

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

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6 Running title: Ground squirrels eavesdrop on lapwing alarm calls
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43
44 **Abstract**

45
46 Animals gather information about their environment from a variety of sources to enable adaptive
47 decision-making behaviour. Eavesdropping on heterospecific alarm calls enhances predator
48 avoidance, reduces time spent vigilant and allows for more time on daily activities such as
49 foraging. If the information is relevant and reliable, individuals that respond to heterospecific
50 signals may benefit from a wider range of information at a low marginal cost. The Cape ground
51 squirrel (*Xerus inauris*) and crowned lapwing (*Vanellus chilensis*) are ground-dwelling species
52 that are taxonomically distant but share similar predators, habitat and anti-predatory behaviours.
53 We used playback experiments of the alarm calls produced by conspecifics and lapwings to
54 investigate the vigilance responses of adult female Cape ground squirrels. Squirrels responded
55 with greater vigilance to both squirrel and lapwing alarm calls and no changes of vigilance levels
56 were observed in response to a control sound. However, contrary to our predictions, changes in

57 vigilance and time to relax did not differ between conspecific versus heterospecific playbacks.
58 The results from our study suggest that squirrels perceive lapwing alarm calls as relevant and
59 reliable information and that responding to it could increase their survival.

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62 **Keywords**

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

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68 **Introduction**

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

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

82 Eavesdropping is the use of information from signals that are produced by nearby callers
83 that are intended for other receivers (Peake, 2005). Eavesdropping on heterospecific alarm calls

84 could greatly enhance predator avoidance and may lead to less time spent in vigilant behaviour
85 and more time for daily activities such as foraging (Makenbach et al., 2013). Furthermore, by
86 responding to signals beyond their own species, eavesdropping allows individuals to gain a wider
87 range of information about their environment at low marginal costs such as attracting the
88 attention of predators (Aschemeier & Maher, 2011; Magrath et al., 2015; Carlson et al., 2020).
89 Thus, eavesdropping can be a low-cost and low-risk behaviour that can be greatly beneficial
90 (Magrath et al., 2015).

91 The ability to recognize heterospecific alarm calls has been demonstrated in a number of
92 vertebrates, including many species of birds and mammals (see Magrath et al., 2020 for a
93 review). In birds, mixed-species flocks are common and species benefit greatly from
94 eavesdropping by decreasing time spent vigilant (Igic et al., 2019; Ridley et al., 2014).
95 Heterospecific alarm call recognition has also been demonstrated in many mammals (e.g.,
96 *Marmota monax* eavesdrop on *Tamias striatus*, Aschemeier & Maher, 2011; *Odocoileus*
97 *hemionus* eavesdrop on *Marmota flaviventris*, Carrasco & Blumstein, 2012; *Helogale parvula*,
98 eavesdrop on *Paraxerus cepapi*, Morris-Drake et al., 2017; *Xerus inauris* and *Cynictis pencilata*
99 mutually eavesdrop Makenbach et al., 2013, and likewise *Marmota flaviventris* and
100 *Callospermophilus lateralis* mutually eavesdrop, Shriner, 1998). Eavesdropping and the ability
101 to recognize heterospecific alarm calls between broader taxonomic gaps exist but it is unknown
102 how commonly they occur (Schmidt et al., 2008). Examples of avian-mammal eavesdropping
103 include primates responding to avian alarm calls (e.g., *Cercopithecus diana* and *Ceratogymna*
104 *elata*, Rainey et al., 2004; *Cercopithecus aethiops* and *Spreo supervus*, Seyfarth & Cheney,
105 1990), as well as squirrel-bird eavesdropping associations (*Cynomys ludovicianus* and *Athene*
106 *cunicularia hypugaea*, Bryan et al., 2014; *Sciurus carolinensis*, and *Turdus migratorius*,

107 Getschow et al., 2013; *Sciurus vulgaris* and *Garrulus glandarius*, Randler, 2006; Schmidt et al.,
108 2008).

109 In many mixed-species associations, some species are better at acquiring and transferring
110 information than others because of differences in their morphology, ecology and physiology, and
111 these species could be considered “sentinel species” (e.g., *Vanellus chilensis*, Cavalli et al.,
112 2018) or “community informants” (Carlson et al., 2020), providing community-wide (public)
113 information (Breed, 2017). Community informants are species that provide reliable information
114 (information sources; Carlson et al., 2020). However, not all species may be able to take
115 advantage of this public information (Getschow et al., 2013; Magrath et al., 2009; Meise et al.,
116 2018). The ability to detect and interpret heterospecific alarm calls may differ from conspecific
117 calls because of either differences in the call structure or because the heterospecific calls may
118 encode different information from the conspecific calls or both (Getschow et al., 2013). Thus
119 conspecific calls may be more reliable than heterospecific calls (Getschow et al., 2013). However,
120 structural similarity is not a pre-requisite of successful eavesdropping as call similarity did not
121 explain the response of superb fairy-wrens (*Malurus cyaneus*) to heterospecific alarm calls
122 (Magrath et al., 2009) or the response of vervet monkeys (*Cercopithecus aethiops*) to the alarm
123 calls of superb starlings (*Spreo superbus*; Seyfarth & Cheney, 1990).

124 If an individual can recognize heterospecific alarm calls, the value of eavesdropping on
125 these alarm calls can depend on the relevance and reliability of the callers (Magrath et al., 2015;
126 Meise et al., 2018). An alarm call is relevant if it is given to threats that endanger the
127 eavesdropper (i.e., they have predator overlap or vulnerability to the same predators; Carrasco &
128 Blumstein, 2012; Goodale et al., 2010; Meise et al., 2018; Templeton, 2018). It is reliable if
129 those threats are present and not false to avoid wasting time responding to deceptive alarm calls

130 in the absence of predators (Magrath et al., 2015; Searcy & Nowicki, 2005). The ability to
131 recognize relevant and reliable heterospecific alarm calls may increase the eavesdropper's fitness
132 (Meise et al., 2018).

133 The Cape ground squirrel (*Xerus inauris*) and crowned lapwing (*Vanellus coronatus*)
134 belong to taxonomically distant groups. Both are ground-dwelling species of similar size (ground
135 squirrel 23.5-28.2cm, Herzig-Straschil, 1978; crowned lapwings 30-31cm, Hockey et al., 2005)
136 that co-occur in open shortgrass areas of southern Africa where they share similar predators and
137 produce alarm calls in response to potential danger (Hockey et al., 2005; Müller & Manser,
138 2008; Unck et al., 2009; Waterman, 1995). In response to the playbacks of conspecific alarm
139 calls, Cape ground squirrels will either run to their burrow or become more vigilant (Furrer &
140 Manser, 2009) and the vigilance of the squirrels increases with increasing distance to their home
141 burrows (Unck et al., 2009). Cape ground squirrels increase their vigilance in response to
142 heterospecific alarm calls produced by another similar-sized mammal (yellow mongoose,
143 *Cynictis pencilata*; Makenbach et al., 2013). However, it is unknown if they will respond to the
144 alarm calling of a more distantly related lapwing species (Skinner & Chimimba, 2005),
145 especially as spectrograms of their alarm calls reveal very different call structures between the
146 two species (see Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988;
147 Supplemental Figure S1). Lapwing alarm vocalizations consist of repeated calls that increase in
148 rate and volume as a predator nears, whereas squirrel alarm vocalizations are less complex
149 shorter repeated calls (Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988).

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

153 9 mo.) breed. A family group lives in a burrow system separated from other families by a few
154 hundred meters and there is little overlap in the home ranges of different groups (Waterman,
155 1995; Waterman & Archibald, 2019). Most of their time spent above ground is devoted to
156 feeding on grasses (Herzig-Straschil, 1978; Waterman, 1995). Cape ground squirrels use
157 urgency-dependent repeated alarm calls but do not appear to use referential calls (Herzig-
158 Straschil 1978; Furrer & Manser 2009).

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

168 The objective of this study was to determine if Cape ground squirrels eavesdrop on the
169 heterospecific alarm calls of sympatric crowned lapwings. As conspecific calls are predicted to
170 be more reliable and relevant (conspecific reliability hypothesis), we predict that Cape ground
171 squirrels will have the highest response (higher vigilance) and longer time to relax upon hearing
172 a conspecific alarm call, followed by lapwing calls and no response to a control sound.

173 However, if lapwings are community informants (Carlson et al., 2020), then they may be able to
174 detect and assess predator threats as well or better than a squirrel's conspecifics ('community
175 informant' hypothesis) and we predict Cape ground squirrels will have a higher (or equal)

176 response (higher vigilance, longer time to relax) and no response to a control sound. Likewise,
177 their time to relax should be longest upon hearing a conspecific alarm call, but since lapwing
178 alarm calls may offer information about a potential threat, the time to relax should be longer in
179 after hearing a lapwing call than a control sound (Makenbach et al., 2013).

180

181 **Methods**

182 Study site

183 The study was conducted at the S.A. Lombard Nature Reserve located near the town of
184 Bloemhof in the North West Province of South Africa (27°35'S, 25°23'E) from May to August
185 2014 during the dry arid winter (Makenbach et al., 2013). The squirrels on this site have been
186 studied since 2002 (Waterman & Archibald, 2019). The 3,359 ha reserve is made up of open
187 grassland with small patches of bush and scattered trees (Makenbach et al., 2013; van Zyl, 1965).
188 Cape ground squirrels and crowned lapwings commonly occur at this site (Hillegass et al., 2008;
189 Skead, 1974) where they share space but they do not aggregate. Aerial and terrestrial predators
190 that can prey on the ground squirrels and lapwings, and that have been sighted hunting on the
191 reserve, include feral cats (*Felis catus*), black-backed jackals (*Canis mesomelas*), caracals
192 (*Caracal caracal*), martial eagles (*Polemaetus bellicosus*), and southern pale chanting goshawks
193 (*Melierax canorus*; Hockey et al., 2005; Skinner & Chimimba, 2005; Unck et al., 2009). Black-
194 backed jackals, eagles and hawks are active throughout the daytime, and caracals are active in
195 the mornings and late afternoons (Hockey et al., 2005; Skinner & Chimimba, 2006), particularly
196 on our study site, which is closed to the public and has low human disturbance.

197

198 Trapping and handling

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

210

211 Creating and recording playback treatments

212 Heterospecific crowned lapwing and conspecific Cape ground squirrel alarm calls were
213 used in a playback experiment to examine the response of focal squirrels (see supplementary
214 Figure S1 for example spectrograms). Three treatments were used in the playback experiments:
215 Cape ground squirrel alarm calls, crowned lapwing alarm calls, and white noise controls (noise
216 made of many frequencies with equal intensities). In this study, an alarm call refers to a single
217 vocalization, which in Cape ground squirrels has four syllables and in the lapwing has one
218 syllable (Figure S1) and a calling bout contains multiple alarm calls in sequence (Furrer and
219 Manser 2009). Repeated calls or call bouts are common in the alarm signalling of ground
220 squirrels (Blumstein and Armitage 1997; Manser 2001; Warkentin et al. 2001). Cape ground
221 squirrel alarm calls were created by opportunistically recording multiple call bouts, in response

222 to a person approaching a squirrel, in June and July 2011 at a sampling rate of 44.1 kHz using an
223 H4Next Handy Recorder (Zoom Co., Japan; see Makenbach et al., 2013 for details). The alarm
224 call bouts from two different females were manipulated using the phonetics program Praat v. 5.2
225 (University of Amsterdam, The Netherlands). These recorded females were not from the same
226 family groups as the focal animals used in our playbacks (see below). In playback studies,
227 different recordings of the same alarm call should be used to avoid pseudoreplication and many
228 different individuals should be recorded (Kroodsma et al. 2001). However, because of the
229 difficulty of approaching squirrels near enough to record high-quality alarm calls, only
230 recordings of the calling bouts from two different females were usable. We constructed two
231 different files from each individual's original alarm calling bouts, using four consecutive
232 syllables in each recording (see Figure S1) to avoid any wind or other background noise,
233 resulting in a total of four playback files (two from each females; mean length 5.34 ± 0.87 s). As
234 Cape ground squirrels use repeated alarm calls in their call bouts and syllable repetition rate can
235 confer response urgency (Herzig-Straschil, 1978; Furrer and Manser 2009), we chose to use only
236 two repeated complete alarm calls in each playback file. We maintained what appeared to be the
237 natural latency between consecutive Cape ground squirrel calls; the latency in our original
238 recordings was 2.4 s on average (measured by hand in Praat, based on the latency between 82
239 syllables; Makenbach et al., 2013). Because crowned lapwings are extremely difficult to
240 approach (Ward & Maclean, 1988; Müller & Manser, 2008), we were unable to get close enough
241 to any crowned lapwings on our study site to make high-quality recordings. Four different sound
242 files (mean length 1.38 ± 0.79 s) of lapwing alarm bouts recorded in South Africa were
243 downloaded from EcoMedia South Africa (Pond5.com) and were also constructed to play two
244 consecutive calls with the latency from the original recording maintained. Only a single

245 individual was calling in each sound file. As crowned lapwings are non-territorial in winter and
246 can move over large areas, particularly outside the summer breeding season (Skead, 1955;
247 Hockey et al., 2005), it is unlikely they have local dialects. Like Cape ground squirrels, crowned
248 lapwings use repeated alarm calls in their call bouts to confer an response urgency (Müller &
249 Manser, 2008), thus the use of only two repeated alarm calls in each lapwing playback file. In
250 addition, Praat was used to create the white noise playback for the control treatment (three
251 different sound files, mean length 1.85 ± 0.01 s; Makenbach et al., 2013).

252

253 Playback experiments

254 In playback trials, we exposed adult female Cape ground squirrels (one individual from
255 each of 11 social groups as our replicate) to three call treatments: Cape ground squirrel alarm
256 calls, crowned lapwing alarm calls, and white noise. The order, and the specific sound file of the
257 recorded alarm call or white noise within each treatment, were chosen randomly by drawing
258 treatment assignments out of a bag. To avoid habituation, we allowed 48 hours between each
259 trial (Makenbach et al., 2013). A Honeytone amplified speaker (Danelectro Co., Camarillo, CA,
260 USA) and H4n Handy Recorder Zoom (Zoom North America, Ronkonkoma, NY, USA) were
261 used to play the .wav files. The volume of the speaker was adjusted before each treatment to
262 reflect natural amplitude (approximately 55-60 dB SPL, measured 1 m from the speaker using
263 the LogSPL app) of the squirrel alarm calls measured from our original calls. The lapwing calls
264 were similarly standardized, as this amplitude matched the level of naturally occurring alarms we
265 perceived by ear (as in Müller & Manser, 2008), and we similarly matched the volume of the
266 white noise, as differences in volume could cause differential responses in the playbacks. The
267 speaker was placed in close proximity to the burrow areas either before the animals emerged in

268 the morning or, if the animal was already above ground, by approaching the focal squirrel and
269 observing which burrow it went in to. When a squirrel moved back into the burrow, time was
270 given for the squirrel to resurface and resume its activity before immergence such that the
271 individual displayed low vigilance behaviours such as allogrooming or foraging. The speaker
272 was always placed within 15 m of the focal squirrel.

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

280 Each social group observed was considered one experimental unit to prevent pseudo-
281 replication as individuals within a social group are usually closely related and may behave
282 similarly. The same adult female from each social group was used for all three trials. All focal
283 animals were older than 2 years of age (range 2 – 8 years) and there were no offspring present
284 for any trials (see Supplementary file, Table S1, for information on female age and playback
285 used). To minimize disturbance of focal squirrels, we did not trap them during the experimental
286 period, so we did not know if they were pregnant. However, no focal female successfully weaned
287 any offspring in the two months following our playbacks. For each playback trial, all behaviours
288 of the focal individual were recorded using the Recordium app v1.0 on an iPhone 5 (iOS 7) for a
289 minimum of 60s before the treatment being delivered and at least 60 s after the playback. The
290 treatment was only administered if the focal individual was exhibiting low vigilance behaviour

291 or was entirely non-vigilant before the playback (see Table 1 for definitions of vigilance levels
292 based on Unck et al. 2009 and Makenbach et al. 2013). Any time spent out of sight was noted
293 and omitted to ensure 60 s of behavioural data was collected before and 60s after the treatment
294 (after Makenbach et al., 2013). To assess changes in vigilance behaviour, we calculated the mean
295 level of vigilance in the 60 seconds before and after the playback. We categorized the intensity
296 of vigilance using an ordinal scale based on the alarm level (Table 1; after Makenbach et al.,
297 2013), and then calculated the weighted mean level of vigilance based on the proportion of time
298 spent in each vigilance level. Using the change in vigilance takes the natural vigilance level of
299 the focal animal before the playback into account. Finally, we calculated the change in vigilance
300 by subtracting the weighted mean vigilance level before the playback from the weighted mean
301 vigilance level after the playback. The number of other squirrels (kin) in proximity (within 15m)
302 to the focal individual was also recorded. Playbacks were made during the day (0800-17h30) at
303 the burrow cluster where the focal squirrel slept.

304

305 Statistical analyses

306 We tested data for normality using Shapiro-Wilk tests. We could not normalize the
307 proportion of time out of sight during the 60 seconds after the playback because in most trials the
308 values were zero. Thus, we used a Friedman's rank test, blocking on individual, to examine if the
309 proportion of time out of sight differed with treatment. To examine the effects of treatments on
310 the change in vigilance after playback, we used general linear mixed models with animal ID as a
311 random effect and treatment and the number of squirrels within 15 metres as fixed effects. We
312 then used Tukey's Honestly Significant Difference (HSD) pairwise tests for post hoc
313 comparisons. To test the effect of different of alarm calls on the duration of response to the calls,

314 we quantified the amount of time (seconds) it took for an animal to return to the vigilance level it
315 exhibited before the playback event (“time to relax” after Manser et al., 2001). For time to relax,
316 we used logarithmically transformed data in the GLMM with animal ID as a random effect with
317 treatment and the number of squirrels within 15 metres as fixed effects. We then used Tukey’s
318 HSD tests for post hoc comparisons among treatments. All statistical analyses were performed in
319 JMP 14.0 (SAS Institute Inc., Cary, NC, USA) and our level of significance (α) was set at 0.05.
320 Unless otherwise indicated, means \pm SE are reported.

321

322 **Results**

323 To determine if Cape ground squirrels eavesdrop on the alarm calls of crowned lapwings, we
324 conducted playback treatments to 11 individual squirrels from 11 different social groups. The
325 mean number of squirrels within 15 m to the focal animals during playback was 1.55 ± 0.30
326 (range = 0 - 5) and it did not influence changes in vigilance levels in response to the playback
327 (GLMM, $F_{1,18.75} = 0.85$, $P = 0.37$). In only one trial, after a heterospecific playback, did an
328 animal run to a burrow, where she became vigilant at the burrow entrance. Mean duration of ‘out
329 of sight’ after a playback averaged 1.84 ± 0.90 sec (lapwing, 1.73 ± 1.04 sec; conspecific, $2.18 \pm$
330 2.20 sec; white noise, 1.64 ± 1.44 sec) and the percent of time spent ‘out of sight’ in the 60
331 seconds after a playback did not differ by treatment (Friedman’s rank test, $\chi^2_{(2)} = 1.7$, $P = 0.42$;
332 lapwing, 2.9 ± 1.7 %; conspecific, 3.6 ± 3.6 %; white noise, 2.7 ± 2.4 %). The change in
333 vigilance in response to the playback differed among treatments (GLMM, $F_{2,19.96} = 9.47$, $P =$
334 0.001 ; Figure 1). The change in vigilance after conspecific calls did not differ from the change in
335 vigilance after lapwing calls (Tukey’s HSD all pairwise comparison, $t_{20} = -1.22$, $P = 0.46$).
336 However, both the change in vigilance after conspecific and lapwing playbacks were

337 significantly greater than the control (Tukey's HSD all pairwise comparisons: conspecific vs.
338 control, $t_{20} = 4.22$, $P = 0.001$; lapwing vs control, $t_{20} = 3.01$, $P = 0.018$).

339 Treatment also affected the time to relax in the squirrels (GLMM, $F_{2,20} = 7.93$, $P = 0.003$,
340 Figure 2) and there was no effect of number of nearby squirrels (GLMM, $F_{1,16.76} = 0.0006$, $P =$
341 0.98). The time to relax was shorter after the control than either the conspecific or lapwing calls
342 (Tukey's HSD all pairwise comparisons: control versus conspecific, $t_{20} = -3.52$, $P = 0.006$,
343 control versus lapwing, $t_{20} = 3.37$, $P = 0.008$), while the time to relax after the conspecific and
344 lapwing calls did not differ (Tukey's HSD all pairwise comparison, $t_{20} = -0.16$, $P = 0.98$, Figure
345 2).

346

347 **Discussion**

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

354 Using the alarm call bouts of only two individual squirrels to create our playback
355 sequences resulted in limited replication in our experimental design (McGregor et al., 1992;
356 Kroodsma et al., 2001). Using calls from multiple individuals is critical to avoid
357 pseudoreplication in playback studies and ideally we would use a new version of the call from a
358 new individual for each trial (Wiley, 2003). Two other factors may limit our conclusions. Firstly,
359 squirrel exemplars were more than twice as long as the crowned lapwing and white noise

360 exemplars. These differences could have led to more information during the squirrel playbacks
361 than the other two playbacks and may have led to different responses by the squirrels. Secondly,
362 using a non-alarm vocalization from the ground squirrels as a control instead of white noise
363 would have created a more natural comparison (Aschemeier and Maher, 2011). Besides alarm
364 calls, Cape ground squirrels make non-alarm vocalizations focused on conspecifics including
365 growls, play calls, and squeaks. The latter two vocalizations, play calls and squeaks are produced
366 by newborns while in the nest (Herzig-Straschil, 1978). The growl vocalization, which is emitted
367 during aggressive interactions amongst conspecifics, could have been used as a control (Furrer
368 and Manser, 2009). However, this vocalization is made at low volumes in very close encounters
369 between conspecifics (Herzig-Straschil, 1978). During playbacks we would have had to use
370 higher volumes of growls, creating an artificially loud growls, suggesting this vocalization would
371 not be an ideal control. An alternative control would be the use of non-alarm vocalizations of
372 some other species living in the area, similar to the controls used in Aschemeier and Maher
373 (2011). While white noise is synthetic, we used an abrupt onset of the white noise, in a similar
374 way to the abrupt onset of alarm calls.

375 Cape ground squirrels produce alarm calls in the presence of predators (Furrer & Manser,
376 2008) and one benefit of grouping in this species is collective detection, which requires the use
377 of alarm calls to warn group members of danger (Edwards & Waterman, 2011). In addition,
378 Cape ground squirrels live and forage in family groups and spatially their closest callers will be
379 their family members (close kin; Waterman & Archibald, 2019), who would be predicted to be
380 more reliable for inclusive fitness reasons (Hare, 1998; Matrosova et al., 2011; Pollard, 2011;
381 Pollard & Blumstein, 2012). In our experiment, we did not find an effect of the number of
382 squirrels within 15m on response, in contrast to Edwards & Waterman (2011), who found that

383 group size affected levels of vigilance. However, not all of our trials had additional group
384 members nearby. In addition, all our experiments were conducted when the focal animal was
385 near to their burrow, when the effects of nearby squirrels on vigilance are not as important as
386 when they have moved away from the safety of the burrow (Unck et al., 2009). Thus, not
387 detecting an effect of squirrel numbers on the vigilance of the focal animal in our experiments is
388 understandable.

389 Contrary to the conspecific reliability hypothesis, the squirrels were as vigilant upon
390 hearing the alarm calls from heterospecifics as they were from conspecifics. Also, and in contrast
391 to what we predicted, time to relax did not differ after conspecific and lapwing alarm calls and
392 their time to relax was significantly longer after either conspecific or heterospecific alarm calls
393 than after the control. It could be that kinship is an important component of reliability, and thus
394 our use of female calls from a different social group could have affected their vigilance levels
395 and time to relax after conspecific calls. Or other differences in our conspecific calls may have
396 affected the focal animal's response, such as the differences in the lengths of the calls. Although
397 call similarity facilitates call recognition across species (Magrath et al., 2009, 2015; Meise et al.,
398 2018), the alarm call structures of Cape ground squirrels and crowned lapwing are very different
399 (see Furrer & Manser, 2009; Müller & Manser, 2008; Ward & Maclean, 1988). Yet Cape ground
400 squirrels still appear to eavesdrop on the calls of lapwings and respond appropriately with
401 increased vigilance. These findings support the hypothesis that crowned lapwing calls provide
402 relevant and reliable information to Cape ground squirrels.

403 The long latency to relax in Cape ground squirrels after the lapwing call is in contrast to
404 their response after the alarm calls of a closely associated species, the yellow mongoose
405 (Makenbach et al., 2013). In the yellow mongoose study, a long latency in squirrel vigilance

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

414 Perhaps it is the differences that matter more than the similarities. Heterospecific calls
415 may provide information that is not otherwise available to the eavesdropper (Igic et al., 2019),
416 which would support the community informant hypothesis (Carlson et al. 2020). Lapwings may
417 give different information to the squirrels than can either conspecifics or mongooses scanning
418 from ground level (Makenbach et al., 2013; Waterman & Roth, 2007). Birds may be more
419 informant than mammals about approaching predators because of their good vision, complex
420 alarm calls, and because they are often in elevated positions and as a result can see farther than
421 small ground mammals (Lima & Bednekoff, 1999; Magrath et al., 2015). But crowned lapwings
422 spend most of their time on the ground, nesting and foraging, which would limit their ability to
423 see approaching predators in a similar way to the ground squirrels (Edwards & Waterman, 2011;
424 Ward & MacLean, 1988). However, crowned lapwings not only give auditory signals but also
425 visual ones. When a predator is too close, the lapwings fly up over the predator, continue to call
426 loudly, and follow the predator (Ward & Maclean, 1988; Ward, 1989). Thus the lapwing
427 behaviour would allow the squirrels to determine if the threat were nearby and what direction the
428 potential threat was moving (towards or away from the receiver). This visual information differs

429 from anything the squirrels can receive from conspecifics or mongooses, who cannot be seen
430 from far away because they are always close to the ground (Magrath et al., 2015). In other
431 words, these birds can give different information from small terrestrial prey, improving the
432 overall knowledge of predation risk (Magrath et al., 2015) beyond that of just of conspecifics and
433 the mongoose. The use of only the auditory component of lapwing signals in our playback study
434 could have influenced the response of our focal squirrels, yet we still saw a change in the
435 vigilance of the squirrels with only the auditory component.

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

447

448 Supplementary file

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

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

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615 **Figure Legends**

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

620

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

624

625

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

627

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

628



