FACTORS MEDIATING INTER-GROUP ENCOUNTERS IN SAVANNAH BABOONS (PAPIO CYNOCEPHALUS URSINUS)

by

DAWN M. KITCHEN[1,2]), **DOROTHY L. CHENEY**[3]) **and**
ROBERT M. SEYFARTH[1,4]

([1] Department of Psychology, University of Pennsylvania, Philadelphia PA, 19104, USA;
[3] Department of Biology, University of Pennsylvania, Philadelphia PA, 19104, USA)

Summary

Inter-group encounters among baboons range from peaceful to aggressive. During 23 months we observed 110 inter-group interactions involving four groups of chacma baboons in the Okavango Delta, Botswana. Results supported the hypothesis that male behavior functions to prevent extra-group males from gaining access to sexually receptive females. Males were more likely to chase females in their own group when estrous females were present, and their chases targeted estrous females more often than expected. Males also chased members of the opposing group more when estrous females were present. When estrous females were absent, male displays were shorter in duration, involved fewer participants, were less intense, and were more likely to result in peaceful mingling between groups. The alpha male was the individual most actively involved in inter-group chases and displays, but males of all ranks participated, especially when they were in consort with a female. However, males did not cooperate in group defense. While behavior during encounters was affected by the presence of

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estrous females, the outcome of encounters was affected by location and rival group identity. Groups were more likely to approach and displace opponents in the core of their range and more likely to retreat in the periphery. Correcting for location, we also found some evidence for an inter-group dominance hierarchy based on the relative number of males.

Keywords: loud calls, baboons, inter-group dominance, resource defense, female defense.

Introduction

Inter-group interactions in non-human primates range from peaceful mingling to violent clashes with fatal outcomes (reviewed by Cheney, 1987; Fashing, 2001). Among primate species characterized by female philopatry, females are often aggressive participants in inter-group encounters (*e.g.* macaques, blue monkeys, vervets, reviewed in Cheney, 1987), and several studies have suggested that defense of resources explains variation in female behavior (*e.g.* Fashing, 2001; Wich *et al*., 2002; reviewed in Cheney, 1987). Unlike other female-bonded species, however, female savannah baboons (*Papio cynocephalus*) are seldom overtly aggressive toward the members of other groups. As a result, the extent to which female behavior has any influence on the outcome of inter-group encounters in this species is not known. In contrast, male baboons' responses to other groups often include loud calls, chases, and even physical attacks on individuals in both the male's own and the opposing group (chacma, *P. c. ursinus*: Hall & DeVore, 1965; Stoltz & Saayman, 1970; Saayman, 1971; Buskirk *et al*., 1974; Hamilton *et al*., 1975, 1976; Cheney & Seyfarth, 1977; Anderson, 1981; Byrne *et al*., 1987; Hamilton & Bulger, 1992; Cowlishaw, 1995; Henzi *et al*., 1998; yellow, *P. c. cynocephalus*: Altmann & Altmann, 1970; Rasmussen, 1979; olive, *P. c. anubis*: Nagel, 1973; Harding, 1976, 1977; Packer, 1979a; Manzolillo, 1986). Male behavior during inter-group encounters in chacma baboons is the focus of the present study.

Data from previous studies of chacma baboons support the hypothesis that male behavior during inter-group interactions functions primarily to defend females rather than resources (*e.g.* Cheney & Seyfarth, 1977; Anderson, 1981; Cowlishaw, 1995; Henzi *et al*., 1998). Males frequently chase female members of their own group away from rival groups ('herding,' Stoltz & Saayman, 1970; Buskirk *et al*., 1974; Henzi *et al*., 1998; see also Packer, 1979a) and are most likely to chase females when they are in estrus (Cheney

& Seyfarth, 1977; Cowlishaw, 1995). One aim of this paper is to test the 'female defense' hypothesis in more detail, focusing in particular on individual differences among males and their relation to dominance rank.

The 'female defense' hypothesis predicts that male aggression during inter-group encounters should increase when sexually receptive females are present and that male chasing should increase the distance between groups. Because high-ranking males have the greatest access to sexually receptive females (*e.g.* Packer, 1979b; Smith, 1986; Altmann *et al.*, 1988, 1996; Bulger, 1993; Weingrill *et al.*, 2000; Alberts *et al.*, 2003), high-ranking males might be expected to be the most active in defending estrous females from extra-group males (Nunn, 2000; Nunn & Lewis, 2001). However, because multiple females are often in estrus simultaneously, even low-ranking males may have access to some females (*e.g.* Alberts *et al.*, 2003). As a result, thwarting additional male competitors might be beneficial for all male residents.

If female defense were the only factor mediating male behavior during inter-group encounters, the location of an encounter should have little effect on male behavior. Alternatively, males might indirectly defend access to females by defending food resources that limit female reproductive success (*e.g.* Rubenstein, 1986; Wrangham & Rubenstein, 1986). This appears to be the case in at least two species of non-human primates, chimpanzees (Williams *et al.*, in press) and female-bonded black and white colobus (Fashing, 2001). Baboon groups do not defend territories and have over-lapping home ranges (Cheney, 1987; but see Hamilton *et al.*, 1975, 1976). Nevertheless, it is possible that the outcome of inter-group encounters is influenced by their location within rival groups' ranges. Here, we test the 'resource defense' hypothesis by examining whether male behavior and/or the outcome of interactions with specific groups varies systematically according to location. One prediction of the resource defense hypothesis is that males should be most aggressive and least likely to retreat from an inter-group encounter in areas of their home range that are used most frequently and overlap least with other groups, and should be least aggressive and most likely to retreat from encounters in areas that are used least often and overlap most with those of other groups.

To test whether movement patterns following an inter-group encounter differ from those expected by chance, we also compare data on movement before and after inter-group encounters with data on movement in the same

location on days when no inter-group encounter occurred. To test whether any hazard encountered in its path causes the group to change its heading, we also examine movement patterns following encounters with lions, a major predator of baboons (Cheney *et al.*, 2004).

Finally, Hamilton *et al.* (1975, 1976) found evidence that some chacma baboon groups were consistently dominant to others. They suggested that variation in male responses to rival groups was based on inter-group dominance, which in turn was determined largely by the number of males in each group (reviewed by Cheney, 1987). Inter-group dominance could be a consequence of either female or resource defense. In either case, if larger groups (or groups with more males) dominate smaller ones, we would predict that small groups should withdraw from large groups regardless of where the encounter occurs (*e.g.* chimpanzees, Wilson *et al.*, 2001; black howler monkeys, Kitchen, 2004). Moreover, the outcome of inter-group interactions should be more ambiguous and more likely to end in a 'draw' when two groups are approximately the same size or have the same number of males.

Methods

Study site and subjects

Research was conducted in the Moremi Game Reserve, located in the Okavango Delta of Botswana. Grasslands in the delta flood annually, exposing elevated 'islands' edged with forest. Islands can be less than one to hundreds of hectares in size (Hamilton *et al.*, 1976; Ross, 1987; Ellery *et al.*, 1993). During floods, baboons continue to ford the submerged plains and move between islands throughout an approximately 5 km^2 range (Bulger & Hamilton, 1987).

As in other species of Old World monkeys, female chacma 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.*, 2003b). Both males and females form linear dominance hierarchies. Although females acquire ranks similar to those of their mothers, male dominance is determined primarily by age and fighting ability (Kitchen *et al.*, 2003b; Fischer, in press). In most cases, dominance rank orders among males are linear and unidirectional, at least over the short term (Kitchen *et al.*, 2003b).

The main study group, C, has been observed since 1978. All individuals are recognized by face and the matrilineal relatedness of all natal animals is known. Subjects are fully habituated to observers on foot. The data described in this paper were gathered over a 23-month period (June, 1999 through May, 2001). During this time, C group contained 78-88 animals, including 23-29 adult females and 17 different natal and immigrant adult males older 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. The adult sex

ratio in C group varied only slightly throughout this study (range: 2.1-2.6 females/male). We were therefore unable to examine its influence on male behavior (see Henzi *et al.*, 1998).

C group encountered six different groups within or at the boundary of its home range. However, only three groups were encountered frequently enough and in a sufficient variety of locations to examine inter-group dominance.

One group, Q, occupied an adjacent home range south and southeast of C's. Q group has been observed intermittently since 1992 and we could recognize all individuals. During the study, Q group contained 20-31 individuals, including 2-10 adult males. Seven of these males had been born in C and were fully habituated to humans. Other males were approachable to within a few meters, though females were only approachable to within 6-10 meters. We took a bi-weekly census of Q group and continually monitored the dominance ranks of all males.

Two other groups, Z and W, occupied adjacent home ranges north and east of C group. The home ranges of Z and W overlapped, with W occupying the area south and east of Z. Groups Z and W were partially habituated and tolerated observer presence to between 20-40 m. Although observers recognized several individuals in both groups, the groups were large and members were often widely dispersed. We could therefore not always be certain that we could accurately distinguish the groups. In this paper, therefore, we have combined data from encounters with Z and W.

General data collection

We typically located C group between 0500 and 0830 and then followed it for 5-7 hours. Observers (usually three and never fewer than two) distributed themselves throughout the group to maximize coverage of adult males. On a subset of days, two observers traveled with Q group while two observers traveled with C group. All observers were in constant radio contact.

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 non-pregnant female between the swelling periods of estrous cycles. (3) Pregnant: any female with a darkened callosity after a missed estrous cycle. We retroactively approximated conception date as mid-way through the maximum swelling period of the last estrous cycle. (4) Lactating: any female with a nursing offspring, until either her infant died or she resumed sexual cycling. We also recorded the identity of all adult males involved in consortships with estrous females.

An inter-group encounter occurred whenever two groups came to within 300 m of each other. Although C group encountered groups visually or audibly at greater distances, these encounters usually produced mild or no responses.

At the onset of an encounter, at least two observers stayed with the focal group while another observer typically collected data on the opposing group. Data collection continued until the two groups separated by at least 50 meters and lost visual contact with one another. On the rare occasion when C group met the same group twice in one day, we used only data gathered during the first encounter. On five occasions C group met two different groups on the same day. In all cases, however, these encounters were separated by at least 30 min (Mean = 114 min) and occurred on separate islands.

Each observer carried a Psion LZ64 computer and digital audio tape recorder (Sony PCM-M1) with a directional microphone (Sennheiser ME66) for recording spoken commentary during an encounter. Both the tape recorder and the computer were programmed to note the

time of an entry to the nearest second and were used to record the occurrence and duration of all behavior and the identity of all participants. When possible, we noted the same behavior in the opposing group and identified the age/sex class of all participants.

An aggressive display began when the first adult male chased or attacked a member of his own or the opposing group, or produced a loud call. Chases were scored as aggressive displays only if they lasted more than 10 s or covered more than 10 m. The most common loud calls produced during aggressive inter-group displays were 'contest wahoos' (Byrne, 1981; Waser, 1982; Fischer *et al.*, 2002; Kitchen *et al.*, 2003a). Typically, males produced wahoos while they chased another male, female or juvenile member of their own or the opposing group (75% of 72 inter-group displays). However, males also occasionally chased other individuals without producing loud calls (17%) or produced loud calls without chasing anyone (8%).

Two groups were considered to be 'mingling' (Hamilton *et al.*, 1975) if some members of both groups were within 10m of each other and quietly resting or feeding in the absence of aggressive displays.

Determining home range

Using a hand held global positioning system (Magellan GPS, 2000) in combination with an aerial photograph of the area (scale: 1:30,000), one observer determined the group's location throughout the day. An average of three measures per day (range: 1 to 5) were taken at approximately two-hour intervals starting after 0800 (*i.e.* after the baboons' first major move from a sleeping site) and ending before 1500 (*i.e.* before baboons settled into a sleeping site).

We created a scatter plot of location coordinates and conducted a kernel analysis (Worton, 1989; SYSTAT, 1997). The 'core' zone was defined as the area within C group's range that was used most often and contained half of all location coordinates. We then determined the 'intermediate' zone, which included another 25% of the locations used by C group. In terms of area, the intermediate and core zones were approximately equal in size. Finally, the 'peripheral' zone was anywhere outside these zones, including those locations used only rarely by C group. The peripheral zone was approximately three times as large as either the core or intermediate zones. Because the study area floods each year (Ross, 1987) and the baboons' ranging patterns are constrained during the period of high flood (Hamilton *et al.*, 1976), we calculated these zones separately for the flood ($N = 522$ coordinates on 174 days) and non-flood seasons ($N = 454$ coordinates on 158 days).

When another group or a predator was first spotted, one observer immediately took a GPS reading. We then determined whether the encounter had occurred in the core, intermediate or peripheral zone by plotting the coordinate on a scatter plot overlaid with the boundaries of these zones, correcting for season as described above.

Movement following encounters

At 30 min intervals on the half-hour, one observer used the GPS to establish the group's heading (*e.g.* true north $= 0°$ or $360°$). The heading was recorded as 'stationary' if the majority of the group was feeding or resting at the time.

To test whether an inter-group or a predator encounter changed the focal group's heading, one observer first used the GPS to determine the heading directly toward the opposing group or the predator. The same observer then recorded the latency and direction of the first

movement of greater than 50 m by the majority (>85%) of the focal group. We called the difference between these two headings the deflection angle (a_1; see also Henzi *et al.*, 1998).

Following an encounter, all observers compared their notes on movement patterns with the GPS readings. Movements were categorized as follows: toward the opposing group ($0° < a_1 < 45°$); neither toward or away from the opposing group ($45° < a_1 < 90°$); or away from the opposing group ($90° < a_1 < 180°$). No data on movement were recorded in three encounters and only observer notes on movement were available in 30 encounters. Using categories to reflect deflection angles, the data derived from observer notes were highly correlated with the deflection angle derived using GPS data (Spearman rank correlation $r_s = 0.901$, $N = 77$, $p < 0.001$). Although data from the 30 encounters with only observer notes are not reported in deflection angle results, their inclusion would not change our overall results.

Using both observer notes and deflection angles to determine the movement patterns of both C group and the opposing group following encounters, we further categorized encounters as a 'loss' if C group moved away and the opposing group moved toward them, a 'win' if C group moved toward the opposing group and they moved away, or a 'draw' if both groups moved off in opposite directions.

Statistics

We used an analysis of covariance (Sokal & Rohlf, 1995) to examine the relative influences of each independent variable on two continuously distributed dependent variables, display duration and deflection angle. Because the display duration data were not normally distributed, we used a natural log transformation. A backward stepwise selection process (using the general linear model command in SYSTAT, 1997) selected the best model from the following independent variables: presence or absence of estrous females; encounter location (core, intermediate, periphery); and opposing group's identity (Q or Z/W). Likewise, a backward stepwise logistic regression (SYSTAT, 1997) was used to test the relative influence of each of the above predictor variables on the following discretely distributed dependent variables: number of participants (0, 1, 2 or more); any loud call; any chase; any mingling; contest outcome (win or lose). Non-parametric statistics were used for all other analyses. Significance levels were set at $\alpha = 0.05$.

Results

Characteristics of inter-group encounters

There was a distinct difference between male and female behavior during inter-group interactions. When groups initially met, the adult females who were closest to the other group sometimes ran away from the other group toward the core of their own group, without necessarily being pursued by adult males from either group. Females were never observed acting aggressively toward other groups. Conversely, adult and sub-adult males became vigilant and typically moved to elevated positions along the edge of their

group nearest the opposing group (Hamilton *et al.*, 1975 describe 'approach' and 'facing off' behaviors). Some inter-group encounters prompted aggressive chases by adult males. Most chases were directed at other members of the male's own group; males chased other male and/or adult female members of their own group in 59.0% of 100 encounters. However, males occasionally traveled up to several hundred meters from their own group to chase members of the opposing group (Hamilton *et al.*, 1975). These males, in turn, were often chased back by a male from the rival group; in 26.8% of 97 encounters males from either group chased members of the opposing group.

We were able to collect complete behavioral data on C group during 100 of 110 encounters and only loud call or chase data during the remaining 10 encounters. Although 28% of 100 encounters with complete behavioral data resulted in non-aggressive mingling or no behavioral responses, other encounters were characterized by high levels of aggression within or between groups, including the death of a one day-old infant. Because this attack occurred while an extra-group male was running through C group and we were not able to identify the infanticidal male, it was unclear whether the attacker was a resident or not.

Inter-group encounters were at least 1.3 times more likely in the non-flood season, with 49 encounters occurring during the flood season (on 47 of 278 observation days or 1 encounter every 5.7 days) and 61 occurring during the non-flood season (on 58 of 265 observation days or 1 encounter every 4.3 days). Although not statistically significant (Pearson $X_1^2 = 2.16$, $N = 543$, $p = 0.142$), the difference in encounter rates may have occurred because the flood restricted the movements of all groups.

Of 110 inter-group encounters for which we had behavioral and/or movement data, 52 (47%) were with Q group, 54 (49%) with Z or W groups and the remaining four (4%) were with three other infrequently encountered groups. At least one female was in estrus in C group during 93 encounters (85%) and no estrous females were present during 17 encounters (15%). C group encounters were fairly equally distributed between Q and Z/W groups in terms of season, location and presence of estrous females (Table 1).

Although C group spent 50% of its time in the 'core' zone, only 27.3% of all inter-group encounters occurred there, significantly fewer than expected by chance (expected: 50%; $X_1^2 = 11.36$, $N = 30$, $p < 0.001$). The difference was probably due to the infrequent use of C group's core zone by other groups. By contrast, significantly more encounters than expected (42.7% of

TABLE 1. *Number of encounters between C group and either Q or Z/W groups based on estrous female presence in C group, season, and location of encounter*

Estrous Females:	Opponent: Q Group			Opponent: Z/W Group			Total N
	Absent	Present	N	Absent	Present	N	
Flood							
Core Zone	2	5	7	2	4	6	13
Intermediate Zone	3	7	10	1	9	10	20
Peripheral Zone	3	5	8	1	6	7	15
Total N	8	14	25	4	18	23	48
Non-flood							
Core Zone	0	6	6	2	8	10	16
Intermediate Zone	1	13	14	1	11	12	26
Peripheral Zone	1	6	7	0	9	9	16
Total N	2	25	27	3	28	31	58

110 encounters) occurred in the 'intermediate' zone, where C group spent 25% of its time (expected: 25%; $X_1^2 = 13.83$, $N = 47$, $p < 0.001$). This was probably due to the extensive use of this zone by other groups. Finally, while other groups often used the 'peripheral' zone of C group's range, C group spent only 25% of its time in this relatively large area. Only 30% of inter-group encounters occurred in this zone, an encounter rate not different from that expected by chance (expected: 25%; $X_1^2 = 1.10$, $N = 33$, $p > 0.100$).

Rank and participation of males

Throughout the study, 13 (76.5%) of the 17 males who were ever present in C group were involved in at least one inter-group encounter. An average of three C group males were involved in each aggressive display (range: 1-9, including the lowest-ranking male). The alpha male was involved in 75% of 72 encounters when at least one male displayed (or 54% of 100 encounters with complete behavioral data), but at least one other male was involved in 74% of 72 encounters where at least one male displayed (or 53% of 100 encounters). During displays, high-ranking males participated in more wahoo bouts (Spearman rank correlation $r_s = -0.703$, $N = 12$ mean rank positions held by 13 males during 48 inter-group encounters, $p < 0.050$), and produced wahoos at a faster rate ($r_s = -0.645$, $N = 11$ rank positions, $p < 0.050$) than did low-ranking males.

Effect of estrous female presence

Although access to estrous females was correlated with male rank, there were often several females in estrous simultaneously. As a result, more than one male might be involved in a consortship on a given day (see Alberts *et al.*, 2003). Of the 0-6 consorting males present in C group during all inter-group encounters, an average of 29.2% were involved in aggressive displays. Of the 6-13 non-consorting males present, an average of 12.1% were involved in aggressive displays. Thus consorting males were more than twice as likely to participate than non-consorting males. Of the 17 males present in C group over the course of the study, six displayed during more than six inter-group encounters (range = 6-27 encounters per male) and were involved in a consort during more than ten encounters (range = 10-36 per male). Five of these six males were more likely to be involved in an aggressive display when they were in a consort with an estrous female than when they were not (Wilcoxon signed ranks test, one-tailed $T = 1$, $N = 6$, $p < 0.050$).

The presence of estrous females affected male aggressive displays in several ways. The presence of estrous females was the only predictor of how many males joined displays (by loud calling and/or chasing); two or more males were more likely than one male to participate in inter-group displays when estrous females were present than when they were not (Fig. 1; multinomial logistic regression $X_2^2 = 6.45$, $N = 106$, $p = 0.040$). Males displayed for longer durations (Fig. 1; ANOVA $F_{1,89} = 4.40$, $N = 91$, $p = 0.039$) when at least one estrous female was present in the group than when no such females were present. Additionally, males were more likely to produce wahoos when at least one estrous female was present (50.0% of 92 encounters) than when no estrous females were present (17.7% of 17 encounters; Table 2).

When at least one estrous female was present in C group, females were more likely to be chased (62.2% of 82 encounters) than when no estrous females were present (29.4% of 17 encounters; Table 2). The presence of estrous females did not, however, affect the probability that an adult male or a juvenile would be chased (Table 2). When females were chased, males targeted estrous females. Correcting for the total number of available females in each reproductive category, 17.9% of available estrous females were chased compared with 6.9% of available pregnant, 8.8% of available lactating, and
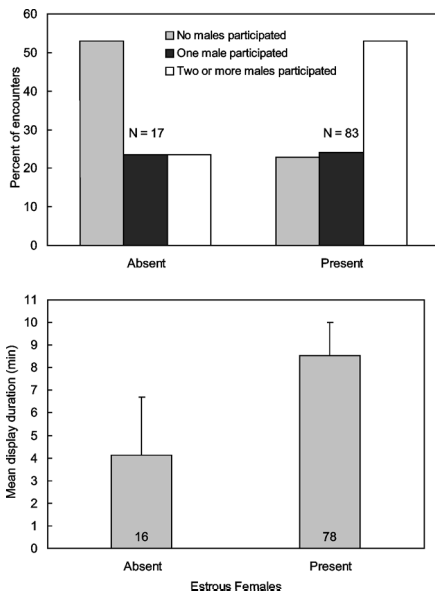
Fig. 1. (a) The percent of encounters when no males, one male or two or more males participated in an inter-group encounter based on the presence of estrous females and (b) the mean ± SE duration of displays produced by all adult males in C group during inter-group encounters based on the presence of estrous females in their group. N = number of encounters.

1.5% of available non-estrous cycling females ($N = 112$ cases in which all victims could be identified).

C group males were more likely to chase members of the opposing group when rival males chased members of C group (Pearson $X_1^2 = 9.28$, $N = 97$, $p = 0.002$). Because these responses were correlated, we tested which factors influenced whether or not either group chased members of the other. We found that males from either group were more likely to chase members of the opposing group when estrous females were present in C group than when they were absent (Fig. 2; Table 2). Neither the oldest males (see Kitchen *et al.*, 2003b for age estimates) nor the alpha male from C group ever chased members of the opposing group.

The two groups involved in an encounter were more likely to mingle non-aggressively on days when no females were in estrus in C group (17.7% of 17 encounters) than when at least one was in estrus (4.3% of 93 encounters; Table 2).

TABLE 2. *Factors affecting the occurrence of male displays and mingling between two groups**

Response Variable[†]	Predictor Variable	Odds ratio	DF	T-ratio	p	Model X^2	Model DF	Model p
Loud calls	Estrous female absent	0.2**	1,103	−2.2	0.03	5.8	1	0.016
Chase C females	Estrous female absent	0.3	1,93	−2.2	0.03	5.4	1	0.020
Chase opposing group	Estrous female absent	0.2	1,91	−1.8	0.07	5.2	1	0.022
Two groups mingle	Estrous female absent	4.6	1,104	1.9	0.06	3.1	1	0.079

* Results based on a binomial logistic regression with presence of estrous females, location, and group identity as predictor variables. A backward stepwise selection process identified the best model, shown above.

[†] Model selection failed to identify any significant predictors of C group males chasing other male or juvenile group members.

** The odds ratio compares the probability of an event occurring with the probability of it not occurring. In this cell, the odds ratio of 0.2 indicates that a wahoo was five times more likely when estrous females were present than when absent, calculated as:

$$\frac{(p_{\text{wahoo − estrous female absent}})/(p_{\text{wahoo − estrous female present}})}{(p_{\text{no wahoo − estrous female absent}})/(p_{\text{no wahoo − estrous female present}})}.$$
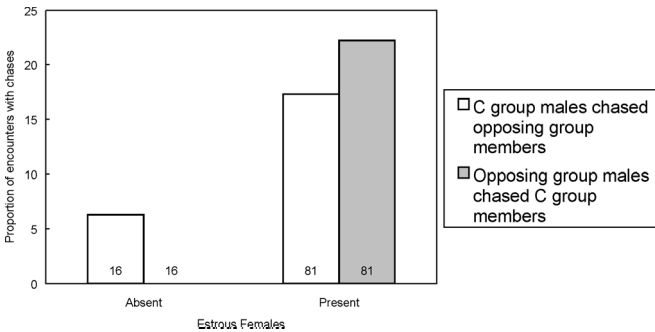

Fig. 2. The percent of encounters resulting in chases of an opposing group member by a C group male and vice versa based on the presence of estrous females in C group. Numbers within histogram indicate sample size.
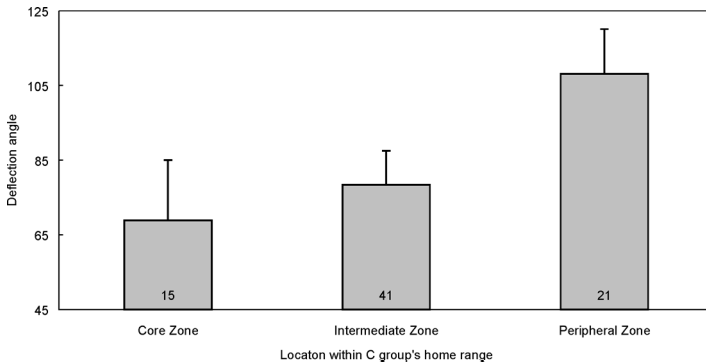
Fig. 3.   The mean ± SE deflection angle taken by C group following inter-group encounters based on the location within its home range. Numbers within histogram indicate sample size.

Neither C group's deflection angle nor the number of encounters that they 'won' were influenced by estrous female presence; C group was equally likely to move off when estrous females were present (49.2% of 65 encounters) or absent (41.7% of 12 encounters). Additionally, male behavior (*i.e.* frequency of chasing) did not affect C group movement patterns following an inter-group encounter (Pearson $X_2^2 = 0.11$, $N = 69$, $p = 0.945$).

Effect of location and rival group identity

Male aggressive behavior was not influenced by the location of the inter-group encounter. Although males in C group gave loud calls and chased females more frequently in their core zone than in the peripheral zone when meeting Z/W, these were non-significant trends, and the characteristics of male aggression during encounters with Q group were unrelated to location.

In the peripheral zone of their home range, C group males produced wa-hoos (Pearson $X_1^2 = 3.90$, $N = 31$, $p = 0.048$) and chased female members of their own group (Pearson $X_1^2 = 4.64$, $N = 27$, $p = 0.031$) more when meeting Q group than when meeting Z/W group.

Although male aggressive behavior was not influenced by the location of the inter-group encounter, C group's deflection angle (mean ± SE = 84.6 ± 6.7°) became increasingly larger as encounters occurred in more peripheral zones (Fig. 3; ANOVA $F_{2,73} = 5.71$, $N = 76$, $p = 0.005$). C group moved away from the opposing group most frequently in the peripheral zone of its home range and moved toward the opposing group most frequently in the

core zone (Pearson $X_1^2 = 10.87$, $N = 61$, $p = 0.006$), regardless of which group they faced.

To ensure that changes in movement were based on location and not just on chance, we compared the change in heading (or 'angle of deflection') before and after an encounter with a similar angle calculated during the same season at approximately the same time and place on a day with no inter-group encounters. C group was more likely to change its direction of movement when it encountered other groups in the peripheral zone (mean $\pm$ SE $= 72.62 \pm 11.85°$) than when no groups were encountered in this zone (mean $\pm$ SE $= 37.62 \pm 8.88°$; Wilcoxon signed ranks test $T = 44.5$, $N = 21$, ties $= 1$, $p < 0.050$). However, C group was no more likely to change its direction of movement on encounter days than on non-encounter days in its intermediate (encounter: mean $\pm$ SE $= 53.75 \pm 11.30°$; non-encounter: mean $\pm$ SE $= 42.75 \pm 12.37°$; $T = 77.0$, $N = 20$, ties $= 1$, $p > 0.100$) or core zones (encounter: mean $\pm$ SE $= 43.20 \pm 10.37°$; non-encounter: mean $\pm$ SE $= 27.33 \pm 6.98°$; $T = 42.5$, $N = 15$, ties $= 1$, $p > 0.100$).

To determine whether any hazard in its path altered C group's movement, we calculated C group's angle of deflection following 25 encounters with lions (11 non-flood and 14 flood days). Following these encounters, C group drastically changed its deflection angle (mean $\pm$ SE $= 125.2 \pm 8.9°$), consistently moving away from the lions. Unlike encounters with other baboon groups, heading changes following encounters with lions were unaffected by the location of the encounter; C group was equally likely to move away from lions in the core, intermediate, and peripheral zones of its range (Kruskal-Wallis $H_2 = 0.07$, $N = 25$, $p = 0.968$).

Examining just inter-group contests with clear winners and losers, outcome was influenced by both location and rival group identity (binomial logistic regression $X_3^2 = 23.1$, $N = 80$, $p = 0.001$), but not by the presence of estrous females. We used post-hoc comparisons to first describe the effects of location while controlling for rival group identity. When facing Q group, C group was more likely to 'win' (displace the opposing group) in the core and intermediate zones and more likely to 'lose' (be displaced by the opposing group) in the peripheral zone (Fig. 4; Pearson $X_2^2 = 5.57$, $N = 40$, $p = 0.062$). When facing Z/W group, C group was increasingly less likely to win as the encounters occurred in more peripheral zones (Fig. 4; Pearson $X_2^2 = 10.53$, $N = 40$, $p = 0.005$).
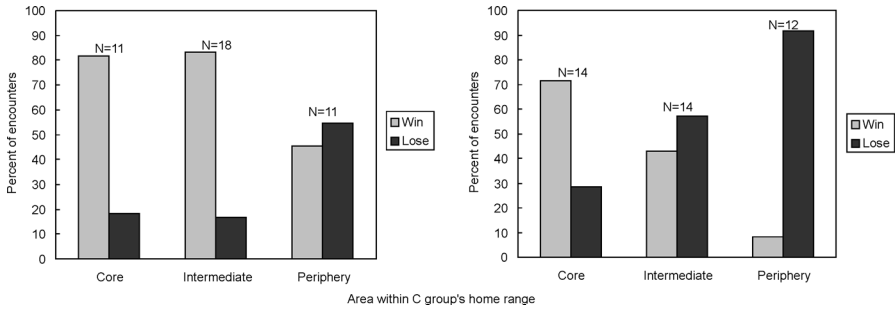
Fig. 4. The percent of encounters that C group won or lost when interacting with (a) Q group and (b) Z/W group, based on the location of the encounter within C group's home range.

Second, we used post-hoc comparisons to describe the effects of rival group identity while controlling for location. In the core zone, rival group identity had no effect on the outcome of encounters (Fig. 4; Pearson $X_1^2 = 0.37$, $N = 25$, $p = 0.546$). However, C group lost more encounters with Z/W group than with Q group in both the intermediate (Fig. 4; Pearson $X_1^2 = 5.72$, $N = 32$, $p = 0.017$) and the peripheral zone (Fig. 4; Pearson $X_1^2 = 4.10$, $N = 23$, $p = 0.043$). Throughout the study, there were always more males in C group than in the smaller Q group. Although a complete census of Z and W groups was often difficult, our estimates suggest that both groups were larger and contained more males than C. Perhaps not surprisingly, therefore, C group tended to be more successful against Q group than against Z/W group.

Of the encounters that ended in a 'draw' (both groups moving off in the opposite direction), most occurred in the intermediate zone (60.9%) compared to the peripheral (13.0%) or core zones (26.1%; Pearson $X_2^2 = 8.44$, $N = 23$, $p = 0.015$). Although more of the encounters that ended in a draw occurred when meeting Z/W group (60.9%) than when meeting Q group (39.1%), this was not a significant difference (Pearson $X_1^2 = 1.09$, $N = 23$, $p = 0.297$).

Because we were able to monitor the relative numbers of males between C and Q groups, we examined these encounters more closely (Fig. 5). Relative numbers appeared to be most important in C group's intermediate zone. In this zone, Q group won an encounter or it ended in a draw more often when the relative numbers of males were approximately equal ($X_1^2 = 4.44$,
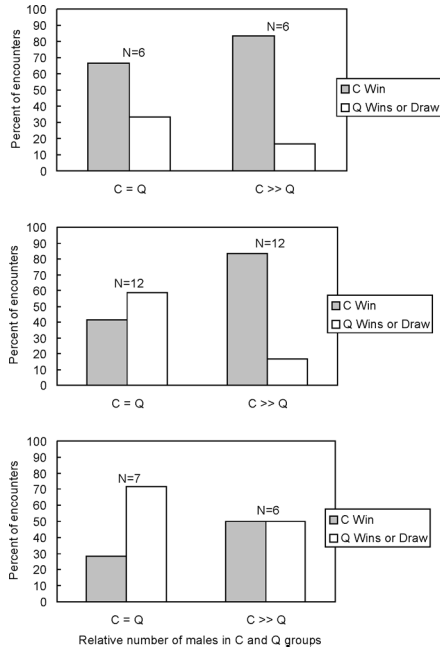
Fig. 5.   The percent of contests won by C or Q group when encounters occurred in the (a) core, (b) intermediate, or (c) peripheral zone of C's home range when C and Q groups had a relatively equal number of males (C:Q males 1.1 to 1.7:1) and when C group had more than twice as many males (C:Q males 2.2 to 6.5:1).

$N = 24$, $p = 0.035$), despite the fact that overall Q group was still smaller than C group.

Discussion

As in several previous studies (*e.g.* Cheney & Seyfarth, 1977; Cowlishaw, 1995), we found strong evidence supporting the hypothesis that male chacma baboons' behavior during inter-group encounters functions to prevent males in other groups from gaining access to sexually receptive females. Aggressive male displays, including chases and loud calls, occurred during 72% of all encounters. When an encounter occurred, males were significantly more likely to chase females if one or more estrous females were present than if they were not, and when chasing occurred estrous females were targeted significantly more often than expected. The presence of estrous females had

no effect on chases of adult males or juveniles. When estrous females were absent from C group, male aggressive displays were shorter in duration, involved fewer adult male participants, were less likely to involve loud calls and chases, and were more likely to result in mingling than when estrous females were present.

Males from the opposing group approached C group and chased C group members more frequently when estrous females were present than when they were not (see also Rasmussen, 1979; Manzolillo, 1986; Henzi *et al.*, 1998), and these chases often resulted in counter-chases by males from C group. Because most sub-adult males eventually leave their natal groups and adult males may transfer between several groups during their lifetimes, these forays may serve as 'reconnaissance missions,' allowing males to assess the number and reproductive state of extra-group females. Two observations support this view: of the 17 transfers that occurred during this 23-month study, at least 47% occurred during an inter-group encounter, and those individuals who would have the least to gain by transferring into a new group, the alpha male and old, low-ranking males, never approached or chased members of the opposing group.

Theory suggests that non-alpha males in multi-male groups of unrelated individuals with high reproductive skew should not invest in group defense, and only the alpha male should actively defend the group (*e.g.* Nunn, 2000; Nunn & Lewis, 2001). In our study population, high-ranking males have significantly greater access to estrous females than do low-ranking males (Bulger, 1993). High-ranking males also participated in more inter-group encounters, and produced wahoo vocalizations more frequently and at faster rates during inter-group encounters than did low ranking males (see also Kitchen *et al.*, 2003b; Fischer, pers. comm.). However, the alpha male was not the only individual to engage in sexual consortships, nor was he the only male to engage in aggressive displays and chasing during inter-group encounters. Several females were often in estrous simultaneously, allowing even middle- and low-ranking males to engage in consortships. At least one male other than the alpha male participated in 74% of all encounters, and nine different males (including the lowest-ranking male) were involved in at least one encounter. Males of all ranks were more likely to be involved in an aggressive display when they were in a consort with an estrous female than when they were not. Results suggest that it may have been in the reproductive

interests of many males to prevent extra-group males from gaining access to estrous females.

However, unlike males in other multi-male species (*e.g.* capuchins: Janson, 1986; Perry, 1996; lions: Grinnell *et al.*, 1995; chimpanzees: Wilson *et al.*, 2001; howler monkeys: Kitchen, 2004), male baboons in our study did not engage in cooperative group defense. Chases by male baboons during inter-group encounters were more likely to be directed at a male member of the chaser's own group than at male members of the opposing group. In this respect, male inter-group displays were very similar to their intra-group contests (Kitchen *et al.*, 2003b). Male-male competition is thus focused primarily on access to females, and males treat extra-group and intra-group rivals similarly.

If female defense were the only factor mediating inter-group contests, we would expect the location of an encounter to have no effect on group movement. In fact, however, group movement during and after inter-group encounters was influenced by location and the identity of the opposing group, but not by the presence of estrous females. Regardless of the number of estrous females present, C group was more likely to move away from groups it encountered on the periphery of its range and more likely to move toward the same groups when it encountered them in its core or intermediate zones. Similarly, C group was more likely to win encounters in its core zone and lose them in its periphery. 'Draws' were most common in the intermediate zone, which was also the zone of highest inter-group range overlap. C group's tendency to withdraw when it encountered a potential inter-group threat in peripheral areas but advance when a similar threat was encountered in a core area was unlikely to have been influenced by individuals' relative familiarity with these areas. In the absence of an inter-group encounter, C group rarely changed its heading from one measurement to another (30 min later), regardless of where it was in its range. When C group encountered lions it changed its heading markedly, regardless of location. We therefore conclude that the baboons' unyielding response to other groups in core and intermediate areas was due to their willingness to defend these areas against intruders, or at least their unwillingness to be deterred from a particular route.

What remains unclear is whether males, females or both drive this behavior. We found little support for the hypothesis that males successfully used chasing to move (or 'herd') groups away from male competitors (but see Henzi *et al.*, 1998). Although chasing increased the distance between males

in the opposing group and individual estrous females over the short term, neither the frequency of chasing nor the presence of estrous females was correlated with the subsequent movement of C group. Despite their lack of overt aggression during inter-group contests, there might be a subtle influence of females or other group members on group movement. However, like other observers (*e.g.* Kummer, 1971) we found it difficult to determine precisely what the stimulus was for a group's movement in a particular direction.

As in other studies of non-human primates (*e.g.* Hamilton *et al.*, 1975, 1976; Wilson *et al.*, 2001; Kitchen, 2004; reviewed in Cheney, 1987), the relative number of males in opposing groups appeared to play at least some role in the nature of inter-group interactions. While C group consistently outnumbered Q group in both total group size and number of males, C group was generally smaller and contained fewer males than Z/W group. Controlling for location, clear wins favored the group with more males; C group was more likely to move away from Z/W group than from Q group. In encounters between C and Q groups, the contest outcome was least clear when the numbers of males in the two groups was most equal.

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