



Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability

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Alarm calls can provide nontarget receivers with potentially life-saving information on predation risk. However, patterns of eavesdropping among species may be shaped by the reliability of the intercepted information, that is, the degree to which the alarm call represents a pertinent threat to the eavesdropping species ('relevance'). Prey are predicted to respond strongly to alarm calls from species that are attacked by the same predator guild, whereas species consumed by a larger or different subset of the carnivore community may act as a less reliable source of predator information. We used a playback experiment to examine whether the degree of antipredator responses to heterospecific alarm calls varied with the reliability of the calling species in three large African mammals: impala, *Aepyceros melampus*, common wildebeest, *Connochaetes taurinus*, and plains zebra, *Equus quagga*. Alarm calls of all three species were broadcast randomly to herds of their own species or to either of the other two species. In accordance with the reliability hypothesis, we found that all species reacted strongly to zebra alarm calls. Lions are the primary predator of zebra and represent a significant threat to all three prey species. In contrast, impala are consumed by a greater number of predators, and their alarm calls evoked weaker, mixed responses in the other two species.

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Alarm calls are prevalent in the antipredator repertoires of birds and mammals (Caro, 2005; Klump & Shalter, 1984; Zuberbühler, 2009). These vocalizations can serve to alert conspecifics to impending danger (Klump, Kretzschmar, & Curio, 1986; Turner, 1973; Wheeler, 2008), confuse or deter predators (for review, see Wheeler, 2008), or recruit nearby individuals to engage in joint defence (Cheney & Seyfarth, 1985; Rohwer, Fretwell, & Tuckfield, 1976). The conspicuous nature of alarm calling presents the opportunity for bystanders to hear and interpret the signals, an act known as 'interceptive eavesdropping' (e.g. McGregor, 2005; McGregor & Dabelsteen, 1996; Templeton & Greene, 2007). Eavesdropping on heterospecifics can shape species interactions, such as promoting the formation of mixed-species associations, with concomitant effects on community structure and, thus, has important implications for community ecology (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Holt, 2007; Schmidt, Dall, & van Gils, 2010; Seppanen, Forsman, Monkkonen, & Thomson, 2007).

Eavesdropping provides nontarget receivers with information on immediate danger that can reduce the probability of

encountering or being captured by predators, a strong selection pressure for recognizing and responding to the calls of sympatric species (Fichtel, 2004; Magrath, Haff, Fallow, & Radford, 2015; Seppanen et al., 2007; Shriner, 1998). Playback experiments have demonstrated appropriate antipredator responses to heterospecific alarm calls within a variety of taxonomic groups (e.g. primates: Fichtel, 2004; Ramakrishnan & Coss, 2000; Zuberbühler, 2000, 2001; sciurids: Blumstein & Armitage, 1997a; Shriner, 1998; birds: Magrath, Pitcher, & Gardner, 2007; Magrath, Pitcher, & Gardner, 2009; Templeton & Greene, 2007), although the extent of eavesdropping behaviours within vocally communicating species has not been well defined (Lea, Barrera, Tom, & Blumstein, 2008; Magrath et al., 2015). Currently, little is known about the factors that determine the extent to which a given species should capitalize upon the alarm calls of another species (Caro, 2005; Magrath et al., 2009, 2015).

Eavesdropping appears to be common in social species that form mixed-species associations (reviewed in Goodale, Beauchamp, & Ruxton, 2017), although it can even occur in nonsocial species as well (Lea et al., 2008). Sociality predisposes individuals to use acoustic signals to warn conspecifics of danger (Blumstein, 1999; Blumstein & Armitage, 1997b), and close heterospecific groupings present an opportunity for members to learn the specific alarm vocalizations of other prey (Bshary & Noe, 1997; Goodale & Kotagama, 2005; Magrath et al., 2009; Sullivan, 1984;

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Zuberbühler, 2000). In addition to augmenting the advantages of group formation via dilution effects and predator deterrence (Curio, 1978; Lima, 1995), mixed-species associations may provide information from heterospecific alarm calls that complements the vocalizations of conspecifics, thereby improving overall knowledge of predation risk (Goodale & Kotagama, 2005; Guatier-Hion, Quris, & Gautier, 1983; Magrath et al., 2015; Nuechterlein, 1981). Associating with a second species that can better detect or communicate danger could provide benefits that exceed the cost of feeding competition, especially if the associating species have divergent diets (Goodale & Kotagama, 2005; Goodale et al., 2010; Seppanen et al., 2007). There is evidence that exploiting heterospecific alarm calls in polyspecific associations can allow utilization of riskier foraging patches (Bshary & Noe, 1997; Guatier-Hion et al., 1983; Ridley, Wiley, & Thompson, 2014) or a reduction in time spent on vigilance (Bell, Radford, Rose, Wade, & Ridley, 2009; Bshary & Noe, 1997; Burger, 1984; Flower, 2011; Ridley & Raihani, 2007).

However, the advantages of intercepting alarm calls are only realized if the two species are vulnerable to the same predators (Kitchen, Bergman, Cheney, Nicholson, & Seyfarth, 2010; Magrath et al., 2009). Otherwise, heterospecific alarm calls are unreliable signals in that there is a low probability that the calls signify danger to the eavesdropper, and there is little selective pressure to respond to them (Goodale et al., 2010; Magrath et al., 2007, 2009; Seppanen et al., 2007). The 'relevance' component of signal reliability, as described by Magrath et al. (2009), varies for each caller–interceptor pair based on vulnerability to overlapping suites of predators. As the number of mutual threats increases, so too does the relevance of the heterospecific's calls (Magrath et al., 2009, 2015; Searcy & Nowicki, 2005). The importance of alarm call reliability in a broad sense on interceptor response has only been examined in a small handful of cases and the significance of relevance as a selective pressure for developing eavesdropping behaviours remains relatively unexplored (Kitchen et al., 2010; Magrath et al., 2009; Rainey, Zuberbühler, & Slater, 2004a, 2004b).

We designed a series of playback experiments to examine the importance of reliability of heterospecific alarm calls, in terms of relevance of predation threat, on the antipredator behaviours of three sympatric herbivores: impala, *Aepyceros melampus*, common wildebeest, *Connochaetes taurinus*, and plains zebra, *Equus quagga*. Each of these species produces an acoustically characteristic alarm call: zebra bray, whinny and snort; wildebeest snort; and impala primarily bark. Thus, there is little chance of mistaking a heterospecific call for that of a conspecific. To our knowledge, auditory eavesdropping behaviours have not previously been investigated in these species despite their use of acoustic alarm calls, sociality and frequent tendency to form mixed-species associations. Other studies have examined changes in vigilance between conspecific and heterospecific groupings of these species, but ours is the first to experimentally disentangle an eavesdropping 'many eyes' (or, in this case, ears) effect from dilution or predator deterrence effects (Pays, Ekor, & Fritz, 2014; Périquet et al., 2012; Schmitt, Stears, Wilmers, & Shrader, 2014). In addition, listening for signals of pertinent threats may provide information at a lower cost and therefore be a more commonly utilized behaviour than visually monitoring other species for threat-reaction cues.

These three species differ substantially in body mass, and consequently, predation risk. Previous research suggests that larger predators exploit a wider range of prey sizes, with a strong correlation between predator mass and maximum prey size (Hopcraft, Olf, & Sinclair, 2010; Radloff & DuToit, 2004). That is to say, all predators have the capacity to take down smaller animals, but only large predators typically handle large prey. Four predator species are present within our study system: lion, *Panthera leo* (161.5 kg),

leopard, *Panthera pardus* (55 kg), cheetah, *Acinonyx jubatus* (50 kg), and African wild dog, *Lycaon pictus* (25 kg) (Kingdon, 1977). These carnivores opportunistically consume all focal prey species; however, adult zebra and wildebeest are underselected by smaller predators relative to their abundance, whereas impala are vulnerable to a greater proportion of the predator community (Hayward, 2006; Hayward, Henschel, O'Brien, Hofmeyr, Balme, & Kerley, 2006; Hayward, Hofmeyr, O'Brien, & Kerley, 2006; Hayward, O'Brien, Hofmeyr, & Kerley, 2006; Tambling & Du Toit, 2005). The reliability hypothesis predicts that impala would therefore have the least relevant calls to intercept, as they may be alarming at predators that do not represent a threat to the larger herbivores. The alarm calls of zebra, the largest prey, should be relevant to all prey species, with wildebeest forming an intermediate in terms of relevance between the two (Cheney & Seyfarth, 1990; Hopcraft et al., 2010; Magrath et al., 2009). Juveniles are vulnerable to a greater number of predator species than adults (e.g. Sinclair, 2003), and we therefore additionally predicted that the presence of offspring in herds of wildebeest and zebra might increase the responsiveness of adults to the alarm calls of smaller herbivores.

METHODS

Study Site

We gathered data during June and August 2016 in Pilanesberg National Park (25°08'–25°22'S; 26°57'–27°13'E), North West Province, South Africa. The site covers approximately 580 km² of hilly savannah terrain, and contains habitats ranging from mixed *Acacia* and broad-leaf bushveld to open grasslands (Adcock, Hansen, & Linderman, 1998). Daily temperatures during the study period ranged from 12 °C to 25 °C. Since the park's establishment in 1979, diverse populations of large herbivores and predators have been reintroduced. Large carnivores currently inhabiting the park include lion, leopard, cheetah and African wild dog.

Study Animals

We focused our study on the three most prevalent herbivore species: impala, common wildebeest and plains zebra. These species are frequently found in mixed-species associations (Kiffner, Kioko, Leweri, & Krause, 2014; Sinclair, 1985). While all large carnivores present within the reserve consume each of the focal prey species, the smaller carnivores (cheetah, wild dog and leopard), preferentially prey on the impala, the smallest prey species (average body mass: 35.4 kg), whereas wildebeest and zebra (145 kg and 197 kg, respectively) are primarily preyed upon by the apex predator, lions (Hayward, Henschel, et al., 2006; Hayward, Hofmeyr, et al., 2006, Hayward, O'Brien, et al., 2006; Radloff & DuToit, 2004). Lions will attack smaller animals when the opportunity presents itself, and represent a significant threat to all prey species (Scheel & Packer, 1995).

Playback Recordings

We elicited alarm calls from each focal species using a life-size, two-dimensional model of a stalking lion (1.15 x 2.2 m) constructed from a high-quality photograph mounted on durable backing. This model was mounted on a wooden trolley that could be wheeled past a herd of animals with a 30 m rope. The resultant alarm calls were extracted from high-quality video recordings of these 'predator encounters', which were undistorted by wind, nonfocal animal calls or other loud noises. Videos were recorded using a Lumix DMC-FZ70 camera (Panasonic; Osaka, Japan). The vocalizations

elicited by the model sound, to humans, identical to calls produced in response to actual predators (Supplementary Fig. S1). No research to date has examined whether large African herbivores give referential alarm calls when confronted with specific carnivore species, but previous work established that zebra, wildebeest and impala produce alarm calls when confronted with all large carnivores present at Pilanesberg (Palmer & Packer, n.d.) and these calls are indistinguishable to the human ear. To prevent possible effects of familiarity, the recordings were taken from experiments performed in other reserves outside Pilanesberg (e.g. Hare & Atkins, 2001). We extracted two alarm call segments for each herbivore species, elicited during separate predator model encounters, which were used interchangeably throughout the experiment. Due to constraints on time and access to the park imposed by other ongoing research projects and high tourist volume, we chose to prioritize procuring adequate sample sizes of responses towards each pair of exemplars rather than increasing the number of exemplars per stimulus but obtaining lower overall statistical power. We later tested to confirm that there was no difference in focal response to unique exemplars.

All playback recordings were prepared using video-editing software (Microsoft Windows Movie Maker, v.2012; <https://windows-movie-maker.en.softonic.com/>). For each ungulate species, we extracted 5 s clips with the best signal-to-noise ratio and replicated these extracts three times with 5 s intervals of silence in between. In our previous experience examining herbivore responses to both real and simulated predators, we typically observed that these species would alarm collectively for a few seconds, followed by a brief pause, and a renewal of alarming if the perception of threat persisted. We attempted to mimic this pattern in the design of our playback exemplars. We composed a total of four types of playbacks, with two unique versions of each alarm call: (1) impala alarm, (2) wildebeest alarm, (3) zebra alarm and, as a control, (4) vehicular noise. In the field, each playback recording was broadcast at approximately the same volume of 80 ± 2 dB SPL, as measured at 5 m distance so as to match natural sound levels and to be clearly audible at our maximum experimental range of 130 m (weighting level A, fast response; Mini Sound Level Meter, Martel Electronics, Yorba Linda, CA, U.S.A.).

Experimental Protocol

We drove transects along the main park roads throughout the reserve from 0730 hours to 1600 hours to locate individuals of the three study species. Pilanesberg is a popular tourist destination and animals are highly habituated to vehicle traffic; we observed no evidence that our activity disturbed the behaviour of the animals. Trials were conducted during periods with minimal wind or road noise and when no other vehicles were present. We positioned our vehicle within 130 m of the herd such that there were no obstructions between the speaker and the herds (mean distance = 52.5 m; range 7–130 m). Playbacks were not conducted if species other than zebra, wildebeest or impala were present within 100 m of the focal group, such that focal groups were either monospecific or a heterospecific association of focal species. Playbacks were initiated when all group members had acclimated to the vehicle presence and had resumed a nonvigilant state (i.e. performing little or no scanning while feeding or resting, with heads and ears oriented downwards; typically, this state was reached within 2–3 min of our arrival). The playback stimuli were loaded onto an Apple iPhone 4 (Apple Inc., Cupertino, CA, U.S.A.) and for each encounter, a randomly determined stimulus selected from a list generated each day a priori was broadcast out of the open window of the vehicle using a OontZ Angle 3 portable wireless speaker system (Cambridge SoundWorks, North Andover, MA,

U.S.A.). To minimize the possibility of resampling the same individuals, playbacks were performed at least 500 m apart on the same day (further than the sound from our playback recordings can carry) and at least 24 h apart at the same location. On average, experiments were conducted (mean \pm SD) 2.76 ± 2.40 km and 2.9 ± 2.4 days apart. We were not able to follow a paired design, in which focal herds were sequentially subjected to different alarm calls to control for the unique behaviours of each group, as none of the animals in Pilanesberg were individually tagged. It is likely that we ultimately exposed the same individuals to different recordings; however, given the factorial nature of our design (three possible species sampled with one of eight randomly drawn playback recordings), there is a low probability that the same individuals were exposed more than once to the same playback treatment.

We recorded herd size, age–sex composition, mixed-species composition (presence or absence of either of the other two study species within 50 m of the focal species) and distance to the speaker, as well as date, time and habitat type ('open': minimal trees or shrubs with grass less than 10 cm tall; 'grasslands': minimal trees or shrubs with grass greater than 10 cm tall; or 'thickets': dense trees or shrubs). A total of 176 trials were conducted across all factorial combinations (three species \times four playback stimulus types), with a mean \pm SD of 16.7 ± 3.2 samples for impala per stimulus, 16.8 ± 4.6 samples for wildebeest per stimulus and 10.5 ± 1 samples for zebra per stimulus.

Behavioural Observations

The focal group was filmed during and after each playback. Three focal individuals were chosen haphazardly from the centre and left and right peripheries of the group. If the group contained fewer than three individuals, the responses of each were recorded. If a group recognizably contained both males and females, at least one animal of each sex was selected. The behavioural responses of these focal individuals were recorded from the onset of the playback until they resumed their previous behaviour for >30 consecutive seconds or until they moved out of sight.

We recorded the presence/absence of the following antipredator behaviours: (1) vigilance, including both orientating towards the speaker and scanning the surrounding environment, (2) grouping, defined as a disaggregated herd coming together to form a close association with <1 m between individuals, (3) alarm calling and (4) fleeing. We measured the duration of vigilance and latency to flee, group and alarm-call. All latency measures were calculated from the onset of the playback stimulus.

Statistical Analysis

All analyses were performed in R (v.3.2.3, Core Team, 2015) and results were considered statistically significant at $\alpha = 0.05$. Bonferroni tests were used to correct for multiple comparisons.

For each focal species, the proportion of herds exhibiting antipredator responses after exposure to the two separate versions of the various alarm call exemplars was tested for independence of frequency using contingency tables (Pearson's chi-square test). This was repeated for each type of antipredator response to verify that the focal species displayed comparable responses to the different versions of each alarm playback. We examined differences in response between the alarm calls and the control sound stimulus using the same method.

Incidence and duration of antipredator behaviours were analysed using a priori-defined full models that included covariates for sound stimulus, initial focal herd distance from speaker, herd size, habitat type and a coefficient indicating whether the focal group was herding with heterospecifics ('conspecifics only',

'heterospecifics present', and 'heterospecifics present whose species identity matched that of the playback stimulus'). To avoid overfitting models, and subsequent inflation of covariate significance and estimates, we retained all covariates in the prespecified models rather than performing stepwise selection (as per [Babyak, 2004](#)). For zebra and wildebeest, juvenile presence/absence was also included (our study preceded the annual impala birthing period of early–mid-November; [Jarman, 1979](#)). The proportion of trials in which antipredator behaviours were elicited were compared using binomial generalized linear models (function 'glm'). In cases of perfect separation, we utilized Firth's bias-reduced logistic regression with a binomial family structure (as per [Firth, 1993](#); [Heinze & Schemper, 2002](#); package 'logistf', function 'logistf', [Heinze, Ploner, Dunkler, & Southworth, 2013](#)) and P values were estimated by penalized profile likelihood (package 'MuMIn', [Barton, 2013](#)). We used linear mixed effects models fitted by restricted maximum likelihood to compare the duration of vigilance across treatments (package 'nlme', function 'lme', [Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016](#)). Herd identity was included as a random intercept, to account for correlated similarity in response between focal samples nested within the same herd ([Zuur, Ieno, Walker, Saveliev, & Smith, 2009](#)). For these models, we used a natural log transformation on speaker distance and herd size to normalize the response variable based on visual examination of residual spread.

Additionally, we examined the effect of sound stimulus on latency until first incidence of flight and alarm calling using time-to-event Kaplan–Meier survival analyses with the log-rank statistic (L) for planned pairwise model comparisons (package 'survival', functions 'Surv' and 'survdiff', [Therneau, 2015](#)).

Ethical Note

This study required no invasive sampling or manipulation of animals, and focal individuals experienced minimal distress after temporary exposure to alarm call stimuli. All experiments were conducted in accordance with the University of Minnesota Institutional Animal Care and Use Committee (IACUC protocol no. 1510-33082A).

RESULTS

Each focal species responded in a similar manner to the alternative versions of each alarm call (all behaviours grouped: chi-

square test: all adjusted P values > 0.05). Thus, all responses were analysed together for each separate species.

A significantly higher proportion of recorded alarm calls provoked fleeing, grouping and alarm calling antipredator behaviours than did the controls (chi-square test: impala: $\chi^2_1 = 32.10$, $P < 0.001$; wildebeest: $\chi^2_1 = 13.12$, $P < 0.001$; zebra: $\chi^2_1 = 6.57$, $P = 0.031$), indicating that the focal animals responded to information conveyed by alarm calls rather than to loud noises per se. Wildebeest and zebra never responded to the control playback. Impala did respond to the control in 10% of trials, but only with flight behaviour. In contrast, each study species responded to alarm calls by conspecifics and heterospecifics with antipredator behaviours (fleeing, grouping and/or alarm calling), although to different extents according to the species of the caller.

Incidence of Response

In terms of specific antipredator responses evoked by each stimulus ([Fig. 1](#)), impala were most likely to flee in response to zebra alarm calls, followed by the alarm calls of wildebeest, and least frequently after the playbacks of their own species ($\beta_{zebra} = 3.06$, $\sigma_{zebra} = 0.97$, $P = 0.022$; $\beta_{wildebeest} = 2.25$, $\sigma_{wildebeest} = 0.94$, $P = 0.016$; $\beta_{impala} = 1.55$, $\sigma_{impala} = 1.00$, $P > 0.05$). Wildebeest and zebra flight response did not vary with the identity of the playback species, and in none of the focal species was flight propensity influenced by social or environmental variables. Impala frequently gave alarm calls in response to playbacks from other impala, but not after exposure to calls of other species ($\beta_{impala} = 3.17$, $\sigma_{impala} = 1.67$, $P = 0.029$). Wildebeest most often called in response to zebra ($\beta_{zebra} = 2.82$, $\sigma_{zebra} = 1.59$, $P = 0.025$), but were less likely to alarm if the playback call came from a species that was not present in the immediate vicinity ($\beta_{NotMatch} = -2.54$, $\sigma_{NotMatch} = 1.46$, $P = 0.030$). Alarm calls were only elicited in zebra in response to playbacks of other zebra (12.5% of trials), although this effect was not significant. None of these species showed any differences in grouping propensity in response to the three different playbacks.

Duration of Response

Type of stimulus call significantly predicted duration of vigilance behaviour across all study species, with each responding strongly to zebra ([Table 1](#), [Fig. 2](#)). Impala responded with approximately equal increases in vigilance to the alarm calls of all three

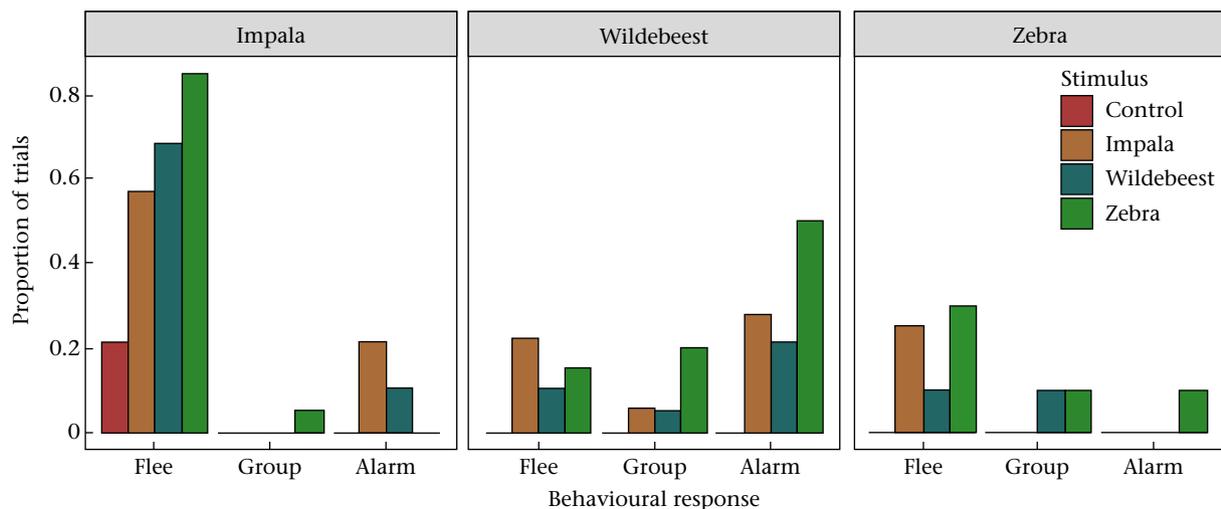


Figure 1. Proportion of trials that contained at least one instance of each specific antipredator behaviour.

Table 1

Fixed-effects coefficient estimates from linear mixed effects models characterizing the total duration of vigilance exhibited during trials in response to playback stimuli, presented with test statistics and standard errors

	Impala				Wildebeest				Zebra			
	Value	SE	<i>t</i>	<i>P</i>	Value	SE	<i>t</i>	<i>P</i>	Value	SE	<i>t</i>	<i>P</i>
Intercept	−68.04	32.03	−2.12	0.036	−4.12	58.31	−0.07	0.944	−37.97	59.05	−0.64	0.523
Stimuli: Impala	22.10	10.85	2.04	0.047	15.53	23.32	0.67	0.508	84.79	25.19	3.37	0.002
Stimuli: Wildebeest	18.19	9.24	1.97	0.054	54.92	24.07	2.28	0.027	68.73	24.00	2.86	0.008
Stimuli: Zebra	21.93	9.01	2.43	0.018	64.65	24.37	2.65	0.011	112.49	22.77	4.94	0.000
log (speaker distance)	13.35	5.81	2.30	0.025	20.22	12.92	1.56	0.124	13.69	14.71	0.93	0.359
log (herd size)	−0.42	3.30	−0.13	0.900	−6.70	8.69	−0.77	0.444	15.12	10.98	1.38	0.179
Habitat: Open	20.28	15.71	1.29	0.202	−48.59	24.38	−1.99	0.051	−24.05	27.29	−0.88	0.385
Habitat: Thickets	28.76	16.17	1.78	0.081	−27.35	29.75	−0.92	0.362	−56.00	26.93	−2.08	0.046
Juveniles Present	N/A	N/A	N/A	N/A	−16.32	32.58	−0.50	0.618	47.12	26.35	1.79	0.084
Other species not matching	13.25	9.16	1.45	0.154	−33.35	21.26	−1.57	0.123	−58.89	27.93	−2.11	0.044
Other species matching	8.42	15.09	0.56	0.579	−46.76	38.29	−1.22	0.227	−11.69	29.84	−0.39	0.698

P values highlighted in bold are statistically significant at $\alpha < 0.05$ and those in bold and italic are trending towards significance ($\alpha < 0.10$).

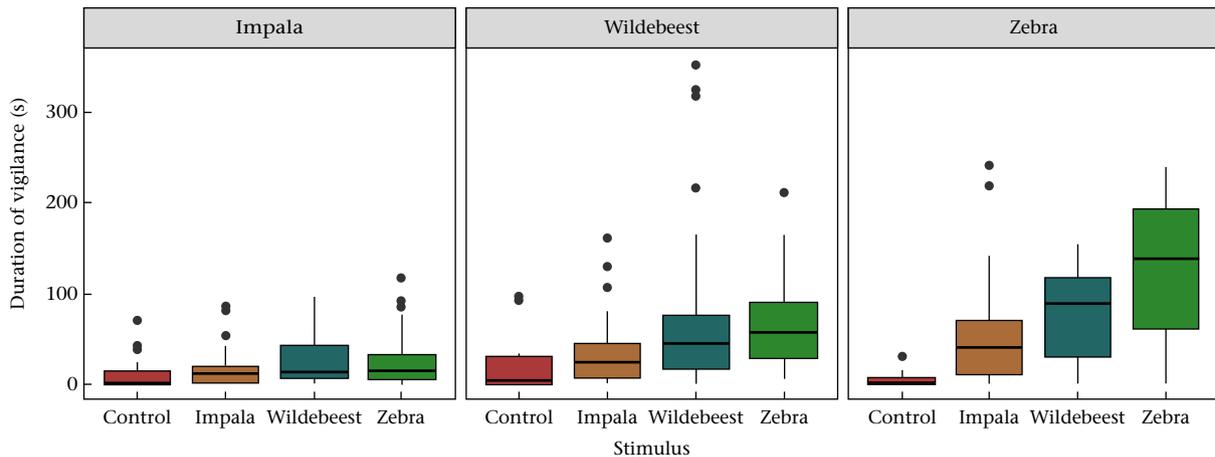


Figure 2. Duration of vigilance across treatments for each focal species. Box plots depict the median (dark line), first and third quartiles (box), and range (whiskers).

species, and vigilance increased with the initial distance between the speaker and the herd. Wildebeest increased their vigilance in response to zebra and wildebeest calls, but not to impala calls. Zebra responded most strongly to calls of their own species, and less strongly, but in equal measure, to calls of impala and wildebeest. Both wildebeest and zebra were sensitive to the surrounding environment: wildebeest decreased their vigilance levels in open areas and zebra decreased their vigilance in densely thicketed areas. Zebra also spent less time engaged in vigilance if the calling species did not match the species present in their immediate vicinity.

Latency to Respond

Impala fled most swiftly in response to zebra alarm calls and were slower to respond to wildebeest and impala playbacks

(Table 2, Fig. 3a). Wildebeest were quickest to flee after exposure to impala alarm calls (Table 2, Fig. 3b), while flight responses in zebra did not vary across stimulus species (Table 2, Fig. 3c). Impala produced alarm calls soonest after exposure to wildebeest and impala playbacks (Table 2, Fig. 3d). Wildebeest responded most swiftly to zebra calls, followed by impala calls, and with least alacrity to calls of their own species (imperceptible from response to control; Table 2, Fig. 3e). Zebra only called after exposure to other zebra calls (Table 2, Fig. 3f).

DISCUSSION

This is one of the first studies to examine reliability of signal information as a selective pressure for heterospecific call discrimination within nonavian vertebrate taxa. We found evidence that large mammalian prey eavesdrop on heterospecific alarm calls and

Table 2

Log-rank statistics (*L*) from pairwise survival analysis comparisons used to determine differences in latency to flee and to produce alarm calls in response to playback stimuli

Pairwise comparison	Latency to flee						Latency to alarm					
	Impala		Wildebeest		Zebra		Impala		Wildebeest		Zebra	
	<i>L</i>	<i>P</i>	<i>L</i>	<i>P</i>	<i>L</i>	<i>P</i>	<i>L</i>	<i>P</i>	<i>L</i>	<i>P</i>	<i>L</i>	<i>P</i>
Control vs Impala	15.395	0.000	4.195	0.041	4.829	0.028	5.571	0.018	5.268	0.022	0.000	1.000
Control vs Wildebeest	11.873	0.001	0.874	0.350	3.601	0.058	3.440	0.064	1.417	0.233	0.000	1.000
Control vs Zebra	43.537	0.000	1.175	0.278	3.043	0.081	0.000	1.000	10.951	0.001	0.000	1.000
Wildebeest vs Impala	0.311	0.577	5.976	0.015	0.291	0.590	1.243	0.265	4.978	0.026	0.000	1.000
Wildebeest vs Zebra	12.823	0.000	0.157	0.692	0.232	0.630	4.910	0.027	18.650	0.000	2.700	0.100
Zebra vs Impala	5.030	0.025	4.901	0.027	0.005	0.942	10.255	0.001	3.342	0.068	2.235	0.135

P values indicate whether the two time-to-event curves overlap, that is, whether the latency to respond towards the two stimuli are the same. *P* values highlighted in bold are statistically significant (curves are distinct) at $\alpha < 0.05$ and those in bold and italic are trending towards significance ($\alpha < 0.10$).

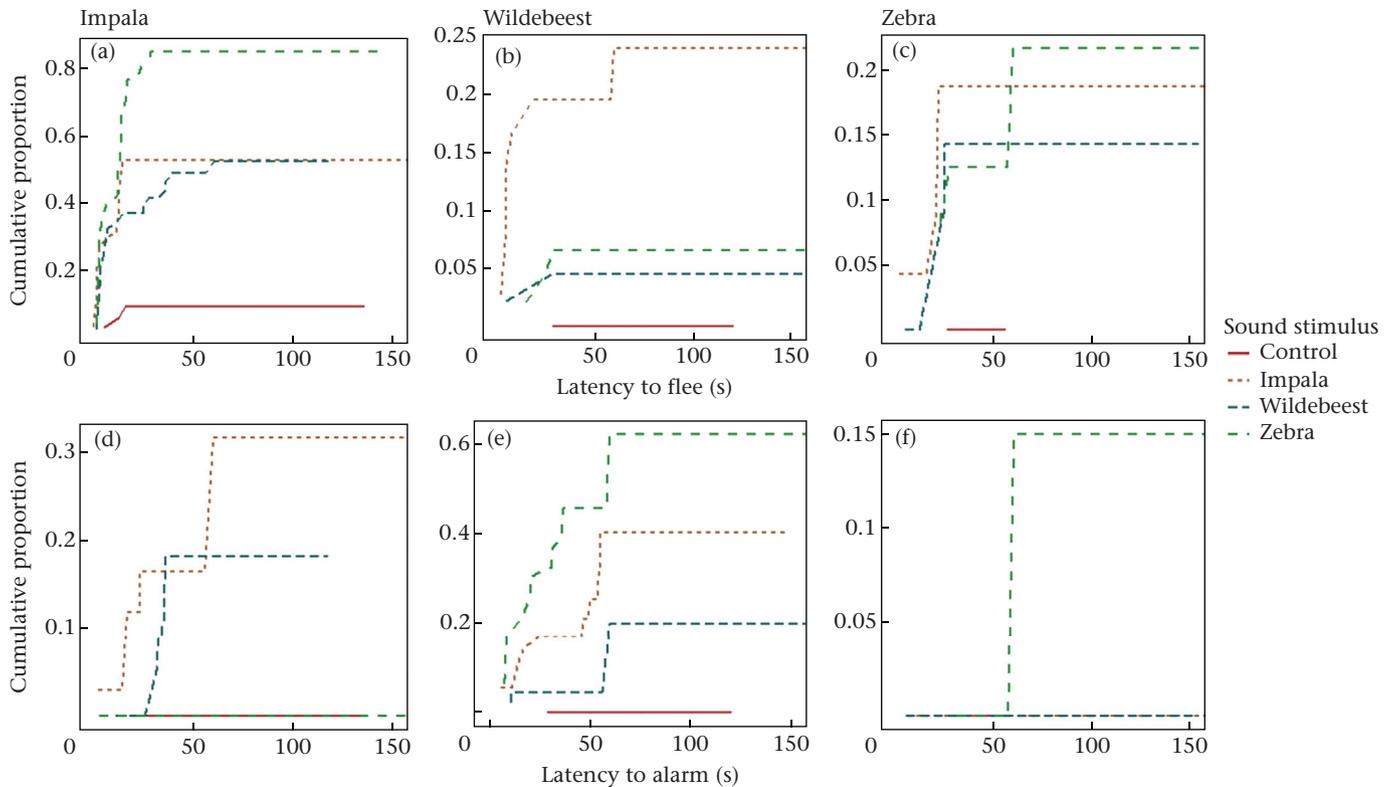


Figure 3. Cumulative incidence curves of Kaplan–Meier survivorship functions for latencies to flee (a, b, c) and alarm (d, e, f) after exposure to each playback stimulus.

respond with a variety of antipredator behaviours. The degree to which these species react to intercepted information appears to reflect, at least in part, the overlap in predator guild as predicted by the reliability hypothesis (Magrath et al., 2009, 2015). Consistent, rapid antipredator responses towards the alarm calls of zebra suggest that all prey species considered this largest-bodied species as the most reliable indicator of imminent danger. Zebra were largely unaffected by the calls of smaller prey species, while impala, which are consumed by the widest range of predators, reacted strongly to all alarm calls. Wildebeest, intermediate in size and vulnerability, reacted to zebra and impala alarm calls with different types and intensities of antipredator response.

In the smaller species, zebra calls elicited the longest durations of vigilance and swiftest and most frequent cases of either alarm calling (wildebeest) or flight (impala). Wildebeest calls were not highly heeded by the larger zebra, but evoked responses in smaller impala that were either on-par (duration of vigilance, latency to flee and alarm) or greater (incidence of flight) than those initiated by conspecific impala playbacks. Interestingly, in wildebeest, the calls of impala provoked swifter incidences of flight than did the calls of conspecifics, even though the impala playback did not have an influence on whether flight ultimately resulted during an experiment. Fleeing swiftly from calls with a lower probability of representing a true threat may be a result of balancing the cost of immediate flight and quick return to foraging versus the ongoing costs of monitoring for predators (Cooper & Blumstein, 2014; Samia, Nomura, & Blumstein, 2013). Prior studies have used the propensity to flee as a proxy for severity of perceived risk, while our results suggest that immediate flight might not always indicate high levels of fear (see Stankowich & Blumstein, 2005; Stankowich & Coss, 2006). The only behaviour impala displayed that was most strongly provoked by conspecifics was frequency of alarm calling. Alarm calling, rather than a relocation behaviour such as flight, may

indicate that impala felt lower levels of threat; however, given that predator overlap and therefore reliability with conspecifics is 100% (for groups of comparable age–sex composition), we suggest that impala may rely on alarm calls to manipulate conspecific behaviour, such as to gather or maintain a defensive group (Cheney & Seyfarth, 1985; Owens & Goss-Custard, 1976), evoke similar outbursts of vocalizations in order to confuse the predator (Cresswell, 1994; Sherman, 1985) or assist/alert potential kin (Sherman, 1977). None of our focal species felt threatened enough by the playbacks to form defensive groupings.

It is significant and unexpected that larger heterospecifics also frequently evoked stronger responses in these species than conspecific calls, despite the idea that perfect overlap with conspecifics in terms of predation threat would hypothetically equate with strong signal reliability of these calls. However, we only considered one facet of reliability, and did not address two other components of signal reliability that may have affected our results: (1) the degree to which the calling species can distinguish between threatening and nonthreatening stimuli ('discrimination') and (2) the likelihood that the calling species will produce false alarm calls to usurp resources from competitors ('deception') (Kostan, 2002; Magrath et al., 2009, 2015). It has been demonstrated that both primates and scurids can learn to associate the identity of callers with their past reliability in terms of both discrimination and deception and reduce their responsiveness to these signallers accordingly (e.g. Cheney & Seyfarth, 1988; Hare & Atkins, 2001). Deception is difficult to confirm without rigorous experimental protocols, and although we cannot rule out the possibility of heterospecific deception (e.g. Flower, 2011; Munn, 1986), we do not consider this possibility further here. Discrimination, however, could have contributed to the type and strength of antipredator response. Although we have not measured the propensity of each species to call at nonthreatening stimuli under natural conditions,

the rate of response to the control stimulus indicates that impala are the least discriminatory species, while wildebeest and zebra are the highly discerning species. The high rate of false antipredator responses in impala, coupled with the large variety of predators that prey on them and hence the low relevance of their calls to larger species, could make impala calls of overall low reliability for other species.

The type and intensity of response appeared to be dictated primarily by calling species: overall, there were very few social and environmental factors that influenced antipredator behaviours throughout this experiment. Contrary to our predictions, responsiveness of larger herbivores to the alarm calls of smaller prey did not increase when vulnerable offspring were present, although in zebra we did see a nonsignificant trend ($P = 0.08$) in this direction. All species appeared to pay less attention to the alarm calls if they did not appear to originate from the immediate vicinity. Wildebeest and zebra were less likely to alarm-call and decreased their levels of vigilance, respectively, if the playback came from a species other than the ones they were currently herding with, while impala decreased their overall duration of vigilance if the sound was initiated from a greater distance away. Habitat also played a minor role in influencing the magnitude of response. Wildebeest were least vigilant after exposure to alarm calls in open areas. Lions, which represent a significant threat to wildebeest, utilize woody vegetation to facilitate their ambush hunting strategies (Hopcraft, Sinclair, & Packer, 2005), this may reflect a perception that underlying risk levels in these spaces were lower, or may be a result of enhanced visibility due to minimal vegetation obstructions. However, this makes it more difficult to interpret our finding that zebra displayed the lowest overall vigilance in thicketed areas, despite the fact that lions are also their primary predator.

It is outside of the aims of our research to address how each species is able to recognize that the calls of other species are indicative of predation threat. The alarm calls of these three species are highly divergent, minimizing the probability that these species rely on convergent acoustic qualities in heterospecific calls (e.g. Aubin, 1991; Jurisevic & Sanderson, 1998). Recognition could occur through some form of associative learning, in which the heterospecific alarm call must be predictably associated with predation risk (Griffin & Galef, 2005; Shettleworth, 1998; Shriner, 1999). Even if the eavesdropping species does not necessarily see the predator itself, simply observing an escape response or other antipredator reaction may be sufficient to trigger a similar response in a naïve observer (reviewed in Griffin, 2004). Associative learning will occur faster if there are ample opportunities for learning, such as regular membership in mixed-species herds (Fichtel, 2004; Ramakrishnan & Coss, 2000; Valone, 2007), but will be hindered if the discriminatory abilities of the calling species are poor, as there will be fewer direct pairings between stimuli (Magrath et al., 2015). Mixed-species associations for these species were observed at similar frequencies across Pilanesberg, with approximately one-fifth of all associations containing at least one of the other focal species (from our data, impala: 17.9%; wildebeest: 23.9%; zebra: 23.9%); however, potentially poor discrimination by impala (discussed above) may further contribute to weak antipredator responses in other prey species.

In conclusion, we have shown that impala, wildebeest and zebra eavesdrop on the alarm calls of each other, and thereby collect relevant information about predation risk within their shared area. Furthermore, the intensity of antipredator response (proxy for level of perceived threat) differs based on the identity of the calling species and the associated overlap in predation risk. This finding is in accordance with the predictions of the reliability hypothesis, which state that the relevance of the call, in terms of how likely it is that the signaller is indicating that a shared threat has been

detected, dictates the strength of antipredator response in the eavesdropper. In addition, response type and level may be shaped by the reliability of the callers and the ability of the interceptors to learn to associate the alarm calls with predation threat.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version at <https://doi.org/10.1016/j.anbehav.2017.12.018>.

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