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The Silent Bared-Teeth Face and the Crest-Raise of the Mandrill (*Mandrillus sphinx*): a Contextual Analysis of Signal Function

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Abstract

The functions of two visual signals of the mandrill [silent bared-teeth face (SBTF) and crest-raise (CR)] were investigated by quantifying the probability of each signal occurring across a set of distinct contexts. The motivation for the investigation was twofold: (1) SBTF had been interpreted in diverse and sometimes contradictory ways, and (2) CR had been interpreted as a distinct signal from SBTF, despite indications that the two signals grade into one another. In our investigation we considered four functions for both SBTF and CR (threat, submissive, conciliatory, and ambivalent), and we made specific predictions about the relative probability that a signal with each of these functions should occur in different contexts. To determine if SBTF and CR represent a single graded signal, we analyzed them separately and together. We predicted that if they represent a single graded signal, then they should exhibit similar patterns of occurrence across contexts when they were analyzed separately, and that these patterns should be strengthened when they were analyzed together. The results showed that both SBTF and CR met the predictions for conciliatory signals, occurring most often in non-aggressive, non-hostile contexts and least often in aggressive, hostile contexts. The results were also consistent with the hypothesis that SBTF and CR represent a single graded signal.

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Introduction

One of the fundamental goals in the study of animal communication is to determine the functions of animal signals. Frequently, this goal is accomplished by identifying salient contexts and determining how often signals occur in these contexts (Bradbury & Vehrencamp 1998). When contextual analyses are conducted in a systematic, quantitative manner they provide a common standard for determining signal function, thus facilitating comparisons across different animal species and different human observers.

The use of a quantitative, contextual-based methodology has proven especially useful in investigations of visual signaling in primates. A number of studies, for example, have investigated teeth-baring and relaxed open-mouth displays across the primate order, and these studies have been used to retrace the likely evolutionary history of these displays (Preuschoft 1995; Preuschoft & van Hooff 1997). Teeth-baring, in particular, appears to be homologous to the human smile, as originally hypothesized by van Hooff (1972). Moreover, the combined quantitative contextual data on teeth-baring in many different primate species supports the interpretation that this signal originated as a defensive or protective behavior and only gradually became a sign of submission, and eventually a friendly signal (van Hooff & Preuschoft 2003).

The function of the silent bared-teeth face (SBTF) of the mandrill (*Mandrillus sphinx*), an Old World monkey endemic to the tropical rain forests of equatorial west Africa, has not been as rigorously documented as the function of teeth-baring in many other primate species. In fact, the mandrill SBTF is noteworthy for the breadth of interpretations different observers have made concerning its function. This signal, wherein the lips are curled back in a horizontal figure eight shape, revealing the canines and premolars, and the crest is erected while the head is shaken repeatedly from side to side, has been variously interpreted as: an 'expression of threat' reminiscent of 'tearing at an opponent' (Andrew 1963, p. 65); a 'strong social attraction, at times mixed with a tendency to attack or to flee' (van Hooff 1967, p. 34); a 'friendly approach' (Bernstein 1970, p. 281); a 'general expression of well being' (Fiedler 1972, p. 427); a 'type of fear grimace' (Redican 1975, p. 111); a 'threat face' (Emory 1975, p. 321); a 'light menace' that 'has nothing friendly about it' (Jouventin 1975, p. 457); a signal whose 'message is in truth friendly and is often an appeasement made toward a threatening animal' (Davis 1976, p. 8); an 'ambivalent approach-flight manifestation' (Gautier & Gautier 1977, p. 933); a 'threat' (Kawata 1980, p. 216); a 'smile' or 'greeting' (Mellen et al. 1981, p. 217); and a 'reassurance gesture' (Feistner 1989, p. 73).

The contradictions among different observers' interpretations of SBTF do not appear to be attributable to variation in the length of observation. These contradictions exist between observers who observed over shorter periods (hours or days) and also between observers who observed over longer periods (weeks or months). One possible explanation for the differences in interpretation of SBTF's function may be that many interpretations were based solely on qualitative observations. To our knowledge, no investigation of SBTF in mandrills has quantified its probability of occurrence across contexts, although this methodology can effectively resolve discrepancies between different observers' functional interpretations and also correct those interpretations that are erroneous (e.g. Johnston 1973; Seeley 1992; Biesmeijer 2003).

Within the mandrills' repertoire there is another signal, crest-raise (CR), which, like SBTF, has not been subjected to a quantitative analysis across different contexts. This signal, which is characterized by a momentary erection of the sagittal crest, appears to resemble SBTF because SBTF is itself characterized by the erection of the crest. Several observers, in fact, have hypothesized that CR and SBTF might represent a single signal because they grade so closely together (P. Jouventin pers. comm.; J. Mellen pers. comm.; R. Sellin pers. comm.; Laidre & Yorzinski pers. obs.). Moreover, the absence of CR in one of the more detailed mandrill ethograms (Emory 1975) may be a consequence of the observer implicitly lumping CR with SBTF. We are aware of only two studies that have explicitly distinguished CR from SBTF (Kawata 1980; Feistner 1989), and both have interpreted CR as a threat.

The objective of this paper is to conduct a quantitative contextual analysis of SBTF and CR in order to (1) assign a function to each of these signals, and (2) test the hypothesis that SBTF and CR represent a single graded signal. In our analysis we consider four possible functions for each of the two signals: threat, submissive, conciliatory, and ambivalent. (These functions were chosen because the interpretations of previous observers have all fallen into one of these four main categories.) To assign functions to SBTF and CR we make predictions about the relative probability that a signal with a specified function will occur in different contexts. We then test these predictions by quantifying the probability of each signal occurring across these contexts. To test the hypothesis that SBTF and CR represent a single graded signal, we analyze these signals separately, as if they were two discrete signals, and together, as if they were a single graded signal. We predict that if SBTF and CR represent a single graded signal, then they should exhibit similar patterns of occurrence across contexts when they are analyzed separately, and that these patterns should be strengthened when they are analyzed together.

Methods

Study Groups and Enclosures

From Jan. 2002 to Jan. 2003 we collected over 700 h of quantitative observations on the visual communication of 11 mandrills housed in three different captive groups in zoos in the USA. Four individuals were observed at the Rosamond Gifford Zoo in Syracuse, NY, USA for a total of 490 h. An adult male, an adult female, and their two juvenile female offspring were housed together in an approx. $9 \times 8 \times 5$ m (length $\times$ width $\times$ height) indoor enclosure. Three individuals were observed at the Buffalo Zoological Gardens in Buffalo, NY, USA for a total of 110 h. An adult female, her juvenile female daughter, and another juvenile female were housed in an approx. $12 \times 6 \times 4$ m outdoor, naturalistic enclosure. Four individuals were observed at the Staten Island Zoo in New York, NY, USA for a total of 100 h. An adult male and three adult females were housed in an approx. $9 \times 7 \times 4$ m indoor enclosure.

Sampling Regimes and Recording Equipment

The first phase of the study (175 h) was conducted on the Syracuse group from Jan. 2002 to May 2002. During this phase we applied continuous focal animal sampling (Altmann 1974) to identify and record communication signals and social contexts. In addition, a Canon 3CCD digital video camcorder (model GL1 NTSC;

Canon, Lake Success, NY, USA) was used to document each signal on film (exemplars of the signals discussed in this paper have been stored in the Visual Media Collections of the Cornell Laboratory of Ornithology's Macaulay Library; these clips will soon be viewable through the laboratory's website [http://www.birds.cornell.edu], but until that time, clips can be obtained by sending a self-addressed, stamped envelope and blank CD to the corresponding author).

In the second phase of the study, which lasted from Jun. 2002 to Jan. 2003, we adopted a revised sampling regime in which each of us had a specific role that only he or she carried out. One observer (M.E.L.) made a continuous record of signals his focal individual directed toward and received from other individuals including any allogrooming, copulation, play, and agonism involving his focal individual. Behavioral and time records were made by speaking into a microcassette recorder and glancing at a digital watch.

The other observer (J.L.Y.) used continuous behavior sampling (Martin & Bateson 1993, p. 87) to record the interactions between individuals in the entire group. She continually scanned all group members and recorded the exact start and stop times of allogrooming, copulation, play, and agonism that involved individuals besides the other observer's focal individual. The small size of our study groups (less than, or equal to four individuals), the small size of the groups' enclosures, and the prominence of the interactions ensured that essentially all interactions were detected.

In both phases of the study, the two observers generally observed the groups simultaneously between 09.00 and 18.00 hours from a public viewing location. Observations on a group were typically continuous for either a 3 or 6 h block and were never ceased when individuals were interacting.

Description of Signals and Definition of Possible Signal Functions

Silent bared-teeth face and CR are illustrated in Fig. 1 and described in the Introduction. For both SBTF and CR we consider four possible functions: threat, submissive, conciliatory, and ambivalent. These different signal functions can be defined as follows: A threat function only includes aggressive signals. These signals can provoke attack when directed by subordinates and can predict attack when directed by dominants. A submissive function only includes signals given chiefly by subordinates. These signals appease existing aggression and preempt potential aggression. A conciliatory function only includes friendly signals given by both dominants and subordinates. These signals indicate an absence of hostility and aggressive intentions. Finally, an ambivalent function only includes signals that poorly advertise the sender's intentions. These signals sometimes indicate aggressive intentions and sometimes indicate non-aggressive intensions, doing so in approximately equal measure.

Demarcation of Contexts

We recognized four types of interactions: allogrooming, copulation, play, and agonism. Allogrooming began when an individual gently passed its fingers or

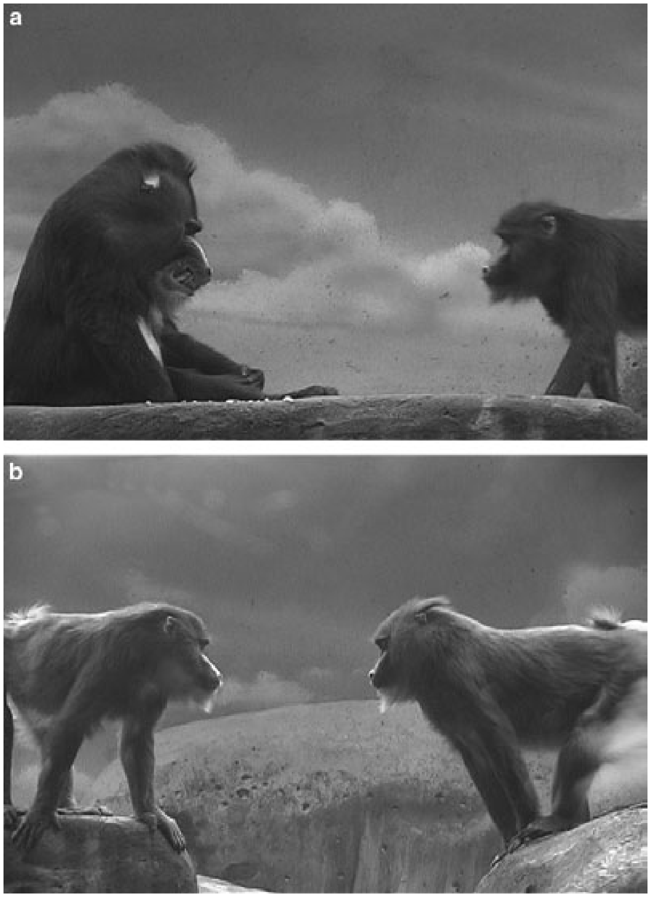

Fig. 1: Pictures of silent bared-teeth face and crest-raise: (a) the adult male (left) in the Staten Island group directing silent bared-teeth face to an adult female; (b) an adult female (right) in the Staten Island group directing crest-raise to another adult female

mouth through the fur of another individual and ended when the individuals ceased this activity, failing to resume it within 20 s. Copulation began when a male mounted an estrous female, achieving intromission, and ended when the male dismounted the female. Play began when juveniles engaged in mutual pushing, pulling, gnaw wrestling, and self-handicapping and ended when the individuals ceased this activity, failing to resume it within 20 s. Agonism began when one individual directed an overtly aggressive or threat signal toward another individual and ended when the individuals ceased looking at one another and stopped directing signals at one another for 10 s. Overtly aggressive signals included hitting, chasing, and biting (Nagel & Kummer 1974) and threat signals included head bob, lunge, slap ground, and stomp (Emory 1975; Kawata 1980; Mellen et al. 1981; Feistner 1989).

The four interactions (allogrooming, copulation, play, and agonism) were used to generate ten mutually exclusive and exhaustive contexts: prior-to-groom (1 min prior to allogrooming); during-groom; prior-to-copulate (1 min prior to copulation); during-copulate; prior-to-play (1 min prior to play); during-play; prior-to-agonism (10 s prior to agonism); during-agonism (from agonism's start up to the last overtly aggressive or threat signal within an agonistic interaction); after-agonism (from the last overtly aggressive or threat signal within an agonistic interaction to 15 s after agonism's end); and nothing (a 30 min period in which none of the other nine contexts occurred).

Predictions of Signals Occurring within Contexts

The 10 contexts we demarcated represent discrete periods in which there is an indication of the state of relations between the interacting individuals. Specifically, the prior-to-groom, during-groom, prior-to-copulate, during-copulate, prior-to-play, and during-play contexts are contexts in which individuals are engaged in or are preparing to engage in non-aggressive, non-hostile interactions. During these contexts we would expect individuals to advertise friendly, non-aggressive intentions. The prior-to-agonism context is a context in which the actions of one individual either elicited spontaneous aggression from the receiver or predicted immediate aggression from the sender. The during-agonism context is an intensely hostile context in which individuals are aggressing against, or attempting to appease one another, or both. The after-agonism context is a context in which individuals have the opportunity to reconcile following an aggressive incident. Finally, the nothing context is a baseline context in which individuals are engaged in none of these activities.

Based on this a priori framework for each context, it is possible to predict the likelihood that a signal with a specified function will occur in one context vs. another. For a conciliatory signal, our predictions are as follow:

1 More likely to occur in the prior-to-groom vs. prior-to-agonism context
2 More likely to occur in the during-groom vs. during-agonism context
3 More likely to occur in the prior-to-copulate vs. prior-to-agonism context
4 More likely to occur in the during-copulate vs. during-agonism context
5 More likely to occur in the prior-to-play vs. prior-to-agonism context
6 More likely to occur in the during-play vs. during-agonism context
7 More likely to occur in the after-agonism vs. prior-to-agonism context

For a threat signal, our predictions are the opposite of those for a conciliatory signal: replace *more likely* with *less likely* in predictions 1–7. For an ambivalent signal, replace *less likely* with *equally likely* in predictions 1–7 of a conciliatory signal. For a submissive signal our predictions are the same as for a conciliatory signal except for predictions 2, 4, and 6. As a submissive signal is employed to appease aggression, it would be more likely to occur in the during-agonism context vs. the during-groom (or during-copulate or during-play) context.

Statistical Analyses and Aggregation of Individuals into Classes

We used age (A = adult; J = juvenile, i.e. 2–5 yr), sex (M = male; F = female) and dominance (d = dominant; s = subordinate; determined based on approach-avoid interactions) to aggregate individuals into classes. This aggregation generated five pairs of age-sex-dominance classes: AFd & AFs; AM & AF; AF & J; AM & J; and Jd & Js. (Note that sex is not delineated for the J class as our study groups contained only female juveniles).

To determine if SBTF and CR have a threat, submissive, conciliatory, or ambivalent function we performed a mixed-model ANOVA for each signal that was exchanged between dyads from the five pairs of age-sex-dominance classes. The dependent variable in the model was dichotomous (signal present in vs. absent from context) and context was defined as a fixed factor while dyad and the interaction between dyad and context were defined as random factors. For each case in which a signal was directed from one age-sex-dominance class to another we report the overall *F*-test for context, the fixed factor.

To test each of our predictions (see previous subsection) we performed multiple pair-wise contrasts of different contexts. The Bonferroni method was applied to control the overall alpha level at 0.05 for each series of contrasts. For example, if five contrasts were performed when a signal was directed from individuals in one age-sex-dominance class to individuals in another class, then one of these contrasts would be considered significant only if it yielded $p < 0.01$. All tests were two-sided and only significant contrasts are reported in the Results section. The mixed-model analyses were based exclusively on data deriving from the second phase of the study and these analyses were run using the GLIMMIX macro of SAS v8.2 (SAS Institute, Inc.; Littell et al. 1996). This program calls the PROC MIXED procedure repeatedly and models a dichotomous dependent variable with a binomial logit function, as in logistic regression. Figures in the Results section show least square mean $\pm$ SE of the probability of a signal being present in each context when the signal was directed from one age-sex-dominance class to another.

Results

Silent bared-teeth face was exchanged between dyads in all pairs of age-sex-dominance classes and a significant difference existed in the probability of SBTF occurring in different contexts when the signal was directed between individuals in many of these classes (see Table 1). The probability of SBTF occurring in non-aggressive, non-hostile contexts (such as the prior-to-groom, during-groom, prior-to-copulate, and after-agonism contexts) was generally higher than the probability of the signal occurring in aggressive, hostile contexts (such as the prior-to-agonism and during-agonism contexts; see Fig. 2). The contrast tests supported this overall inspection, showing that when directed between individuals in one or more pairs of age-sex-dominance classes the probability of SBTF occurring was significantly higher in (1) the prior-to-groom compared with the

Table 1: Results (p-values) of the overall *F*-test of context and the seven possible pair-wise contrasts of contexts when silent bared-teeth face was directed from individuals in one age-sex-dominance class to individuals in another class

Directed by_ received by	Overall *F*-value	PG vs. PA	DG vs. DA	PC vs. PA	DC vs. DA	PP vs. PA	DP vs. DA	AA vs. PA
AFd_AFs	0.0005	0.0001	NS	–	–	–	–	0.0005
AFs_AFd	0.005	0.001	NS	–	–	–	–	NS
AM_AF	0.01	0.005	NS	0.005	NS	–	–	NS
AF_AM	NS	NS	NS	NS	NS	–	–	NS
AF_J	NS	NS	NS	–	–	–	–	NS
J_AF	0.005	NS	0.05	–	–	–	–	0.005
AM_J	0.005	–	–	–	–	–	–	0.005
J_AM	NS	–	–	–	–	–	–	NS
Jd_Js	NS	NS	NS	–	–	NS	NS	NS
Js_Jd	NS	NS	NS	–	–	NS	NS	NS

Context abbreviations: PG, prior-to-groom; DG, during-groom; PC, prior-to-copulate; DC, during-copulate; PP, prior-to-play; DP, during-play; PA, prior-to-agonism; DA, during-agonism; AA, after-agonism.
Age-sex-dominance class abbreviations: AF, adult female; AM, adult male; J, juvenile; d, dominant; s, subordinate (AM always dominant over AF and adults always dominant over J in our study groups).
The p-values are only indicated when significant; the actual values were at or below the given threshold. NS, not significant and '–', not applicable (i.e. dyads from that pair of age-sex-dominance classes did not engage in both of the contexts being contrasted).

prior-to-agonism context, (2) the during-groom compared with the during-agonism context, (3) the prior-to-copulate compared with the prior-to-agonism context, and (4) the after-agonism compared with the prior-to-agonism context (see Table 1 for results of all contrasts).

Predictions 1, 2, 3, and 7 of a conciliatory signal were therefore strongly met for SBTF. And although the contrast tests for predictions 5 and 6 of a conciliatory signal were not significant, both these predictions were still well supported: SBTF, when directed from dominant to subordinate juveniles, attained a higher mean probability in the prior-to-play compared with the prior-to-agonism context, and a higher mean probability in the during-play compared with the during-agonism context (see Fig. 2).

Crest-raise was exchanged between dyads in nearly all the same pairs of age-sex-dominance classes as SBTF, except we did not observe it directed from juveniles to adult males or females. The probability of CR occurring was far less than SBTF across all contexts (compare Figs 2 and 3). CR's highest mean probability of occurrence, which was in the prior-to-groom context when the signal was directed from subordinate to dominant adult females, was less than a third of SBTF's highest mean probability of occurrence (0.26 compared with 0.95). The only overall *F*-test indicating that a significant difference existed in the probability of CR occurring in different contexts was when the signal was directed

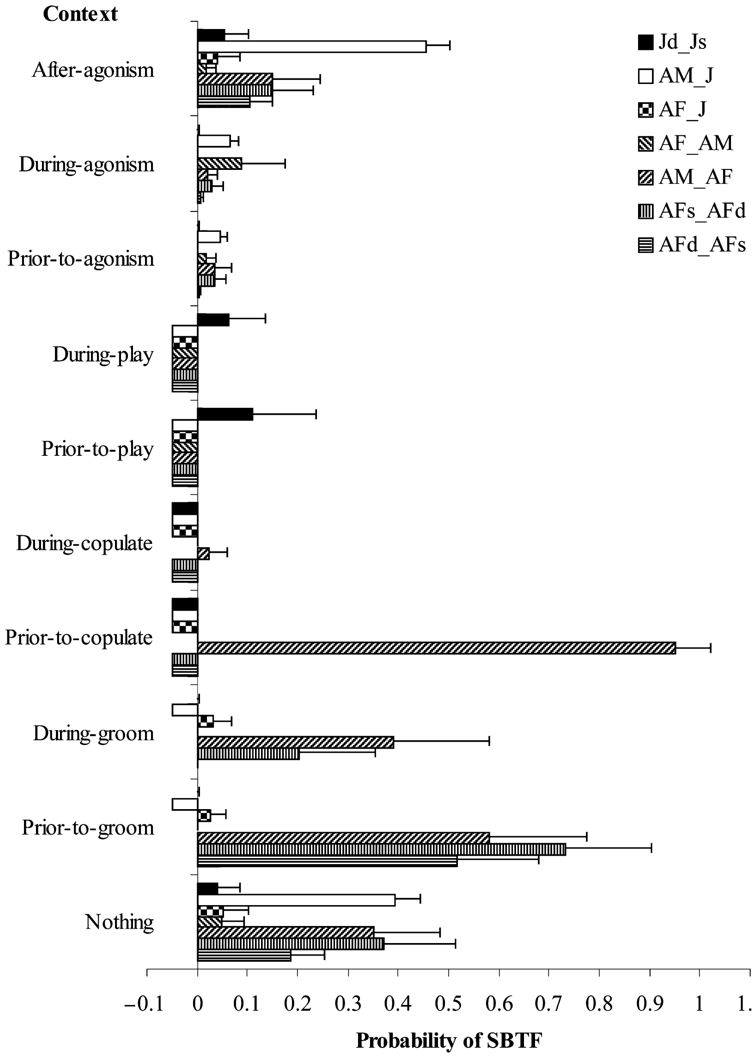

Fig. 2: The probability of silent bared-teeth face (SBTF) occurring in each context when this signal was directed from individuals in one age-sex-dominance class to individuals in another class. Abbreviations for age-sex-dominance classes are as in Table 1. The first age-sex-dominance class that is listed directed the signal and the second age-sex-dominance class that is listed received the signal. For example, 'AFd_AFs' indicates the signal was directed from dominant to subordinate adult females. A negative probability value for a pair of age-sex-dominance classes in a particular context denotes that this pair was not observed to engage in that context. The probability of SBTF is not shown when this signal was directed from juveniles to adult females, from juveniles to adult males, and from subordinate to dominant juveniles because these probabilities were too low to appear at the given scale. Context sample sizes for each pair of age-sex-dominance class are given in Table 2

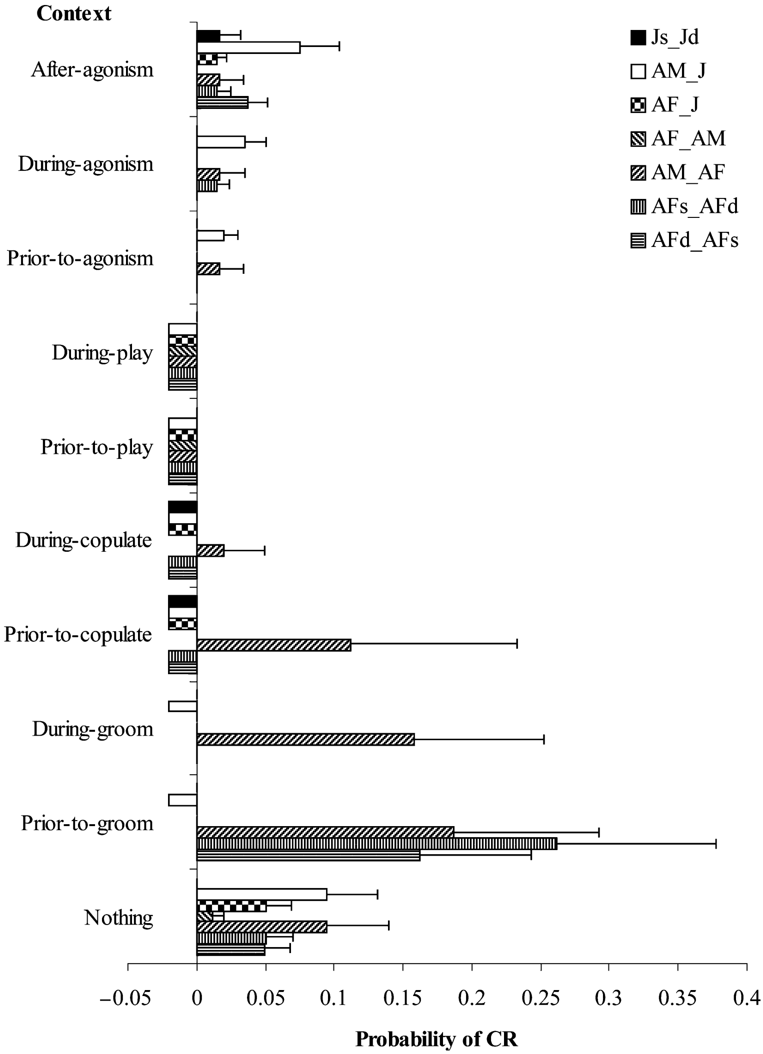

Fig. 3: The probability of crest-raise (CR) occurring in each context when this signal was directed from individuals in one age-sex-dominance class to individuals in another class. Notation as in Fig. 2. The probability of CR is not shown when this signal was directed from dominant to subordinate juveniles because these probabilities were too low to appear at the given scale

from subordinate to dominant adult females. Equally uninformative were the contrast tests, which did not produce a single significant result.

A comparison of CR and SBTF's probability distributions across contexts showed that these probability distributions were very similar. Both CR and SBTF showed the following patterns: (1) when directed from dominant to subordinate adult females, from subordinate to dominant adult females, and from adult males

Table 2: Sample sizes for all contexts for each age-sex-dominance class pair along with the total number of dyads within each age-sex-dominance class pair

	Age-sex-dominance class pair				
Context	AFd & AFs	AM & AF	AF & J	AM & J	Jd & Js
Nothing	100	255	140	176	30
Prior-to-groom	11	81	50	–	7
During-groom	11	81	55	–	10
Prior-to-copulate	–	21	–	–	–
During-copulate	–	21	–	–	–
Prior-to-play	–	–	–	–	22
During-play	–	–	–	–	26
Prior-to-agonism	141	40	143	259	35
During-agonism	141	40	143	259	37
After-agonism	140	40	143	259	38
No. of dyads	3	4	4	2	2

The sample size given indicates the total number of opportunities either age-sex-dominance class in the pair had to direct a signal in that context. '–' indicates that dyads from that pair of age-sex-dominance classes did not engage in the context.

to adult females the mean probability of occurrence was higher in the prior-to-groom compared with the prior-to-agonism context; (2) when directed from adult males to adult females the mean probability of occurrence was higher in the during-groom compared with the during-agonism context and higher in the prior-to-copulate compared with the prior-to-agonism context; and (3) when directed from dominant to subordinate adult females, from subordinate to dominant adult females, from adult females to juveniles, and from adult males to juveniles, the mean probability of occurrence was higher in the after-agonism compared with the prior-to-agonism context (see Figs 2 and 3).

When SBTF and CR were analyzed together as a single signal the results closely matched those obtained when SBTF was analyzed alone. The only difference was that two previously non-significant contrasts became significant: (1) when the combined signal was directed from subordinate to dominant adult females its probability of occurring in the after-agonism context was significantly greater than its probability of occurring in the prior-to-agonism context and (2) when the combined signal was directed from adult males to adult females its probability of occurring in the during-groom context was significantly greater than its probability of occurring in the during-agonism context. Two of the predictions for a conciliatory signal (2 and 7) were thus strengthened when SBTF and CR were analyzed as if they were one signal.

Discussion

A diversity of functions has been suggested for SBTF, including aggressive and non-aggressive functions. Our quantitative analysis provides strong evidence that SBTF has a conciliatory function, and not a threat, submissive, or ambivalent function, as previously suggested. Whereas earlier arguments for SBTF having a conciliatory function have rested largely on observations of how often SBTF occurred during only one context, namely play (Mellen et al. 1981; Feistner 1989), we have provided evidence for a conciliatory function by looking at many additional contexts. Specifically, we found that in exchanges between a variety of age-sex-dominance classes this signal occurred with especially high probabilities in non-aggressive, non-hostile contexts, and that, in most cases, the probability of SBTF occurring in non-aggressive, non-hostile contexts was greater (often significantly) than the probability of it occurring in aggressive, hostile contexts.

Our results fail to support the interpretation that SBTF has a submissive function because (a) SBTF was given often not just by subordinates but also by dominants, and (b) SBTF was given less often in hostile contexts (where the sender would need to appease aggression) compared with non-hostile contexts (where sender would need to advertise friendly intentions). Likewise, our results fail to support the interpretation that SBTF has a threat function because SBTF was given very infrequently prior to and during aggressive contexts. Finally, our results also fail to support the interpretation that SBTF has an ambivalent function as the probability of this signal occurring in non-aggressive, non-hostile contexts was very different from the probability of this signal occurring in aggressive, hostile contexts.

Unlike our analysis of SBTF, our analysis of CR failed to produce statistically significant results. Nevertheless, two functions can be eliminated for CR. First, CR does not appear to have submissive function because it was given often by dominants and subordinates. Second, CR does not appear to have a threat function (as suggested by previous observers) because (1) CR occurred infrequently prior to and during aggressive contexts, and (2) CR occurred frequently during allogrooming (more often than in any other context) whereas threat signals never occurred during allogrooming (our contexts could not have been mutually exclusive if they had).

The lack of statistically significant results for CR may indicate that CR is a discrete signal with an ambivalent function (i.e. CR poorly advertises the sender's intentions). An alternative interpretation, however, is that CR possesses a conciliatory function and that it represents only a small portion of a graded signal (of which SBTF forms the other, larger portion). A small portion of a signal could be expected to occur less often and hence have lower probabilities of occurrence across contexts compared with the other, larger portion of the signal (as was true for CR compared with SBTF). And these lower probabilities of occurrence could have effectively reduced the power of contrast tests, accounting for the lack of statistical significance in the CR results. This graded signal interpretation is preferable to the ambivalent signal interpretation because both of our predictions were supported for the SBTF/CR graded hypothesis: (1) when CR was analyzed as a discrete signal it had probability distributions across contexts that were very similar to SBTF, and (2) when CR and SBTF were analyzed together the results closely matched those when SBTF was analyzed alone (except with some contrast tests being strengthened). We therefore suggest that CR is not a discrete signal with an ambivalent function, but rather that CR, in combination with SBTF, represents a single, graded conciliatory signal.

Preuschoft & van Hooff (1997) and van Hooff & Preuschoft (2003) have suggested that variation in the function of facial displays across primate species can at least be partially explained by varying social organizations. Although mandrill social organization has not yet been completely documented, recent work by Abernethy et al. (2002) has shown that multiple adult male mandrills typically inhabit the same group and that these males remain only seasonally present within the groups, otherwise living solitarily. Additional work by Setchell & Dixson (2001a,b) on the ontogeny of coloration in mandrills has suggested that the bright coloration (particularly the red) exhibited by adult males functions as an intrasexual signal, communicating information about a male's current state. It seems likely therefore that previously solitary adult males that join the same group may evaluate one another's coloration and use this information to avoid conflicts with superior opponents. We suggest that SBTF and CR, when used between adult males, may serve a similar function, although in a more immediate time window. That is, SBTF and CR may allow adult males to advertise non-hostile intentions to one another, and thereby avoid constant, costly battling and also reconcile when battles do occur. Recent observations we made on semi-free ranging groups in Gabon provide preliminary support for this hypothesis: adult males both within the same group and in different groups frequently directed SBTF and CR when passing one another without engaging in a fight afterwards, and when passing one another immediately after having engaged in a fight. Thus, similar to exchanges between other age-sex classes, exchanges between adult males suggest that SBTF and CR possess a conciliatory function.

Baring the teeth and raising the crest is not unique to mandrills. Many animals are known to possess some form of bared-teeth or CR signal within their communication repertoire (van Hooff 1972). In most primates baring the teeth serves either a conciliatory function (e.g. Tonkean macaques: Thierry et al. 1989) or a submissive function (e.g. Rhesus macaques: de Waal & Luttrell 1985; Barbary macaques: Preuschoft 1992), whereas in canids this same signal can serve a threat function (Darwin 1872). Raising the crest has not been reported often in primates, but in birds this signal can serve a threat function (e.g. Stellar's jay: Brown 1964) or a submissive function (e.g. Fox sparrow: Hailman 1977). To accurately compare a signal's function across different species and different observers it is necessary to have a common standard for making and evaluating functional inferences. A quantitative contextual analysis provides such a standard. As Slater (1983, p. 20) has noted: 'But there is a limit to the extent that others can take on trust the "judgment of the skilled observer" when it is on this basis alone that the role of a behavior pattern has been assessed. Ultimately, precise quantitative analysis is called for, both to achieve a detailed understanding and to present results which may be appraised and repeated by others.'

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