mantel test, $Z = -0.10$, $p = 0.30$). Among the dyads that exchanged at least one intense greeting, there was no significant difference in the number of greetings initiated by the dominant and by the subordinate member of the dyad (Wilcoxon test, $n = 50$, dominant = 1.46 ± 1.50 ; subordinate = 0.96 ± 1.09 ; $z = -1.81$; $p = 0.07$). Furthermore, there was no significant relationship between an individual's relative rank within the dyad and the likelihood of initiating a grooming bout (Wilcoxon test, $n = 18$, dominant = 5.20 ± 6.35 ; subordinate = 4.50 ± 7.11 ; $z = -0.32$, $p = 0.75$) or in the total duration of grooming performed (Wilcoxon test, $n = 18$, dominant = 382.6 ± 595.95 s; subordinate = 589.6 ± 934.23 ; $z = -1.68$; $p = 0.09$).

Dyads that exchanged a higher number of grooming bouts were more likely to participate in intense greeting interactions (simple Mantel test, $Z = 0.48$, $p < 0.0001$; Fig. 2a). Furthermore, dyads that spent a higher proportion of time in contact or proximity, also exchanged intense greetings more frequently (simple Mantel test, $Z = 0.47$, $p < 0.001$; Fig. 2b). However, when time in contact or proximity was controlled for grooming time, this relationship was no longer significant (partial Mantel test, $Z = 0.08$, $p = 0.46$).

There was no significant correlation between intense greetings and aggression exchanged within dyads (simple Mantel test, $Z = -0.07$, $p = 0.46$), even when aggression was controlled for time spent in contact or proximity (partial Mantel test, $Z = -0.12$, $p = 0.22$).

The number of less intense greetings exchanged was not correlated to distance in rank (simple Mantel test, $Z = -0.15$, $p = 0.14$), contact or proximity

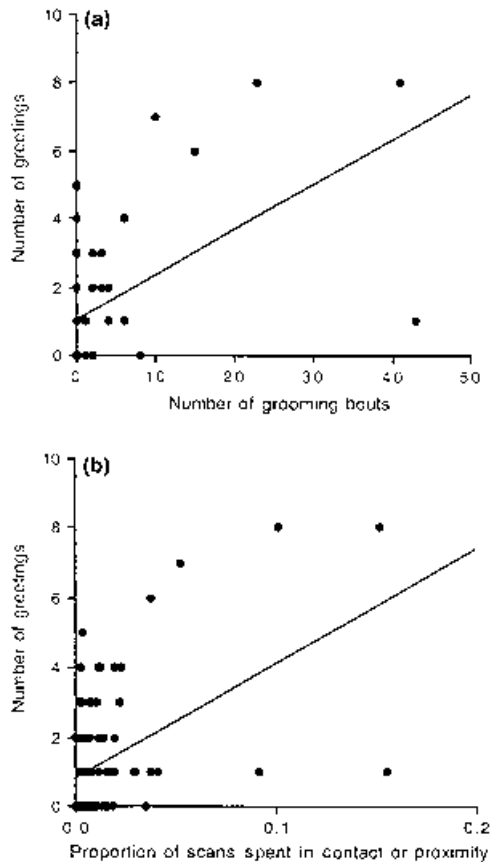


Fig. 2: (a) Relationship between the number of grooming bouts and number of intense greetings exchanged within particular dyads. (b) Relationship between the proportion of scans members of a dyad spent in contact or proximity and the number of intense greetings exchanged

(simple Mantel test, $Z = 0.18$, $p = 0.07$), grooming bouts (simple Mantel test, $Z = 0.10$, $p = 0.27$), or aggression (simple Mantel test, $Z = -0.04$, $p = 0.71$).

The Context of Occurrence of Greetings

If greetings, and in particular intense greetings, are associated with specific social interactions between males, they should occur in close temporal association with such events. For example, if greetings serve an aggressive or submissive function, they should occur in close temporal association with episodes of aggression or in situations potentially involving competition such as mating or feeding in close proximity. On the contrary, if greetings reflect a form of communication about social relationships (i.e., the history of previous interactions between two individuals) instead of any specific interactions between males, they are not expected to be temporally associated with any particular events or contexts. If anything, greetings may be associated with the exchange of affiliation (e.g., grooming) or agonistic support, i.e., with social interactions that, along with greetings, are expected to be exchanged frequently between males with good social relationships.

To evaluate these hypotheses, first, we investigated all social and non-social events that preceded, within 1 min, the occurrence of intense greetings. These events included, among others, activities such as aggression, agonistic support, grooming, mating, or feeding. Secondly, we investigated how many intense greetings were followed, within 1 min, by an episode of dyadic aggression vs. an episode of grooming or agonistic support. Finally, we investigated how many episodes of aggression, with or without agonistic support, were followed by greetings (both intense and less intense) or grooming.

Of the 120 intense greetings for which information was available, only one of them was preceded by dyadic aggression, two by aggression with agonistic support, and five of them by male–male allogrooming. The vast majority of greetings were preceded, within 1 min, by non-social activities such as feeding or grooming alone, walking, or resting. These non-social activities accounted for approx. 88% of the males' time budgets, and approx. 91% of all intense greetings occurred during these activities. Of the 105 intense greetings for which information was available, only one of them was followed by aggression between the same two males. In contrast, 17 of them were followed by allogrooming between the same two males. The same member of the dyad was observed to initiate both the greeting and the grooming 15 of 17 times.

A total of 85 episodes of male–male aggression were recorded during the focal observations. In 11 of these episodes, the focal male either gave or received agonistic support from a third male. Only one episode of dyadic aggression was followed, within 1 min, by a greeting between former opponents (an intense greeting). Three of the 11 episodes of agonistic support were followed by a greeting (two intense and one less intense) between the focal male and the supporting male. These greetings were all initiated by the supporting male. In two episodes of aggression, the focal male received less intense greetings from a third

male not involved in the conflict. These greetings may also be interpreted in the context of agonistic support.

Agonistic support was also often followed by grooming. Specifically, in five of the 11 observed cases of agonistic support, the provider and the receiver of support exchanged grooming within 1 min after the intervention. The intervening male and supported male were equally likely to initiate grooming. In two cases, aid was followed by the supporting male initiating both a greeting and a bout of grooming.

Discussion

Male–male greetings were relatively common social interactions in our study group. For example, intense greetings (which represented about 40% of total greetings) were exchanged between about half of all possible male–male pairs. Some individuals, however, were involved in greeting interactions more than others, and some male–male dyads exchanged greetings at a much higher rate than other dyads. Our data suggest that variation in the occurrence of greetings is not accounted for by individual characteristics such as dominance rank or aggressiveness. Furthermore, the occurrence of greetings does not appear to be temporally contingent upon any specific events such as episodes of aggression, or competition over feeding or mating. Instead, our data suggest that the differences among male–male dyads in the exchange of greetings reflect differences in the quality of their social relationships.

The view that greetings express submissive behavior and are used by subordinate males to appease dominants in situations with a high risk of aggression is inconsistent with several findings. The relationship between individual rank and intense greetings was opposite to that expected if greetings had a submissive function. Low-ranking males were more involved in greetings than high-ranking males, and in particular, they received more greetings than dominants. Less intense greetings showed no clear relationship with rank. Furthermore, involvement in intense greeting interactions with other males was not predicted by the frequency of aggression exhibited or received. In particular, only one of 85 episodes of aggression between two individuals was immediately followed by a greeting between the former opponents, and this association could have arisen by chance. This finding argues against the hypotheses that greetings serve an aggressive or submissive function, or that they are used for post-conflict reconciliation. As close temporal association with aggression is part of the operational definition of reconciliation (Aureli & de Waal 2000), the fact that greetings did not immediately follow aggression makes it highly unlikely that they serve a reconciliatory function. Most greetings were preceded by non-social activities such as walking, feeding alone, or resting. These activities accounted for approx. 88% of the males' time budgets, and approx. 91% of all intense greetings occurred during these activities, suggesting that the occurrence of greetings was relatively random. This result is consistent with a previous field study of savanna baboons in which 98% of all male–male greetings occurred in

a neutral context, such as during traveling, resting, or foraging (Smuts & Watanabe 1990).

Our results do not support the view that greetings ‘may be regarded as a quasi-aggressive behaviour ... aimed at testing a potential or actual rival’s tendencies during competition’ (Colmenares 1991a, p. 50). Colmenares (1990, 1991a,b) has argued that, in hamadryas baboons and their hybrids, greetings occur in the same context as physical aggression (e.g., competition over resources, agonistic bouts, reconciliation, and recruiting/inhibiting support) and that aggression and greetings may be considered alternative strategies of conflict resolution. Although it is possible that greetings have a different function in different *Papio* species, we believe that most data reported so far for all baboons, including the Guinea baboons of this study, are consistent with the hypothesis proposed by Smuts & Watanabe (1990) that greetings allow two males to exchange information about their relationship, i.e., their past and future interactions, independently from the context.

Dominance does not appear to be an aspect of the male–male relationship that is immediately relevant to the occurrence of greetings. In our study, rank distance between members of a dyad did not predict the frequency of greetings exchanged, and the relative ranks of the two males did not predict who initiated the greeting. In contrast, frequent exchange of intense greetings within particular dyads of males was associated with high frequency of grooming and elevated time spent in contact or proximity. In other words, greetings were frequent between males that had good-quality relationships. Similar to greetings, other measures of affiliation were not clearly associated with dominance rank. In particular, the exchange of grooming within male–male dyads was relatively symmetrical. Although a very small percentage of greetings occurred in the context of aggression, these few greetings appeared to be associated with polyadic interactions and agonistic support. In particular, these greetings were initiated by the individual providing support and directed to the individual being aided. Grooming was also relatively common in this context. A correlation between greetings and agonistic support has also been reported by Colmenares (1990, 1991a,b) in a captive colony of hamadryas baboons, yellow baboons, and their hybrids.

We believe that the specific function of greetings, or at least of the most intimate and intense forms of this interaction, is to allow two males to test the strength of their social bond and/or express their present and future commitment to the relationship (see also Smuts 2002). Specifically, low-ranking males may use greetings to gather information on the dominants’ willingness to tolerate and support them. The intimate nature of intense greetings is such that they would be allowed by only very tolerant and supportive males. In addition to tolerating greetings initiated by subordinates, dominant males may initiate greeting interactions to communicate their willingness to accept the subordinates’ presence in their group, and their availability as potential allies. Consistent with the potential riskiness and cost of these interactions, intense greetings are particularly well suited to the honest exchange of information about one’s intentions and

commitments. Other affiliative signals such as lipsmacking, or even grooming, appear to be much cheaper than greetings and therefore more suitable for deceitful communication.

Our findings and their interpretation are consistent with those of other primate studies. For example, in studies of white-faced capuchin monkeys (*Cebus capucinus*), Perry (1997) and Perry et al. (2003) reported that individuals engaged in costly, risky social behaviors such as tail-pulling, inserting their fingers into another individual's nose, and rubbing their faces into the body of other group members. Perry et al. (2003) argued that the function of these interactions is to test the strength of social bonds because a positive response from the recipient, or even the toleration of such behaviors, would be indicative of a good relationship and the willingness to further invest in the bond. Similarly, Manson (1999) argued that female capuchins handle the infants of their grooming partners and allies as a way to test the strength of their bonds.

Males or females in different species may have different reasons to test the strength of their social bonds with greetings or other risky behaviors. The relatively high rate of greetings among the male Guinea baboons of this study may be accounted for, in part, by the social organization of this species, and in part by the captive environment. Guinea baboons have been poorly studied, particularly in the field, but the available evidence suggests that their social organization shares some characteristics with that of hamadryas baboons and other *Papio* species (see Barton 2000, for a recent discussion of *Papio* taxonomy and social organization). Similar to the hamadryas, Guinea baboons appear to live in large and loosely structured social units (troops) that fission into multi-male subgroups which further subdivide into harem-like groups (clans or parties) (Dunbar & Nathan 1972; Boese 1975; Sharman 1981; Galat-Luong & Galat 2003). These clans typically include one or two males and several adult females and their offspring (Dunbar & Nathan 1972; Boese 1975). Mating appears to occur mostly within the small clans (Boese 1975; Maestriperi et al., unpubl.). How the clans are formed and maintained in Guinea baboons is not well known. Adult males, however, do not kidnap and herd females the way hamadryas males do (Kummer 1968; Dunbar & Nathan 1972).

Maintaining good relationships may be advantageous to the males that live in the same clan and interact with the same females. This would reduce the probability of costly fights, maintain cohesiveness within the clan, and reduce the probability that the clan may be taken over by other males or that the females may spontaneously leave the clan and join another one. Good male-male relationships may also be important between males of different clans, when the clans reunite together at the sleeping sites or when the multi-male subgroups travel and forage together (see Kummer 1968; Swedell 2002, for hamadryas baboons). Thus, pressure to maintain good-quality relationships between males both within and between clans may have favored the evolution of high rates of greetings in Guinea baboons as a way to continuously test and strengthen social bonds. More generally, high rates of greetings or other forms of ritualized affiliative interactions are expected to occur in socially living primate species in

which there is a high potential for severe male–male aggression (e.g., because of male body size, canine tooth size, and temperament) but in which there are also substantial benefits to maintaining good relationships with particular males (e.g., tolerance, or coalition formation, or cooperation for group defense). Such species may include the baboons, some macaques, and chimpanzees.

The variability in environmental and social settings in which baboon greetings have been studied so far (e.g., captivity vs. field, groups with many males vs. groups with few males, and groups with hybrids vs. groups without hybrids) makes it difficult to compare absolute rates of greeting interactions across different studies. However, it is reasonable to hypothesize that stable groups with a relatively high number of adult males living in a confined environment, such as the group of this study, may exhibit higher rates of male–male greetings than those that have different demographics or live in other environments. Although the bond-testing hypothesis of greetings can be investigated with any social group in any environment, to fully understand their adaptive value and evolution among baboons, more studies are needed comparing free-ranging populations of all the different *Papio* species.

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