

Male baboon responses to experimental manipulations of loud “wahoo calls”: testing an honest signal of fighting ability

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Abstract Among male chacma baboons (*Papio hamadryas ursinus*), rank positions in the dominance hierarchy are fiercely contested. Physical fighting is costly but relatively rare in this species. Instead, disputes are frequently resolved using displays that include loud, repetitive “wahoo” (two-syllable bark) vocalizations. We previously found that males of all ranks adjust their contest behavior based on the relative fighting ability of opponents and that length of the second syllable (“hoo” duration), calling rate, and fundamental frequency reliably indicate fighting ability. To test whether males indeed attend to hoo duration when assessing opponents, we designed two sets of playback experiments in which

call sequence pairs were identical except for this single modified feature. In experiment 1, we used calls recorded from high-ranking males unfamiliar to all subjects. In experiment 2, callers were familiar rivals that ranked one position below subjects in the dominance hierarchy. In paired analyses, subjects in both experiments responded more strongly to sequences with more intense signal features (most commonly associated with high-quality males) compared to sequences with relatively less exaggerated features (most often associated with low-quality males). Results suggest that males can use acoustic features to both indirectly evaluate strangers and to monitor the changing condition of those rivals that present the biggest intragroup threat to their position in the dominance hierarchy. Taken together with our previous research, baboons appear to follow a classic assessor strategy—signal features related to rank and condition are salient to males and directly affect their propensity to respond to rivals.

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Introduction

Loud, repetitive calling is a prominent feature of competitive displays among males in many vertebrates. When either the mode of call delivery and/or specific acoustic features of a call are energetically costly to produce, loud call displays may function as honest signals of fighting ability, such that only high-quality males produce the most exaggerated versions (Zahavi 1975; Grafen 1990; reviewed in Vehrencamp 2000). According to evolutionary game theory, individuals should use such honest signals to assess their rival's relative fighting ability and avoid contests they would likely lose (e.g., Maynard Smith 1974, 1982; Parker 1974; Parker and

Rubenstein 1981; Enquist and Leimar 1983; reviewed in Bradbury and Vehrencamp 1998).

There are many examples demonstrating an honest link between loud call displays and fighting ability in animals (e.g., amphibians—Ryan and Brenowitz 1985; Bee et al. 1999; Bee and Gerhardt 2001; Bee 2002; birds—Krebs et al. 1978; Yasukawa et al. 1980; Dabelsteen and Pedersen 1990; Shackelton and Ratcliffe 1994; Galeotti et al. 1997; Otter et al. 1997; Furlow et al. 1998; Rehsteiner et al. 1998; Christie et al. 2004; Price et al. 2005; Cardoso et al. 2007; nonprimate mammals—Clutton-Brock et al. 1979; Poole 1989, 1999; Reby and McComb 2003; Sanvito et al. 2007; Wyman et al. 2008; primates—Steenbeek et al. 1999; Kitchen et al. 2003b, 2005a; Fischer et al. 2004; Harris 2006; Harris et al. 2006). However, the fact that reliable information is available in loud calls is not sufficient to determine whether listeners actually attend to those signal features. The most appropriate test of this question is to quantify male responses to paired playback experiments. Playbacks allow researchers to systematically manipulate a single acoustic feature and thereby determine the specific characteristics that affect responses (e.g., amphibians—Davies and Halliday 1978; Arak 1983; Given 1987; Wagner 1989; birds—Leonard and Horn 1995; Beecher et al. 1996; Slabbekorn and ten Cate 1997; Burt et al. 2001; Mennill and Ratcliffe 2004; Mager et al. 2007; bats—Behr et al. 2009; red deer—Clutton-Brock and Albon 1979; Reby et al. 2005; sea lions—Charrier et al. 2011). Here, we describe results of playback experiments testing whether listeners attend to an acoustic feature previously found to correlate with fighting ability in a nonhuman primate—chacma baboons (*Papio hamadryas ursinus*).

As in many other species of Old World monkeys living in large multimale, multifemale groups, male chacma baboons usually immigrate into neighboring groups as adults (at approximately 9–10 years of age), although some males in this population remain in their natal group and can rise to alpha positions (e.g., Hamilton and Bulger 1990; Beehner et al. 2005). The male dominance hierarchy is linear and stable in the short term, but males frequently engage in fierce competition with one another over positions (Kitchen et al. 2003b), likely because rank confers reproductive benefits (Cowlshaw and Dunbar 1991; Bulger 1993; Weingrill et al. 2000). At our site, alpha male tenure lasts only 9 months on average and challenges are common even among the lower-rank positions, with reversals between males of adjacent rank occurring at a rate of 1.5 times per month (Hamilton and Bulger 1990; Palombit et al. 2000; Kitchen et al. 2003b).

When contests escalate to physical fights, substantial and even potentially fatal injuries have been observed in this population (Smith 1986; Bulger 1993; Kitchen et al. 2005a). As in other species of animals, however, the majority of contests between males seldom escalate beyond the level of threat displays. Among male chacma baboons, these

displays include repetitive “wahoo” vocalizations (a two-syllable bark; Fischer et al. 2002; Kitchen et al. 2003b, 2005a) that are often but not always accompanied by running, leaping through trees, and chases. Displays can last for up to an hour and appear to require considerable stamina, because even high-ranking males seem to be exhausted after a long display bout. Thus, although less risky than fighting, wahoos displays are likely costly to produce and therefore have the potential to reliably indicate fighting ability.

Several lines of evidence indicate that at least three specific features—duration of the “hoo” component, fundamental frequency, and calling rate—are honest signals of male fighting ability in baboons. First, these are the very acoustic features that reliably separate (a) “contest” wahoos from “alarm” wahoos elicited only by predators (Fischer et al. 2002; Kitchen et al. 2003a) and (b) adult male wahoos from the loud barks of adult females and juvenile males (with these differences developing around puberty—Fischer et al. 2002; see also Ey et al. 2007). Second, these three features are related to male rank; high-ranking males tend to produce wahoos at a faster rate with longer “hoo” components and higher fundamental frequencies than low-ranking males (Kitchen et al. 2003b; Fischer et al. 2004). Third, these features degrade as a male ages or after a male—even a high-ranking one—grows exhausted within a protracted calling bout (Kitchen et al. 2003b; Fischer et al. 2004) suggesting they are costly (see Fischer et al. 2004 for discussion that suggests signal honesty is less likely maintained because wahoos are “index” or “conventional” signals as described in Vehrencamp (2000)). Fourth, individual males are more likely to produce the most exaggerated versions of these features when they are facing rivals of similar rank (Kitchen et al. 2003b, 2005a). However, the hypothesis that these features of wahoos are functionally significant from the listener’s perspective can only be tested experimentally, in the absence of the many visual cues that are available during displays.

In our playback experiments, we manipulated a single acoustic feature of contest wahoos—the duration of the “hoo” component—because of its salience in these calls and the ease with which its duration can be manipulated experimentally. Because short versions of this acoustic feature are more often associated with subordinate, low-quality, or exhausted individuals (Kitchen et al. 2003b, 2005a; Fischer et al. 2004), we predicted that wahoos with a short hoo would prompt weaker overall responses than wahoos with a long hoo.

In the first set of experiments, we controlled for any experience the listener might have had with the caller by presenting subjects with wahoos recorded from high-ranking but unfamiliar males. Using the calls of strangers in playback experiments is common and serves to maximize responses by some listeners (dear-enemy hypothesis—Fisher 1954; e.g., Bee and Gerhardt 2001; Bee 2003; Tripovich et al.

2008; but see Bergman 2010). We predicted that the wahoos of apparently dominant males (with long hoo) would elicit stronger responses from subjects than the wahoos of apparently subordinate males (with short hoo). Moreover, because high-ranking immigrants pose a comparatively greater threat to the mating opportunities of dominant resident males than those of subordinate males (low-ranking males' access to females being already constrained), we predicted that high-ranking males would show stronger responses than low-ranking males to the playback trials.

Most empirical tests of male vocal assessment have traditionally focused on strangers, based on the assumption that animals residing within the same group can more easily rely on other cues to monitor a rival's condition. To test whether familiar rivals show differential responses to each other solely based on variation in the acoustic cues contained in their calls, we presented subjects in a second experiment with wahoos recorded from individuals who ranked immediately below them in the dominance hierarchy. Our previous research has demonstrated that these lower- and adjacently ranked males are the most direct threat to a subject's current position in the dominance hierarchy (Kitchen et al. 2003b, 2005a,b). Because subjects served as their own control, we did not predict any effect of subject rank on responses in this experiment.

Methods

Study site and subjects

Research was conducted from July 2003 to August 2004 (experiment 1) and from February to May 2006 (experiment 2) in the Okavango Delta, a seasonally flooded swampland in northwestern Botswana (Hamilton et al. 1976). The main study group had been observed since 1978 (Cheney and Seyfarth 2007). Subjects were fully habituated to observers on foot, all individuals were identifiable, and the matrilineal relatedness of all natal animals was known. The group numbered from 65 to 73 individuals with a total of 8–14 adult males in the group on any given day (numbers fluctuated due to emigration, immigration, maturation, and death). Rank positions among males were calculated daily as part of a long-term study at the site using both 10-min focal animal samples and ad lib recordings (Cheney and Seyfarth 2007). Only approach-retreat interactions were used to determine ranks (details in Kitchen et al. 2003b).

General vocal recording and analysis

Vocalizations were recorded as part of ongoing behavioral studies (Cheney and Seyfarth 2007). Contest wahoos were recorded from known individuals during male–male competition using Sennheiser ME80 or ME66 directional microphones

(Wennebostel, Germany) and either Marantz PMD660 solid state, compact flash recorders (Tokyo, Japan; experiment 2), or SONY WM-DC6 Analog or TCD-D100 DAT recorders (Tokyo, Japan; experiment 1).

Only high-quality calls (i.e., relatively free of background noise with a high signal-to-noise ratio) were used for analysis and playback stimuli. Call features were quantified using Cool Edit (Syntrillium Software, Phoenix, AZ, USA) and custom LMA 8.4 software (Schrader and Hammerschmidt 1997). Cool Edit was also used to create stimuli for playbacks.

Experiment 1 stimuli

In our first set of experiments, we presented subjects with the calls of unfamiliar males—two high-ranking immigrant males (DG and EN) who had died 3 and 5 years previously and had not resided with any of the current adult male subjects in the group.

Of the wahoos available, we chose five wahoos from DG and six wahoos from EN that fell in the upper half of their hoo as measured by the distribution of hoo lengths (Table 1). Using these “long hoo” calls (mean=0.32 s), we created five “short hoo” calls by shortening the hoo by an average of 53 % to 0.15 s (done by starting at the hoo onset point, highlighting a section of 150 ms in duration, and removing any energy after that point; Fig. 1). This duration was chosen because it was the shortest hoo duration common to both DG and EN (Table 1). Although our previous work had demonstrated variation between males in the acoustic features of their wahoos (e.g., Fischer et al. 2002, 2004), we found very little variation within the hoo syllable of a given wahoo (e.g., F0 and other frequency elements did not modulate). Hoo syllables, however, decline in amplitude at the end of the call. To simulate this decline, we used the fading function in Cool Edit on the very end of our modified calls. Thus, our methods yielded long hoo and short hoo versions of each call (Table 1), with all other acoustic features held as constant as possible.

From these, we created paired sequences where the number of wahoos (five) was identical, but one sequence in a pair used the long hoo versions of each of the calls and one used the short hoo versions. However, each call, short or long, occupied the same position in the series. The average calling rate of 19.5 calls/min was approximately the same as the average natural wahoo rate (17.1 calls/min; Kitchen et al., unpublished) in this population. Although we duplicated the intercall interval pattern between sequences (mean pause, 276 ms), the wahoos were longer in the long hoo than in the short hoo sequences. Thus, the duration of sequences was still slightly longer and the rate slightly higher in the long (mean duration, 15.8 s; mean calling rate, 19 calls/min) than in short hoo sequences (mean duration, 15.0 s; mean calling rate, 20 calls/min).

Table 1 The typical duration of the “hoo” syllable of wahoos from two callers used in experiment 1 as well as the mean hoo duration of the original calls chosen as stimuli and the mean result of a modification (shortening the hoo) to those originals

Male	Male's typical hoo Mean, range	Original/long hoo Mean±SD	Modified/short hoo ^a Mean±SD
DG	224 ms, 135–380 ms ($N=26$ wahoos)	303.2±40.8 ms ($N=5$ wahoos)	150±0 ms ($N=5$ wahoos)
EN	251 ms, 155–415 ms ($N=20$ wahoos)	330.8±44.0 ms ($N=6$ wahoos)	150±0 ms ($N=6$ wahoos)

^a Shortening the hoo. All other acoustic features were held constant in long and short hoo version of each stimulus

Because we had more stimuli from EN, we created two versions of EN's wahoos sequences that minimized repeats and changed the original order of the calls. We used the DG set and the two sets of EN sequences approximately equally in experimental trials ($N_{DG}=3$, $N_{EN1}=3$, $N_{EN2}=2$) and we attempted to play each sequence pair to a high-, mid-, and low-ranking subject (we were unable to play EN2 to a midranking subject). Although Kroodmsa et al. (2001) consider any multiple use of the same call sequence to be pseudoreplication, Wiley (2003) notes that there are clear problems with complete avoidance of repeating the same stimulus in certain conditions. This was the case in our study; only by repeating trials using the same call sequence on subjects of different rank (low, middle, and high) could we test for an effect of rank as well as an effect of sequence type (long or short hoo).

Experiment 2 stimuli

In our second set of experiments, we compared the responses of subjects to variation in a current resident male's calls (baboons can distinguish among the vocalizations of individuals; e.g., Cheney et al. 1995). In these trials, we always presented a subject with the call of a male ranking directly below him in the hierarchy because our previous research suggested that this male represents the greatest threat to the subject's rank position (Kitchen et al. 2005a,b).

After determining the average duration and range of each calling male's hoo component from their natural wahoo bouts (Table 2), we chose three high-quality wahoos from each of these six males. Because we had a more limited number of recordings for these males, we were not able to collect as many high-quality calls at the upper end of the hoo

Fig. 1 Spectrogram (frequency×time) examples of **a** the modified “short hoo” version and **b** the modified “long hoo” version of a wahoo from male DG used in creating a set of playback sequences in experiment 1. Calls were modified by removing a 150 ms section of the end of the hoo component in the original call

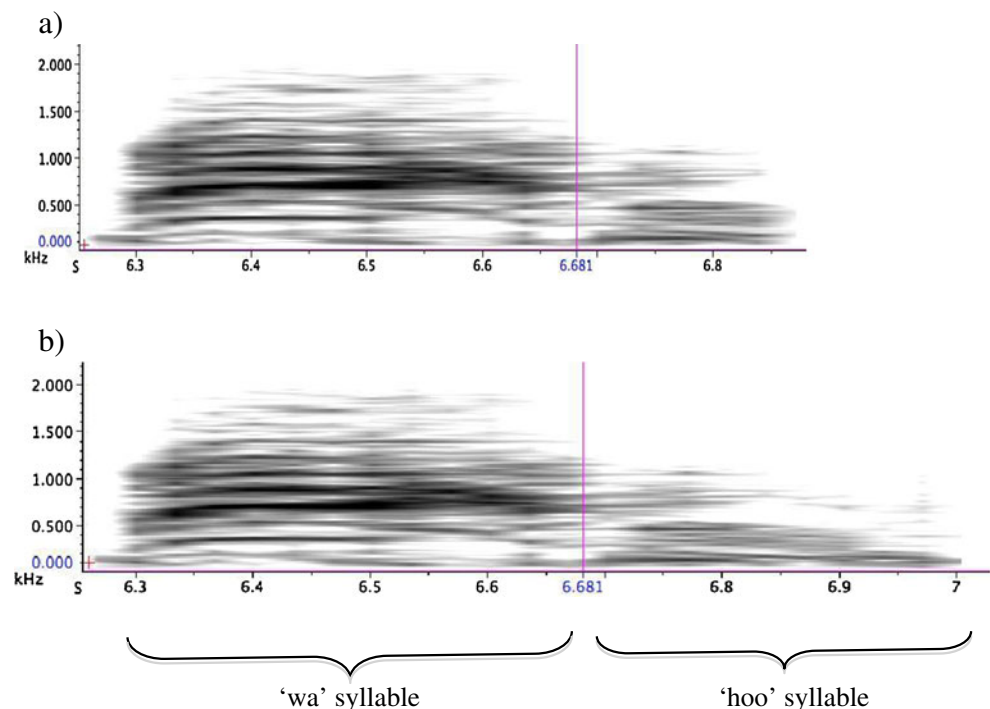


Table 2 The typical duration of the “hoo” syllable of wahoos from six callers used in experiment 2, as well as the mean hoo duration of three original calls chosen as stimuli and the mean result of two modifications (elongating and shortening the hoo) to those originals

Male	Male's typical hoo Mean, range	Original call Mean±SD	Long hoo version ^a Mean±SD	Short hoo version ^a Mean±SD
DY	260 ms, 167–466 ms (<i>N</i> =14 wahoos)	294±40 ms (<i>N</i> =3 wahoos)	464±43 ms (<i>N</i> =3 wahoos)	133±5 ms (<i>N</i> =3 wahoos)
EF	188 ms, 0–287 ms (<i>N</i> =41 wahoos)	172±19 ms (<i>N</i> =3 wahoos)	268±9 ms (<i>N</i> =3 wahoos)	33±31 ms (<i>N</i> =3 wahoos)
FT	157 ms, 0–363 ms (<i>N</i> =9 wahoos)	258±28 ms (<i>N</i> =3 wahoos)	333±8 ms (<i>N</i> =3 wahoos)	0±0 ms (<i>N</i> =3 wahoos)
HA	222 ms, 0–444 ms (<i>N</i> =54 wahoos)	263±12 ms (<i>N</i> =3 wahoos)	395±24 ms (<i>N</i> =3 wahoos)	90±7 ms (<i>N</i> =3 wahoos)
NA	256 ms, 0–433 ms (<i>N</i> =20 wahoos)	341±7 ms (<i>N</i> =3 wahoos)	405±20 ms (<i>N</i> =3 wahoos)	136±8 ms (<i>N</i> =3 wahoos)
RY	233 ms, 0–434 ms (<i>N</i> =33 wahoos)	271±28 ms (<i>N</i> =3 wahoos)	370±30 ms (<i>N</i> =3 wahoos)	65±11 ms (<i>N</i> =3 wahoos)

^a Modifications. All other acoustic features were held constant in long and short hoo version of each stimulus

duration range as we had in experiment 1. Therefore, calls were manipulated differently. We first chose calls that were near the individual male's mean hoo duration (Table 2), and then either shortened or elongated the hoo component by cutting approximately an average of 72 % (SE=±4 %) or repeating an average of 45 % (SE=±4 %) from the middle section of the hoo component (Fig. 2). This method yielded long and short hoo durations that were near either the upper or lower range of a male's repertoire (Table 2), with all other acoustic features held constant (including any amplitude decline at the end of the call).

Next, we combined the modified versions of wahoos from a given caller so that they were in the same order in both long and short hoo sequences. Average calling rate in both sequences was 56 wahoos/min, which simulates a fast rate but one which is frequently produced in this population (calling rates can exceed 60 wahoos/min; Kitchen et al., unpublished). Although we kept the intercall interval pattern generally the same between sequences, we slightly elongated these pauses in short hoo sequences (mean, 821 ms) compared to long hoo sequences (mean, 500 ms). However, inevitably, the duration of sequences was still slightly longer and the rate slightly

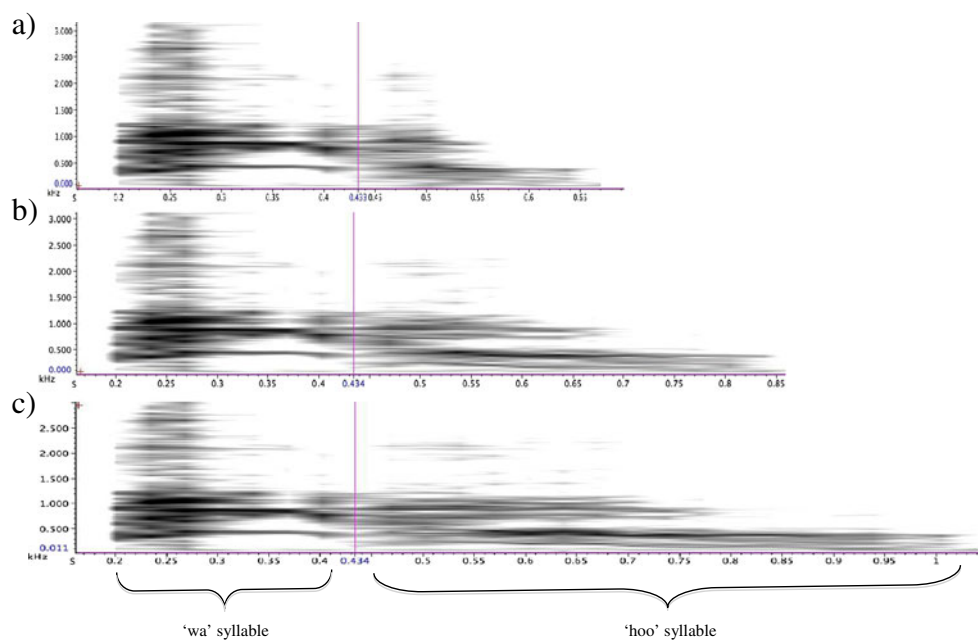


Fig. 2 Spectrogram (frequency×time) examples of **a** the modified “short hoo” version, **b** the original, and **c** the modified “long hoo” version of a wahoo from male DY used in creating a set of playback

sequences in experiment 2. Calls were modified by removing or repeating approximately 50 % of the midsection of the hoo component in the original call

higher in the long (mean duration, 5.7 s; mean calling rate, 58 calls/min) than in the short hoo sequences (mean duration, 5.3 s; mean calling rate, 54 calls/min).

General experimental protocol

Because baboon wahoos are loud (audible for over 1 km; personal observation) and low in frequency (strongest energy concentrated between 0.25 and 2 kHz; Fischer et al. 2002), playbacks required the use of a large speaker and considerable amplification. We used an Electro-Voice SX-2000 loudspeaker (Burnsville, MN, USA, 82×66×43 cm) powered by a Pioneer GM149-X922 amplifier (Tokyo, Japan) and either a Sony PCM-M1 digital tape recorder (Tokyo, Japan; experiment 1) or a Marantz PMD660 recorder (Tokyo, Japan; experiment 2) to broadcast sound.

To ensure that call amplitude was similar within and between sequences, we calibrated the minimum and maximum amplitude of all recordings in the field using the “fast” response and “C” weighting settings of a Realistic sound pressure level meter (RadioShack, Fortworth, TX, USA, referenced at 20 μ Pa, accurate at ± 2 and 114 dB). The maximum range (90–95 dB at 5 m for all sequences) was within the normal range of this species (mean natural amplitudes=92 dB at 5 m, $N=14$; Kitchen et al. 2003a). Additionally, all sequences sounded realistic to experienced human observers.

To obscure its view from all group members, broadcast equipment was positioned behind natural vegetation (mean \pm SE speaker–subject distance; experiment 1–80 \pm 3 m, range=50–100 m; experiment 2–58 \pm 4.3 m, range=42–100 m). This distance is within the range at which natural wahoo interactions occur both within and between groups (Kitchen et al. 2004). In experiment 2, another observer followed the resident male whose calls were played to ensure he was over 150 m or more from the broadcast equipment at trial onset.

Observers were in contact via two-way radios so that trials could be aborted if necessary. To reduce the potential for habituation, trials were conducted at a low rate (natural rate=1 wahoo bout/per observation day; mean \pm SE experimental rate; experiment 1–32 \pm 9 days apart, range=4–84 days; experiment 2–46 \pm 25 days apart, range=9–167 days) and human observers frequently followed baboons with cameras or setup broadcasting equipment on days when no playback occurred. We randomized the order of playbacks and waited to conduct trials until subjects were alone (defined as >2 m from any other animal; Cheney and Seyfarth 2007) and not engaged in social interaction (i.e., feeding or resting but not sleeping). No playbacks were conducted if wahoos had been heard or if another group or predator had been encountered in the previous hour.

Although 14 adult males resided in our study group during experiment 1, our ability to complete trials on more than eight males ($N=16$ paired trials) was hampered due to both

demographic changes and logistical difficulties in moving the large loudspeaker through high floodwaters. Nine immigrant adult males resided in the group during experiment 2, for a total of eight possible subjects. However, only six subjects ($N=12$ paired trials) were tested because the two lowest-ranking males did not wahoo frequently enough for us to record suitable exemplars of their calls for use in playbacks. No male was tested twice with the same stimulus and none of the subjects used in experiment 1 appeared as subjects in experiment 2.

We measured subjects' responses using frame-by-frame analysis of video recordings in Windows Movie Maker 5.1 (Microsoft 2007). We measured latency and duration of orientation toward the speaker as well as latency, duration, distance, and direction moved. Latency was measured from playback onset and duration was measured for up to 1 min after playback onset. For duration of “look” responses, we subtracted any time spent looking toward the direction of the speaker in the minute before the trial from the duration of looking after onset.

Statistics

Because response variables are often correlated (e.g., subjects that look quickly also tend to look for long time periods) and because a response in one category might preclude one in another (e.g., it is difficult for a subject to look directly at the speaker when moving), we combined all response variables using a principal components analysis (PCA; McGregor 1992) in SPSS 19.0 (IBM SPSS Statistics, Armonk, NY, USA). The resulting principal component scores functioned as an index of response strength, with high values indicating strong move and/or look responses. We accepted any principal component scores with eigenvalues greater than 1.0.

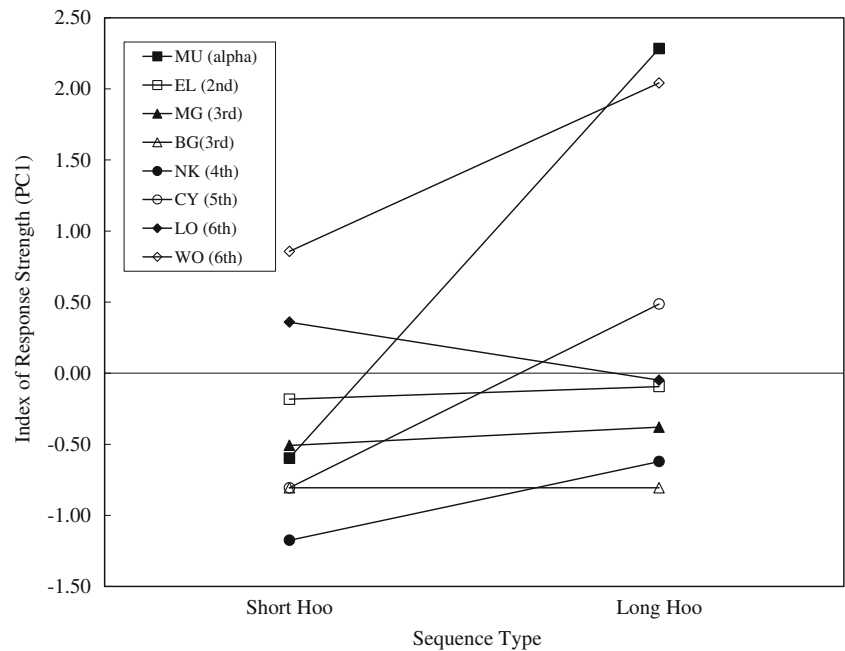
We analyzed the relationship of the principal component score with our main independent variable of interest (long vs. short hoo sequence type) and each of the following four potentially confounding effects: speaker–subject distance, subject's dominance rank (mean \pm SE; experiment 1–3.8 \pm 0.5, range=alpha to sixth-ranked male; experiment 2–3.3 \pm 0.5, range=alpha to sixth-ranked male), order in which sequences were played, and caller identity (only necessary in experiment 1). Given our small sample sizes, we used nonparametric statistics (Sokal and Rohlf 1995). Alpha was set at 0.05 and all analyses were two-tailed.

Results

Experiment 1: unfamiliar callers

The PCA of the five look and move responses resulted in one principal component score (hereafter PC1; eigenvalue=3.48) that explained 69.6 % of the variance in the data. All variables

Fig. 3 Responses of eight male baboon subjects to playback sequences of unfamiliar callers with short vs. long hoo components in their wahoos vocalizations. PC1 is a composite score where larger values mean stronger look and move responses. Males are listed in descending order based on their average rank position during the study



had high loading scores on PC1 (look latency, -0.52; look duration, 0.92; move latency, -0.86; move duration, 0.87; move distance, 0.93). Thus, high PC1 values reflected strong overall responses (e.g., short latencies and long durations).

We found that long hoo sequences elicited stronger looking responses than short hoo sequences in seven of eight paired trials (Wilcoxon signed ranks test, $T=3$, $N=7$, ties=1, $P=0.039$; Fig. 3), with one subject having the opposite response (LO, one of the two lowest-ranking males). Results were similar if we examined each response variable (look latency, move latency, etc.) separately (Table 3).

Examining five potentially confounding effects, we found no relationship between PC1 and sequence order (Friedman test, $\chi^2_1=1.29$, $N=8$, $P=0.257$) or caller identity (Kruskal–Wallis test using average per male, $H_1=0.56$, $N=8$, $P=0.456$). Even though the highest-ranking male (MU; Fig. 3) had the strongest overall response to the long hoo, we found no overall relationship between PC1 and subjects' dominance rank (Spearman correlation, long hoo— $r_s=0.096$, $N=8$, $P=0.820$; short hoo— $r_s=0.309$, $N=8$, $P=0.456$). Although we also found no

effect of speaker–subject distance on PC1 in the short hoo condition ($r_s=0.161$, $N=8$, $P=0.704$), results approached statistical significance in the long hoo condition ($r_s=0.659$, $N=8$, $P=0.076$). This result was driven by two of the five separate response variables; when hearing a long hoo, males moved for longer time periods ($r_s=0.775$, $N=8$, $P=0.024$) and for longer distances ($r_s=0.725$, $N=8$, $P=0.042$) if the speakers were farther away. No other relationships between the four potentially confounding effects and the separate response variables that made up PC1 (e.g., look latency and move latency) were found (data not shown).

In sum, baboon subjects of all ranks were quantifiably more interested in the calls of unfamiliar males when wahoos had a long rather than a short hoo syllable.

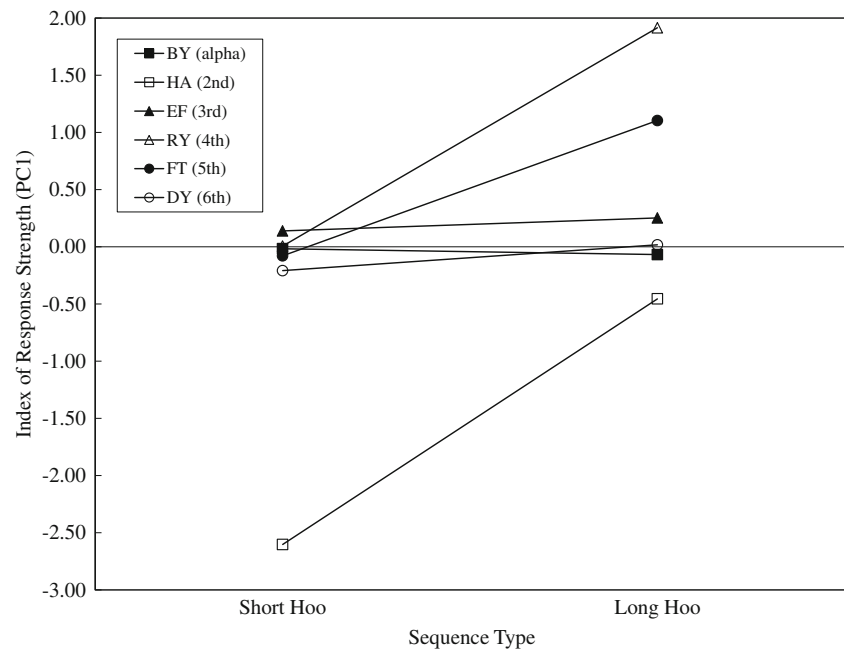
Experiment 2: familiar callers

Although all trials elicited a look response in experiment 2, no subjects moved in the 1 min following playback broadcast. Using only look responses, the PCA resulted in only

Table 3 The relationship in experiment 1 (unfamiliar callers, $N=16$ trials on 8 subjects) of playback sequence type on responses including the principal component score (PC1), a composite index that combines all other responses

Response (mean±SE)	Long hoo	Short hoo	Wilcoxon signed ranks T	Ties	P
Look latency (s)	5.7±3.1	16.6±6.9	2	2	0.047
Look duration (s)	18.8±8.4	9.1±5.2	2	2	0.047
Move latency (s)	38.7±8.5	43.6±8.3	6	3	0.688
Move duration (s)	13.5±5.0	3.1±1.5	1	3	0.063
Move distance (m)	8.0±4.0	1.7±0.9	1	3	0.063
PC1	0.4±0.4	-0.4±0.2	3	1	0.039

Fig. 4 Responses of six male baboon subjects to playback sequences of familiar callers (rivals ranking directly below subjects in the hierarchy) with short vs. long hoo components in their wahoos vocalizations. PC1 is a composite score where larger values mean stronger look responses. Males are listed in descending order based on their average rank position during the study



one principle component (hereafter PC1; eigenvalue=1.27) that explained 63.3 % of the variance in the data. The two variables each had high loading scores on PC1 (look latency, -0.80 ; look duration, 0.80). Thus, high PC1 values reflect strong overall look responses (i.e., short look latencies and long look durations).

We found that long hoo sequences elicited stronger looking responses than short hoo sequences in five of six paired trials (Wilcoxon signed ranks test, $T=1$, $N=6$, ties=0, $P=0.031$; Fig. 4), with one subject (the alpha male, BY) having the reverse response. Results were similar if we examined each response variable (look latency, move latency, etc.) separately (Table 4).

Examining three potentially confounding effects, we found no relationship between PC1 and subjects' rank (Spearman correlation; long hoo— $r_s=0.543$, $N=6$, $P=0.266$; short hoo— $r_s=-0.343$, $N=6$, $P=0.787$), sequence order (Friedman test— $\chi^2_1=0.67$, $N=8$, $P=0.414$) or speaker–subject distance (long hoo— $r_s=0.543$, $N=6$, $P=0.266$; short hoo— $r_s=-0.232$, $N=6$, $P=0.721$). No relationship with the three potentially confounding effects was found when the response variables that made up PC1 (look latency and duration) were examined

separately, with one exception; the latency to orient toward the speaker was shorter when the speaker was closer ($r_s=0.880$, $N=6$, $P=0.021$).

In sum, baboon subjects of all ranks were quantifiably more interested in the calls of familiar males when wahoos had a long rather than a short hoo syllable.

Discussion

Using playback experiments, we found evidence that male chacma baboons attend to the duration of the hoo component of wahoos, which is one of the three features that we previously found to be reliable indicators of rank and stamina (Kitchen et al. 2003b, 2005a; Fischer et al. 2004). Although previous playback experiments with this population demonstrated that male baboons monitor changing social context and intragroup relationships via vocalizations (e.g., Kitchen et al. 2003a, 2005b; Bergman et al. 2006; Crockford et al. 2007), this is the first study to focus on a specific acoustic attribute (syllable length) and its value in male–male competition. Because only a limited number of exemplars and

Table 4 The relationship in experiment 2 (familiar callers, $N=12$ trials on six subjects) of playback sequence type on responses including the principal component score (PC1), a composite index that combines all other responses

Response (mean±SE)	Long hoo	Short hoo	Wilcoxon signed ranks T	Ties	P
Look latency (s)	0.8±0.3	3.1±2.8	7	0	0.281
Look duration (s)	7.3±2.9	2.1±0.6	0	0	0.016
PC1	0.5±0.4	-0.4±0.4	1	0	0.031

subjects were used in our study (which is often the case in playback studies on primate species), we are aware there are limits to the inferential strength of our conclusions (reviewed in Fischer et al. 2013). However, in light of the fact that various exemplars and subjects were used in both experiments and results were comparable, we feel confident that our claims are justified.

Our results follow the predictions of evolutionary game theory (Maynard Smith 1974, 1982) and closely mirror the classic studies of Clutton-Brock et al. (1979), who demonstrated that the roaring rate of male red deer (*Cervus elaphus*) was not only an honest signal of fighting ability, but also one that males attend to in experimental trials (Clutton-Brock and Albon 1979; see also Reby and McComb 2003; Reby et al., 2005). Although frequently tested in birds (citations in the “Introduction” section), whether mammals other than red deer use this strategy has only been confirmed in bats (*Saccopteryx bilineata*; Behr et al. 2009) and sea lions (*Neophoca cinerea*; Charrier et al. 2011). Like red deer, bats, and sea lions, male chacma baboons are quantifiably more interested in the sounds of threatening rivals than in rivals that sound comparatively weak. Although we focused on syllable length here, male baboons likely evaluate multiple traits simultaneously (Payne and Pagel 1997), which has been proposed in studies of other animals (e.g., birds—Cardoso et al. 2007; antelope—Bro-Jørgensen and Dabelsteen 2008; dogs—Taylor et al. 2011). In baboons, this might include visual cues and other acoustic features such as fundamental frequency and calling rate (e.g., Engh et al. unpublished data).

In experiment 1, we also predicted that there would be an effect of subject identity on responses to unfamiliar rivals (reviewed in Nunn 2000; Kitchen and Beehner 2007). Because high-ranking resident males in this population experience the highest mating success, they have the most to lose if a dominant immigrant enters the group. Indeed, previous research on the same group of baboons has shown males whose reproductive opportunities are most threatened by potential immigrants—alpha males and males in consortship with receptive females—were more likely to be involved in aggressive displays during intergroup encounters (Kitchen et al. 2004). However, although the alpha male showed the strongest response to the calls of a potential immigrant, there was no overall relationship between dominance rank and male response strength in our current study.

As predicted, we also did not find an effect of dominance rank on subjects' responses in experiment 2. All but one subject responded more strongly to their adjacently ranked rival's long hoo than short hoo calls. Because more intense calls may reflect a male's motivation or ability to challenge a higher-ranking rival, it may be beneficial for even mid- and low-ranking males to attend to the acoustic structure of adjacently ranked rival's calls. Although dominant males in this population of baboons experience the greatest mating

success, reproductive skew is not complete and the alpha male does not sire all infants (Moscovice et al. 2010). As a result, mid- and low-ranking males do have some mating opportunities—opportunities that may be at risk if they fall even lower in rank.

Results from the playback experiment described here suggest that males attend to at least one specific feature of loud calls, hoo duration, that correlates with their fighting ability and condition (Kitchen et al. 2003b, 2005a; Fischer et al. 2004). Previous playback experiments have demonstrated that male baboons are capable of using loud calls to monitor a variety of social relationships within their group (e.g., Kitchen et al. 2005b; Crockford et al. 2007). Furthermore, males of all ranks are much more likely to wahoo at, chase, fight, and even injure males who are close to them in rank (Kitchen et al. 2003b). Such contests increase in frequency in the few weeks leading up to rank reversals (Kitchen et al. 2005a). Taken together, these results suggest that males actively attend to the behavior and social interactions of rivals in order to take advantage of any vulnerability that are able to detect.

Regardless of whether variation in signal features represents fighting ability and condition or arousal and motivation (e.g., Poole 1989; Burmeister et al. 2002), male baboons of all ranks attend to disparity among vocalizations produced by both familiar and unfamiliar rivals. Although the predictions of evolutionary game theory have rarely been tested in mammals, it is likely that assessment of rivals via an honest signal is a pervasive strategy used by males in all species characterized by strong intrasexual competition.

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