Eavesdropping of an African ground squirrel on the heterospecific alarm calls of a noisy ground-nesting bird.

Running title: Ground squirrels eavesdrop on lapwing alarm calls

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Abstract

Animals gather information about their environment from a variety of sources to enable adaptive decision-making behaviour. Eavesdropping on heterospecific alarm calls enhances predator avoidance, reduces time spent vigilant and allows for more time on daily activities such as foraging. If the information is relevant and reliable, individuals that respond to heterospecific signals may benefit from a wider range of information at a low marginal cost. The Cape ground squirrel (*Xerus inauris)* and crowned lapwing (*Vanellus chilensis*) are ground-dwelling species that are taxonomically distant but share similar predators, habitat and anti-predatory behaviours. We used playback experiments of the alarm calls produced by conspecifics and lapwings to investigate the vigilance responses of adult female Cape ground squirrels. Squirrels responded with greater vigilance to both squirrel and lapwing alarm calls and no changes of vigilance levels were observed in response to a control sound. However, contrary to our predictions, changes in vigilance and time to relax did not differ between conspecific versus heterospecific playbacks. The results from our study suggest that squirrels perceive lapwing alarm calls as relevant and reliable information and that responding to it could increase their survival.

Keywords

Vigilance; predator risk; crowned lapwings; Cape ground squirrels; playback experiment; alarm calls

Introduction

Animals gather information about their environment from a variety of sources, including information they gather directly (personal information) and information they obtain through others (socially acquired or public information), to enable adaptive decision-making behaviour (Dall et al., 2005; Danchin et al., 2004; Magrath et al., 2015). This information can be essential for survival particularly when individuals alert group mates of potential threats, such as when producing alarm calls.

The response to alarm calls may be to run to shelter, increase vigilance or mob the potential predator (Sherman, 1985; Dutour et al., 2019) and the ability to respond appropriately to a call can be either innate (e.g., white-browed scrubwren, *Sericornis frontali*, Platzen & Magrath, 2004) or learned (e.g., Belding's ground squirrels, *Urocitellus beldingi*, Mateo & Holmes, 1997). In addition to information gained from conspecific alarm calls, information on potential predators may also be gained by eavesdropping on the signals or cues made by heterospecific individuals (Magrath et al., 2015; Meise et al., 2018).

Eavesdropping is the use of information from signals that are produced by nearby callers that are intended for other receivers (Peake, 2005). Eavesdropping on heterospecific alarm calls could greatly enhance predator avoidance and may lead to less time spent in vigilant behaviour and more time for daily activities such as foraging (Makenbach et al., 2013). Furthermore, by responding to signals beyond their own species, eavesdropping allows individuals to gain a wider range of information about their environment at low marginal costs such as attracting the attention of predators (Aschemeier & Maher, 2011; Magrath et al., 2015; Carlson et al., 2020). Thus, eavesdropping can be a low-cost and low-risk behaviour that can be greatly beneficial (Magrath et al., 2015).

The ability to recognize heterospecific alarm calls has been demonstrated in a number of vertebrates, including many species of birds and mammals (see Magrath et al., 2020 for a review). In birds, mixed-species flocks are common and species benefit greatly from eavesdropping by decreasing time spent vigilant (Igic et al., 2019; Ridley et al., 2014). Heterospecific alarm call recognition has also been demonstrated in many mammals (e.g., *Marmota monax* eavesdrop on *Tamias striatus*, Aschemeier & Maher, 2011; *Odocoileus hemionus* eavesdrop on *Marmota flaviventris,* Carrasco & Blumstein, 2012; *Helogale parvula*, eavesdrop on *Paraxerus cepapi*, Morris-Drake et al., 2017; *Xerus inauris* and *Cynictis pencillata* mutually eavesdrop, Makenbach et al., 2013, and likewise *Marmota flaviventris* and *Callospermophilus lateralis* mutually eavesdrop, Shriner, 1998). Eavesdropping and the ability to recognize heterospecific alarm calls between broader taxonomic gaps exist but it is unknown how commonly they occur (Schmidt et al., 2008). Examples of avian-mammal eavesdropping include primates responding to avian alarm calls (e.g., *Cercopithecus diana* and *Ceratogymna elata*, Rainey et al., 2004; *Cercopithecus aethiops* and *Spreo supervus*, Seyfarth & Cheney, 1990), as well as squirrel-bird eavesdropping associations (*Cynomys ludovicianus* and *Athene cunicularia hypugaea*, Bryan et al., 2014; *Sciurus carolinensis,* and *Turdus migratorius,* Getschow et al., 2013; *Sciurus vulgaris* and *Garrulus glandarius*, Randler, 2006; Schmidt et al., 2008).

In many mixed-species associations, some species are better at acquiring and transferring information than others because of differences in their morphology, ecology and physiology, and these species could be considered "sentinel species" (e.g., *Vanellus chilensis*, Cavalli et al., 2018) or "community informants" (Carlson et al., 2020), providing community-wide (public) information (Breed, 2017). Community informants are species that provide reliable information (information sources; Carlson et al., 2020). However, not all species may be able to take advantage of this public information (Getschow et al., 2013; Magrath et al., 2009; Meise et al., 2018). The ability to detect and interpret heterospecific alarm calls may differ from conspecific calls because of either differences in the call structure or because the heterospecific calls may encode different information from the conspecific calls or both (Getschow et al., 2013). Thus conspecific calls may be more reliable than heterospecific calls (Getshow et al., 2013). However, structural similarity is not a pre-requisite of successful eavesdropping as call similarity did not explain the response of superb fairy-wrens (*Malurus cyaneus*) to heterospecific alarm calls (Magrath et al., 2009) or the response of vervet monkeys (*Cercopithecus aethiops*) to the alarm calls of superb starlings (*Spreo superbus*; Seyfarth & Cheney, 1990).

If an individual can recognize heterospecific alarm calls, the value of eavesdropping on these alarm calls can depend on the relevance and reliability of the callers (Magrath et al., 2015; Meise et al., 2018). An alarm call is relevant if it is given to threats that endanger the eavesdropper (i.e., they have predator overlap or vulnerability to the same predators; Carrasco & Blumstein, 2012; Goodale et al., 2010; Meise et al., 2018; Templeton, 2018). It is reliable if those threats are present and not false to avoid wasting time responding to deceptive alarm calls in the absence of predators (Magrath et al., 2015; Searcy & Nowicki, 2005). The ability to recognize relevant and reliable heterospecific alarm calls may increase the eavesdropper's fitness (Meise et al., 2018).

The Cape ground squirrel (*Xerus inauris*) and crowned lapwing (*Vanellus coronatus*) belong to taxonomically distant groups. Both are ground-dwelling species of similar size (ground squirrel 23.5-28.2cm, Herzig-Straschil, 1978; crowned lapwings 30-31cm, Hockey et al., 2005) that co-occur in open shortgrass areas of southern Africa where they share similar predators and produce alarm calls in response to potential danger (Hockey et al., 2005; Müller & Manser, 2008; Unck et al., 2009; Waterman, 1995). In response to the playbacks of conspecific alarm calls, Cape ground squirrels will either run to their burrow or become more vigilant (Furrer & Manser, 2009) and the vigilance of the squirrels increases with increasing distance to their home burrows (Unck et al., 2009). Cape ground squirrels increase their vigilance in response to heterospecific alarm calls produced by another similar-sized mammal (yellow mongoose, *Cynictis pencillata*; Makenbach et al., 2013). However, it is unknown if they will respond to the alarm calling of a more distantly related lapwing species (Skinner & Chimimba, 2005), especially as spectrograms of their alarm calls reveal very different call structures between the two species (see Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988; Supplemental Figure S1). Lapwing alarm vocalizations consist of repeated calls that increase in rate and volume as a predator nears, whereas squirrel alarm vocalizations are less complex shorter repeated calls (Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988).

Female Cape ground squirrels are semi-fossorial and live in permanent egalitarian kin groups of one to five adult females and up to nine sub-adults of either sex (Waterman, 1995; Hillegass et al., 2008). There is no dominance hierarchy within a group, and all adult females (>

9 mo.) breed. A family group lives in a burrow system separated from other families by a few hundred meters and there is little overlap in the home ranges of different groups (Waterman, 1995; Waterman & Archibald, 2019). Most of their time spent above ground is devoted to feeding on grasses (Herzig-Straschil, 1978; Waterman, 1995). Cape ground squirrels use urgency-dependent repeated alarm calls but do not appear to use referential calls (Herzig-Straschil 1978; Furrer & Manser 2009).

Crowned lapwings are ground-nesting insectivores, feeding primarily on termites (*Odontotermes* sp*;* Ward & Maclean, 1988). Crowned lapwings live in small groups (most likely family groups) or at times in large flocks (Ward & Maclean, 1988). Crowned lapwings scan frequently for predators and their vigilance is not affected by conspecific group size (Ward & MacLean, 1988). Like the southern lapwing (*Vanellus chilensis*) of South America, which could be described as a community informant species (Carlson et al., 2020) because of their loud alarm calls and aggressive behaviour towards potential intruders (Cavalli et al., 2018), crowned lapwings also make very loud alarm calls and mob potential predators (Ward & Maclean, 1988). These vocalizations are also urgency-dependent repeated calls (Müller & Manser 2008)

The objective of this study was to determine if Cape ground squirrels eavesdrop on the heterospecific alarm calls of sympatric crowned lapwings. As conspecific calls are predicted to be more reliable and relevant (conspecific reliability hypothesis), we predict that Cape ground squirrels will have the highest response (higher vigilance) and longer time to relax upon hearing a conspecific alarm call, followed by lapwing calls and no response to a control sound. However, if lapwings are community informants (Carlson et al., 2020), then they may be able to detect and assess predator threats as well or better than a squirrel's conspecifics ('community informant' hypothesis) and we predict Cape ground squirrels will have a higher (or equal) response (higher vigilance, longer time to relax) and no response to a control sound. Likewise, their time to relax should be longest upon hearing a conspecific alarm call, but since lapwing alarm calls may offer information about a potential threat, the time to relax should be longer in after hearing a lapwing call than a control sound (Makenbach et al., 2013).

Methods

Study site

The study was conducted at the S.A. Lombard Nature Reserve located near the town of Bloemhof in the North West Province of South Africa (27°35’S, 25°23’E) from May to August 2014 during the dry arid winter (Makenbach et al., 2013). The squirrels on this site have been studied since 2002 (Waterman & Archibald, 2019). The 3,359 ha reserve is made up of open grassland with small patches of bush and scattered trees (Makenbach et al., 2013; van Zyl, 1965). Cape ground squirrels and crowned lapwings commonly occur at this site (Hillegass et al., 2008; Skead, 1974) where they share space but they do not aggregate. Aerial and terrestrial predators that can prey on the ground squirrels and lapwings, and that have been sighted hunting on the reserve, include feral cats (*Felis catus*), black-backed jackals (*Canis mesomalas*), caracals (*Caracal caracal*), martial eagles (*Polemaetus bellicosus*), and southern pale chanting goshawks (*Melierax canorus*; Hockey et al., 2005; Skinner & Chimimba, 2005; Unck et al., 2009). Black-backed jackals, eagles and hawks are active throughout the daytime, and caracals are active in the mornings and late afternoons (Hockey et al., 2005; Skinner & Chimimba, 2006), particularly on our study site, which is closed to the public and has low human disturbance.

Trapping and handling

To identify individuals for playbacks, we trapped Cape ground squirrels using Tomahawk live traps (15x15x50cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with a mix of peanut butter and birdseed at the beginning of the field season. Upon capture, we transferred and restrained individual squirrels in a cone-shaped handling bag (Koprowski, 2002), where they were identified (see below on permanent identification), weighed, sexed, and checked for reproductive condition. All ground squirrels were permanently tagged with a passive integrated transponder (PIT tag, AVID Inc., Folsom, LA) for long term identification. We also applied a unique and laterally symmetrical dye mark to each squirrel (Rodol D; Lowenstein and Sons, New York, NY), which allowed us to temporarily identify them from a distance. Animals were released at the location where they were caught. All experimental procedures were approved by the University of Manitoba Animal Care Committee (protocol F10-030).

Creating and recording playback treatments

Heterospecific crowned lapwing and conspecific Cape ground squirrel alarm calls were used in a playback experiment to examine the response of focal squirrels (see supplementary Figure S1 for example spectrograms). Three treatments were used in the playback experiments: Cape ground squirrel alarm calls, crowned lapwing alarm calls, and white noise controls (noise made of many frequencies with equal intensities). In this study, an alarm call refers to a single vocalization, which in Cape ground squirrels has four syllables and in the lapwing has one syllable (Figure S1) and a calling bout contains multiple alarm calls in sequence (Furrer and Manser 2009). Repeated calls or call bouts are common in the alarm signalling of ground squirrels (Blumstein and Armitage 1997; Manser 2001; Warkentin et al. 2001). Cape ground squirrel alarm calls were created by opportunistically recording multiple call bouts, in response to a person approaching a squirrel, in June and July 2011 at a sampling rate of 44.1 kHz using an H4Next Handy Recorder (Zoom Co., Japan; see Makenbach et al., 2013 for details). The alarm call bouts from two different females were manipulated using the phonetics program Praat v. 5.2 (University of Amsterdam, The Netherlands). These recorded females were not from the same family groups as the focal animals used in our playbacks (see below). In playback studies, different recordings of the same alarm call should be used to avoid pseudoreplication and many different individuals should be recorded (Kroodsma et al. 2001). However, because of the difficulty of approaching squirrels near enough to record high-quality alarm calls, only recordings of the calling bouts from two different females were usable. We constructed two different files from each individual's original alarm calling bouts, using four consecutive syllables in each recording (see Figure S1) to avoid any wind or other background noise, resulting in a total of four playback files (two from each females; mean length 5.34± 0.87s). As Cape ground squirrels use repeated alarm calls in their call bouts and syllable repetition rate can confer response urgency (Herzig-Straschil, 1978; Furrer and Manser 2009), we chose to use only two repeated complete alarm calls in each playback file. We maintained what appeared to be the natural latency between consecutive Cape ground squirrel calls; the latency in our original recordings was 2.4 s on average (measured by hand in Praat, based on the latency between 82 syllables; Makenbach et al., 2013). Because crowned lapwings are extremely difficult to approach (Ward & Maclean, 1988; Müller & Manser, 2008), we were unable to get close enough to any crowned lapwings on our study site to make high-quality recordings. Four different sound files (mean length 1.38 ± 0.79s) of lapwing alarm bouts recorded in South Africa were downloaded from EcoMedia South Africa (Pond5.com) and were also constructed to play two consecutive calls with the latency from the original recording maintained. Only a single individual was calling in each sound file. As crowned lapwings are non-territorial in winter and can move over large areas, particularly outside the summer breeding season (Skead, 1955; Hockey et al., 2005), it is unlikely they have local dialects. Like Cape ground squirrels, crowned lapwings use repeated alarm calls in their call bouts to confer a response urgency (Müller & Manser, 2008), thus the use of only two repeated alarm calls in each lapwing playback file. In addition, Praat was used to create the white noise playback for the control treatment (three different sound files, mean length 1.85 ± 0.01s; Makenbach et al., 2013).

Playback experiments

In playback trials, we exposed adult female Cape ground squirrels (one individual from each of 11 social groups as our replicate) to three call treatments: Cape ground squirrel alarm calls, crowned lapwing alarm calls, and white noise. The order, and the specific sound file of the recorded alarm call or white noise within each treatment, were chosen randomly by drawing treatment assignments out of a bag. To avoid habituation, we allowed 48 hours between each trial (Makenbach et al., 2013). A Honeytone amplified speaker (Danelectro Co., Camarillo, CA, USA) and H4n Handy Recorder Zoom (Zoom North America, Ronkonkoma, NY, USA) were used to play the .wav files. The volume of the speaker was adjusted before each treatment to reflect natural amplitude (approximately 55-60 dB SPL, measured 1 m from the speaker using the LogSPL app) of the squirrel alarm calls measured from our original calls. The lapwing calls were similarly standardized, as this amplitude matched the level of naturally occurring alarms we perceived by ear (as in Müller & Manser, 2008), and we similarly matched the volume of the white noise, as differences in volume could cause differential responses in the playbacks. The speaker was placed in close proximity to the burrow areas either before the animals emerged in the morning or, if the animal was already above ground, by approaching the focal squirrel and observing which burrow it went in to. When a squirrel moved back into the burrow, time was given for the squirrel to resurface and resume its activity before immergence such that the individual displayed low vigilance behaviours such as allogrooming or foraging. The speaker was always placed within 15 m of the focal squirrel.

Observations of ground squirrels were made 50-100 m away from the focal animal, from either a tower (~6m high) or in a hide on top of a vehicle using 10×50 binoculars (Nikon 763908 BU) and a 20–45×60 spotting scope (Bushnell Corp., KS, USA) mounted on a monopod or tripod. A Kestrel 3000 Pocket Weather Meter (Nielsen Kellerman, Chester, PA, USA) was used to record the average wind speed (km/hr) over a 2 min period. Observations and trials were not made during wind speeds >18 km/hr to reduce the chance that wind would affect squirrel behaviours (Makenbach et al., 2013; Sloan & Hare, 2004).

Each social group observed was considered one experimental unit to prevent pseudo-replication as individuals within a social group are usually closely related and may behave similarly. The same adult female from each social group was used for all three trials. All focal animals were older than 2 years of age (range 2 – 8 years) and there were no offspring present for any trials (see Supplementary file, Table S1, for information on female age and playback used). To minimize disturbance of focal squirrels, we did not trap them during the experimental period, so we did not know if they were pregnant. However, no focal female successfully weaned any offspring in the two months following our playbacks. For each playback trial, all behaviours of the focal individual were recorded using the Recordium app v1.0 on an iPhone 5 (iOS 7) for a minimum of 60s before the treatment being delivered and at least 60 s after the playback. The treatment was only administered if the focal individual was exhibiting low vigilance behaviour or was entirely non-vigilant before the playback (see Table 1 for definitions of vigilance levels based on Unck et al. 2009 and Makenbach et al. 2013). Any time spent out of sight was noted and omitted to ensure 60 s of behavioural data was collected before and 60s after the treatment (after Makenbach et al., 2013). To assess changes in vigilance behaviour, we calculated the mean level of vigilance in the 60 seconds before and after the playback. We categorized the intensity of vigilance using an ordinal scale based on the alarm level (Table 1; after Makenbach et al., 2013), and then calculated the weighted mean level of vigilance based on the proportion of time spent in each vigilance level. Using the change in vigilance takes the natural vigilance level of the focal animal before the playback into account. Finally, we calculated the change in vigilance by subtracting the weighted mean vigilance level before the playback from the weighted mean vigilance level after the playback. The number of other squirrels (kin) in proximity (within 15m) to the focal individual was also recorded. Playbacks were made during the day (0800-17h30) at the burrow cluster where the focal squirrel slept.

Statistical analyses

We tested data for normality using Shapiro-Wilk tests. We could not normalize the proportion of time out of sight during the 60 seconds after the playback because in most trials the values were zero. Thus, we used a Friedman’s rank test, blocking on individual, to examine if the proportion of time out of sight differed with treatment. To examine the effects of treatments on the change in vigilance after playback, we used general linear mixed models with animal ID as a random effect and treatment and the number of squirrels within 15 metres as fixed effects. We then used Tukey’s Honestly Significant Difference (HSD) pairwise tests for post hoc comparisons. To test the effect of different of alarm calls on the duration of response to the calls, we quantified the amount of time (seconds) it took for an animal to return to the vigilance level it exhibited before the playback event ("time to relax" after Manser et al., 2001). For time to relax, we used logarithmically transformed data in the GLMM with animal ID as a random effect with treatment and the number of squirrels within 15 metres as fixed effects. We then used Tukey's HSD tests for post hoc comparisons among treatments. All statistical analyses were performed in JMP 14.0 (SAS Institute Inc., Cary, NC, USA) and our level of significance (α) was set at 0.05. Unless otherwise indicated, means ± SE are reported.

Results

To determine if Cape ground squirrels eavesdrop on the alarm calls of crowned lapwings, we conducted playback treatments to 11 individual squirrels from 11 different social groups. The mean number of squirrels within 15 m to the focal animals during playback was 1.55 ± 0.30 (range = 0 - 5) and it did not influence changes in vigilance levels in response to the playback (GLMM, $F_{1,18.75} = 0.85$, $P = 0.37$). In only one trial, after a heterospecific playback, did an animal run to a burrow, where she became vigilant at the burrow entrance. Mean duration of 'out of sight' after a playback averaged 1.84 ± 0.90 sec (lapwing, 1.73 ± 1.04 sec; conspecific, 2.18 ± 2.20 sec; white noise, 1.64 ± 1.44 sec) and the percent of time spent 'out of sight' in the 60 seconds after a playback did not differ by treatment (Friedman's rank text, $\chi^2_{(2)} = 1.7$, $P = 0.42$; lapwing, 2.9 ± 1.7 %; conspecific, 3.6 ± 3.6 %; white noise, 2.7 ± 2.4 %). The change in vigilance in response to the playback differed among treatments (GLMM, $F_{2,19.96} = 9.47$, $P = 0.001$; Figure 1). The change in vigilance after conspecific calls did not differ from the change in vigilance after lapwing calls (Tukey's HSD all pairwise comparison, $t_{20} = -1.22$, $P = 0.46$). However, both the change in vigilance after conspecific and lapwing playbacks were significantly greater than the control (Tukey’s HSD all pairwise comparisons: conspecific vs. control, $t_{20} = 4.22$, $P = 0.001$; lapwing vs control, $t_{20} = 3.01$, $P = 0.018$).

Treatment also affected the time to relax in the squirrels (GLMM, $F_{2,20} = 7.93$, $P = 0.003$, Figure 2) and there was no effect of number of nearby squirrels (GLMM, $F_{1,16.76} = 0.0006$, $P = 0.98$). The time to relax was shorter after the control than either the conspecific or lapwing calls (Tukey’s HSD all pairwise comparisons: control versus conspecific, $t_{20} = -3.52$, $P = 0.006$, control versus lapwing, $t_{20} = 3.37$, $P = 0.008$), while the time to relax after the conspecific and lapwing calls did not differ (Tukey’s HSD all pairwise comparison, $t_{20} = -0.16$, $P = 0.98$, Figure 2).

Discussion

The conspecific reliability hypothesis predicts that the intensity of vigilance behaviour should be higher in response to conspecific calls than in response than heterospecific calls (Magrath et al., 2009; Getschow et al., 2013). However, we found that Cape ground squirrels responded similarly to both conspecific and heterospecific alarm calls, supporting the hypothesis that Cape grounds squirrels eavesdrop on the heterospecific alarm calls of sympatric crowned lapwings as information denoting potential danger.

Using the alarm call bouts of only two individual squirrels to create our playback sequences resulted in limited replication in our experimental design (McGregor et al., 1992; Kroodsma et al., 2001). Using calls from multiple individuals is critical to avoid pseudoreplication in playback studies and ideally we would use a new version of the call from a new individual for each trial (Wiley, 2003). Two other factors may limit our conclusions. Firstly, squirrel exemplars were more than twice as long as the crowned lapwing and white noise exemplars. These differences could have led to more information during the squirrel playbacks than the other two playbacks and may have led to different responses by the squirrels. However, Cape ground squirrels alarm calls are not functionally referential (Furrer and Manser, 2009). Secondly, using a non-alarm vocalization from the ground squirrels as a control instead of white noise would have created a more natural comparison (Aschemeier and Maher, 2011). Besides alarm calls, Cape ground squirrels make non-alarm vocalizations focused on conspecifics including growls, play calls, and squeaks. The latter two vocalizations, play calls and squeaks are produced by newborns while in the nest (Herzig-Straschil, 1978). The growl vocalization, which is emitted during aggressive interactions amongst conspecifics, could have been used as a control (Furrer and Manser, 2009). However, this vocalization is made at low volumes in very close encounters between conspecifics (Herzig-Straschil, 1978). During playbacks we would have had to use higher volumes of growls, creating an artificially loud growls, suggesting this vocalization would not be an ideal control. An alternative control would be the use of non-alarm vocalizations of some other species living in the area, similar to the controls used in Aschemeier and Maher (2011). While white noise is synthetic, we used an abrupt onset of the white noise, in a similar way to the abrupt onset of alarm calls.

Cape ground squirrels produce alarm calls in the presence of predators (Furrer & Manser, 2008) and one benefit of grouping in this species is collective detection, which requires the use of alarm calls to warn group members of danger (Edwards & Waterman, 2011). In addition, Cape ground squirrels live and forage in family groups and spatially their closest callers will be their family members (close kin; Waterman & Archibald, 2019), who would be predicted to be more reliable for inclusive fitness reasons (Hare, 1998; Matrosova et al., 2011; Pollard, 2011; Pollard & Blumstein, 2012). In our experiment, we did not find an effect of the number of squirrels within 15m on response, in contrast to Edwards & Waterman (2011), who found that group size affected levels of vigilance. However, not all of our trials had additional group members nearby. In addition, all our experiments were conducted when the focal animal was near to their burrow, when the effects of nearby squirrels on vigilance are not as important as when they have moved away from the safety of the burrow (Unck et al., 2009). Thus, not detecting an effect of squirrel numbers on the vigilance of the focal animal in our experiments is understandable.

Contrary to the conspecific reliability hypothesis, the squirrels were as vigilant upon hearing the alarm calls from heterospecifics as they were from conspecifics. Also, and in contrast to what we predicted, time to relax did not differ after conspecific and lapwing alarm calls and their time to relax was significantly longer after either conspecific or heterospecific alarm calls than after the control. It could be that kinship is an important component of reliability, and thus our use of female calls from a different social group could have affected their vigilance levels and time to relax after conspecific calls. Or other differences in our conspecific calls may have affected the focal animal's response, such as the differences in the lengths of the calls. Although call similarity facilitates call recognition across species (Magrath et al., 2009, 2015; Meise et al., 2018), the alarm call structures of Cape ground squirrels and crowned lapwing are very different (see Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988). Yet Cape ground squirrels still appear to eavesdrop on the calls of lapwings and respond appropriately with increased vigilance. These findings support the hypothesis that crowned lapwing calls provide relevant and reliable information to Cape ground squirrels.

The long latency to relax in Cape ground squirrels after the lapwing call is in contrast to their response after the alarm calls of a closely associated species, the yellow mongoose

(Makenbach et al., 2013). In the yellow mongoose study, a long latency in squirrel vigilance occurred only after conspecific alarm calls (Makenbach et al., 2013). Individuals are expected to direct energy to eavesdrop on more reliable and relevant information from species sharing habitat and predators to reduce time spent vigilant (Igic et al., 2019; Palmer & Gross, 2018). Yellow mongoose and Cape ground squirrels share burrows, are of similar body size and share predators, suggesting that alarm calls from mongooses would be as relevant as alarms from lapwings (Makenbach et al., 2013; Waterman & Roth, 2007). If nothing else, the mongoose and squirrel are more similar ecologically and thus the squirrels should have responded longer to the mongoose rather than the lapwings.

Perhaps it is the differences that matter more than the similarities. Heterospecific calls may provide information that is not otherwise available to the eavesdropper (Igic et al., 2019), which would support the community informant hypothesis (Carlson et al. 2020). Lapwings may give different information to the squirrels than can either conspecifics or mongooses scanning from ground level (Makenbach et al., 2013; Waterman & Roth, 2007). Birds may be more informant than mammals about approaching predators because of their good vision, complex alarm calls, and because they are often in elevated positions and as a result can see farther than small ground mammals (Lima & Bednekoff, 1999; Magrath et al., 2015). But crowned lapwings spend most of their time on the ground, nesting and foraging, which would limit their ability to see approaching predators in a similar way to the ground squirrels (Edwards & Waterman, 2011; Ward & MacLean, 1988). However, crowned lapwings not only give auditory signals but also visual ones. When a predator is too close, the lapwings fly up over the predator, continue to call loudly, and follow the predator (Ward & Maclean, 1988; Ward, 1989). Thus the lapwing behaviour would allow the squirrels to determine if the threat were nearby and what direction the potential threat was moving (towards or away from the receiver). This visual information differs from anything the squirrels can receive from conspecifics or mongooses, who cannot be seen from far away because they are always close to the ground (Magrath et al., 2015). In other words, these birds can give different information from small terrestrial prey, improving the overall knowledge of predation risk (Magrath et al., 2015) beyond that of just of conspecifics and the mongoose. The use of only the auditory component of lapwing signals in our playback study could have influenced the response of our focal squirrels, yet we still saw a change in the vigilance of the squirrels with only the auditory component.

Our results support that Cape ground squirrels eavesdrop on crowned lapwing calls, suggesting that they collect important information on predation risk from more than just conspecifics. Ignoring heterospecific alarm calls could result in death. The ability of lapwings to fly up and follow potential predators provides reliable and relevant information that is not available to the squirrels via conspecifics or through other ground-dwelling neighbours and may allow the squirrels to allocate more time to foraging and reduce the energy needed to assess risk. Future studies should be aimed at determining if crowned lapwings are eavesdropping on Cape ground squirrel alarm calls making it a mutualistic relationship. Associations between heterospecific eavesdropping species are beginning to be understood. Identifying how information on predators is spread and used by prey communities (particularly eavesdropping) is an important component to our understanding of interspecific interactions.

Supplementary file

Figure S1. Spectrogram examples of alarm calls of a) crowned lapwing (call ID 1) and b) Cape ground squirrel (call ID 3).

Table S1. List of the specific recordings each focal female squirrel received.

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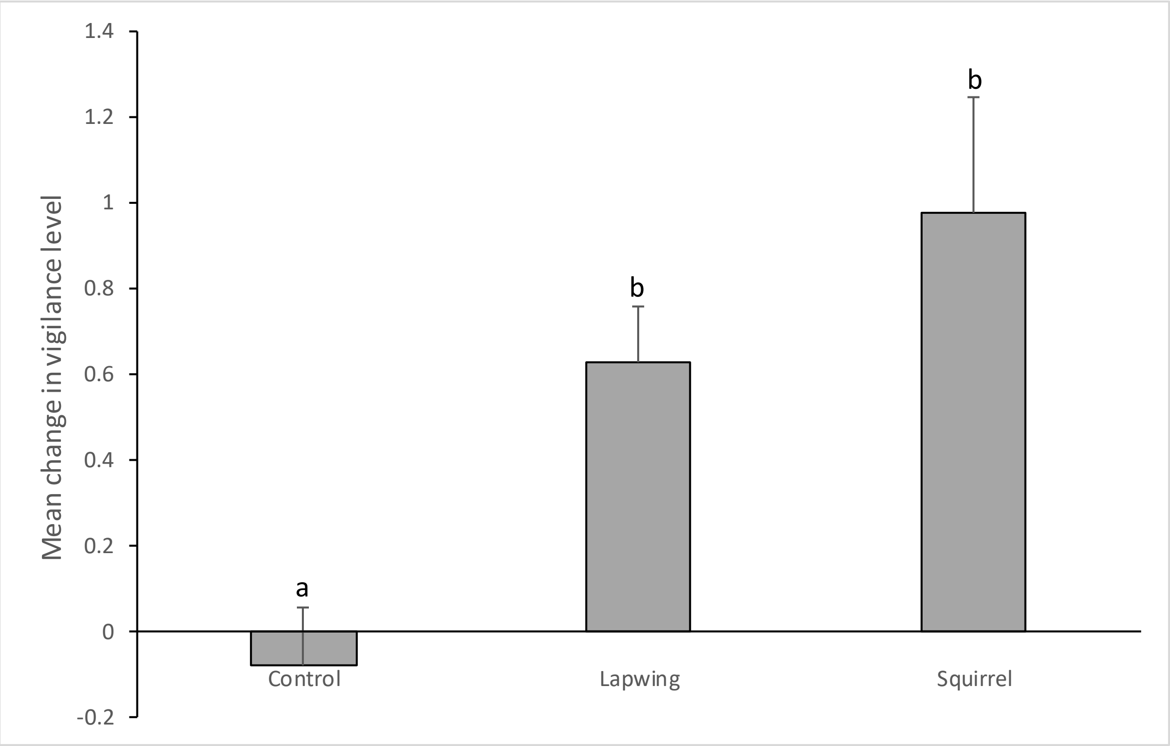
Figure Legends

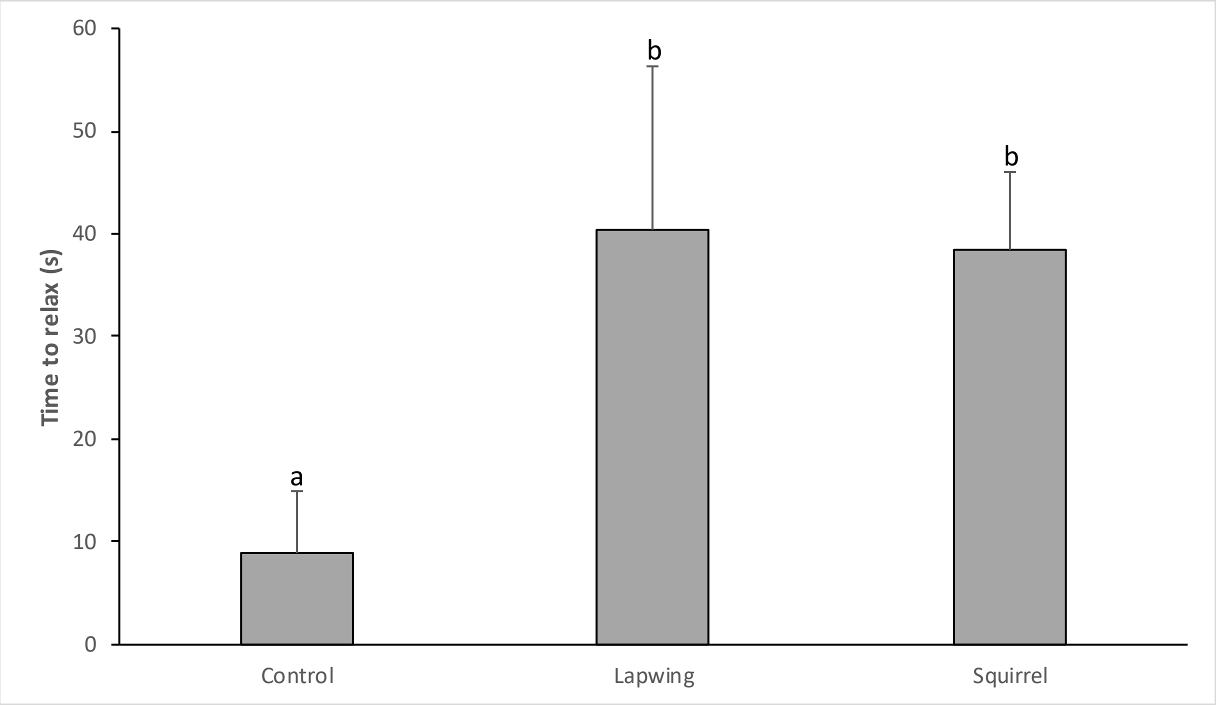
Figure 1. Change in levels of vigilance (mean ± SE) of 11 female Cape ground squirrels in a 60 second period before and after a playback using control (white noise), crowned lapwing calls (heterospecific calls) and ground squirrel calls (conspecific calls). Bars with different letters indicate significant differences ($P < 0.05$; Tukey's HSD).

Figure 2. Duration of time to resume the vigilance level before playback (time to relax, mean ± SE) of Cape ground squirrels ($N = 11$ individuals) following playback experiments. Bars with different letters indicate significant differences ($P < 0.05$; Tukey's HSD).

Table 1. The ordinal scale of vigilance levels (lowest to highest) in Cape ground squirrels.

Vigilance level	**Description**
0 (non-vigilant)	Head below shoulders sitting on two feet, with or without feeding; standing on four feet with or without feeding; walking; grooming; digging
1 (low-vigilance)	Head just above shoulders or at shoulder height, sitting upright hunched on two feet without extending legs, feeding
2 (mid-vigilance)	Vertical (standing on hind legs) while feeding or head above shoulders upright, hunched on two feet but not feeding
3 (high-vigilance)	Vertical (standing or sitting on hind legs, spine straight), not feeding; scanning surroundings


Mean change in vigilance level
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
a
b
b
Control
Lapwing
Squirrel


60
50
40
30
20
10
0
Time to relax (s)
a
b
b
Control
Lapwing
Squirrel