

Comparing responses of four ungulate species to playbacks of baboon alarm calls

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Abstract A growing body of evidence suggests that a wide range of animals can recognize and respond appropriately to calls produced by other species. Social learning has been implicated as a possible mechanism by which hetero-specific call recognition might develop. To examine whether familiarity and/or shared vulnerability with the calling species might influence the ability of sympatric species to distinguish heterospecific alarm calls, we tested whether four ungulate species (impala: *Aepyceros melampus*; tsessebe: *Damaliscus lunatus*; zebra: *Equus burchelli*; wildebeest: *Connochaetes taurinus*) could distinguish baboon (*Papio hamadryas ursinus*) alarm calls from other

loud baboon calls produced during intra-specific aggressive interactions ('contest' calls). Overall, subjects' responses were stronger following playback of alarm calls than contest calls. Of the species tested, impala showed the strongest responses and the greatest difference in composite response scores, suggesting they were best able to differentiate call types. Compared with the other ungulate species, impala are the most frequent associates of baboons. Moreover, like baboons, they are susceptible to both lion and leopard attacks, whereas leopards rarely take the larger ungulates. Although it seems possible that high rates of association and/or shared vulnerability may influence impala's greater ability to distinguish among baboon call types, our results point to a stronger influence of familiarity. Ours is the first study to compare such abilities among several community members with variable natural histories, and we discuss future experiments that would more systematically examine development of these skills in young ungulates.

Keywords Heterospecific alarm calls · Baboon · Impala · Tsessebe · Wildebeest · Zebra

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Introduction

Many animals respond to alarm calls produced by members of other species. Such 'eavesdropping' (e.g., McGregor and Dabelsteen 1996) has been demonstrated both within taxonomic groups (e.g., birds: Forsman and Monkkonen 2001; Magrath et al. 2007, 2009; Templeton and Greene 2007; primates: Fichtel 2004; Oda 1998; Oda and Masataka 1996; Ramakrishnan and Coss 2000; Zuberbühler 2000; marmots and squirrels: Blumstein and Armitage 1997; Shriner 1998) and between them. For example, a number of mammalian

and reptilian species respond to bird alarm calls (e.g., vervet monkeys, *Chlorocebus aethiops*: Seyfarth and Cheney 1986; red squirrels, *Sciurus vulgaris*: Randler 2006; Gunther's dik-diks, *Madoqua guentheri*: Lea et al. 2008; banded mongooses, *Mungos mungo*: Müller and Manser 2008; Galápagos marine iguanas, *Amblyrhynchus cristatus*: Vitousek et al. 2007). Similarly, hornbills (*Ceratogymna* spp.) can discriminate among primate alarm calls (Rainey et al. 2004a, b).

In some cases, interspecific signal recognition may occur as a result of the conservation or convergence of acoustically similar signal attributes (Aubin 1991; Brown et al. 2000; Jurisevic and Sanderson 1998; de Kort and ten Cate 2001; Johnson et al. 2003; Marler 1957; Mirza and Chivers 2001). In other cases, however, listeners respond appropriately to alarm calls that are acoustically very different from their own (e.g., Lea et al. 2008; Magrath et al. 2009; Templeton and Greene 2007; see also Shriner 1999; Vitousek et al. 2007), suggesting that responses are learned. For example, juvenile vervet monkeys residing in groups that regularly hear the alarm calls given by superb starlings (*Spreo superbus*) respond appropriately to playback of these calls at an earlier age than juvenile vervets living in groups with lower rates of exposure (Hauser 1988). Similarly, several studies have demonstrated that subjects respond to the alarm calls produced by sympatric, but not allopatric, species (e.g., Fichtel 2004; Magrath et al. 2009; Ramakrishnan and Coss 2000; also see Nocera et al. 2008 for experiments on migratory birds).

To date, no study has attempted to determine whether different species residing within the same community vary in the strength of their responses to another species' alarm calls, or the degree to which any such differences reflect association patterns with the calling species. To examine this question, we conducted playback experiments to test whether the alarm calls produced by chacma baboons (*Papio hamadryas ursinus*) elicit anti-predator behavior from four sympatric species of ungulates that vary in their exposure to baboons and in their susceptibility to predation (impala: *Aepyceros melampus*; tsessebe: *Damaliscus lunatus*; wildebeest: *Connochaetes taurinus*; zebra: *Equus burchelli*).

When encountering lions (*Panthera leo*) or leopards (*P. pardus*), female and juvenile baboons produce single-syllable harsh barks, while males produce two-syllable 'alarm wahoos' (Fischer et al. 2001, 2002). Because these alarm calls are loud and highly conspicuous (Busse 1982; Cowlishaw 1994; Kitchen et al. 2003), sympatric ungulates may learn to associate the calls with predator presence and benefit from these warning signals.

Predator encounters are not the only contexts that elicit loud calls from baboons. Some other loud calls—for example, the screams produced by females and juveniles during aggressive intraspecific interactions—are acoustically dis-

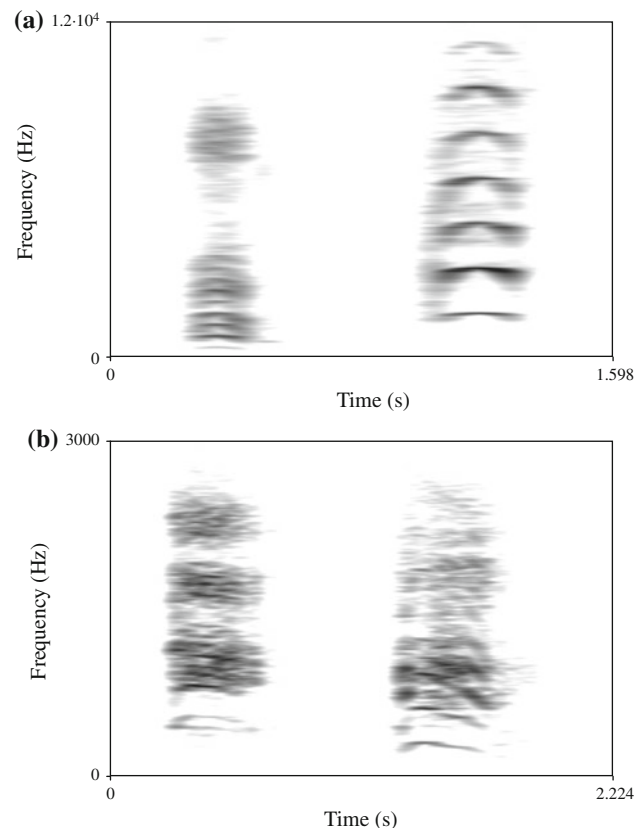


Fig. 1 Example spectrograms of call types used in playback sequences: **a** shows an adult female alarm bark followed by the same female's scream. **b** shows an adult male alarm wahoo followed by the same male's contest wahoo

tinct from alarm barks (Fig. 1a). Others, however, are acoustically similar to alarm calls and difficult for humans to discriminate by ear. In particular, these include the loud 'contest wahoos' produced by males during aggressive disputes with other males (Fig. 1b; Fischer et al. 2002; Kitchen et al. 2003). To test whether the four ungulate species discriminate among baboon loud call types, we contrasted each species' response to baboon alarm calls (alarm wahoos and barks) with its response to the contest wahoos and screams given by baboons during aggressive interactions with conspecifics.

Although impala, zebra, wildebeest, and tsessebe often hear baboon loud calls, for two reasons we predicted that impala would be most accurate in discriminating between alarm and contest calls. First, although all four species come into contact with baboons, only impala regularly intermingle with baboons at close range, both at our study site and in other areas of Africa (e.g., Washburn and DeVore 1961; see "Materials and methods"). Consequently, impala are more likely to experience a close juxtaposition of baboon alarm calls and predators, which may facilitate their ability to associate these calls with danger. Second, baboons are vulnerable to predation by both leopards and

lions, and always give alarm calls when they encounter these predators. Indeed, predation by leopards and lions is the primary cause of mortality among adults and juveniles in this population of baboons (Cheney et al. 2004). However, although all four ungulate species are vulnerable to lion predation (see **Materials and methods**), only impala are susceptible to high rates of predation by leopards (Radloff and DuToit 2004). Thus, in contrast to the other three ungulate species, impala are almost invariably vulnerable to a predator that elicits alarm calls from baboons, giving them more opportunities to form an association between the two stimuli.

Materials and methods

Study site and population

Research was conducted in the Okavango Delta in north-western Botswana. Grasslands in this region flood annually, usually between June and October, leaving elevated islands edged with forest exposed (Ellery et al. 1993; Hamilton et al. 1976). Because vehicles were needed for experiments, playbacks could not be conducted during periods of extensive flooding.

The four ungulate species tested represented all possible herbivore subjects in the area; other species either presented logistical problems or were encountered too rarely. Although impala, zebra, wildebeest, and tsessebe are all relatively abundant within the baboons' range, they vary in their association with them. Based on years of daily study at this site, we have observed impala frequently, zebra occasionally, wildebeest rarely, and tsessebe almost never intermingling with baboons. Impala and baboons likely overlap due to their diet and habitat preferences. Impala and baboons spend a majority of their time in woodland areas. During 1,828 h of feeding observations from 1999 to 2001, we found that baboons spent 73% of their time in woodlands (unpublished data). Similarly, Okavango Delta impala were located in woodlands during 77% of observations ($n = 264$ observations; van Bommel et al. 2006). When together in woodlands, impala exploit fruits and seeds dropped from trees by baboons (e.g., Hansen et al. 1985; Newton 1989). In fact, the mixed diet of impala has been found to overlap more with the diet of baboons than with the diets of the other three ungulate species (Codron et al. 2006, 2007). In contrast, tsessebe, wildebeest, and zebra are primarily grazers who feed in open grasslands (Estes 1991; Kingdon 1988), although there are several differences in the diet and habitat preferences of these three species (see Codron and Codron 2009). For example, although zebra prefer open habitats, they spend approximately 16% of their time in woodlands (Fischhoff et al. 2007; see also Kingdon 1988), and they have been the

second most common associates of baboons during our daily observations.

The four ungulate species also differ in their vulnerability to leopards. Leopards (24–61 kg) are considerably smaller than lions (124–188 kg) and concentrate mainly on smaller prey species found in woodlands (Radloff and DuToit 2004). Based on average body size (impala: 47.5 kg; tsessebe: 127 kg; wildebeest: 212 kg; zebra: 307.5 kg; Radloff and DuToit 2004), impala are most vulnerable and zebra least vulnerable to leopard predation. On the other hand, although all four species are susceptible to lion predation (Radloff and DuToit 2004), lions in Southern Africa prefer large prey species (190–550 kg; Hayward and Kerley 2008). Additionally, although three of the ungulates tested in our study were shown to be among the top five preferred prey of South African lions (Lehmann et al. 2008; tsessebe were not present in the study), more wildebeest (24% of 591 kills) were captured than zebra (8%) or impala (9%).

Playback stimuli

Baboon loud calls were recorded from known individuals in a fully habituated group that had been the subject of detailed behavioral observation since 1978 (e.g., Cheney et al. 2004). Vocalizations were recorded using a Sennheiser ME66 directional microphone and a Sony PCM-M1 digital tape-recorder. Although alarm calls used in trials had been recorded during observed encounters with lions, there is no evidence that alarm calls given in response to lions differ from those given in response to leopards (Fischer et al. 2001, 2002).

Using software for waveform analysis (Cool Edit 2000, Syntrillium Software) and natural calling bouts as templates, we constructed four unique pairs of baboon call sequences. One sequence in each pair consisted of alarm calls recorded during a lion encounter (i.e., adult male alarm wahoos and juvenile and adult female alarm barks); the other sequence in the pair consisted of calls recorded during a male-male aggressive contest that involved the chasing of females and juveniles (i.e., adult male contest wahoos and juvenile and adult female screams). Baboons commonly produce both types of vocal sequences: contests occur once every 11 h of observation (Kitchen et al. 2003) and alarms occur every 17 h, when night time predator attacks are included (unpublished data).

For the sequences in each pair, calling order of individuals were matched for age and sex (e.g., adult male first, then adult female) and each sequence included different calls from several individuals (mean: 5 individuals/sequence). Within any given pair, alarm call sequences did not differ significantly from contest sequences in the proportion of loud calls produced by each age/sex class (mean \pm SE: $40.8 \pm 3.2\%$ of calls/sequence from adult males), the total

number of calls (mean \pm SE: 26.3 ± 0.8 calls/sequence), the overall bout duration (mean \pm SE: 12.55 ± 0.68 s), or the duration of pauses between calls (mean \pm SE: 0.32 ± 0.07 s; Wilcoxon signed ranks tests, all $P > 0.100$). Therefore, the rate, number of calls, and types of participants in each paired sequence provided no information about context.

Calls were broadcast using a Sony PCM-M1 recorder and an Electro-Voice SX-2000 loudspeaker (82 cm \times 66 cm \times 43 cm) amplified by a Pioneer GM-X922 amplifier. We calibrated recordings in the field by measuring peak amplitude of the whole sequence from 5 m using a Realistic sound level meter (referenced at 20 μ Pa, accurate to ± 2 dB at 114 dB) to ensure that amplitude remained constant within and between paired sequences (average range was 88–95 dB) and matched natural levels (Kitchen et al. 2003).

Experimental protocol

We conducted playback trials from April–May of 2001 and from February–May 2006. To ensure that the same group of animals was not tested twice, approximately half of the trials were conducted on each side of a river. For trials conducted on the same side on the same day, we traveled 3 km between trials, ensuring that a tested group did not hear a trial conducted on another group.

The vehicle carrying broadcast equipment was positioned behind natural vegetation (mean speaker–subject distance = 74.8 m; range = 60–91 m). One observer filmed all responses from a second, unhidden vehicle positioned perpendicular to the first (mean camera–subject distance = 166 m; range = 81–300 m). No playbacks were conducted if baboon loud calls had been heard or if a predator had been seen in the previous hour.

Playbacks were initiated when all group members were in a relaxed state (i.e., performing little or no scanning while feeding or resting, with heads and ears oriented down). Each trial involved playback of both call sequences, the second separated from the first by a duration of at least 5 min. After playing one sequence, we waited until the group returned to its prior relaxed state and then waited an additional 5 min before playing the second sequence.

In half of the paired trials, the alarm call sequence was played first followed by the contest call sequence (impala: $n = 3$ of 6 trials; tsessebe: $n = 3$ of 5; wildebeest: $n = 2$ of 4; zebra: $n = 2$ of 5). In the other half, the contest call sequence was played first. Each ungulate species was played each of the four paired sequences at least once. We originally aimed to conduct eight paired trials on each species but were unable to do so due to flooding, which restricted vehicle use.

Most playbacks occurred when the subject was in close proximity only to members of its own species. In three

paired trials, however, subjects were in visual range (approximately 100 m) of another ungulate species. In these cases, care was taken to ensure that subjects were facing away from the other species at the onset of playback. In one other pair of trials involving zebra, the subjects were within approximately 30 m of a group of impala. It was therefore unclear whether the subjects could see the impala in their peripheral vision (see “Results”).

Data analysis

Subjects were filmed for 25 s prior and for 25 s after onset of the first call in a sequence. Using frame-by-frame analysis, we measured four dependent responses: (1) latency to orient toward the speaker, (2) duration of looking toward the speaker, (3) latency to move at least 1 m (excluding movements associated with feeding or with conspecific interactions), (4) rate of moving (total distance moved over duration of movement). All latency measures were calculated from the onset of the first vocalization in a sequence. We calculated duration by subtracting the amount of time spent moving or looking toward the speaker in the 25 s prior to playback from the total amount in the 25 s after call onset. We also recorded the direction of movements.

We completed 20 paired trials (impala: $n = 6$; tsessebe: $n = 5$; wildebeest: $n = 4$; zebra: $n = 5$). For our main analyses, we randomly chose one individual from the center of the group to serve as the representative subject of that group. We attempted to use the same subject for both call sequences ($n = 14$ paired trials), but on six occasions it was not completely clear if we had correctly located the same subject for the second call sequence (it was sometime difficult to keep track of specific individuals in the 5 or more minutes between trials because animals mingled and sometimes moved in and out of surrounding vegetation). However, an analysis based on the average response of all animals filmed per trial did not differ from results based on one randomly chosen subject (see below).

Due to small sample size, we used non-parametric statistics (Sokal and Rohlf 1981) to examine the effect of call sequence type, species identity, species average weight, and five potentially confounding effects (call sequence order, subject’s group size, speaker–subject distance, camera–subject distance and year tested) on subject responses. For separate analyses of call sequence type and species identity we used a Mann–Whitney U test because, unlike Wilcoxon signed ranks test, it can handle samples as low as 4 in each treatment (White 1952; SYSTAT 2007). To obtain exact P values for Spearman rank correlations, we used free software developed by McDonald (2009).

Because of our small sample size, we also calculated the magnitude of effects for non-parametric tests (following Nakagawa and Cuthill 2007) using software developed by

Coe (2000). We report Hedges' d statistic of standardized mean differences (which corrects for upward bias in sample sizes of less than 10 in each group: Hedges and Olkin 1985) and 95% confidence intervals (CI). Following Cohen (1988), we refer to effect sizes greater than 0.20, 0.50 and 0.80 as small, moderate and large, respectively.

Both to increase our sample size and to examine the relative effects of our two main predictor variables, we used a generalized linear mixed model (GLMM: McCulloch and Searle 2001; SYSTAT 2007) to analyze responses of all animals filmed for the entire trial. This resulted in the following sample sizes: impala: $n = 23$ in 6 groups; tsessebe: $n = 20$ in 5 groups; wildebeest: $n = 26$ in 4 groups; zebra: $n = 28$ in 5 groups. Because the responses of multiple individuals in a group are not fully independent, we avoided pseudoreplication by including a random effect for group identity.

For all analyses, alpha was set at 0.050. However, in cases of multiple testing of the same data set, we used Holm's (1979) sequential Bonferroni transformation: $\alpha/(\text{number of tests} - (\text{rank number of individual result in ascending order of degree of significance}) + 1)$. For example, if there were three tests of the same data, then the most significant result could only be accepted at $P < 0.017$, the second most significant at $P < 0.025$, and the third at $P < 0.05$.

Results

Correlation of response variables

Several dependent variables were moderately to strongly correlated (Spearman rank correlation, look latency vs.

look duration: $r_s = -0.42$, look latency vs. move latency $r_s = 0.36$, look latency vs. move rate $r_s = -0.37$; look duration vs. move latency: $r_s = -0.19$; look duration vs. move rate: $r_s = 0.16$; move latency vs. move rate: $r_s = -0.95$). For example, subjects that were quick to look toward the speaker also looked for long periods of time. Therefore, we combined all four continuous variables using a Principal Components Analysis (PCA: SYSTAT 2007; for rationale see McGregor 1992).

For the analysis using only one subject per group (Table 1), PCA resulted in two principal components (hereafter PC1 and PC2) with eigenvalues greater than 1.0. PC1 (eigenvalue 1.96) explained 49.1% of the variance in the data and PC2 (eigenvalue 1.18) explained 29.6%. Because dependent variables all loaded this component in the same direction (look latency: -0.56 , look duration: 0.42, move latency: -0.88 , move rate: 0.84), high PC1 scores reflected strong overall responses (i.e., short latency to look, long look duration, short latency to move and fast rate of movement). Conversely, look and move responses loaded in opposite directions for PC2 (look latency: -0.58 , look duration: 0.75, move latency: 0.32, move rate: -0.43). Thus, whereas high PC2 scores reflected strong look responses and weak move responses, low PC2 scores reflected only weak look responses (no subjects moved without looking). Because PC1 provided a stronger and unambiguous summary of look and move responses, we restrict our discussion to this component.

For the GLMM analysis using multiple subjects per group (Table 2), PCA resulted in two principal components (hereafter PC1b and PC2b) that had eigenvalues greater than 1.0. PC1b (eigenvalue 2.09) explained 52.3% of the variance in the data and PC2b (eigenvalue 1.30) explained 32.6%. Once again, based on component loadings (look latency: -0.72 ,

Table 1 Mean \pm SE of responses by one randomly chosen subject to 40 trials based on species identity and sequence type

	Impala ($n = 6$ pairs)	Tsessebe ($n = 5$ pairs)	Wildebeest ($n = 4$ pairs)	Zebra ($n = 5$ pairs)
<i>Alarm sequences</i>				
Look latency (s) ^a	0 \pm 0	1.20 \pm 0.58	0 \pm 0	1.00 \pm 1.00
Look duration (s)	15.17 \pm 4.27	20.80 \pm 2.01	16.25 \pm 3.17	14.20 \pm 2.67
Move latency (s) ^a	4.33 \pm 1.96	15.40 \pm 4.01	21.75 \pm 3.25	15.40 \pm 5.30
Move rate (m/s)	3.00 \pm 0.79	0.90 \pm 0.46	0.13 \pm 0.13	0.62 \pm 0.30
PC1 ^b	1.49 \pm 0.35	0.35 \pm 0.40	-0.28 ± 0.20	0.10 \pm 0.34
<i>Contest sequences</i>				
Look latency (s)	0.33 \pm 0.33	3.40 \pm 2.71	7.75 \pm 5.92	7.00 \pm 4.62
Look duration (s)	11.25 \pm 3.17	15.60 \pm 4.63	11.75 \pm 4.80	7.00 \pm 2.24
Move latency (s)	19.33 \pm 1.82	22.90 \pm 2.10	21.75 \pm 3.25	24.60 \pm 0.40
Move rate (m/s)	1.22 \pm 0.45	0.20 \pm 0.20	0.25 \pm 0.25	0.20 \pm 0.20
PC1	0.04 \pm 0.23	-0.50 ± 0.11	-0.73 ± 0.54	-0.98 ± 0.29
<i>Average difference between alarm and contest PC1 scores</i>				
	1.45	0.85	0.45	1.08

^a If subjects did not look or move during trial, latency was recorded as 25 s

^b A composite score developed using a Principal Components Analysis (see text)

Table 2 Mean \pm SE of responses by multiple subjects per group to 40 trials based on species identity and sequence type

	Impala (<i>n</i> = 23)	Tsessebe (<i>n</i> = 20)	Wildebeest (<i>n</i> = 26)	Zebra (<i>n</i> = 28)
<i>Alarm sequences</i>				
Look latency (s) ^a	0.27 \pm 0.20	1.10 \pm 0.31	7.00 \pm 2.99	4.21 \pm 2.39
Look duration (s)	15.55 \pm 3.06	18.10 \pm 1.67	11.00 \pm 2.41	11.07 \pm 1.83
Move latency (s) ^a	6.46 \pm 2.03	16.90 \pm 2.73	24.00 \pm 1.00	16.64 \pm 2.64
Move rate (m/s)	2.46 \pm 0.53	0.75 \pm 0.29	0.04 \pm 0.04	0.64 \pm 0.25
PC1b ^b	1.49 \pm 0.24	0.45 \pm 0.25	−0.60 \pm 0.21	0.08 \pm 0.26
<i>Contest sequences</i>				
Look latency (s)	0.17 \pm 0.17	3.80 \pm 2.40	9.08 \pm 2.96	7.07 \pm 2.12
Look duration (s)	14.33 \pm 2.60	15.80 \pm 2.98	10.15 \pm 2.39	8.71 \pm 1.51
Move latency (s)	18.08 \pm 1.13	22.90 \pm 2.10	24.00 \pm 1.00	23.43 \pm 0.89
Move rate (m/s)	1.18 \pm 0.32	0.10 \pm 0.10	0.08 \pm 0.08	0.26 \pm 0.12
PC1b	0.46 \pm 0.15	−0.25 \pm 0.23	−0.70 \pm 0.22	−0.57 \pm 0.16
<i>Average difference between alarm and contest PC1b scores</i>				
	1.03	0.70	0.10	0.65

^a If subjects did not look or move during trial, latency was recorded as 25 s

^b A composite score developed using a Principal Components Analysis (see text)

look duration: 0.52, move latency: −0.83, move rate: 0.78), high PC1b scores reflected strong overall responses (i.e., short latency to look, long look duration, short latency to move and fast rate of movement). Look and move responses again loaded in opposite directions from each other in PC2b (look latency: 0.52, look duration: −0.75, move latency: −0.43, move rate: 0.53). This time, however, low PC2b scores reflected strong look responses and weak move responses, while high PC2b scores reflected weak look responses in the absence of movement. For the same reason given above, we restrict our discussion to PC1b.

In all analyses, the patterns of results remained unchanged if we replaced Principal Component scores with individual dependent variables.

Potentially confounding effects

We found that PC1 response scores were not affected by camera–subject distance (alarm: *n* = 20, r_s = −0.287, P = 0.221; contest: *n* = 20, r_s = −0.255, P = 0.278), speaker–subject distance (alarm: *n* = 20, r_s = −0.290, P = 0.215; contest: *n* = 20, r_s = −0.162, P = 0.495), sequence order in paired trials (Mann–Whitney test, U_1 = 257, P = 0.123), or year tested (Mann–Whitney test, U_1 = 127.5, P = 0.482). The size of the subject's group rarely changed between sequences in a paired trial and we also found no effect of group size on responses (alarm: *n* = 20, r_s = −0.163, P = 0.491; contest: *n* = 20, r_s = −0.101, P = 0.671).

General results

In 30 of the 40 playbacks when animals within the group responded to a call sequence, subjects resumed baseline behavior and were considered 'relaxed' (defined above)

within a few seconds to a minute after the broadcast ended. In the remaining 10 playbacks, animals took up to 10 min or more to relax. Nine of these 10 cases followed playback of an alarm sequence.

When subjects moved following a broadcast (*n* = 21 of 40 playbacks; 65% of alarm trials and 40% of contest trials), they either turned abruptly 180° to face the speaker or traveled at least their body length and up to 60 m (average = 12 m). Subjects were more likely to travel toward the speaker (*n* = 16 or 76.2% of playbacks) than away (*n* = 5 or 23.8%; χ^2_1 = 5.76, P = 0.016). However, patterns did not differ between alarm and contest trials (i.e., subjects moved toward speakers in 77% of alarm and 75% of contest trials).

Effect of species identity

We found *species differences in the overall strength of responses* (Kruskal–Wallis Test, H_3 = 10.14, P = 0.017; Fig. 2). In a non-parametric post hoc test, we found that impala (*n* = 6) had stronger PC1 scores than all other species combined (*n* = 14) in both the alarm (mean \pm SE, impala: 1.49 \pm 0.35; non-impala: 0.08 \pm 0.19; Mann–Whitney test, U_1 = 74.00, P = 0.008) and contest conditions (impala: 0.04 \pm 0.23; non-impala: −0.74 \pm 0.18; Mann–Whitney test, U_1 = 69.00, P = 0.026). Results remained the same if we ran six separate post hoc tests pairing each of the four species, and effect sizes of all impala/non-impala pairs were moderate to large (Table 3). In the only paired trial conducted on a mixed-species group—when the zebra subject might have been able to see impala (see [Materials and methods](#))—members of the two species responded differently: whereas impala responded to both sequence types, the zebra only responded to the alarm sequence.

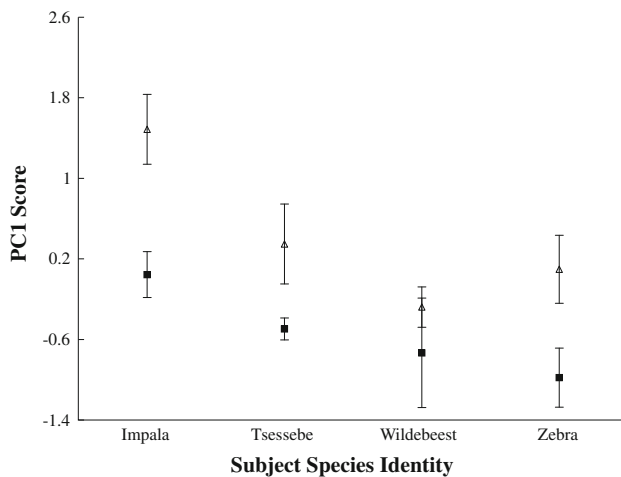


Fig. 2 Using one subject per group, mean \pm SE composite response scores (PC1) based on species identity and sequence type (alarm sequence: *open triangles*; contest sequence: *filled squares*). Species are listed in ascending size order. PC1 was calculated using a Principal Components Analysis for four dependent variables (see text); higher scores indicate a stronger response

Table 3 Effect sizes and confidence intervals of response difference between two species based on sequence type

Species pairs	Alarm sequences	Contest sequences
	d^a (95% CI)	d (95% CI)
Impala vs. Tsessebe	1.20^b (−0.09 to 2.49)	1.10 (−0.17 to 2.38)
Impala vs. Wildebeest	2.23 (0.63 to 3.83)	0.87 (−0.45 to 2.19)
Impala vs. Zebra	1.54 (0.19 to 2.89)	1.54 (0.19 to 2.89)
Tsessebe vs. Wildebeest	0.78 (−0.59 to 2.14)	0.28 (−1.04 to 1.60)
Tsessebe vs. Zebra	0.27 (−0.98 to 1.51)	0.87 (−0.42 to 2.17)
Zebra vs. Wildebeest	0.52 (−0.82 to 1.85)	−0.26 (−1.58 to 1.07)

^a Standardized mean difference with Hedges correction

^b Moderate to large effects in bold

Effect of sequence type

Although all four species had larger PC1 scores during alarm trials than contest trials (Table 1; see also below), we found *species variation in the ability to differentiate sequence types*. Impala demonstrated the best ability to discriminate the two sequence types (Mann–Whitney test, $U_1 = 34.00$, $P = 0.010$). Specifically, impala subjects showed shorter latencies to orient toward the speaker, looked toward the speaker for a longer duration, began moving sooner, and moved at faster rates following playback of alarm than contest call sequences. Although differences in alarm and contest PC1 responses of zebra were the second largest, results did not reach statistical significance (based on Holm’s sequential Bonferroni transformation) for any non-impala species (Mann–Whitney test, tsessebe:

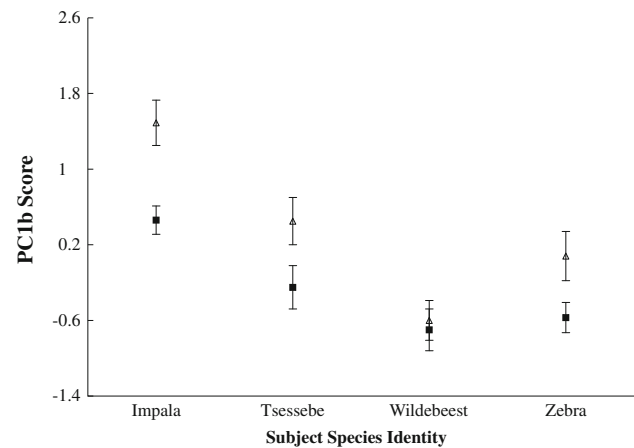


Fig. 3 Using multiple subjects per group, mean \pm SE composite response scores (PC1b) based on species identity and sequence type (alarm sequence: *open triangles*; contest sequence: *filled squares*). Species are listed in ascending size order. PC1b was calculated using a Principal Components Analysis of four dependent variables (see text); higher scores indicate a stronger response

$U_1 = 17.00$, $P = 0.347$; wildebeest: $U_1 = 11.00$, $P = 0.386$; zebra: $U_1 = 23.00$, $P = 0.028$). Effect sizes were moderate to large for all species (impala: $d = 1.86$, 95% CI = 0.50 to 3.21; tsessebe; $d = 1.18$, 95% CI = −0.17 to 2.52; wildebeest: $d = 0.48$, 95% CI = −0.93 to 1.88; zebra: $d = 1.34$, 95% CI = −0.03 to 2.71).

Relative effects of sequence type and species identity

Using the responses of multiple individuals filmed per group and a random effect of identity, we found that both sequence type (GLMM, $F_{1,73} = 15.96$, $P = 0.000$) and species identity (GLMM, $F_{3,73} = 20.25$, $P = 0.000$) had strong influences on PC1b (Fig. 3), but not the interaction between the two variables (GLMM, $F_{3,73} = 1.59$, $P = 0.200$).

As a post hoc test of this larger sample size, we examined the effect of sequence type on each species separately (with a random effect for group identity). As with the smaller subset of data, we found that impala had larger differences in alarm and contest PC1b responses (GLMM, $F_{1,16} = 14.16$, $P = 0.002$) than any other species (GLMM, tsessebe: $F_{1,14} = 4.17$, $P = 0.060$; zebra: $F_{1,22} = 4.53$, $P = 0.045$; wildebeest: $F_{1,21} = 0.13$, $P = 0.718$). Although impala, tsessebe and zebra had stronger look and move responses to the alarm than to the contest sequences (Table 2), only the impala scores were significantly different using the conservative Holm’s Bonferroni transformation. Conversely, wildebeest had the smallest difference between their alarm and contest composite scores (Fig. 3) and showed no difference between the two trials in their average move responses (Table 2).

Relationship between body weight and response strength

The overall response strength of PC1 was inversely correlated to the average body size of the species tested (Spearman correlation, alarm sequences: $n = 20$, $r_s = -0.540$, $P = 0.014$; contest sequences: $n = 20$, $r_s = -0.591$, $P = 0.006$). However, the difference between responses in each alarm-contest pair was not correlated with the focal species' average body size (Spearman correlation, $n = 20$, $r_s = -0.183$, $P = 0.441$).

Discussion

Several previous studies have suggested that at least some animals are able to discriminate between the different loud calls of other species. For example, vervet monkeys react differently to the alarm calls produced by superb starlings in response to raptors as opposed to terrestrial predators (Seyfarth and Cheney 1986; see also references in “Introduction”). Our results are consistent with these findings and are the first to suggest that vulnerability and/or familiarity with the calling species may affect heterospecific responses to alarm calls among multiple species living within the same community. With one exception (wildebeest move responses; Table 1), subjects in all four ungulate species showed stronger look and move responses to alarm call sequences than to aggressive contest sequences, even though both sequence types were similar in pattern, amplitude and duration. Among subjects, impala showed the strongest reaction to both sequence types and also the biggest difference in composite responses to the two sequences, whereas wildebeest had the weakest and least differentiated responses. Although effect sizes suggest that the impala data are biologically meaningful, larger sample sizes are required to determine if the non-impala species (particularly zebra and tsessebe) are consistently able to differentiate sequence types.

Our experiments do not address which acoustic cues ungulates use to recognize baboon alarm calls. In contrast to males' alarm and contest wahoos, females' and juveniles' alarm barks are easily distinguished from screams (Fischer et al. 2001). It therefore seems probable that ungulate responses were guided primarily by the acoustically different calls produced by females and juveniles in alarm as opposed to aggressive contexts. Although it seems less likely that the highly graded male contest and alarm wahoos can be distinguished by other species, female baboons can differentiate these calls (Kitchen et al. 2003), and there is some evidence that birds can differentiate subtle acoustic differences in the alarm calls of other species (e.g., Rainey et al. 2004a, b; Templeton and Greene 2007).

These experiments also do not allow us to determine whether ungulates learn to discriminate alarm calls from aggressive contest calls, or whether they are innately equipped to respond to the sounds of baboon alarm barks and/or alarm wahoos while ignoring screams and/or contest wahoos. Such an innate skill could be simply explained if there was some acoustic convergence between baboon alarm calls and the alarm calls produced by these four ungulate species. However, these species' alarm calls consist primarily of snorts (e.g., Caro et al. 2004) that share few acoustic similarities with any baboon calls.

Given that the strongest difference in response to the two baboon call sequences was manifested by impala—the species with the most exposure to baboons—it seems possible that learning might play a role in the ability to discriminate among baboon calls. Impala are the most likely species to hear a baboon alarm call in conjunction with the sighting of a predator, the most robust way to learn the association between two stimuli (e.g., Mineka and Cook 1993). Even if impala do not always see the predator that evoked the baboons' alarm calls, simply observing an escape response—even in another species—may be sufficient to trigger a similar response in a naïve observer (Cook et al. 1985; Mathis et al. 1996; reviewed in Griffin 2004). Once again, impala have more opportunities than the other ungulates to associate baboon alarm calls with the escape responses of others (see also review of ‘public information’: Valone 2007). Furthermore, zebra showed the second strongest difference in response to the two baboon sequence types and they are the second most common associates of baboons at our study site. In order to adequately test the hypothesis that association patterns influence heterospecific call learning, a series of playback tests could be conducted on young ungulates with varying levels of exposure to baboons and their vocalizations (e.g., Hauser 1988; Ramakrishnan and Coss 2000; Fichtel 2004; Magrath et al. 2009).

Factors other than degree of exposure might also explain the differences in the four ungulate species' responses to the playback sequences. Perhaps due to their vulnerability to both leopards and lions, impala are highly vigilant compared to other ungulates (Underwood 1982). For impala, baboon alarm calls are almost invariably associated with a predator to which they are susceptible; impala consequently have many opportunities to form an association between the two stimuli. In contrast, the association frequency between a baboon alarm call and a significant predator may be considerably lower for the other species, which are rarely eaten by leopards (Radloff and DuToit 2004). Like baboons (Cowlshaw 1994), impala are vulnerable to leopard predation because of their relatively small size (Radloff and DuToit 2004). Furthermore, impala and baboons, unlike the other ungulates tested, are more likely to encounter

leopards because they share the predator's woodland habitat.

Ideally, we would have tested between the size and habitat hypotheses by including a large woodland ungulate such as kudu (*Tragelaphus strepsiceros*) in our experiment; unfortunately, this proved impossible because kudu are shy and elusive. Instead, we used average species weights as an approximation of susceptibility (Radloff and DuToit 2004). Although we found that overall response strength and body size were inversely correlated, we did not find a relationship between the subject species' body size and differences in composite scores to the two sequence types. This suggests that the heightened sensitivity of impala to all baboon loud calls does not explain why they are also better able to differentiate the two sequence types relative to the other ungulates tested. Although this suggests a stronger role of familiarity than vulnerability in learning to associate baboon calls with predators, we cannot completely rule out the effect of shared predation risk.

In addition to alerting other prey to the presence of a predator, alarm calls may also function to dissuade predators (reviewed in Caro 1995; Hasson 1991). When subjects in our experimental trials moved, they were significantly more likely to travel toward the speaker rather than away from it. Although it is possible that the animals were moving toward the caller to gather more information, it is also true that natural predator encounters frequently result in ungulates following predators (Caro et al. 2004; personnel observation). By moving toward an ambush-hunting predator such as a lion, an ungulate is able to monitor its location and presumably thwart its attempts at a surprise attack. An observational study in the Ivory Coast demonstrated that a radio-collared leopard would move away from alarm-calling monkeys faster than expected by chance (Zuberbühler et al. 1999). Future studies should experimentally test whether hearing the alarm calls of their potential prey in the absence of visual cues also deters ambush-hunting predators such as lions.

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Conflict of interest statement The authors declare that they have no conflict of interest.

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