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Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks

Abstract Males in multi-male groups of chacma baboons (*Papio hamadryas ursinus*) in Botswana compete for positions in a linear dominance hierarchy. Previous research suggests that males treat different categories of rivals differently; competitive displays between males of similar rank are more frequent and intense than those between disparately ranked males. Here we test whether males also respond differently to male–male interactions in which they are not directly involved, using playbacks of the loud 'wahoo' calls exchanged between competing males in aggressive displays. We played paired sequences of vocal contests between two adjacently ranked and two disparately ranked males to ten subjects, half ranking below the signalers in the call sequences and half above. Subjects who ranked above the two signalers showed stronger responses than lower-ranking subjects. Higher-ranking subjects also responded more strongly to sequences involving disparately ranked, as opposed to adjacently ranked opponents, suggesting that they recognized those individuals' relative ranks. Strong responses to sequences between disparately ranked opponents might have occurred either because such contests typically involve resources of high fitness value (defense of meat, estrous females or infants vulnerable to infanticide) or because they indicate a sudden change in one contestant's condition. In contrast, subjects who ranked lower than the signalers responded equally strongly to both types of sequences. These subjects may have been able to distinguish between the two categories of opponents but did not respond differently to them because they had little to lose or gain by a rank reversal between males that already ranked higher than they did.

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Introduction

It has been hypothesized that the ability to recognize 'third-party' relationships should be advantageous whenever individuals live in large social groups (e.g., Harcourt 1988, 1992; Cheney and Seyfarth 1990). In order to compete successfully within such groups, it would seem to be advantageous for individuals to recognize who outranks whom, who is closely bonded to whom, and who is likely to be allied with whom. The ability to adopt a third party's perspective, and discriminate the ranks and social relationships that exist among others based on observations alone, may therefore be of great selective benefit (reviewed in Cheney and Seyfarth 2004). A growing body of evidence suggests that non-human primates do recognize the relative ranks of others (vervet monkeys, *Cercopithecus aethiops*: Cheney and Seyfarth 1990; baboons, *Papio hamadryas ursinus*: Bergman et al. 2003; bonnet macaques, *Macaca radiata*: Sinha 1998; capuchin monkeys, *Cebus capucinus*: Perry et al. 2004; sooty mangabeys, *Cercocebus torquatas atys*: Range and Nöe 2004). For example, in playback experiments, female baboons respond more strongly to vocal sequences that are inconsistent with the female dominance hierarchy than to sequences that are consistent with it (Cheney et al. 1995).

There is currently much less evidence for third-party rank recognition in non-primates, largely because few studies of non-primate animals have attempted to investigate this question. If the recognition of third-party relationships is adaptive whenever individuals live in large social groups composed of individuals of varying degrees of genetic relatedness and competitive ability, we should find evidence for third-party rank recognition in a variety of taxa in addition to non-human primates. Indeed, recent research on free-ranging hyenas (*Crocuta crocuta*), whose social structure is very similar to that of many Old World Monkeys, has suggested that, like monkeys, hyenas

choose allies based on their own, their opponent's, and their ally's relative ranks (Engh et al. 2004). Similarly, male great tits (*Parus major*) appear able to infer their own dominance relative to that of a rival by combining direct experience with information gathered by 'eavesdropping' on interactions between the rival and another bird (Peake et al. 2002). Transitive inference demands that an individual be able to evaluate the relative rank or value of items within a list (e.g., inferring that if A>B and B>C, then A>C). A recent laboratory study of transitive inference in two species of closely related corvids has indicated that social pinyon jays (*Gymnorhinus cyanocephalus*) learn transitive lists more rapidly and accurately than less social scrub jays (*Aphelocoma californica*) (Bond et al. 2003). The paucity of data on transitive inference in other highly social species of birds and mammals, however, currently prevents any systematic comparison between primates and other animals.

To date, most studies of third-party rank recognition in non-human primates have focused on female Old World monkeys, whose ranks remain stable for years at a time. In most species of Old World monkeys, females are philopatric and matrilineal rank is inherited, whereas males disperse as adults and rank is largely determined by fighting ability. Because rank reversals among males are common, it may be more difficult for individuals to keep track of transient male dominance hierarchies than stable female ones. Only one study has considered rank recognition among male Old World monkeys. In that study, Silk (1993, 1999) found that captive male bonnet macaques consistently recruited alliances partners on the basis of their opponent's and their ally's relative ranks, even though males changed ranks often.

Males in multi-male groups of baboons form linear dominance hierarchies in which high-ranking individuals gain preferential access to food and estrous females (e.g., Packer 1979; Altmann et al. 1988, 1996; Bulger 1993; Weingrill et al. 2000; Alberts et al. 2003). Among chacma baboons in the Okavango Delta of Botswana, male dominance hierarchies are linear and stable over short periods of time, but rank reversals are common, occurring at a rate of one to two per month (Kitchen et al. 2003b). Male–male competition frequently takes the form of displays that include loud calls, chases of other group members and/or physical fights with other adult males. High-ranking males display more frequently than low-ranking males, but regardless of rank all males compete more frequently and more intensely with opponents of similar, rather than disparate, rank (Kitchen et al. 2003b, 2004). These observations suggest that males distinguish between different categories of opponents, and that they change their own display behavior depending on their opponent's rank relative to their own.

Aggressive displays between two males do not occur in a vacuum; other group members see or hear displays, including in particular the loud 'wahoo' vocalizations that are typically exchanged by contesting males (Fischer et al. 2002, 2004; Kitchen et al. 2003b, 2004). Males may therefore be able to monitor the condition and status of their rivals without directly participating in displays. It remains unclear, however, whether male baboons are capable of third-party rank recognition (i.e., the ability to infer the relative ranks and status of other individuals through observation alone).

To investigate whether male chacma baboons recognize other males' relative ranks, we conducted playback experiments that simulated wahoo contests between adjacently and disparately ranked males. In paired trials, male subjects were played wahoo sequences involving two signalers who occupied either adjacent or more disparate ranks in the current male dominance hierarchy. Because subjects in these experiments always ranked either above or below both of the signalers involved in the wahoo contest, an ability to differentiate between the two categories of opponents would require subjects to recognize their opponents' relative ranks.

On the assumption that males do recognize each others' relative ranks, we predicted that subjects would respond more strongly to wahoo contests involving disparately ranked opponents than to those involving adjacently ranked opponents. This result could occur for two reasons. First, aggressive displays between two disparately ranked males may indicate a sudden change in one of the contestant's condition. Second, in the Okavango population, displays between disparately ranked opponents occur 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 (Kitchen et al. 2004; see also Palombit et al. 1997).

We further predicted that subjects who ranked higher than the apparent contestants would respond more strongly to the wahoo sequences than subjects who ranked lower than the contestants. This prediction was based on the observation that high-ranking males are generally more responsive to aggressive displays than low-ranking males (Kitchen et al. 2003b). Moreover, males who already rank below two contestants are unlikely to have their ranks affected by a potential rank reversal. In contrast, males who currently rank above two contestants may subsequently be challenged themselves if one of the contestants rises in rank.

Methods

Study site and population

Playback experiments were conducted in the Moremi Game Reserve, Botswana, between October 2000 and April 2001 (for a site description see Hamilton et al. 1976; Ross 1987; Kitchen et al. 2003b). The main study group, C, has been observed since 1977 (e.g., Bulger and Hamilton 1987; Cheney et al. 2004). All individuals are easily identifiable and the matrilineal relatedness of all natal animals is known. Subjects are fully habituated to observers on foot. During this study, C group contained 78–88 animals, including 22–25 adult females and 17 different natal and immigrant males 8.5 years or older. The mean number of adult males on any given day was 12. The number of males fluctuated due to immigrations, emigrations, maturation and death. Male ranks were

determined by the direction of approach–retreat interactions and were updated daily (Kitchen et al. 2003b).

Playback stimuli

The experiment's design assumed that males could recognize the wahoos of other resident males. This assumption was based both on acoustic analysis demonstrating consistent variation among the wahoos of individual males (Fischer et al. 2002, 2004) and on the well-documented ability of non-human primates to recognize others by voice alone (reviewed in Snowdon 1990; Cheney et al. 1995).

Playback sequences were constructed from recordings obtained during naturally occurring wahoo contests involving known individuals (Kitchen et al. 2003b; Fischer et al. 2004). Although 'contest' wahoos differ acoustically from 'alarm' wahoos given in response to predators, there is no evidence that contest wahoos differ acoustically across competitive contexts, for example, when given during fights over resources as opposed to dominance contests (Fischer et al. 2002).

Recordings were made with a Sennheiser ME80 directional microphone and a Sony PCM-M1 digital tape-recorder. We used software for waveform analysis (Cool Edit 2000, Syntrillium Software, Phoenix, Ariz.) to construct paired sequences of calls containing six wahoos from two different males (i.e., three different calls from each male), with each call in the series separated by 1 s of silence. Thus each playback sequence contained the same number of wahoos, played at the same rate. Sequences were an average of 8.7 s in duration, which falls within the natural range of display duration (Kitchen et al. 2003b). In 'adjacent' sequences, one male's wahoos alternated with the wahoos of a male currently adjacent to him in rank (Table 1). In 'disparate' sequences, the same male's wahoos alternated with the wahoos of a male currently separated from him by at least three steps in rank (Table 1). Five different signalers served as the 'same' male in the paired sequences. Seven signalers served as adjacently ranked males, and five as disparately ranked males. In total, we constructed 16 different call sequences, which were used in ten paired trials. Some sequences were used more than once, but playbacks of these sequences were separated by at least 10 days (mean=45 days).

For each paired sequence, the signaler that was common to both calls was the first to wahoo. The remaining five calls were arranged into one of five different sequences (e.g., 'high-low-high-high-low-low' or 'high-low-high-low-high-low'). The patterns of calling in sequences simulated natural wahoo exchanges, and there was no effect of the sequence used on results (Kruskal-Wallis, latency to look: $H_4=0.51$, $n=10$, $P=0.973$; duration of look: $H_4=3.04$, $n=10$, $P=0.552$). Sequences within the same paired trials followed the same calling pattern.

Under natural conditions, male baboons are more likely to participate in wahoo contests with males who are adjacent to them in rank than with males of disparate rank (Kitchen et al. 2003b). Some closely ranked males rarely engage in wahoo contests, however, while some disparately ranked males are frequently involved in such contests. To control for the possibility that subjects might respond more strongly to disparate sequences simply because they were more novel than adjacent sequences, we attempted to combine pairs of signalers based on their natural interaction rates (determined during a 23-month study, Kitchen et al. 2003b). Paired sequences were therefore composed of adjacently and disparately ranked males who were naturally heard wahooing either relatively frequently or rarely (Table 2). Whenever possible we attempted to err on the conservative side, using a disparate pair that was naturally heard more frequently than the adjacent pair.

Baboon wahoos are loud vocalizations, audible for at least 1 km and with typical mean amplitudes of over 90 dB at 5 m. Because they are also relatively low frequency calls, with most energy concentrated between 0.25 kHz and 2 kHz (Fischer et al. 2002), they require a large loudspeaker and considerable amplification for playback. In these experiments, we used an Electro-Voice SX-2000 loudspeaker (Burnsville, Minn.; 82 cm×66 cm×43 cm) powered by a Pioneer GM-X922 amplifier (Tokyo, Japan). Calls were calibrated both within and between sequences using a Realistic sound level meter (Radio Shack, Fort Worth, Tex.; referenced at 20 µPa, accurate to ±2 dB at 114 dB) and had a mean amplitude of 93 dB (range =91–96 dB) at 5 m from the playback source and a mean amplitude of 64 dB (range =60–66 dB) at 75 m through vegetation (see also Kitchen et al. 2003a).

Experimental protocol

Subjects were all males resident in C group during the period when playbacks were conducted. We were able to complete two matched trials for ten subjects; two other subjects emigrated from the group before both trials could be completed. Half of the subjects ranked above the signalers used in each of the paired trials (mean rank difference between subjects and the higher-ranking male in the sequence =2 rank positions; Table 1), and half of the subjects ranked below the signalers (mean rank difference between subjects and the lower-ranking male in the sequence =4 rank positions; Table 1). Note that middle-ranking subjects (i.e., males ranking in the middle one third of the hierarchy, or ranks 5–8 in a 12-male group) were used in both types of trials. Thus, not all subjects ranking above signalers were very high-ranking and not all subjects ranking below signalers were very low-ranking.

All playbacks were conducted following a period of at least 1 h when no wahoos of any type had been heard, no predators or other baboon groups had been sighted, and no male–male aggression had occurred. While one observer remained with the subject, a second observer placed the speaker at a mean distance of 55 m from the subject (range 51–60 m). A third observer located the two males whose calls were to be played to ensure that they were not visible to the subject when the calls were broadcast. The speaker was placed in

Table 1 Subjects and sequence pairs used in playback experiments

Subject	Subject's rank	Adjacent sequence	No. of ranks separating adjacent signalers	Disparate sequence	No. of ranks separating disparate signalers
PO	1	RY–TW	1	RY–TH	3
SO	2	RY–PO	1	RY–TH	3
RY	3	TW–TH	1	TW–AU	3
VE	5	TH–BJ	1	TH–WA	3
TH	6	BJ–AP	1	BJ–AU	4
AP	7[a]	RY–TW	1	RY–TH	5
BJ	7[a]	PO–SO	1	PO–VE	4
SX	8	PO–RY	1	PO–VE	3
AU	9	PO–BJ	1	PO–TH	5
WA	11	VE–TW	1	VE–TH	3

[a]These two subjects held the same rank because they were tested at different times during the study

Table 2 Rate of natural wahoo contests by pairs of signaling males used in playback experiments

Subject	Subject's rank relative to signalers	Adjacent sequence	# Natural wahoo contests between adjacent signalers[a]	Disparate sequence	# Natural wahoo contests between disparate signalers[a]
PO	Higher	RY–TW	3	RY–TH	21
SO	Higher	RY–PO	12	RY–TH	21
RY	Higher	TW–TH	4	TW–AU	0
VE	Higher	TH–BJ	2	TH–WA	6
TH	Higher	BJ–AP	0	BJ–AU	0
AP	Lower	RY–TW	3	RY–TH	21
BJ	Lower	PO–SO	5	PO–VE	14
SX	Lower	PO–RY	12	PO–VE	14
AU	Lower	PO–BJ	2	PO–TH	25
WA	Lower	VE–TW	2	VE–TH	1

[a] Number of times that the two signalers were naturally observed to engage in wahoo contests with each other (Kitchen et al. 2003b)

the same relative direction as the two males whose calls were to be played; these males were always at least 100 m from the speaker at the time of the broadcast. Observers were in contact via two-way radios, so that trials could be aborted if the subject moved, oriented in the direction of the speaker, or became involved in a social interaction.

Playbacks were conducted in habitats of low visibility and only when subjects were at least 2 m from all other individuals and feeding or sitting with their heads oriented downward and away from the speaker. Subjects were filmed for a minimum of 15 s prior to playback and for 30 s afterwards.

The order of presentation of adjacent and disparate wahoo sequences was randomly determined for each subject. All playbacks were separated by at least 4 days (mean =10 days) and trials involving the same subject were separated by at least 1 week (mean =20 days). Playbacks were therefore conducted at approximately one quarter the rate of naturally occurring contest wahoos (once per 11.3 h of observation, excluding dawn 'choruses'; Kitchen et al. 2003a).

Using a Sony DVCAM (Tokyo, Japan), we quantified all videotaped responses at 30 frames/s. We scored four categories of responses: (1) latency to look toward the speaker, (2) duration of looking toward the speaker, (3) latency to move at least 3 m (this distance was chosen to exclude movements associated with feeding), and (4) duration of moving. All latency measures were calculated from the onset of the first wahoo in a sequence. All duration measures were calculated from the onset of the first response. We calculated duration measures by subtracting the amount of time spent looking toward the speaker in the 15 s prior to playback from the total amount in the 15 s after playback onset. Based on both observation and previous playback experiments of wahoos (Kitchen et al. 2003a), we predicted that subjects' primary response to playback sequences would be to orient toward the speaker. Because the playback sequences were of short duration and simulated a low intensity contest (see Kitchen et al. 2003b), we did not predict a strong movement response. Following each trial, a 45-min focal animal sample (Altmann 1974) was conducted on the subject, and observers remained with the group for at least 1 h.

Results

Upon hearing the wahoo sequences, most subjects startled, ceased feeding and oriented immediately toward the speaker. In 19 of 20 trials, males looked toward the speaker before completion of the playback recording.

We used each subject's mean reaction to the two call sequences (i.e., disparate and adjacent sequences) to examine whether higher-ranking subjects showed overall stronger responses than lower-ranking subjects. Subjects who were dominant to two signaling males looked toward the speaker for longer durations than subjects who were subordinate to them (Fig. 1; Mann-Whitney U-test, n_1=5, n_2=5, U=3, P=0.047). Higher-ranking subjects also had shorter latencies to look toward the speaker than lower-ranking subjects, but this result did not reach statistical significance (lower-ranking subjects: mean±SE=1.61 ±0.95; higher-ranking subjects: mean±SE=0.72±0.14; U=17, P=0.347).

The strong response of dominant male subjects was largely a consequence of these males responding more strongly to disparate wahoo sequences than to adjacent sequences. All five of the higher-ranking subjects looked toward the speaker for significantly longer periods following playback of the disparate sequence than playback of the adjacent sequence (Fig. 2; Wilcoxon signed ranks test, n=5, 0 ties, Z=2.02, P=0.043).

In contrast, subjects who were subordinate to the signaling males looked toward the speaker for an approximately equal duration upon hearing both the disparate and the adjacent wahoo sequences (Fig. 2;
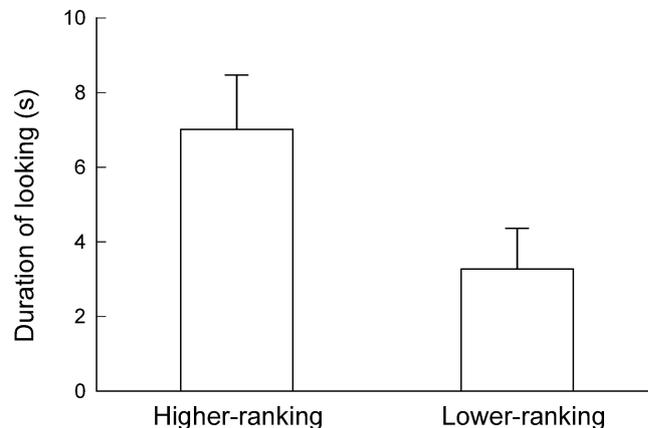

Fig. 1 The mean (+SE) duration that subjects looked toward both types of playback sequences when they were either higher- or lower-ranking than the signalers
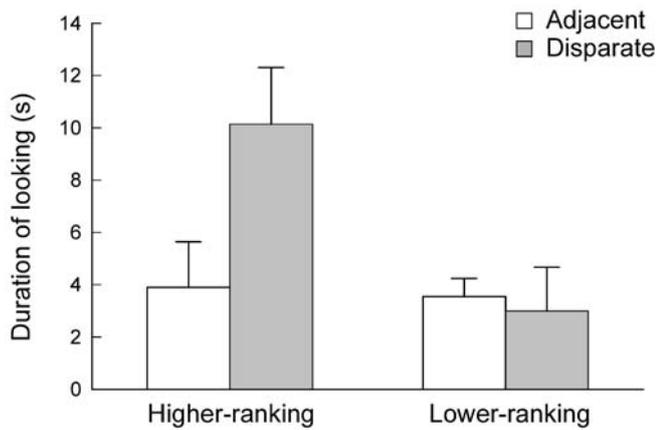
Fig. 2 The mean (+SE) duration that higher- and lower-ranking subjects responded to adjacent and disparate wahoo sequences

Wilcoxon signed ranks test, $n=5$, 0 ties, $Z=-0.67$, $P=0.500$).

Only one call sequence caused a subject to move. This was a disparate sequence played to a subject ranking higher than both signalers. This male began moving approximately 4 s after all calls ended (i.e., within 13 s of call onset) and moved for 10 s, traveling 20 m toward the speaker. The male then sat and continued to look in the direction of the speaker for over 2 min after the recording ended.

For both higher- and lower-ranking subjects, latency to look toward the speaker was similar following playbacks of disparate and adjacent wahoo sequences (Wilcoxon signed ranks test, $n=5$, higher-ranking subjects: $Z=0.14$, $P=0.893$; lower-ranking subjects: $n=5$, 1 tie, $Z=0.37$, $P=0.715$). Because the same signaler always appeared first in both the adjacent and the disparate wahoo sequence, the lack of a difference in subjects' latency to respond is not surprising.

We also examined observational data to determine whether subjects' responses to playback sequences might have been influenced by the frequency of the signalers' naturally occurring wahoos. We found no obvious effect. Subjects did not orient for longer durations upon hearing two signalers who naturally engaged in few wahoo contests than to those who engaged in many contests (Spearman rank correlation, $n=20$, $r_s=0.148$, $P>0.50$). Similarly, subjects' responses did not appear to be influenced by the frequency of their natural interactions with the second signaler in the wahoo sequence (i.e., the signaler who was unique to that sequence). There was no correlation between orientation duration and the natural frequency of wahoo contests between the subject and the second signaler ($n=20$, $r_s=-0.048$, $P>0.50$).

Discussion

When played sequences of wahoos mimicking a vocal contest between two other males, subjects who ranked higher than the apparent contestants responded more

strongly (i.e., by looking in the direction of the speaker for longer durations) than subjects who ranked lower. Under natural conditions, high-ranking males participate more frequently and more intensely in vocal contests than do low-ranking males (Kitchen et al. 2003b, 2004). Moreover, the same males typically participate less often and less intensely in aggressive displays when they fall in rank (Kitchen et al. 2003b; Fischer et al. 2004). Rather than being an inherent attribute of particular individuals, therefore, high responsiveness appears to be an attribute of high rank. It seems likely that these results reflect the higher motivation, superior physical condition and/or different hormonal levels of high-ranking males (T.J. Bergman, J.C. Beehner, D.L. Cheney and R.M. Seyfarth, unpublished data).

Males who ranked higher than the apparent contestants responded significantly more strongly to wahoo sequences involving disparately ranked opponents than to sequences involving adjacently ranked ones. In contrast, subjects who ranked lower than the contestants showed no difference in their response to adjacently ranked and disparately ranked opponents.

High-ranking males' strong responses to contests between disparately ranked opponents were not simply a result of the relative novelty of these contests. Instead, it seems probable that high-ranking subjects recognized that a contest between two disparately ranked rivals represented either a potentially significant change in the condition or status of one of the contestants or a dispute over a resource of high fitness value. In contrast, males who were subordinate to the apparent contestants may have responded more weakly to playback sequences because they had little to gain or lose from a rank reversal between males who already ranked higher than they, and little chance of competing successfully for a valuable resource.

The results presented here do not allow us to identify the mechanisms used by males to assess each others' relative ranks. Although males may keep track of each other's exact ordinal positions in the dominance hierarchy, it is also possible that they simply identify some individuals as holding similar ranks and others as holding very different ones. Whatever the precise mechanisms underlying males' responses, our results suggest that at least some males monitor competitive interactions in which they are not directly involved. Moreover, a male's own relative rank appears to influence his interest level. Overall, these results support previous observations suggesting that male monkeys recognize each other's relative ranks even when their ranks change often (Silk 1993, 1999).

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