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Contextual Factors Meditating Contests Between Male Chacma Baboons in Botswana: Effects of Food, Friends and Females

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*We examined aggressive displays among male chacma baboons (*Papio ursinus*) over a 23-mo period in the Okavango Delta of Botswana. High-ranking males were more likely than middle- or low-ranking males to participate in displays. Regardless of rank, all males were more likely to participate in chases or physical fights if their opponent's rank was similar to their own. Most chases and fights, including those that led to injuries, were also between similarly-ranked males. The rate of both aggressive displays and approach-retreat interactions increased in the weeks before rank reversals, suggesting that rank challenges were preceded by a period when males assessed each others' competitive ability and/or motivation. Aggressive displays between disparately-ranked opponents occurred most frequently in contests involving resources of high fitness value: the defense of meat, the defense of estrous females, and the protection of infants against infanticidal attacks. Silent displays were more likely to occur in these three contexts than were displays that occurred as part of more slowly escalating interactions, in which opponents first exchanged calls. Results suggest that competitive encounters among male baboons follow patterns predicted by evolutionary game theory.*

KEY WORDS: baboons; friendships; mate-guarding; infanticide; displays; dominance hierarchy.

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Many species of primates live in large multimale groups in which males compete with each other for dominance rank and access to food and mates. Among chacma baboons (*Papio ursinus*) in the Okavango Delta of Botswana, groups can contain as many as 14 adult males that have immigrated from neighboring groups and that are usually unrelated to each other. Competitive interactions often take the form of vigorous displays that include loud calls, chases of other group members, and aggressive fights that occasionally result in severe injury (Stoltz and Saayman, 1970; Saayman, 1971; Buskirk *et al.*, 1974; Smith, 1986; Bulger, 1993; Drews, 1996; Kitchen *et al.*, 2003). The loud, two-syllable wahoo calls produced by males during aggressive displays appear to serve as honest indicators of stamina and competitive ability (Kitchen *et al.*, 2003; Fischer *et al.*, 2004); high-ranking males participate in more wahoo contests and call more vigorously than low-ranking males do, and males are more likely to engage in prolonged vocal contests with adjacently-ranked opponents than with disparately-ranked ones. Although the majority of aggressive displays include wahoos by at least one participating male, males do not always produce wahoos and in some displays all males remain silent. We describe the nonvocal behavior of males during aggressive displays and test several predictions regarding the effects of a male's own rank, his opponent's rank, and context on patterns of behavior.

First, we determine whether high-ranking males are more likely than lower-ranking males to participate in aggressive displays. A previous analysis of vocal contests revealed a strong correlation between male rank and wahoo production (Kitchen *et al.*, 2003; Fischer *et al.*, 2004), leading us to predict a similar correlation between rank and other types of aggressive behavior during displays. It remains possible, however, that all males are equally likely to engage in aggressive displays, but that high-ranking males are more likely to produce vocalizations during these displays. This could occur, for example, because loud calls require more stamina and endurance, or because loud calls signal a greater willingness to escalate aggression.

Second, we examine the frequency and intensity of aggressive displays between closely-ranked, as opposed to disparately-ranked, opponents. Evolutionary game theory predicts that contests should occur more frequently and be more likely to escalate to costly physical fights when opponents are closely matched rather than disparately matched because the outcome is less predictable (Maynard Smith, 1982). Our previous analysis revealed that vocal contests between disparately-ranked males are less frequent and less intense than those between closely-ranked males (Kitchen *et al.*, 2003), and we predicted that other features of aggressive displays would follow the same patterns.

We further explore whether any targeting of adjacently-ranked males during aggressive displays is simply an artifact of spatial proximity. For example, if low-ranking males occupy peripheral locations within the group, high-ranking males might be less likely to target low-ranking males than other nearby high-ranking males. To test this hypothesis we examine the rate of approach-retreat interactions to determine if males interact more with similarly-ranked than disparately-ranked individuals. We assume that this baseline measure of nonaggressive interactions reflects proximity between two males. If males do not interact more with similarly-ranked males during nonaggressive interactions than expected by chance, this would suggest that males specifically seek out similarly-ranked rivals during aggressive displays.

Additionally, we examine rates of aggressive displays and approach-retreat interactions in the weeks prior to rank reversals to determine whether ascending males targeted adjacently-ranked males with which they eventually switched ranks. Game theory predicts that individuals should assess a dominant opponent's competitive ability before challenging him. Just prior to a reversal, potential challengers should therefore increase not only the frequency of aggressive displays with their higher-ranking opponent, but also the frequency of less aggressive, less costly approach-retreat interactions.

Next, we investigate the context of aggressive displays to determine if any qualitative differences exist between the displays of closely-ranked and disparately-ranked opponents. Both theoretical (e.g., Parker, 1974; Parker and Rubenstein, 1981) and empirical work (e.g., Sigurjónsdóttir and Parker, 1981; Austad, 1983; Riechert, 1984; Grinnell *et al.*, 1995) suggest that, when the benefits of winning (or the costs of losing) are high, contestants may escalate an interaction even with a far superior opponent. Although uncommon, vocal contests between disparately-ranked male baboons do occur (Kitchen *et al.*, 2003). We therefore anticipated that aggressive displays between unmatched opponents might also occasionally escalate to chases and physical fights. Specifically, we predicted that fights between disparately-ranked opponents would be more likely to involve a tangible, high-value resource than fights between closely-ranked opponents. Based on previous observations, we identified three resources that appeared to be of sufficiently high value to provoke aggression between unequal opponents: meat, estrous females, and the defense of infants against infanticide. In our study population, males compete over meat (e.g., squirrels, young ungulates, vervets) and subordinate males aggressively resist attempts by higher-ranking individuals to take meat from them. Similarly, males of all ranks compete to form consortships with estrous females, and low-ranking males will often forcefully defend themselves against attempts by higher-ranking males to take over their consortships (Hausfater, 1975; Packer, 1979; Smith, 1986; Bulger, 1993). Finally, males of all ranks form friendships with lactating females whose infants are vulnerable to infanticide (Palombit *et al.*, 1997, 2000). Males defend their female friends (and thus their dependent infants) against potentially infanticidal attacks by other males, and even very low-ranking males will confront high-ranking males when they harass female friends carrying small infants.

Game theory also predicts that contests should typically begin with displays that are of low cost and escalate only slowly to more costly fights (reviewed in Bradbury and Vehrencamp, 1998; Vehrencamp, 2000). However, because the defense of meat, estrous females, and female friends with infants seems to be of high value to baboons, we predicted that disputes involving these resources would be more likely than other disputes to escalate to fights and chases without preceding wahoo vocalizations.

METHODS

Study Site and Subjects

This research was conducted in the Moremi Game Reserve, located in the Okavango Delta of Botswana (for study site details see Hamilton *et al.*, 1976; Ross, 1987; Ellery *et al.*, 1993; Cheney *et al.*, 2004). The main study group, C, has been observed since 1978. All individuals are identifiable and the matrilineal relatedness of all natal baboons is known. Subjects are fully habituated to observers on foot. During the study (June 1999 through May 2001), C group contained 78–88 individuals, including 23–29 adult females and 17 different natal and immigrant adult males greater than 8.5 years of age. The mean number of adult males on any given day was 12. The number fluctuated due to immigrations, emigrations, maturation and death. As in other species of Old World monkeys, female baboons remain in their natal groups throughout their lives, while males usually immigrate to neighboring groups after approximately 8.5 years of age (Kitchen *et al.*, 2003; Cheney *et al.*, 2004). Male dominance is determined primarily by age and fighting ability (Kitchen *et al.*, 2003; Fischer *et al.*, 2004).

Data Collection

We typically located a group between 0500 and 0830 h and then followed it for 5–7 h. During the daily census, we classified the reproductive state of each adult female as either: 1) estrous: any female with a visible perineal swelling (e.g., Hausfater, 1975); 2) cycling: any nonpregnant female between the swelling periods of estrous cycles; 3) pregnant: any female with paracallosal skin that appeared pink in color after a missed estrous cycle (we retroactively approximated conception date as midway through the maximum swelling period of the last estrous cycle); or 4) lactating: any female with a nursing offspring, until either her infant died or she resumed sexual cycling.

On most days, observers (usually three and never fewer than two) distributed themselves throughout the group in an attempt to maximize observation of adult males. We maintained contact via 2-way radios. Each observer carried a Psion LZ64 computer and a digital audio tape recorder (Sony PCM-M1) with a directional microphone (Sennheiser ME66). Both the tape recorder and the computer are programmed to note the time of an entry to the nearest s. We conducted focal animal and *ad libitum* sampling (Altmann, 1974) on all adult males. We selected focal subjects from a randomized list; whenever possible, no individual was sampled twice until all males had been sampled once. We sampled all males for approximately 3 h per mo, for a total of 3,560 focal animal samples.

During focal sampling, we recorded continuous data on all interactions involving the subject and other group members for a 10-min period, including approaches, supplants, threats, chases, and physical fights. Threats included head bobs, stares with raised eyebrows, slaps on the ground, and lunges. Threats were usually accompanied by multisyllable, staccato vocalizations called threat-grunts. A chase occurred when one male pursued another group member for more than 5 m, without making contact or physically fighting.

The onset of an aggressive display was said to occur when one or more resident adult males chased or attacked another group member or produced a loud call during daylight hours (i.e., data on predawn choruses were not included). Two displays occurring on the same day had to be separated by at least 1 h. The results we present in this paper deal only with displays that occurred in the context of within-group aggression. We discuss aggressive displays during inter-group encounters elsewhere (Kitchen *et al.*, 2004).

We identified three contexts for aggressive displays. 1) Meat: when two or more males competed over a prey item. We noted all changes in ownership of meat during the contest. 2) Consortship: when two or more males competed over access to an estrous female. We noted any change in the identity of the consorting male during or following the aggressive display. 3) Friends: when a male threatened or chased a male that had attacked or threatened one of his lactating female friends that was carrying her infant. Infants in the population are vulnerable to infanticide through 1 yr of age (Palombit *et al.*, 2000; Cheney *et al.*, 2004). We determined male-female friendships through *ad libitum* data and 10-min focal male samples, using criteria established by Palombit *et al.* (1997).

Dominance Rank

We established male dominance ranks using focal animal samples (see above) and recalculated them daily. We defined dyadic dominance relations according to the direction of approach-retreat interactions and submissive behaviors (threats, chases, and fights were not used to determine rank relationships). Submissive behaviors included the fear grimace (lips pulled back exposing clenched teeth), fear bark (a cough-like vocalization; Cheney *et al.*, 1995) and lean-away (animal glances at and then turns head and extends body away from approaching dominant). Because not all dyads interacted during daily focal samples, we also used *ad libitum* data on approaches and retreats to determine whether any change in rank order had occurred.

Although dominance rank orders were typically linear and unidirectional, a few triangular rank relations (F > G, G > H, and H > F) were stable over several mos. Because each male in these triads outranked one individual and was outranked by another, we assigned all three males the same rank for purposes of analysis. As in other populations of baboons, the male dominance hierarchy in C group was stable over the short term (Hausfater, 1975; Packer, 1979; Bulger, 1993; Alberts *et al.*, 2003; Kitchen *et al.*, 2003).

In every aggressive display, we assigned a dominance rank to each participant based on his place in the hierarchy at the time. The highest-ranking male was assigned rank 1, the second-ranking male was rank 2, and so on. During the 23-mo study, two different individuals held the alpha, or first, rank. An average of 3.2 males occupied each of the 12 rank positions (range = 2–6), and each male occupied an average of 3.4 different ranks (range = 2–7).

RESULTS

Frequency and Nature of Displays

Aggressive displays involving one or more resident adult males occurred once every 10.1 h of observation (based on 2880 h of observation). Overall, we were able to record complete behavioral data on all males during 286 displays involving 17 different adult males occupying 12 different rank positions (mean = 37.6 displays/male; range = 3–117 displays/male).

The majority of displays (74.5%) involved at least two males (mean = 2.26 males/display; range = 1–7 males).

During 64% of 286 observed displays, at least one male produced wahoos, while 36% of displays were completely silent. Even during the 183 displays that included at least one male wahooing, however, other male participants often remained silent and chased females or other males without producing calls.

A majority of aggressive displays included chases of one or several other group members. Males chased other males in 57.0% of displays; on average, males chased 1.2 males per display (range = 1–4 males chased/male). By comparison, males chased females in 68.2% of displays, and on average chased 1.3 females per display (range = 1–6 females chased/male).

Physical fights usually occurred when a male that was being pursued by another male stopped running and turned to face his opponent. The males then used their hands to slap and scratch and their large canines to slash and bite each other (Drews, 1996). Physical fights involving one or more dyads occurred during 29.0% of the 286 displays.

Despite physical contact, the majority of fights did not result in a visible external injury to either participant. Of the 93 physical fights during 83 displays, 36.6% resulted in injury to one or both participants. We recorded the location of injuries for 40 of 44 injured males during a physical fight. Most injuries (87.5% of 40) were to the face or shoulder and relatively few (12.5%) were to other parts of the body.

In our initial analysis, we examined aggressive displays with and without wahoos separately. However, with the exception of aggression that occurred over tangible resources (see below), we found no differences in patterns of behavior or rank of participants. Therefore, we combined data from silent and vocal displays in most of the analyses below.

Effect of Rank

Chases

High-ranking males were more likely than low-ranking males to chase other males (Fig. 1; Spearman correlation $r_s = -0.909$, $n = 12$ rank positions occupied by 16 males in 163 displays, $p < 0.001$), and to fight other males (Spearman correlation $r_s = -0.919$, $n = 12$ rank positions by 93 dyads in 83 displays, $p < 0.001$).

Males chased other males that were both higher- and lower-ranking than themselves. To compare the effects of rank disparity between two males on the direction of chases, we used Friedman's nonparametric

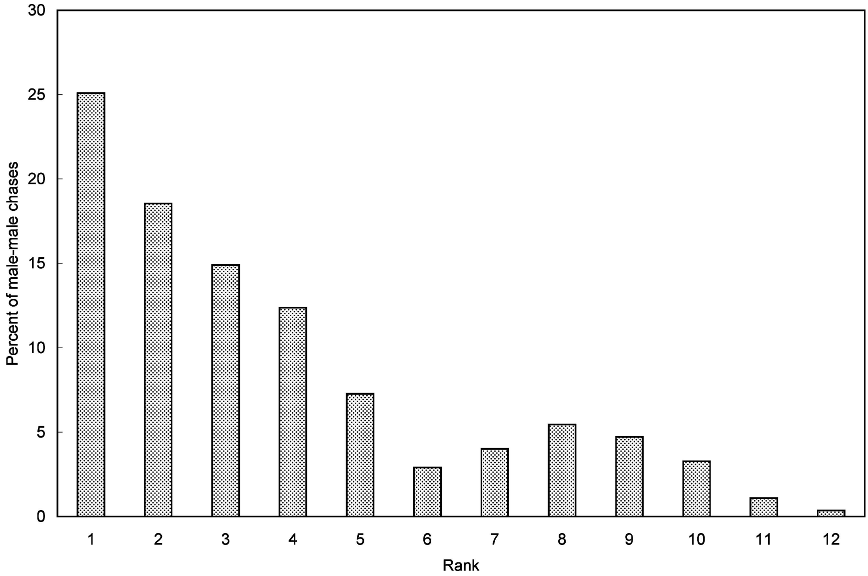

Fig. 1. The percent of 275 male-male chases involving males of different ranks in the dominance hierarchy. Note that the *y*-axis runs from 0–30%.

method for randomized blocks, with the direction of the chase (i.e., higher-ranking male chasing lower-ranking male or vice versa) as treatments and rank differences (i.e., adjacent, 2 positions etc.) as blocks (Sokal and Rohlf, 1995, pp. 440ff). Regardless of the rank difference between two opponents, high-ranking males chased low-ranking males more often than the reverse ($\chi^2 = 7.40, n = 275, df = 2, p = 0.025$).

To test whether closely-ranked males were more likely than disparately-ranked males to engage in aggressive displays, we first tested whether overall participation decreased as the difference in rank between contestants increased. For this and the following analyses, we included all chases by individual males within a display, although each dyad was only counted once per display ($n = 275$ male-male chases). Although males chased other males that occupied ranks up to 10 positions different from themselves in the dominance hierarchy, results revealed a sharp decline in participation as rank differences increased (Spearman correlation $r_s = -0.985, n = 10$ rank position differences occupied by 16 males participating in 163 displays, $p < 0.001$).

We then compared the frequency with which males of different ranks chased other males with the frequency that would have been expected had males been equally likely to chase males of any rank. To calculate expected probabilities, we assumed that all individuals were equally likely to interact with all possible opponents and then calculated how many interactions would have involved adjacently-ranked individuals, how many would have involved individuals separated by two rank positions, and so on (e.g., in a group of 12, the second-ranked male had a 2 in 11 chance of interacting with an adjacently-ranked male).

Regardless of the direction of the chase, the observed distributions of chases during displays are significantly different from expected (Fig. 2; $\chi^2 = 74.12$, $n = 275$, $df = 3$, $p < 0.001$). Post-hoc paired comparisons revealed that chases of adjacently-ranked males and males separated by two rank positions occurred significantly more often than expected ($\chi^2 = 41.76$, $n = 158$, $df = 1$, $p < 0.001$). Chases of males separated by three or four rank positions occurred no more frequently than expected ($\chi^2 = 0.33$, $n = 70$, $df = 1$, $p > 0.100$), and chases involving males separated by 5 to 10 rank positions occurred significantly less often than expected ($\chi^2 = 32.03$, $n = 47$, $df = 1, p < 0.001$).

These results suggest that males selectively sought out similarly-ranked opponents. It remains possible, however, that high rates of interaction between males of similar rank occurred simply as a consequence of the overall frequent participation by high-ranking males. Given that high-ranking males were more likely than others to participate in chases, it naturally follows that a disproportionate number of chases involved closely-ranked, high-ranking individuals.

To test between these two hypotheses, we used data from Fig. 1 to calculate the probability that a male occupying a specific rank would participate in a chase. For example, out of 275 chases, the probability that the alpha male would be involved was 0.251 and the probability that the third-ranking male would be involved was 0.149. Based on their overall probability of participation, therefore, the probability that any dyadic interaction would involve the first- and third-ranking males is $0.251 \times 0.149 = 0.037$. For each dyad we then compared the observed frequency with the frequency that would have been expected based on the two males' overall rates of interaction.

Males in 10 of 11 rank positions interacted in displays more often than expected with individuals that were closely-ranked (either adjacently-ranked or two steps away in the hierarchy; Wilcoxon signed ranks test $Z = -2.80$, $n = 12$, ties $= 1, p = 0.005$). We therefore conclude that males did not chase opponents whose ranks were similar to their own simply as a consequence of high-ranking individuals participating at high rates in aggressive displays. Regardless of their absolute rates of participation, individuals of all ranks interacted with similarly-ranked opponents at higher rates than expected.

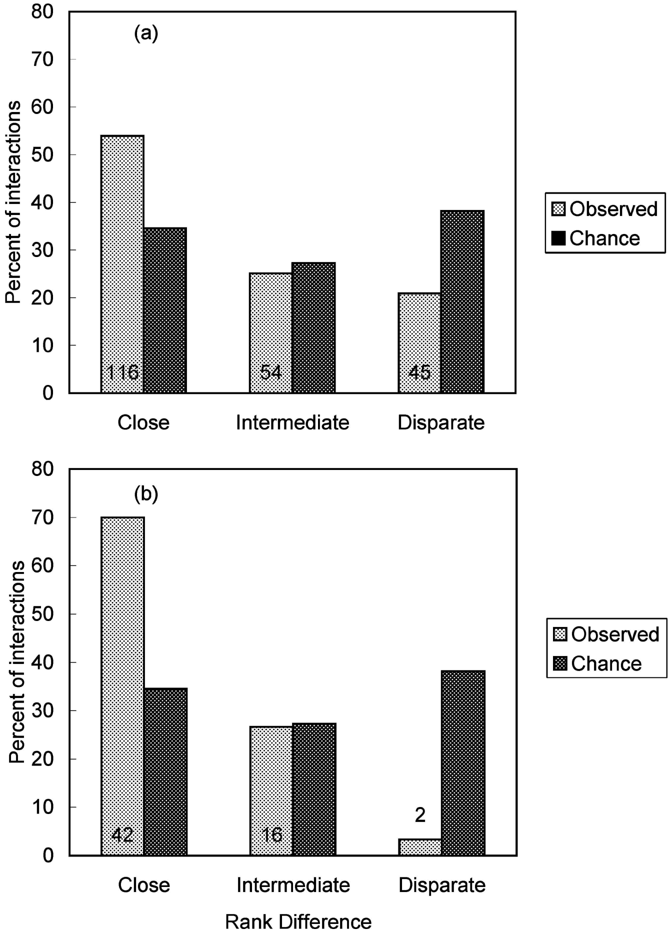

Fig. 2. Rank position differences between two males involved in a chase compared with expected values when (a) the higher-ranking male chased the lower-ranking male and (b) the lower-ranking male chased the higher-ranking male. Close = 1–2 rank differences; Intermediate = 3–4 rank differences; Disparate = 5–10 rank differences. Note that chases were still more likely to be directed at lower-ranking rivals than higher-ranking rivals (see text).

It is also possible that males targeted closely-ranked opponents in aggressive displays because they were more likely to be in close proximity to such individuals and to interact generally at high rates with them. To test this hypothesis, we examined the frequency of 12 males' approach-retreat interactions with all other males in the group during the 23 mo-study (mean = 43.2 h of focal sampling per male). We then determined each male's frequency of approach-retreat interactions with the two males that were adjacent to him in the dominance hierarchy and compared this value with the frequency of his approach-retreat interactions with all other males in the group. If males interacted with adjacently-ranked males no more than expected by chance, 18.2% (2/11 in a group of 12 males) of the approach-retreat interactions of most males should have occurred with adjacently-ranked males, and in the cases of the alpha male and the lowest-ranking male, 9.0% (1/11 in a group of 12 males) should have occurred with adjacently-ranked males. We found that approach-retreat interactions between adjacently-ranked males constituted an average of 20.8% (range = 14.6–27.2%) of all approach-retreat interactions. Seven males interacted more with adjacently-ranked males than expected, and five males interacted with such individuals less than expected (Wilcoxon signed ranks test $Z = -1.33$, $n = 12$, $p = 0.182$). Results therefore suggest that, although males targeted similarly-ranked males during chases and fights, they did not interact with these males nonaggressively more than expected by chance.

Physical Fights

When a male-male chase ended in aggressive physical contact we called the entire interaction a fight (i.e., we did not include fight data in the above chase analyses). To test whether closely-ranked males were more likely than disparately-ranked males to fight, we first tested whether overall participation in fights decreased as the difference in rank between contestants increased. Although males fought with other males that were separated from them by as many as 11 rank positions, results revealed a sharp decline in participation as rank differences increased (Spearman correlation $r_s = -0.840$, $n = 11$ rank positions by 93 dyads during 83 displays, $p < 0.010$).

We then compared the frequency with which males of different ranks fought with other males with the frequency that would have been expected had males been equally likely to fight with males of any rank (as calculated above). We pooled data from all displays involving individuals separated by three or more rank positions because of the small number of fights involving males of greatly disparate ranks. The rank relationship between two opponents in a fight was different than expected by chance ($\chi^2 = 42.86$, $n = 93$, $df = 2$, $p < 0.001$); displays were more likely to escalate to physical fights when males were close in rank (i.e., separated by 1 or 2 rank positions) than when they were disparately-ranked (i.e., separated by 3–11 rank positions; Fig. 3).

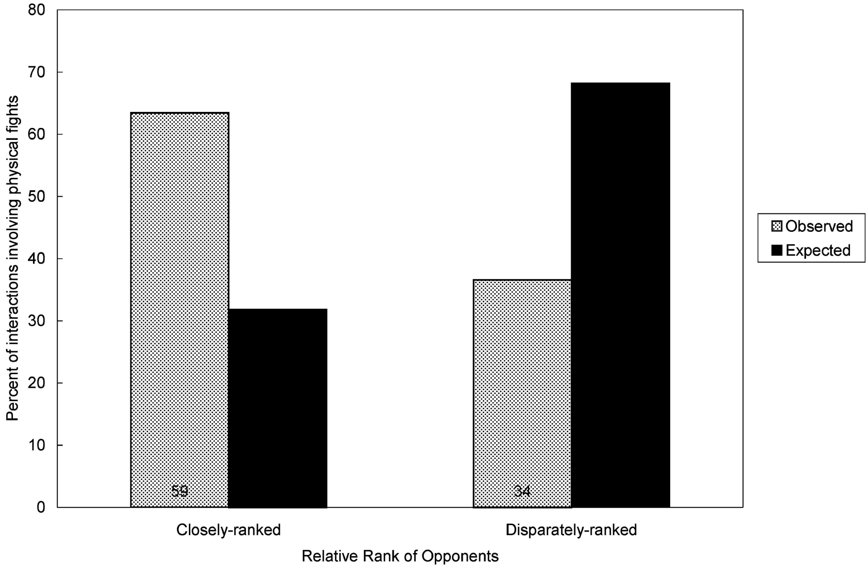

Fig. 3. Rank position differences between males involved in physical fights compared with expected values. Close = 1–2 rank differences; Disparate = 3–11 rank differences.

Once again, these results suggest that males selectively escalated contests with similarly-ranked opponents. However, it is possible that high rates of fighting between males of similar rank occurred simply as a consequence of frequent interaction by high-ranking males with other males of high rank. We used the same methods presented previously to test between these two hypotheses.

During displays, males in 12 of 12 rank positions fought more often than expected with individuals that were closely-ranked (Wilcoxon signed rank tests $Z = 3.06, n = 12, p = 0.002$). We therefore conclude that individuals of all ranks engaged in fighting at higher rates than expected when they faced similarly-ranked opponents.

Injuries

Injuries were more likely to occur during fights between closely-ranked males (75% of 44 fights) than between rivals separated by three or more rank positions ($\chi^2 = 11.00$, $df = 1$, $p = 0.001$). Only slightly more injuries (59.1% of 44) were sustained by the lower-ranking participant than by the high-ranking participant. However, all cases in which the lower-ranking of the two opponents injured the higher-ranking male occurred among dyads that were separated by three or fewer rank positions.

Rank Reversals

Permanent rank reversals (i.e., reversals whose outcomes lasted at least one mo), occurred at an average rate of 1.6 per mo and involved males in all positions of the dominance hierarchy (mean rank of ascending males = 6.6; range = 2–12). We observed the exact date of 26 of these reversals and were able to estimate the outcome of 10 additional reversals within 1–3 days.

Of the 26 observed rank reversals, 19 (73.1%) followed an aggressive display involving the two males (the other seven reversals may have been preceded by a display that we did not observe).

To determine whether two males were more or less likely to engage in aggressive displays with each other just prior to reversing ranks, we compared the frequency of their aggressive displays and approach-retreat interactions in the two weeks immediately prior to the rank reversal with a control period—the third and fourth weeks prior to the reversal. For each reversal, we examined the behavior of three males (e.g., males ranked A > B > C before the reversal and B > A > C after the reversal): the ascending male (B), the adjacently-ranked male that was usurped (A), and the adjacently-ranked, control male whose rank did not change (C). Complete data for the pre-reversal period were available for 23 of 26 permanent reversals; data for the control period existed for 22 of these cases.

Approach-Retreat Interactions

An increase in the rate of approach-retreat interactions between males that ultimately reversed ranks might be indicative of an increase in their efforts to assess each other's competitive ability and motivation to fight. To explore this issue, we compared males' behavior in the two weeks immediately prior to rank reversals with their behavior during the control period. We analyzed 138.3 h of focal samples on the ascending and usurped males in 22 dyads involved in permanent rank reversals (mean = 6.0 h of focal sampling per dyad). Seven males were usurped and eight males were usurpers more than once. In all but one case, however, successive rank reversals involving the same male occurred with different rivals. In the one case in which the same two males reversed ranks twice, the second reversal occurred 6 mo after the first, when each male occupied a very different rank position than in the previous reversal. Approach-retreat interactions between males that reversed ranks occurred on average 1.6 times/h in the

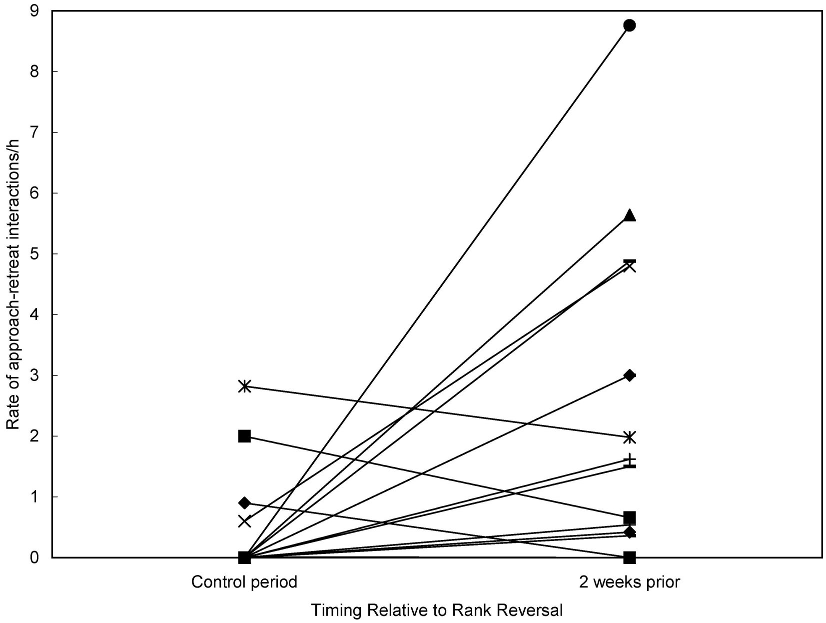

Fig. 4. The rate of approach-retreat interactions between males that reversed ranks during the two weeks prior to their rank reversal compared with their rate of approach-retreat interactions during the two-week control period (definitions in text). For seven dyads, the rates were zero prior to the reversal and in the control period and these overlapping points are not visible on the figure.

two weeks preceding the rank reversal, a rate that was 5.3 times higher than during the two-week control period. Comparing each dyad separately, the rate of approach-retreat interactions was higher before the rank reversal than during the control period for 11 dyads, lower for only 4 dyads, and the same for 7 dyads (Fig. 4; Wilcoxon signed ranks test $Z = -2.30, n = 22$, ties $= 7, p = 0.020$).

It remains possible that males did not specifically target the individuals with which they reversed ranks, but instead became generally more interactive with all males prior to a rank reversal. We therefore compared each male's rate of approach-retreat interactions with the two males that occupied rank positions adjacent to him in the dominance hierarchy: the higher-ranking male that he eventually usurped and the lower-ranking control male whose relative rank remained the same. For this analysis, we examined 102.8 h of focal sampling on 23 triads (ascending (B), usurped (A) and control males (C)) during the two weeks prior to the rank reversal (mean = 4.5 h of focal sampling per triad). Three reversals involved the same three

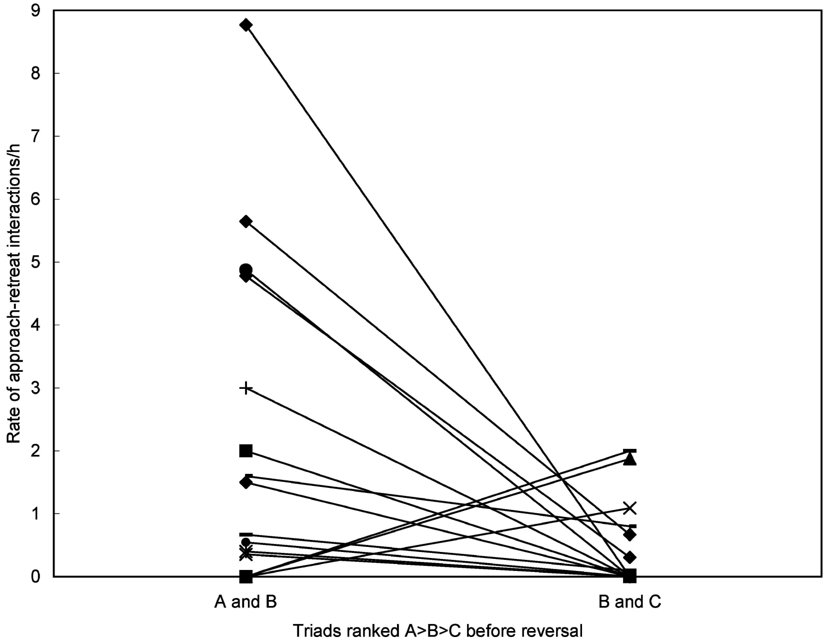

Fig. 5. The rate of approach-retreat interactions between the male that ultimately fell in rank (male A) and his usurper (male B) during the two weeks prior to their rank reversal, compared with male B's rate of approach-retreat interactions with the adjacently-ranked control male (C) during the same time period (definitions in text). For seven males, the interaction rates with both male A and male C were zero and these overlapping points are not visible on the figure.

males, but the roles of the three males differed (e.g., ascending vs. control) in each case. We found that ascending males' approach-retreat interaction rates with control males occurred on average 0.3 times/h, a rate that was 5.4 times lower than that with the usurped males. Thirteen of the ascending males interacted at higher rates with the males whose rank they ultimately usurped than with the control males, only three interacted at lower rates, and seven interacted at the same rate (Fig. 5; Wilcoxon signed ranks test $Z = -2.30, n = 23, \text{ties} = 7, p = 0.021$).

Aggressive Displays

We predicted that patterns of male-male aggressive displays would be similar to those of approach-retreat interactions prior to a rank reversal. We counted male participation in all chases and fights in the two-week pre-reversal period (not including the day of the rank reversal) and in the two-week control period for 23 dyads. Aggressive displays in the two weeks preceding the reversal increased for 11 dyads, decreased for only 2 dyads, and remained the same for 10 dyads (Wilcoxon signed ranks test $Z = -2.67$, $n = 23$, ties $= 10, p = 0.008$).

When we compared ascending males' aggressive interactions with both the usurped male and the control male in the pre-reversal period, we found that 11 of 23 ascending males chased and fought more with the male immediately above them in the hierarchy (the usurped male) than with the male immediately below them in the hierarchy (the control male). For only one ascending male the rate was lower, while for 11 others the rate was the same (Wilcoxon signed ranks test $Z = -2.83, n = 23$, ties $= 10, p = 0.005$). There was some evidence, therefore, that males increased their challenges of higher-ranking individuals prior to rank reversals, and no evidence that they avoided each other.

Effect of Context

As noted earlier, most aggressive displays were preceded and accompanied by wahoos. Some displays, however, escalated to chases or fights without any preceding exchange of wahoos. Because chasing and fighting is potentially more risky than wahooing, we predicted that displays would be more likely to involve chases and fights without prior wahoos when the contestants were competing over meat, estrous females, or the defense of female friends and their vulnerable infants. We also predicted that displays without wahoos would be more likely to occur when males chased opponents higher-ranking than themselves. Thus, in the following analyses on chases and fights, we examined displays with and without wahoos separately.

Chases

Approximately half of all chases (45.1% or 124 of 275) occurred either in the context of meat defense (21.0% of 124 explained chases), defense of estrous females (39.5% of 124), or defense of lactating female friends and their vulnerable infants (39.5% of 124). As predicted, silent displays were more likely to occur in one of these three contexts (64.0% of 89 chases with no wahoos) than were chases preceded by wahoos (36.0% of 186 chases with wahoos; $\chi^2 = 19.09$, $df = 1, p < 0.001$). Contrary to our predictions, however, these contexts did not account for cases when males

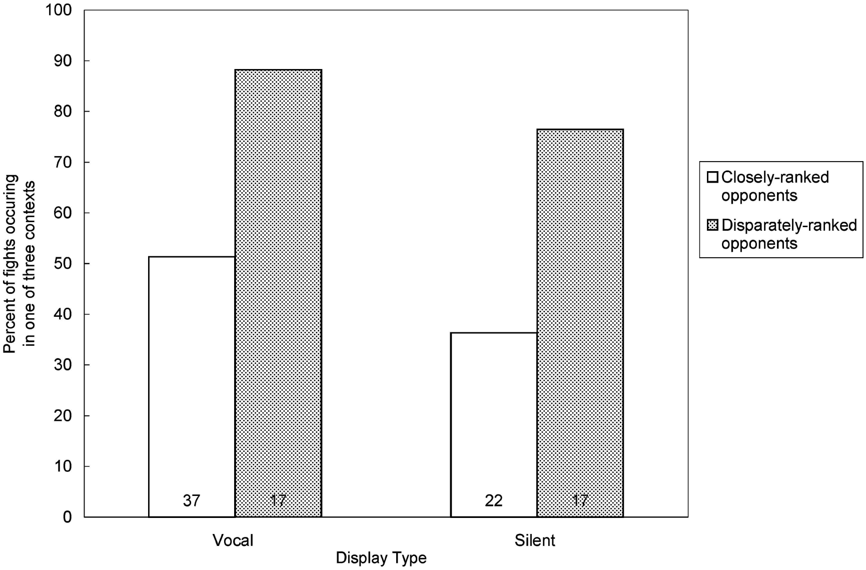

Fig. 6. The proportion of physical fights between closely-ranked and disparately-ranked opponents that occurred in one of the three contexts described in the text. Closely-ranked opponents: 1–2 rank differences; Disparately-ranked opponents: ≥3 rank differences.

chased opponents higher-ranking than themselves (displays with wahoos: $\chi^2 = 2.27$, $n = 186$, $df = 1$, $p = 0.132$; silent displays: $\chi^2 = 0.001$, $n = 89$, $df = 1, p = 0.976$).

Physical Fights

More than half of all physical fights (63.4% or 59 of 93) occurred either when males were defending meat (13.5% of 59 explained fights), estrous females (42.4% of 59), or female friends and their infants (44.1% of 59). As predicted, fights between disparately-ranked males were more likely than fights between closely-ranked males to occur in one of these three contexts (Fig. 6). This was true both of fights that were accompanied by wahoos and those in which the opponents remained silent (fights with wahoos: $\chi^2 = 6.80, n = 54, df = 1, p = 0.009$; silent fights: $\chi^2 = 6.21, n = 39, df = 1$, $p = 0.013$). Unlike male-male chases, however, silent fights were no more likely to occur in one of these three contexts (53.8% of 39 fights with no wahoos) than were fights preceded by wahoos (63.0% of 54 fights with wahoos; $\chi^2 = 0.78, df = 1, p = 0.377$).

Injuries

Half (54.5%) of 44 observed injuries occurred during fights over estrous females, meat, or a lactating female friend. As predicted, injuries incurred during fights between disparately-ranked opponents were more likely to occur in these three contexts (81.8% of 11 fights between males separated by three or more rank positions) than injuries incurred between closely-ranked opponents (45.5% of 33 fights; $\chi^2 = 4.40, df = 1, p = 0.036$).

DISCUSSION

Elsewhere we reported that the frequency and intensity of vocal contests varies according to both absolute male rank and the number of ranks separating opponents (Kitchen *et al.*, 2003). When this analysis is expanded to incorporate the chases and fights that often accompany vocal contests or that occur during silent displays, the patterns remain the same.

First, high-ranking males were more likely than low-ranking males to participate in aggressive displays. This result could have occurred because these males were more motivated to defend their rank and/or because only these males were in sufficiently good condition to participate in energetic displays.

Second, regardless of their frequency of participation, males of all ranks were more likely to engage in displays with males of similar rank than with males of disparate rank. Additionally, most physical fights, particularly those that resulted in injury, occurred between similarly-ranked opponents. This pattern did not occur simply because males of similar rank were more likely to be in proximity to each other, because they did not engage in approach-retreat interactions with adjacently-ranked males more than expected by chance. As predicted by evolutionary game theory, males seemed to avoid participating in contests with far superior opponents but appeared willing to engage in escalated contests with closely-matched rivals.

Finally, males that reversed ranks increased both their rate of approach-retreat interactions and the frequency of their displays against each other in the weeks immediately preceding the reversal. It seems likely that males used these interactions to monitor their rivals' motivation and/or condition.

Evolutionary game theory predicts that aggression between males of very disparate competitive abilities (in this case, very disparate ranks) should only occur when the value of winning a contest is exceptionally high. We identified three contexts that might motivate males to engage in risky contests with far superior opponents: the defense of meat, estrous females, or vulnerable infants of lactating female friends. As predicted, silent displays were more likely to occur in these high-value contexts than were displays that occurred as part of more slowly escalating interactions, in which opponents first exchanged wahoos. Likewise, the seemingly anomalous fights between disparately-ranked males occurred more often in high-value contexts than did fights between closely-ranked males. Finally, rank reversals between closely-matched rivals seldom (26%) occurred during one of these three contexts. Here again, the nature of aggressive interactions between similarly-ranked males were qualitatively different from those between disparately-ranked males.

Defending estrous females or infants could result in present or future fitness benefits to a male, and these two contexts were the most common cause of fights. However, it seems unlikely that there are such high fitness benefits to defending meat. Baboons do not regularly acquire meat and meat is not a nutritional requirement for adult males. Consequently, it is unclear why meat should be so highly prized that males would risk injury from far superior opponents to retain it.

Taken together, our results suggest that rank maintenance among male chacma baboons follow patterns predicted by evolutionary game theory. Males seem to avoid interactions that they are likely to lose unless the value of winning is exceptionally high. Whereas contests between adjacently-ranked males seem to occur in the context of rank maintenance or challenge, contests between disparately-ranked males occur over more tangible resources.

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REFERENCES

Alberts, S. C., Watts, H. E., and Altmann, J. (2003). Queuing and queue-jumping: Long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim. Behav*. 65: 821–840.

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour* 49: 227–265.

Austad, S. N. (1983). A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Anim. Behav*. 31: 59–73.

Bradbury, J. W., and Vehrencamp, S. L. (1998). *Principles of Animal Communication*, Sinauer, Sunderland, Mass.

Bulger, J. (1993). Dominance rank and access to estrous females in male savanna baboons. *Behaviour* 124: 89–122.

Buskirk, W. H., Buskirk, R. E., and Hamilton, W. J. (1974). Troop-mobilizing behavior of adult male chacma baboons. *Folia Primatol*. 22: 9–18.

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., Kitchen, D. M., Palombit, R. A., Rendall, D., and Silk, J. B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int. J. Primatol.* 25: 401–428.

Cheney, D. L., Seyfarth, R. M., and Silk, J. B. (1995). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: Evidence for causal reasoning? *J. Comp. Psych.* 109: 134–141.

Drews, C. (1996). Contexts and patterns of injuries in free-ranging male baboons (*Papio cynocephalus*). *Behaviour* 133: 443–474.

Ellery, W. N., Ellery, K., and McCarthy, T. S. (1993). Plant distribution in island of the Okavango Delta, Botswana: Determinants and feedback interactions. *Afr. J. Ecol.* 31: 118–134.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., and Cheney, D. L. (2004). Baboon loud calls advertise male quality: Acoustic features and their relation to rank, age, and exhaustion. *Behav. Ecol. Sociobiol.* 56: 140–148.

Grinnell, J., Packer, C., and Pusey, A. E. (1995). Cooperation in male lions: Kinship, reciprocity, or mutualism? *Anim. Behav*. 49: 95–105.

Hamilton, W. J., Buskirk, R. E., and Buskirk, W. H. (1976). Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology* 57: 1264–1272.

Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). *Contributions to Primatology, Vol 7*. Karger, Basel.

Kitchen, D. M., Cheney, D. L., and Seyfarth, R. M. (2004). Factors mediating inter-group encounters in chacma baboons (*Papio cynocephalus ursinus*). *Behaviour* 141: 197–218.

Kitchen, D. M., Seyfarth, R. M., Fischer, J., and Cheney, D. L. (2003). Loud calls as an indicator of dominance in male baboons, *Papio cynocephalus ursinus*. *Behav. Ecol. Sociobiol.* 53: 374–384.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*, Cambridge University Press, Cambridge.

Packer, C. (1979). Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav*. 27: 37–45.

Palombit, R. A., Seyfarth, R. M., and Cheney, D. L. (1997). The adaptive value of "friendships" to female baboons: Experimental and observational evidence. *Anim. Behav*. 54: 599–614.

Palombit, R., Cheney, D., Seyfarth, R., Rendall, D., Silk, J., Johnson, S., and Fischer, J. (2000). Male infanticide and defense of infants in chacma baboons. In van Schaik, C., and Janson, C. (eds.), *Infanticide by Males and Its Implications*, Cambridge University Press, Cambridge, pp. 123–152.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol*. 47: 223–243.

Parker, G. A., and Rubenstein, D. I. (1981). Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav*. 29: 221–240.

Riechert, S. E. (1984). Games spiders play III: Cues underlying context-associated changes in agonistic behaviour. *Anim. Behav*. 32: 1–15.

Ross, K. (1987). *Okavango: Jewel of the Kalahari*, Macmillan, New York.

Saayman, G. S. (1971). Behavior of the adult males in a troop of free-ranging chacma baboons. *Folia Primatol.* 15: 36–57.

Sigurjónsdóttir, H., and Parker, G. A. (1981). Dung fly struggles: Evidence for assessment strategy. *Behav. Ecol. Sociobiol*. 8: 219–230.

Smith, K. S. (1986). Dominance and mating strategies of chacma baboons, *Papio ursinus*, in the Okavango Delta, Botswana. PhD. dissertation, University of California, Davis.

Sokal, R. R., and Rohlf, F. J. (1995). *Biometry*, 3rd edn., Freeman, New York.

Stoltz, L. P., and Saayman, G. S. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Ann. Transvaal Mus*. 26: 99–143.

Vehrencamp, S. (2000). Handicap, index, and conventional elements of bird song. In Espmark, Y., Amundsen, T., and Rosenqvist, G. (eds.), *Animal Signals: Signalling and Signal Design in Animal Communication* Tapir, Trondheim, Norway, pp. 277–300.