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Assessing blue wildebeests' vigilance, grouping and foraging responses to perceived predation risk using playback experiments

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ABSTRACT

Two aspects of reactive antipredator behaviour are still unclear for ungulates. First, when there is a direct predation threat, how do prey balance antipredator and social vigilance to learn a predator's location and assess the risk? Second, how do an individual's group and environment affect its responses? We tested the responses of adult females in 101 groups of wildebeest to playbacks of lion roars or car noises in Etosha National Park, Namibia. We analysed how the times they spent in different types categories of vigilance, and their within-group density, were affected by the playbacks and how a range of social and environmental variables affected those responses. Females increased their antipredator vigilance but not their social vigilance, after lion roars but not car noises, suggesting that they mostly relied on their own vigilance rather than social information to try to find the source of the lion roars. Females' antipredator vigilance increased more when they were further from cover and with other prey species, suggesting that both circumstances increased their perception of risk. They 'bunched' more after lion roars than car noises and their bite rates decreased as they bunched. Animals' use of social information about threats is likely to be context-dependent.

1. Introduction

Predator avoidance behaviours can carry costs to prey, and these costs of "risk effects" can be as high or higher than those of direct predation itself (Creel and Christianson, 2008). Antipredator behaviours can be either proactive or reactive (Caro, 2005; Creel, 2018); proactive behaviours reduce predation risk in the absence of a known predator, while reactive ones are responses to the detection of a predator. One antipredator behaviour, scanning for danger (vigilance), can be either reactive (in response to auditory, visual or olfactory stimuli signalling the presence of a predator) or proactive (reviewed by Elgar, 1989; Roberts, 1996). Vigilance can impose a feeding cost when animals stop foraging or chewing to scan for danger (Houston et al., 1993; Brown, 1999; Djagoun et al., 2013; Robinson and Merrill, 2013). This cost can be affected by many social (e.g., group size and composition, density of group members) and environmental (e.g., distance to cover, wind, local predator density) factors. For example, prey animals have been found to spend less time foraging and more in vigilance when group size and within-group density decrease (e.g., Smith and Cain III, 2009; reviewed by Beauchamp, 2013), when predation risk is increased (e.g. for mothers with young, Hunter and Skinner, 1998), when predator cues are present (van der Meer et al., 2012) and in risky conditions (e.g., in high wind speeds, Carter and Goldizen, 2003; or when close to cover, Matson et al., 2005). In a study of elk (*Cervus elaphus*) preyed upon by wolves (*Canis lupus*), Liley and Creel (2008) found the elks' vigilance to be affected by variables relating to the elk themselves (e.g. groups were more vigilant when they included cows and had a higher proportion of calves), by variables relating to the local wolf packs (e.g. vigilance was higher when there were more than ten wolves and they were within one kilometre of the elk), and even, albeit to a lesser extent, by environmental variables (vigilance was higher farther from cover). These examples illustrate the challenge of investigating the drivers of vigilance behaviour and its costs.

The foraging-vigilance trade-off is further complicated to assess as some species can be simultaneously vigilant and handle food, thus reducing the cost of vigilance (e.g., Blanchard and Fritz, 2007; Périquet et al., 2012). Vigilance whilst chewing reduced the cost of vigilance on foraging time by up to 35% in elk and bison (*Bison bison*) (Fortin et al., 2004), but the noise associated with chewing likely reduces vigilance quality (Blanchard and Fritz, 2007). Thus, both the cost and

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effectiveness of vigilance can be better understood by investigating whether animals interrupt chewing for vigilance or do both simultaneously (Favreau et al., 2015).

Although the literature mainly focuses on vigilance as an antipredator strategy, vigilance can also be used to gather social information, yet most studies have not quantified these types of vigilance separately. Individuals can use social vigilance (vigilance facing towards conspecifics) to locate and assess resources by picking up cues from group members (Fernandez-Juricic et al., 2005; Favreau et al., 2015), or to find mates or social partners. In the context of antipredator behaviour, social vigilance may be used to detect threats by using cues about risk from conspecifics' behaviour (such as heightened alertness and flight initiation) (Caro, 2005; Ellard and Byers, 2005; Blank, 2019). Social vigilance can also be used as a form of risk assessment (Blank, 2019), for instance by allowing an individual who does not know the location of a threat to determine the direction in which informed conspecifics are looking, speeding up its own visual discovery of the threat (Pays et al., 2013). Bighorn sheep (*Ovis canadensis*) were more likely to copy the vigilance of others in their group (an example of behavioural contagion) if the individual being copied had been vigilant without chewing, which was more common in induced vigilance than routine vigilance (McDougall and Ruckstuhl, 2018). This shows that these sheep were using social vigilance to learn of others' sensing of possible danger. Goitered gazelles (*Gazella subgutturosa*) notice when another gazelle freezes in an alarm posture, look in the same direction as that animal and sometimes approach it to be able to search for danger from the alarmed animal's viewpoint (Blank, 2019). Compared to the vast number of studies of direct antipredator vigilance, few have explicitly considered whether and how individuals use social vigilance to learn about possible danger from predators, in addition to other uses of social vigilance, such as watching potential competitors or mates.

Prey animals also form large and dense groups to reduce predation risk (Jarman, 1974). The main benefits of aggregation include collective vigilance (Lima, 1995), dilution of risk (Roberts, 1996), individuals putting others between themselves and danger (selfish herd effect, Hamilton, 1971), the possibility for group defense (reviewed by Caro, 2005), and the potential to confuse predators by reducing the predator's ability to focus on a target individual (Landeau and Terborgh, 1986; reviewed by Caro, 2005). By grouping, individuals can reduce other antipredator behaviours such as vigilance (Treves, 1998). However, there are two aspects to grouping – group size and within-group density ('bunching') – and these can be changed independently. Increasing group size is generally a proactive antipredator behaviour (Creel et al., 2014), whereas increasing within-group density due to bunching is most likely to be a reactive antipredator behaviour. African elephants (*Loxodonta africana*) bunched together when they heard playbacks of lion roars (McComb et al., 2011). While bunching may provide protection, it likely also carries costs. Little is known about these potential costs but impala increased step rates when foraging in denser groupings, probably in response to increased intraspecific competition (Smith and Cain III, 2009).

To investigate two reactive antipredator responses (vigilance patterns and bunching) of blue wildebeest (hereinafter 'wildebeest') and how these were affected by social and environmental variables, we studied the responses of wildebeest to playbacks of lion roars in Etosha National Park in northern Namibia. Predator simulation studies (reviewed by Blumstein et al., 2008; Hettena et al., 2014) have not yet been used to investigate whether prey use both antipredator and social vigilance as reactive responses to predator stimuli. Such studies should provide a better understanding of the ways in which prey seek information about predators (directly, or via group members) after being first alerted to their presence, and the cost associated with this information gathering (intensity of vigilance). While prey might be expected to respond to predator stimuli by trying to find the predator visually themselves (antipredator vigilance), a prey individual might be able to find a predator more quickly by using social vigilance to determine whether a group member has located the predator, and if so, where it is (Pays et al., 2013; Blank, 2019).

We addressed three aims relating to wildebeests' reactive antipredator behaviours when they heard lion roars, to understand how they might manage the complex trade-offs between antipredator behaviours and food intake. Our first aim was to describe the antipredator behaviours of wildebeest exposed to lions' roars, including patterns of vigilance and bunching. We tested four predictions: 1) that wildebeests would increase both antipredator vigilance and social vigilance after hearing a lion roar, but not after a control playback, to directly detect predators and also to use cues from conspecifics to learn where those predators might be; 2) that wildebeests would bunch after hearing a lion roar; 3) that increases in antipredator vigilance after playbacks would be linked with increases in exclusive vigilance because exclusive vigilance should be more effective than vigilance while chewing; and 4) that increases in social vigilance would be positively correlated with increases in vigilance while chewing because wildebeests would use vision rather than hearing to assess potential knowledge that conspecifics might have about the predator, and thus could afford to use this perhaps less effective form of vigilance.

The second aim of this study was to test how these antipredator responses were affected by social and environmental factors. We predicted that both vigilance and bunching responses would be stronger when the focal individual was in a smaller group of wildebeests (due to safety effects of being in larger groups), when the group contained fewer heterospecifics (because heterospecifics might further dilute the risk to a given individual) and when the individual was in a more dangerous location (close to cover or close to water). Behavioural responses by prey to predators are affected by the 'landscape of fear' (Laundré et al., 2010; Esparza-Carlos et al., 2016). While it is clear that prey should, and do, respond to evidence that predators are nearby, it is less well known how the risks associated with an individual's surroundings (the landscape of fear) affect its response to a predator stimulus and its vigilance strategy (the type and intensity of vigilance used), not just the time it spends in vigilance.

Our third aim was to test whether there was a foraging cost to bunching. Bunching as a reactive antipredator behaviour likely incurs a cost through increasing foraging competition, however the magnitude of this cost is not yet known. We predicted that the more the wildebeest bunched after hearing the lion roar, the more their bite rate would drop during their non-vigilant time, due to increased competition and perhaps time lost in movement.

2. Materials and methods

2.1. Study area

This experiment was conducted in central Etosha National Park (19°10′48.61″S, 15°55′6.98″E), along a network of over 200 km of road transects, during the 2014 dry season (March to November). Etosha has a semi-arid climate, with a mean annual rainfall in the park of 351 mm (Namibian Ministry of Environment & Tourism, unpubl. data). The park is essentially fully fenced, covers 22,270 km^2 and has high predator densities including approximately 500 lions (Bauer et al., 2015) that preferentially hunt for wildebeest (Berry, 1981). There are also leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), but these are unlikely to be significant threats to the wildebeest. During the dry season, most herbivores, including the approximately 2500 wildebeest at Etosha (M. Kasaona, personal communication) concentrate around permanent natural and artificial water sources (du Preez and Grobler, 1977). Waterholes are areas of high prey vulnerability, particularly to lions (Schaller, 1972; Hopcraft et al., 2005). In Hwange National Park, lions preferentially hunt within two kilometers around artificial waterholes (Davidson et al., 2013). Lions, being ambush hunters, also prefer to hunt in areas of thicker cover (Hopcraft et al., 2005). All playbacks were done on short grass plains (le Roux et al., 1988), where wildebeest did most of their foraging.

2.2. Playback catalogue

We observed the effects of recorded lion roars on adult female wildebeest during foraging periods. We developed a catalogue of recordings that included five lion roars to reduce pseudoreplication. Two recordings were obtained from Natural History Media archives (www.naturalhistorymedia.com) and three from a commercial online catalogue (www.sounddogs.com). Each recording included a single male lion from southern Africa vocalizing through deep repetitive roars. All playbacks were standardized to 25 s; lion roar sequences have been found to have durations between 17 and 90 s, with lions in Etosha having shorter roars than elsewhere (Stander and Stander, 1988). As a control stimulus, we used recordings of car noise. Each of the five car recordings was sourced from a commercial sound catalogue (www.sounddogs.com) and consisted of a single car driving along a dirt road. We standardized each car recording to 25 s. The sound of cars driving on dirt roads is common in Etosha and likely to be non-threatening to wildebeest. We chose this sound for our control rather than another animal call as this allowed for similar sound levels between the lion and control playbacks. We loaded all ten playbacks, in WAV format, onto an iPhone 4 (Apple Inc, U.S.A.) and played them through two 180 W speakers (Auto Gear, South Africa) and a 700 WRMS amplifier (Jaycar, Australia) powered by a 12 V battery (Midas Style Powerbooster, U.S.A.). All playbacks were calibrated to natural sound pressures of 115 dB ± 1 dB at one meter (Dick Smith Digital Sound Level Meter Q1362, Australia) (Durant, 2000; Webster et al., 2012). One of the five lion recordings or five car recordings was chosen at random to be played during each sample and the recording code was noted.

2.3. Field data collection

We performed experiments during two sampling sessions daily: (1) beginning at dawn and lasting up to three hours and (2) up to three hours in the afternoon, ending at dusk. Each road transect was driven approximately twice weekly during sampling sessions to locate and sample wildebeest. These are the periods when wildebeest spend the most time foraging (Berry et al., 1982). While lions are most active during the night, they do roar and hunt during the day in this area, albeit to a lesser extent (RJ Dannock, personal observation). A herd of wildebeest containing two or more individuals with nearest neighbour distances less than 100 m was defined as a ‘group’. We selected adult females as focal individuals, thus only mixed herds (those containing adult and juvenile females and males) were observed, not bachelor herds (groups of adult males, with no juveniles or females present) or solitary bulls. Adult females are likely to be under stronger selection to trade off foraging and vigilance optimally due to the resource demands of pregnancy and lactation, and the predation risks involved with having dependent offspring. We also wished to avoid the likely variation in vigilance among age/sex classes (e.g., Childress and Lung, 2003; Winnie and Creel, 2007). Upon encountering a wildebeest group containing females the observer stopped the vehicle, placed the speaker, amplifier, audio player and battery on the ground between 100 m and 300 m from the focal group, and then drove approximately 100 m from the speaker prior to sampling. The recording was set to start playing 10 min after the observer had moved away to ensure that the observer was in place and had collected baseline observations prior to the playback.

Prior to the baseline observations, the observer recorded the date, time, GPS coordinates, distance to cover (areas of dense vegetation, ridges and artificial structures that could hide lions), wind speed, group size (# of wildebeests only), before-playback group area (estimated length × width of group), number of heterospecifics within 50 m of the wildebeest group, grass height (included as a metric of forage availability, not visibility, as grass was never over 0.8 m, which is the height at which a lion’s hunting success increases, Orsdol, 1984) and the recording code assigned to the recording that was played back. The time was transformed into a minutes from sunrise or to sunset variable (for morning or afternoon samples, respectively). This was because the risk of predation was likely higher at sunrise and sunset; lions in Etosha hunt more actively during these times (Stander, 1992). We estimated grass height visually in the field by recording which anatomical part of the wildebeest (base of hoof, ankle, shin, knee or stomach) the grass was nearest to in height. There was no grass above the wildebeests’ stomachs. The height above ground for each of the anatomical parts was calculated using a photograph of an adult female wildebeest at a known distance from the camera and known focal length: base of hoof (1 cm), ankle (11 cm), shin (20 cm), knee (42 cm) or stomach (75 cm). We only recorded the numbers of heterospecifics that compete with wildebeest for food or are depredated by lions (zebra, *Equus quagga burchellii*; springbok, *Antidorcas marsupialis*; oryx, *Oryx gazella*; and red hartebeest, *Alcelaphus buselaphus caama*). Average wind speed in kilometers per hour was measured over the course of one minute using a handheld anemometer (Kestrel 1000 Pocket Weather Meter, Nielsen-Kellerman, U.S.A.).

We selected a focal individual haphazardly (the first foraging adult female wildebeest sighted as the observer looked up; wildebeest groups are sufficiently spread out that these focal individuals were sometimes central and sometimes peripheral). The focal individual’s reproductive state and body condition were recorded. Reproductive state was classed as nil (apparently non-reproductive), noticeably pregnant or lactating, and body condition was ranked using Berry and Louw’s (1982) criteria from one (very poor) to five (excellent). Individuals moved throughout the focal sample, and therefore it was not possible to include the individual’s location in the group in our analyses. Each focal sample consisted of before and after playback periods: five minutes of baseline (before, or pre-playback) observations, then 25 s of lion or control playback, followed by five minutes of short-term response (after, or post-playback) observations. The entire focal sample was video recorded (Canon Legria HFR38, Japan). The distance between the speaker and the focal group was noted and we only conducted playback samples on groups that were between 100 m and 300 m from the speaker at the start of the playback. At the end of the after-playback period we estimated group area again and retrieved the playback equipment. We only sampled one female for each playback to avoid pseudoreplication. Tourists are a common sight for wildebeest at Etosha and thus wildebeest rarely respond to the presence of cars; however, if passing cars did cause a response from the focal wildebeest (i.e., the focal animal changed her behaviour to become vigilant toward a car) or other wildebeests’ reactions affected the focal’s behaviour (e.g., wildebeest alarm called in response to tourists, causing the focal animal to become vigilant), the sample was cancelled and not analysed. To reduce the potential for habituation, no playbacks were done within five kilometers of another playback on the same day.

We recorded vigilance strategy as done by Favreau et al. (2010, 2015). An individual with its head raised was considered vigilant. Vigilance was classified by both type (antipredator or social) and intensity (exclusive or chewing) in a 2 × 2 classification. In antipredator vigilance an individual faced away from its group, including facing toward the speaker while facing away from the group, while in social vigilance it faced towards at least one group member. Vigilance while chewing was considered low intensity vigilance, while exclusive vigilance (done without chewing) was high intensity. Video recorded samples were analysed to quantify the time the focal female spent exhibiting each vigilance type and intensity during the five-minute before and after playback periods of each sample. Antipredator and social vigilance were distinguished based both on the videos and notes recorded while the behaviour was being video recorded. The individual’s bites were counted and their bite rate was recorded as bites per minute of non-vigilant time.

We recorded the within-group densities (before and after the

Table 1
Means ± SE of percentages of time wildebeest spent in four categories of vigilance before playbacks, after playbacks of lions' roars and after playbacks of car noises.

Treatment	Exclusive antipredator vigilance	Exclusive social vigilance	Chewing antipredator vigilance	Chewing social vigilance
Before playbacks	1.28 ± 0.05	0.16 ± 0.01	2.11 ± 0.03	1.98 ± 0.04
After lion roar playbacks	35.67 ± 0.29%	1.13 ± 0.04	1.94 ± 0.05	0.54 ± 0.02
After car noise playbacks	0.70 ± 0.03	0.00 ± 0.00	1.87 ± 0.02	2.49 ± 0.08

playback) as the number of wildebeests per square meter using the data on the group size and area covered by the group collected before and after the playback. ArcMap 10.3′s proximity tool was used to calculate the straight-line distance to the nearest waterhole from the location of each sample.

We collected 101 focal samples including 59 lion playback samples and 42 car playback samples. To control for the potential confounding effect of habituation over the data collection season, we created a date-based categorical variable, called habituation period, characterized by three levels in each of our models: 1) the first third of data collection time, 2) the second third, and 3) the final third.

2.4. Statistical analyses

We addressed Aims 1 and 2 together and again analysed the changes in behaviour from the before-playback period to the after-playback period of the sample for all three behavioural responses (time in antipredator vigilance, time in social vigilance and within-group density). By assessing how the response variables changed, rather than assessing the response variables in the before and after playback periods separately, we were able to consider how each individual's vigilance behaviour changed and whether groups bunched. We first used general linear regressions using the ade4 package (Dray et al., 2015) in R 3.1 (R Development Core Team, 2016) to test for any effect of day of year, wind speed, body condition, grass height and habituation period on our response variables. We found that there were no effects of these on any of our response variables (Table S1). As a result, we did not include these predictor variables in our models.

Changes in time spent in antipredator vigilance, time spent in social vigilance and within-group density were used as the response variables for three linear mixed-effects models, to address Aims 1 and 2. The three models assessed the effects of the playbacks, social variables and environmental variables, including location-based variables, on the response variables. For each of the vigilance models we included playback type, distance to speaker, minutes from sunrise or to sunset, distance to water, distance to cover, group size, the number of heterospecifics and the focal individual's reproductive state as predictor variables. We did not have a sufficient sample size to add the type of cover or species of heterospecifics as additional variables, or to consider possible interaction terms. The within-group density model included the same predictor variables except that it did not include the reproductive state of the focal individual, as within-group density is a group's response, not an individual's. We included the recording code assigned to each lion or car recording that was played back as a random effect in all models to deal with the issue of pseudoreplication caused by reusing predator stimuli (Johnson and Freeberg, 2016).

Prior to modelling, we transformed our response variable data using the Yeo Johnson power transformation to improve normality of variance, stabilize the residuals and improve symmetry (Yeo and Johnson, 2000). Models were run with the *lmer* function from the *nlme* package (Pinheiro, 2015) in R 3.1 (R Development Core Team, 2016). We looked at each model's residual plots, normal probability plots of residuals and histograms to check for model fit. All three models met the assumptions of normality and homoscedasticity.

For Aim 1, we also ran a Spearman's correlation test to determine the Spearman's rho and significance of the correlation between the changes in time spent in exclusive and in antipredator vigilance.

To test Aim 3, we used a Spearman's rank correlation test to determine whether the changes in the bite rate per minute of non-vigilant time response and in the within-group density response were correlated. The responses were determined by looking at the changes in behaviour (bite rate and within-group density) from the before-playback period to the after-playback period of the sample.

3. Results

Across the 101 samples in this study, the sizes of the focal wildebeests' groups varied from 4 to 187 wildebeest ($\bar{x}$ ± SE = 31.94 ± 3.19). All of the sampled groups were mixed herds, which comprised adult females, adult males and juveniles. Wildebeest changed from spending 1.28 ± 0.05% of their time in exclusive antipredator vigilance before playbacks to spending 35.67 ± 0.29% of their time doing so after playbacks of lion roars. There were no major changes in other categories of vigilance after the lion roar playbacks, or in response to playbacks of car noises (Table 1). Groups had an average density of 0.014 ± 0.000 wildebeest per square kilometre during the before playback period, which increased by 164.29% after lion roar playbacks and by 7.14% after car playbacks.

3.1. Aims 1 and 2: Behavioural responses to playbacks and whether these were affected by social and environmental variables

Playback type was the variable that most significantly affected the change in the amount of time spent in antipredator vigilance from before to after the playback (Table 2). When wildebeest were exposed to a lion roar, they increased time spent in antipredator vigilance (Fig. 1). This did not happen in response to the playbacks of cars. Distance to cover and the number of heterospecifics also affected the change in

Table 2
Results of linear mixed-effects model of the factors affecting the antipredator vigilance response of wildebeest. d.f. = 1, 91 in all cases but reproductive state (2, 91). Data were standardized prior to analysis.

	F	*P*	Coefficient	S.E.
Playback type	73.61	< 0.001	Lion: -0.202	Lion: 4.437
Distance to speaker	6.70	0.011	−0.011	0.034
Minutes from sunrise/to sunset	0.93	0.337	−0.061	0.059
Distance to water	1.01	0.317	−0.002	0.001
Distance to cover	6.73	0.011	0.012	0.012
Group size	1.57	0.214	−0.029	0.070
Number of heterospecifics	6.21	0.015	0.002	0.071
Reproductive state	2.18	0.119	Nil: 1.677 Pregnant: 8.957	Nil: 5.639 (*P* = 0.767) Pregnant: 5.363 (*P* = 0.098)

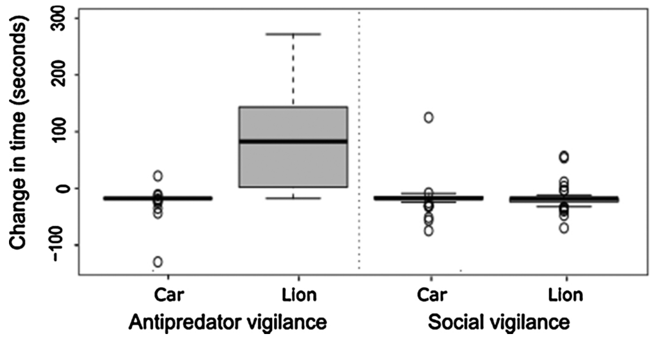

Fig. 1. Effects of playbacks on vigilance strategy (*N* = 101), showing the mean (± S.E.) changes, from before to after the playback, in time spent in antipredator and social vigilance by female wildebeest exposed to control and lion roar playbacks. Plot shows the medians (bold lines in boxes), the upper quartiles (25% percentile, the top lines of the boxes), the lower quartiles (75% percentile, the bottom lines of the boxes), the minimum and maximum values within 1.5 × inter-quartile range (bottom and top whiskers) and any outliers falling outside of the whisker range (circles).

time spent in antipredator vigilance in response to playbacks. Wildebeests increased their time spent in antipredator vigilance more when farther from cover and when more heterospecifics were present. The increase in time spent in antipredator vigilance after lion roar playbacks was highly positively correlated with the increase in time spent performing exclusive vigilance ($r_s = 0.91$, $P = < 0.01$).

When wildebeests were exposed to a lion roar or car playback, they did not significantly change the time they spent in social vigilance (Fig. 1) and no other variables affected the change in the amount of time spent in social vigilance (Table 3).

Wildebeest significantly increased their within-group density (number of wildebeests per meter square) when exposed to a lion roar, but not a car playback (Fig. 2). No other variables had significant effects on the change in within-group density (Table 4).

3.2. Aim 3: was bunching negatively correlated with bite rate?

There was a significant, albeit weak, negative correlation between the change in within-group density as a result of the playback of a lion roar and the change in bite rate per minute of non-vigilant time of individual wildebeests (r_s = -0.286, P = 0.01). Thus, when wildebeest groups had stronger bunching responses, the focal individuals' bite rates decreased more.

4. Discussion

As expected, wildebeests increased their vigilance in response to

Table 3
Results of linear mixed-effects model of the factors affecting the social vigilance response of wildebeests. d.f. = 1, 91 in all cases but reproductive state (2, 91). Data were standardized prior to analysis.

	F	*P*	Coefficient	S.E.
Playback type	0.002	0.964	Lion: 67.491	Lion: 7.867
Distance to speaker	0.110	0.741	−0.158	0.061
Minutes from sunrise/to sunset	1.072	0.303	0.102	0.105
Distance to water	3.737	0.056	0.002	0.002
Distance to cover	0.905	0.344	−0.056	0.021
Group size	0.172	0.679	0.155	0.124
Number of heterospecifics	0.001	0.973	−0.313	0.126
Reproductive state	1.639	0.200	Nil: -19.645	Nil: 9.996 (*P* = 0.052)
			Pregnant: -15.655	Pregnant: 9.508 (*P* = 0.103)

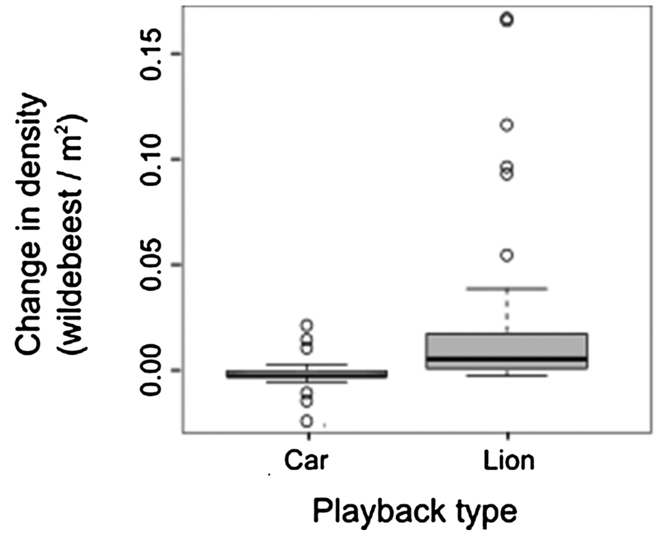

Fig. 2. Effects of playbacks on change in within-group density, showing the mean (± S.E.) change, from before to after the playback, in within-group density (wildebeest per m^2), for wildebeest groups exposed to car and lion roar playbacks. Plot shows the medians (bold line in boxes), the upper quartiles (25% percentile, the top lines of the boxes), the lower quartiles (75% percentile, the bottom lines of the boxes), the minimum and maximum values within 1.5 X inter-quartile range (bottom and top whiskers) and any outliers falling outside of the whisker range (circles).

Table 4
Results of linear mixed-effects model of the factors affecting bunching response of wildebeests. d.f. = 1, 93 in all cases. Data were standardized prior to analysis.

	F	*P*	Coefficient	S.E.
Playback type	36.390	< 0.001	Lion: 0.01	Lion: 0.002
Distance to speaker	0.426	0.516	−0.00001	0.00001
Minutes from sunrise/to sunset	0.105	0.747	0.00001	0.00002
Distance to water	0.512	0.476	-3.5×10^{-7}	5.0×10^{7}
Distance to cover	1.285	0.260	0.00001	5.0×10^{6}
Group size	0.897	0.346	−0.00003	0.00003
Number of heterospecifics	0.339	0.562	0.00002	0.00003

lion roars but not control recordings of car noises. However, contrary to our expectation, the increase in vigilance after the predator stimulus was due only to an increase in antipredator vigilance. There was no increase in social vigilance in response to lion roars. This suggested that the wildebeest relied on their own ability to attempt to locate the calling lion, rather than also using social information to locate the lion by watching their group mates for cues. Increases in antipredator vigilance were highly correlated with increases in exclusive vigilance. The antipredator vigilance response of focal individuals was influenced by three variables in addition to playback type. The farther the individual was from cover that could hide a lion, and the more heterospecific individuals there were with them, the more their vigilance increased following the lion roar playback. Wildebeests also increased their within-group density after hearing lion roars, and this bunching response was not affected by any of the other variables investigated. The increase in antipredator vigilance was negatively correlated with the distance from the focal animal to the speaker.

The lack of an increase in social vigilance after the playbacks of lion roars to wildebeests was unexpected. Social information includes both communication (e.g., alarm signals in this context) and 'inadvertent social information', where individuals gain information from watching others carrying out their own activities (reviewed by Danchin et al., 2004). Wildebeests produce alarm snorts themselves and have been shown to respond to the alarm calls produced by chacma baboons

(*Papio hamadryas ursinus*) that have seen lions (Kitchen et al., 2010). Alarm calls alert conspecifics to the presence of danger, but do not themselves convey the location of that danger. Eastern grey kangaroos (*Macropus giganteus*), herbivores with similar diets and grouping patterns to wildebeests but that do not give alarm calls, can learn about the presence and location of a predator that they cannot see, by noticing the responses of group members to the threat (Pays et al., 2013). For the use of such collective detection to be effective, however, individuals should ideally monitor the vigilance and postures of their group mates. Evidence that this can occur comes from a study of black-tailed prairie dogs (*Cynomys ludovicianus*) that showed that they use a particular display to assess the alertness of nearby conspecifics and then adjust their own vigilance accordingly (Hare et al., 2014).

So why did the wildebeest in our study not increase their social vigilance after hearing the playbacks of lion roars? It is possible that scanning in the direction of the lion roar was likely to provide information on the location of the lion more quickly than social vigilance would have. Whether prey visually search for a predator themselves or attempt to gain information using social vigilance may depend on the size of the predator; perhaps with a smaller predator that was more difficult to locate, the wildebeest would have increased their social vigilance. Another possibility, albeit an unlikely one, was that their background level of social vigilance (just over 2% of their time), which they maintained essentially unchanged in the five minutes after the playbacks, was sufficient to gain any information that could be acquired from conspecifics' responses. It is also possible that the likely response of conspecifics to actually seeing lions would be movements that would be obvious even to a non-vigilant feeding wildebeest, so that increasing their levels of social vigilance would not be necessary. We also do not know how much peripheral vision wildebeests have, but given the location of their eyes this might be considerable, and might allow them to monitor conspecifics without having to face towards them. Finally, wildebeest may not use social information for antipredator purposes at all.

While lions do some of their hunting during the day, they do not normally roar while hunting. Nonetheless, we believe it is reasonable that wildebeests would respond to the roar of a lion, as ungulates often seek to remain aware of the location of nearby predators, regardless of the behaviour of those predators at the time. For example, ungulates will frequently remain near a waterhole for an extended period watching lions that are drinking, rather than flee (AW Goldizen, unpublished observation). However, the fact that lions do not normally roar while hunting may explain the relatively muted reactions of the wildebeest to the roars and the fact that they did not flee.

We had predicted, and did not find, group-size effects on the wildebeests' vigilance and bunching responses, but Kitchen et al. (2010), who played baboon alarm calls to ungulates, including wildebeest, also found no group-size effects on their behavioural responses. The effects of social factors, particularly group size, on foraging and vigilance have been well studied in many species; an increase in group size usually leads to increased foraging time and reduced vigilance through the group-size effect (reviewed by Beauchamp, 2013). Our lack of a significant effect of group size suggests that group size may be more likely to affect prey animals' proactive decisions prior to predator detection than reactive ones in the presence of a predator. However, group size effects have not always been found for proactive vigilance in ungulates either, which could be explained by larger groups being more likely to attract predators in some cases. In contrast to the lack of effects of group size, wildebeest did consider their within-group density in their reactive responses, by bunching after lion playbacks. Predators can be disoriented by dense groupings, reducing their predation success (Landeau and Terborgh, 1986). They may also be more likely to be injured when they attack higher-density groups, due either to cooperative defence by the prey or simply due to the large number of prey moving quickly in close proximity. As FitzGibbon (1990) showed, cheetahs (*Acinonyx jubatus*) preferentially hunt Thomson's gazelles (*Gazella thomsoni*) that are peripheral and have neighbors farther away. Therefore, the increase in within-group density that we found is likely to have been a result of wildebeest moving to more central areas of the group to reduce their predation risk. We had expected that factors such as whether or not heterospecifics were present would affect the bunching response, but this was not the case.

Wildebeests increased their antipredator vigilance after playbacks more when they were further from cover and when there were more heterospecifics in their groups. The first of these findings is surprising, but perhaps was a result of wildebeest being concerned that they could hear the playback, yet could not find anywhere where the source of the playback (lion or car) could be hidden (given that we defined cover as vegetation or topography that could hide a lion). It is also possible that being close to cover is beneficial to wildebeest by facilitating escape from predators or reducing the chance of predators finding them. The latter possibility seems unlikely give that wildebeest generally feed on open plains in groups, and thus would be highly detectable. It is not clear whether escaping from a predator by running into cover would be effective. It would be interesting to know whether the effect of distance to cover differed for lion roar versus car noise playbacks, but this would require a larger sample size than we had. The effect of heterospecifics was also opposite to our prediction. Pays et al. (2014) studied impala in groups without heterospecifics, and in groups with plains zebras, blue wildebeest or greater kudu, in Zimbabwe. At small to medium group sizes, the impalas were less vigilant when with another species, perhaps because these other species were preferred prey of lions. Given that wildebeest are particular targets of lions in Etosha, they may be more vigilant than other heterospecifics there and thus there may be no benefit to them of being in mixed species groups. Instead, the increased disturbance caused by mingling with heterospecifics may explain their increased vigilance response when there were heterospecifics present, perhaps by making it more difficult for a wildebeest to escape from a lion due to the movements of the extra heterospecifics. Alternatively, the presence of the heterospecifics may make a wildebeest groups more likely to be targeted by lions, although this seems unlikely. The lack of any effect of distance to water is not surprising as this would be expected to affect proactive antipredator behaviour more than reactive responses.

Finally, the increase in vigilance facing away from the group (considered to be antipredator vigilance) in response to the lion playbacks was strongly correlated with an increase in exclusive vigilance. This suggests that exclusive vigilance is the main form of vigilance used in response to likely immediate predation risk, as expected if it is indeed a more effective form of vigilance than vigilance while chewing. Although this relationship has been speculated before, this has been rarely studied using predator simulation. Both antipredator responses that we documented in our experiments reduced feeding rates. Wildebeests cannot feed or even chew during exclusive vigilance, and the more they bunched the lower their feeding rates were during their non-vigilant time. However, this measure of the cost of bunching was small. Indeed, if wildebeests return to feeding quite quickly after a predator stimulus, when there is no further evidence of that predator, any reduced feeding rate would have a minimal impact on them.

While these antipredator behaviours are presumably beneficial in reducing predation, less is known about their fitness costs (reviewed by Creel and Christianson, 2008). Most studies that have documented costs of antipredator behaviour have involved invertebrates or small vertebrates (e.g., LaManna and Martin, 2016). It is less clear how significant the costs of anti-predator behaviour are to large herbivores, but these include reduced foraging efficiency due to the use of resource-poor habitats to avoid predators (Valeix et al., 2009), a possible reduction in reproductive success due to physiological effects (Creel et al., 2007) and reduced food intake due to vigilance behaviour (e.g., Fortin et al., 2004). Given the likelihood that behaviours such as vigilance carry at least some cost, animals are thought to carefully balance the benefits and costs of their antipredator behaviours. Animals' apprehensiveness likely falls on a continuum from being non-existent, and thus incurring no cost, in some (likely rare) circumstances, to being high-level and higher cost, likely including exclusive vigilance.

We encourage further studies of the reactive antipredator responses of prey animals, and particularly when and how they use social information to inform these responses. Many animals warn of threats using alarm signals, with an ever increasing number of species known to use different alarm signals for different types of predators or to convey the intensity of the threat (reviewed by Caro, 2005). However, there is still little known about whether communication, intentional or not, occurs about other details of threats, such as the exact location of a predator. An animal should be able to get some information about this from watching its group mates, yet we found no increase in social vigilance after our lion playbacks. Further work is needed to understand the benefit/cost ratios to prey of using antipredator vigilance in reaction to a predator stimulus to try to locate the danger, versus using social vigilance to gain social information on the threat from group members.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.05.021.

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