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1 **Multiple adaptive and non-adaptive processes determine responsiveness to heterospecific alarm**  
2 **calls in African savanna herbivores**

3

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8

9 **Abstract**

10 Heterospecific alarm calls may provide crucial survival benefits shaping animal behaviour. Multi-  
11 species studies can disentangle the relative importance of the various processes determining these  
12 benefits, but previous studies have included too few species for alternative hypotheses to be tested  
13 quantitatively in a comprehensive analysis. In a community-wide study of African savanna herbivores  
14 we here, for the first time, partition alarm responses according to distinct aspects of the signaller-  
15 receiver relationship and thereby uncover the impact of several concurrent adaptive and non-  
16 adaptive processes. Stronger responses were found to callers who were vulnerable to similar  
17 predators and who were more consistent in denoting the presence of predators of the receiver.  
18 Moreover, alarm calls resembling those of conspecifics elicited stronger responses, pointing to  
19 sensory constraints, and increased responsiveness to more abundant callers indicated a role of  
20 learning. Finally, responses were stronger in risky environments. Our findings suggest that mammals  
21 can respond adaptively to variation in the information provided by heterospecific callers but within  
22 the constraints imposed by a sensory bias towards conspecific calls and reduced learning of less  
23 familiar calls. The study thereby provides new insights central to understanding the ecological  
24 consequences of interspecific communication networks in natural communities.

25

26 Keywords: Interspecific communication network, alarm calls, adaptive response, mixed-species  
27 groups, herbivores

**28 Introduction**

29 Most studies investigating the role of communication in animal behaviour have focused on single-  
30 species groups [1, 2]. However, there is increasing interest in information transfer between species,  
31 and its role in shaping behaviours of animals living in mixed-species groups [3-5]. In particular,  
32 communication between species about predation risk often may have substantial fitness  
33 consequences by increasing survival chances during an attack [6, 7]. Although interspecific  
34 communication benefits can be fundamentally important for social dynamics between species [8-  
35 10], the principles underlying behavioural responses to heterospecific informants remain poorly  
36 understood.

37         The value of heterospecific as informants depends on their ability to detect a predator, their  
38 likelihood of emitting an alarm call upon detection, and the extent to which they are vulnerable to  
39 the same predators as the receiver, i.e. the predator overlap [1, 10]. Where the predator overlap is  
40 only partial, the reliability of heterospecific alarm calls may be reduced by ‘false positives’ (i.e.  
41 erroneously indicating a predator when none is present from the perspective of the receiver),  
42 whereas the consistency of a heterospecific alarm caller in denoting predator presence may be  
43 reduced by ‘false negatives’ (i.e. not indicating the presence of a predator from the perspective of  
44 the receiver) [2, 7]. Accordingly, significant differences can be expected in the survival benefits that a  
45 species gains by responding to alarm calls of different heterospecifics.

46         But are animals able to respond adaptively to these differences in the information provided  
47 by heterospecific alarm calling? Some studies have indeed found alarm responses to depend on  
48 predator overlap [11, 12], call reliability and caller consistency [13-16]. Still, other studies indicate  
49 that responses are also influenced by the similarity of the acoustic structure to the conspecific  
50 alarms [17, 18], suggesting that sensory bias limits the ability to extract information from  
51 heterospecific alarm calls. Yet other studies have found a positive correlation between responses to  
52 heterospecific alarm calls and familiarity with the calling species [19-21], indicative of learning.  
53 These hypotheses are not mutually exclusive and responses to heterospecific alarm calls may well be

54 the result of several factors operating simultaneously [6]. However, the limited number of species  
55 included in previous studies of interspecific alarm communication has precluded simultaneous  
56 statistical assessment of the various explanations proposed.

57         The alarm communication network of African savanna herbivores is an ideal system in which  
58 to study the relative importance of the factors purported to influence interspecific communication.  
59 In this system, multiple species are commonly found in mixed-species groups [22, 23], and  
60 heterospecifics therefore have the potential to act as an important source of information about  
61 predation risk. Moreover, the species-rich guild provides pronounced diversity in key ecological  
62 variables, such as morphology, predator vulnerability, and species abundance [24-26], and extensive  
63 variation can therefore be expected in the information content of heterospecific alarms and the  
64 associated detection benefits.

65         In the present study, we first establish the information content of the alarm calls of each  
66 herbivore species by identifying which predators trigger them. This allows us to assess to what  
67 extent species-specific alarms reflect the vulnerability to predators (Table 1, H1). Next, we  
68 investigate the various adaptive and non-adaptive hypotheses proposed to explain the function of  
69 interspecific communication networks (Table 1). Specifically, we test whether herbivores respond  
70 more strongly to alarm calls from species with whom predator overlap is high (H2), alarms calls from  
71 species who are more consistent in indicating when predators of the receiver are present (H3.1),  
72 alarm calls which more reliably indicate a predator to which the receiver is vulnerable (H3.2), more  
73 familiar alarm calls (H4), and alarm calls acoustically similar to those of the receiver (H5).  
74 Additionally, we test if responsiveness to alarm calls depends on environmental factors related to  
75 predation risk (H6). The species-rich study system allows us for the first time, to our knowledge, to  
76 quantitatively test the impact of interspecific relationships on alarm responses, and thereby gain  
77 new insights into the adaptive value of heterospecific alarm communication networks.

78

79 **Methods**

80 *Study system*

81 The study was conducted between September 2015 and October 2016 in the Masai Mara National  
82 Reserve, Kenya, which is part of the Serengeti-Mara Ecosystem and characterised by open savanna  
83 grassland and riverine forests. We focused on the 12 most common species in the herbivore  
84 community: Thomson gazelle (*Gazella thomsonii*, 'Tho'), Grant gazelle (*Gazella granti*, 'Gra'), impala  
85 (*Aepyceros melampus*, 'Imp'), common warthog (*Phacochoerus aethiopicus*, 'War'), ostrich (*Struthio*  
86 *camelus*, 'Ost'), topi (*Damaliscus lunatus*, 'Top'), hartebeest (*Alcelaphus buselaphus*, 'Har'), blue  
87 wildebeest (*Connochaetes taurinus*, 'Wil'), plains zebra (*Equus quagga*, 'Zeb'), African buffalo  
88 (*Syncerus caffer*, 'Buf'), common eland (*Tragelaphus oryx*, 'Ela'), and giraffe (*Giraffa Camelopardalis*,  
89 'Gir'). Their main predators include the lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), leopard  
90 (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and black-backed jackal (*Canis mesomelas*).

91

92 *Ecological and morphological species characteristics*

93 To calculate the relative abundance of the study species, we conducted a total of 66 censuses at  
94 approx. 16-day intervals on three study plains, covering a total of 54km<sup>2</sup>. We then determined  
95 relative abundance of the study species from the mean number of individuals recorded per census.  
96 We used abundance data of all predator species collected by Broekhuis [27] during transects to  
97 calculate relative predator abundance. Vulnerability to predators was quantified using the Jacob's  
98 index [28-32] (transformed to values between 0 and 1, with values close to 1 indicating a high  
99 vulnerability to predators). Since no indices were given for the preference of the black-backed jackal  
100 for Thomson and Grant gazelles, we used the value reported for the closely related springbok  
101 (*Antidorcas marsupialis*) which is similar in size, speed and ecological niche. Body size ratio between  
102 caller and receiver was calculated based on the mean adult body mass [24, 33]. Following Lovich and  
103 Gibbons [34], we calculated the body size ratio as [receiver mass : caller mass] when the receiver  
104 was larger, and [2-(caller mass : receiver mass)] when the receiver was smaller than the caller.

105

106 *Call reliability and caller consistency*

107 To determine the probability with which species-specific alarm calls denoted the various predators  
 108 (i.e. their information content), we conducted a predator simulation experiment where we exposed  
 109 the study species to life-sized lateral photographs of their five main predators (see ‘Study system’)  
 110 and a reedbuck (*Redunca redunca*) as control. The two-dimensional models were presented to  
 111 monospecific groups (for details on the experimental design see S2). Once the first animal in the  
 112 group detected the model (i.e. looked straight at the model with pointed ears), we noted the  
 113 occurrence of alarm calls emitted over the next 5 minutes. We determined the distance to the  
 114 model (using a laser range finder, Bushnell Scout DX 1000 ARC), group size, and the presence of  
 115 young individuals (i.e. less than half the adults’ body shoulder height). In total, we conducted 649  
 116 predator simulations aiming for an even distribution of simulations between the predator-herbivore  
 117 combinations (mean  $\pm$  s.e. = 9.05  $\pm$  0.26).

118 In order to identify the relative importance of falsely negative and falsely positive alarm calls  
 119 in the interspecific communication, we distinguished the value of an alarm caller from the value of a  
 120 single alarm call as information sources. Hence we differentiated between (i) the consistency of an  
 121 alarm caller in denoting the presence of the receiver’s predators whenever these are present, and  
 122 (ii) the reliability of a single alarm call in indicating a predator to which the receiver is vulnerable.  
 123 The caller consistency was calculated as the probability that an alarm call is emitted when the  
 124 signaller is presented with a given predator model, weighted by the relative probability of  
 125 encountering that predator, multiplied by the vulnerability of the receiver to that predator, summed  
 126 over all predators in the system:

$$127 \quad L(i, j) = \sum_{x=1}^n I_{xj} \varepsilon_{ix} A_x,$$

128 where  $i$  denotes the species identity (ID) of the receiver;  $j$  denotes caller species ID;  $n$  denotes the  
 129 number of predator species;  $I_{xj}$  denotes the probability that species  $j$  gives an alarm call in response  
 130 to a model of predator  $x$ ;  $\varepsilon_{ix}$  denotes the preference of predator  $x$  for species  $i$ ; and  $A_x$  denotes the

131 relative abundance of predator  $x$ . A high value of  $L(i,j)$  (close to 1) suggests that species  $j$  is highly  
132 likely to inform about the presence of species  $i$ 's predators.

133 Following Magrath et al. [13], we calculated the reliability of a species' alarm call as:

$$134 \quad V(i,j) = \sum_{x=1}^n C_{xj} \varepsilon_{ix} A_x,$$

135 where  $C_{xj}$  denotes the proportion of alarm calls of species  $j$  elicited by the model of predator  $x$  when  
136 models of all predators are presented with equal frequency. A high value of  $V(i,j)$  (close to 1)  
137 indicates that an alarm call of species  $j$  is likely to be directed to a predator to whom species  $i$  is  
138 highly vulnerable.

139 Note that we thus distinguish callers and calls as being more or less consistent respectively  
140 reliable (a continuous approach) rather than as being true or false (a categorical approach).

141

#### 142 *Acoustic structure of alarm calls*

143 Alarm calls were collected ad libitum during natural predator-prey encounters observed during  
144 previous field work in the study area (2011-2016) using a digital audio recorder (Marantz PMD670)  
145 with a directional microphone (Sennheiser ME67). Given the stereotypic acoustic structure of alarm  
146 calls within each species, we combined all the alarm calls according to species for further analysis  
147 (see S2 for details). We analysed 10 high-quality calls from different individuals of each study species  
148 except the ostrich ( $n = 9$ ) and the eland ( $n = 0$ ; alarm calls were never heard during previous long-  
149 term fieldwork on the species in the study area and therefore considered unimportant, [35]). The  
150 acoustic similarity between alarm calls was quantified as (1-Euclidean distance) using the following  
151 variables: duration, visibility of harmonics, number of distinct structural components, presence of  
152 pulses, the 25% energy quartile, the bandwidth between the 25% and the 75% energy quartiles, and  
153 the 3<sup>rd</sup> dominant frequency, DF3 (because DF1, DF2 and DF3 were highly correlated, we only  
154 included DF3 which showed most interspecific variation and best separated species; for details on  
155 the acoustic analysis see S2). Each measure was standardised by dividing each value by the  
156 maximum value of this measure to ensure equal weighting of variables.



157

158 *Alarm responses*

159 For the playback experiment, we selected six high quality recordings from each of the 11 vocal study  
160 species, three from each sex. As a control we used three recordings of a non-alarm call from the  
161 ring-necked dove (*Streptopelia capicola*), which is frequently heard throughout the study area. Using  
162 a digital sound level meter (UNI-T, model UT352), we determined species-specific alarm call intensity  
163 at 35 m distance in the wild, and subsequently we adjusted playback volume to natural levels by  
164 matching sound level meter measurements at this distance, where average intensity for the study  
165 species ranged from 54dB to 67dB.

166 We conducted a total of 2433 playback experiments following a balanced design in terms of  
167 the species and sex of both caller and receiver (for each caller-receiver combination: mean  $\pm$  s.e. =  
168  $17.7 \pm 0.43$ ). The playback experiments were targeted at animals which were relaxed and foraging  
169 for at least 20s prior to the experiment, and the response was recorded using a digital video camera  
170 (Sony HDR-PJ810E). For each experiment, we recorded wind speed (using an anemometer, Proster  
171 Digital LCD), distance of the focal animal (using the laser rangefinder), group size, and estimates of  
172 grass height and proximity to cover (for details on the playback design see S2).

173 We analysed the playback videos using BORIS (Behavioural Observation Research Interface  
174 Software, [36]). Responses were coded both as a binary variable, where a response was defined as  
175 any behavioural change taking place within 10 seconds after the playback sound, and as continuous  
176 variables, where response strength was measured by the latency to first response, speed of head-  
177 lifting, time until foraging was resumed for at least 10 sec, and number of head-ups and scratches  
178 (S1).

179

180 *Statistical analysis*

181 All analyses were performed in R3.4.0 [37]. Model selection was based on the Akaike Information  
182 criterion for small sample sizes (AICc)(*MuMIn* package, [38]; for full model descriptions see S3 and

183 S4). Results presented refer to the models with the lowest AIC. *P*-values for mixed models were  
184 obtained using the Kenward-Rogers method for linear mixed models and likelihood ratio tests for  
185 generalized linear mixed models (*afex* package, [39]). Integer variables were standardized by mean  
186 centering and scaling by the standard deviation. Final models were checked for overdispersion and  
187 multicollinearity. For linear models, we additionally checked normality and homoscedasticity of  
188 residuals. For three variables the assumption of normality was violated, but after log-transforming  
189 the response variable all model assumptions were met.

190 To assess the information content of alarm calls (H1), we modelled the probability of giving  
191 an alarm call as a function of predator identity using logistic regression (*lme4* package, [40]). Initially,  
192 we included focal species ID, model type (predator/control), and their interaction term as  
193 explanatory variables. This confirmed that all species had a higher probability of giving an alarm call  
194 when presented with a predator model compared to the control ( $n = 626$  experiments;  $b = 1.35$ ,  $z =$   
195  $4.61$ ,  $p < 0.001$ ). We subsequently tested the effect of species-specific predator vulnerabilities on the  
196 probability of alarm calling to the five predator models, including focal species ID, predator  
197 vulnerability, their interaction, distance to the model, group size, and the presence of young as  
198 explanatory variables (M1,  $n = 522$  experiments).

199 To determine species-specific differences in alarm responses, we modelled response  
200 probability as the binary response variable in a logistic regression model with receiver species ID, call  
201 type (conspecific/heterospecific/control), their interaction, grass height, proximity to cover, distance  
202 to speaker, wind speed, and group size as explanatory variables ( $n = 2433$  experiments). As the  
203 response probability differed significantly between control and alarm sounds (conspecific call:  $b =$   
204  $3.20$ ,  $z = 10.00$ ,  $p < 0.001$ , heterospecific call:  $b = 2.37$ ,  $z = 9.62$ ,  $p < 0.001$ ) and individuals were no  
205 more likely to raise their heads during control playbacks than during undisturbed foraging bouts  
206 (Wilcoxon signed rank test:  $V = 55$ ,  $p = 0.117$ ), we removed the control sound from further analyses,  
207 replacing call type with caller species ID (M2,  $n = 2334$  experiments).

208 To assess the adaptive value of alarm calls (H2-H6), we analysed the probability to respond  
209 to heterospecific alarm calls using a binomial mixed effect model with logit-link function with the  
210 following explanatory variables: receiver's body size, body size ratio (including linear and quadratic  
211 terms as we expected the highest responsiveness to callers of the same size), the interaction  
212 between the body size ratio (linear and quadratic term), caller consistency, call reliability, acoustic  
213 similarity and abundance of the caller. Additionally, we included grass height, proximity to cover,  
214 distance to speaker, wind speed, and group size (M2.1,  $n = 2030$  experiments); receiver species ID  
215 was included as a random factor. Response strength was analysed using separate log-linear mixed  
216 models for latency (M2.2,  $n = 1529$  experiments), duration (M2.3,  $n = 1429$  experiments) and speed  
217 of head-lifting (M2.4,  $n = 1466$  experiments), and generalized linear mixed effect models with  
218 negative binomial distribution for the number of head-ups and scratches (M2.5, M2.6,  $n = 1380$   
219 experiments); the explanatory variables and the random factor were the same as in the previous  
220 model.

221

## 222 **Results**

223 *Do information content of alarm calls and receiver responses differ between species?*

224 The study species differed in their general probability of alarm calling when exposed to a predator  
225 model (M1,  $\chi^2_{11,510} = 249.43$ ,  $p < 0.001$ ; figure 1A), and the probability that a species would alarm call  
226 to a given predator model depended on its vulnerability to that predator ( $b = 1.76$ ,  $z = 3.89$ ,  $p <$   
227  $0.001$ ) (H1). This indicates that both the consistency of the caller and the reliability of the alarm calls  
228 differ significantly between species that vary in predator overlap. In line with this finding, individual  
229 species showed pronounced asymmetries in their probability of responding to alarm calls from  
230 different species (M2,  $\chi^2_{11,2322} = 129.00$ ,  $p < 0.001$ ), leading to a directed communication network  
231 among savanna herbivore species (figure 1B). Individuals were generally more responsive to  
232 conspecific alarm calls than to heterospecific alarm calls ( $b = 0.96$ ,  $z = 4.15$ ,  $p < 0.001$ ).

233

234 *Are responses to heterospecific alarm calls adaptive or non-adaptive?*

235 Responsiveness was highest towards alarm calls of similar-sized and slightly larger heterospecifics  
236 (response probability (M2.1), latency (M2.2), duration (M2.3), scratches; Table 2; figure 2B),  
237 indicating that herbivore species with similar predators are more likely to react to each other's alarm  
238 calls (H2). Moreover, larger species were generally less responsive (response probability (M2.1),  
239 latency (M2.2), speed of head-lift (M2.4), scratches (M2.6); Table 2; figure 2A), and the significant  
240 interaction between receiver's body size and the body size ratio indicates that they are less sensitive  
241 to body size differences between caller and receiver (duration (M2.3), scratches (M2.6); Table 2).

242         Responsiveness was furthermore higher to alarm calls from those heterospecifics who were  
243 more consistent as informants (head-ups (M2.5); Table 2; figure 2E), suggesting that receivers are  
244 sensitive to false negatives (H3.1). We found no independent effect of the reliability of the alarm call  
245 itself (M2.1-M2.6, Table 2), suggesting that any effect of emitting false positives was negligible  
246 (H3.2).

247         Responsiveness moreover increased with the abundance of the caller species (response  
248 probability (M2.1), duration (M2.3); Table 2; figure 2C), suggesting that alarm responses are  
249 enhanced by learning (H4). In addition, responsiveness increased with similarity in the acoustic  
250 structure of the call to the receiver's own alarm call (response probability (M2.1), latency (M2.2),  
251 duration (M2.3); Table 2; figure 2D), indicating that sensory constraints affect alarm responses (H5).

252         Finally, responsiveness increased with grass height (response probability (M2.1), duration  
253 (M2.3), head-ups (M2.5), scratches (M2.6); figure 2F), wind speed (response probability (M2.1),  
254 latency (M2.2), duration (M2.3)), and proximity to the caller (latency (M2.2)), whereas no significant  
255 effects were found of proximity to cover, or group size (S4). These results support that the  
256 environmental context can affect alarm responses (H6).

257         These findings show that the responses of African savanna herbivores to heterospecific  
258 alarm calls are shaped by a range of factors which are partly adaptive, as indicated by the effects of  
259 body size similarity, caller consistency, and grass height which affects predation risk, but also partly

260 non-adaptive, notably depending on the acoustic similarity between the con- and heterospecific  
261 calls.

262

### 263 **Discussion**

264 Prey species often obtain information about the presence of predators from heterospecific alarm  
265 calls. Although this use of public information is widespread, we still know little about how individuals  
266 process other species' alarm calls [7]. In the present study, we established the information content  
267 of alarm calls from the community of African savanna herbivores and then quantified species-  
268 specific alarm responses in order to test the relative importance of different adaptive and non-  
269 adaptive processes. Our results indicate that responses to heterospecific calls increase with the  
270 predator overlap between caller and receiver, the consistency of the caller from the perspective of  
271 the receiver and the predation risk in the environment, suggesting that part of the response to  
272 heterospecific alarm calls is adaptive. However, we also found an independent effect of acoustic  
273 similarity, which indicates that perception is limited by sensory constraints. These findings reveal  
274 that the alarm communication network of savanna herbivores is the outcome of multiple forces  
275 acting simultaneously.

276 Both predation and resource limitation are crucial factors in the regulating the herbivore  
277 populations of the African savanna [41], and a primary expectation of our study was therefore that  
278 the study species are optimizing the trade-off between benefits from increased predator detection  
279 and costs from reduced foraging in their responsiveness to heterospecific alarm calls [42, 43]. In  
280 particular, strong selection was expected to favour increased responsiveness to species sharing  
281 similar predators. We indeed found that receivers respond more strongly to alarm calls from similar-  
282 sized or slightly larger species with whom predator overlap is high (H2, Table 1). Receivers may  
283 therefore use an awareness of similarity in predator vulnerability to assess the importance of alarm  
284 calls from heterospecifics.

285           In this study, we moreover distinguished the reliability of a single alarm call in denoting a  
286 predator of the receiver from the consistency of the heterospecific caller in denoting when a  
287 predator of the receiver was present. In doing so, we identified an effect of the consistency of the  
288 caller (i.e. few false negatives, H3.1), but not the reliability of the alarm call (i.e. few false positives,  
289 H3.2). This suggests that it is more important that a heterospecific consistently alarm calls when  
290 encountering a predator of the receiver than whether the heterospecific also gives irrelevant alarm  
291 calls to carnivores which are not predators of the receiver. It is possible that the consistency in  
292 hearing a given heterospecific calling whenever a predator is encountered facilitates learning of the  
293 information content of the alarm call. This explanation is supported by the increased responsiveness  
294 to alarm calls from more abundant species: learning of their alarm calls is likely to be facilitated by  
295 hearing them more frequently (H4). An effect of learning is consistent with the conclusion of a  
296 previous study of fairy-wrens (*Malurus cyaneus*) in which the fact that heterospecific alarms only  
297 elicited alarm responses in sympatry, and not in allopatry, was interpreted as demonstrating a role  
298 of learning [20, 44, 45]. While this single-species study was also able to conclude that call similarity  
299 was 'neither sufficient nor necessary for interspecific recognition' (p. 769), our multi-species study  
300 demonstrates that there is still an additional effect of acoustic similarity on alarm responses at the  
301 community level (H5). This is consistent with other studies which have reported unlearned  
302 responses to acoustically similar heterospecific calls where responses to conspecific alarm calls are  
303 innate [12, 17, 46]. Hence our study suggest that although both awareness of the social environment  
304 and associative learning of acoustic signals shape alarm responses, sensory bias limits the flexibility  
305 in responding adaptively to heterospecifics calls depending on their similarity to that of conspecifics.  
306 Further studies are needed to fully understand the underlying cognitive processes.

307           Our findings also suggest that herbivores adjust their alarm responses to environmental  
308 factors increasing predation risk [47] (H6). Stronger responses were found to alarm calls when heard  
309 on plains with longer grass. This is likely an adaptive precaution since stalking predators are  
310 dependent on cover provided by the grass to get sufficiently close to their prey to launch a

311 successful attack on open plains [48]. It is also conceivable that enhanced food abundance on long  
312 grass swards diminishes the costs from foraging foregone when responding to alarms. Alarm calls  
313 moreover elicited stronger responses when heard from a closer distance, again suggesting adaptive  
314 adjustment to heightened predation risk. Finally, stronger responses under windy conditions can  
315 likewise be explained as an adaptation to increased risk of predation [49]. Ungulates are known to  
316 increase group size and seek safe habitats as antipredator precautions under windy conditions  
317 where their ability to detect predators decreases [50]. Although we only played alarm calls at wind  
318 speeds that assured their detection by the intended receiver, distortion of transmission may still  
319 have impeded the localisation of predators by acoustic and olfactory cues at the higher wind speeds  
320 below this threshold.

321 The array of factors demonstrated to simultaneously influence the responses to  
322 heterospecific alarm calls in this study highlights the importance of multivariate analysis at the  
323 species level in deciphering interspecific alarm communication networks. Insights into the relative  
324 importance of the crucial factors in turn deepen our understanding of the social landscape in which  
325 interspecific interactions unfold. In particular, the role of communication as a driver of social affinity  
326 between species and the formation of mixed-species groups requires an in-depth understanding of  
327 both the information content encoded in alarm calls and how this information is decoded by the  
328 receiver. We have here shown that alarm responses of savanna herbivores are only partly adaptive  
329 and that an appreciation for limitations to adaptation is likely to be critical for understanding the  
330 role of interspecific communication in shaping ecological processes.

331

### 332 **Ethical statement**

333 All experiments adhere to guidelines of the Kenya Wildlife Service and have been approved under  
334 the following permits: NACOSTI/P/14/5838/3377 (Kenyan National Commission for Science,  
335 Technology, and Innovation), KWS/BRM/5001 (Kenya Wildlife Service) and  
336 NCG/MMN/R/R/VOL.V/39 (Narok County Government).

337

338 **Data accessibility**

339 Data are available from the Dryad Digital Repository: doi:10.5061/dryad.mb7dd20.

340

341 **Competing interests**

342 We have no competing interests.

343

344 **Author's contributions**

345 KM collected the field data, designed and performed the statistical analysis, and drafted the  
346 manuscript; DWF contributed to the study design and manuscript preparation; JBJ conceived and  
347 designed the study, contributed to the fieldwork and manuscript preparation. All authors gave final  
348 approval for publication.

349

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356

357

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362



363 **Table captions**

364 Table 1: Hypothetical framework.

365 Table 2: Responsiveness to heterospecific alarm calls in the savanna herbivore community.

366

367 **Figure labels**

368 Figure 1: Communication network of African savanna herbivores. (A) Species-specific differences in  
369 the probability of alarm calling in relation to predator vulnerability. (B) Species-specific dependency  
370 on heterospecific alarm calls. Arrows point to species in which alarm calls elicited a response with  
371 edge weight representing response probability (cut-off point: 0.72). Node-size indicates the number  
372 of species whose alarm calls caused a response (for species abbreviations, see 'Study system').

373

374 Figure 2: Probability of responding to an alarm call in relation to the body size of the receiver, the  
375 body size ratio between caller and receiver (H2), the acoustic similarity between caller and receiver  
376 alarms (H5) and the abundance of the caller (H4) (A-D). Head-up response to alarm calls in relation  
377 to the consistency of the caller (H3.1) and grass height (H6) (E-F). Body size ratio, acoustic similarity,  
378 abundance and consistency of the caller were all scaled between 0 and 1.

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| <b>Hypothesis</b>   | <b>Predictions</b>   | <b>References</b> |
|---|--|-------------------|
| H1: The information content of an alarm call reflects the predator vulnerability of the caller (adaptive)   | Species are more likely to give alarm calls in response to predators to which they are more vulnerable   | [42]              |
| H2: Herbivores respond more strongly to alarm calls from species with similar predators (adaptive)  | Responsiveness is higher to alarm calls from species with body sizes similar to the receiver (proxy measure of predator overlap, see [47,48])                                    | [11,12]           |
| H3: Receivers respond more strongly to more accurate information sources (adaptive)<br>H3.1: Receivers respond more strongly to alarm calls from more consistent informants<br>H3.2: Receivers respond more strongly to more reliable alarm calls | 3.1: Responsiveness is higher to alarm calls from species emitting few false negatives<br>3.2: Responsiveness is higher to alarm calls from species emitting few false positives | [13-16]           |
| H4: Receiver responses are influenced by learning (adaptive, but limited to more familiar calls)  | Responsiveness is higher to calls from more abundant heterospecifics   | [19-21]           |
| H5: Receivers are more sensitive to calls similar to their own (non-adaptive)   | Responsiveness is higher to alarm calls which are acoustically similar to the conspecific alarms   | [17,18]           |

|  |  |      |
|--|--|------|
| H6: Receiver responses are influenced by environmental factors affecting predation risk (adaptive, non-adaptive) | Responsiveness increases with grass height<br>Responsiveness decreases with proximity to cover<br>Responsiveness increases with wind speed<br>Responsiveness decreases with distance to caller<br>Responsiveness decreases with group size | [47] |
|--|--|------|



| Model | Response variable | Statistics | Explanatory variables    |                 |                              |            |                         |                    |                  |                  |                     |              |                    |            |
|-------|-------------------|------------|--------------------------|-----------------|------------------------------|------------|-------------------------|--------------------|------------------|------------------|---------------------|--------------|--------------------|------------|
|       |                   |            | H2                       |                 |                              |            |                         | H3.1               | H3.2             | H4               | H5                  | H6           |                    |            |
|       |                   |            | Receiver body size (RBS) | Body size ratio | Body size ratio <sup>2</sup> | RBS: ratio | RBS: ratio <sup>2</sup> | Caller consistency | Call reliability | Caller abundance | Acoustic similarity | Grass height | Distance to caller | Wind speed |
| M2.1  | Response          | <i>b</i>   | -0.45                    | 6.48            | -4.35                        |            |                         |                    |                  | 0.44             | 1.74                | 0.37         | -0.08              | 0.09       |
|       | probability       | $\chi^2$   | 4.56                     | 16.61           | 7.64                         |            |                         |                    |                  | 5.57             | 31.94               | 31.47        | 2.04               | 2.82       |
|       |                   | <i>p</i>   | <0.05                    | <0.001          | <0.01                        |            |                         |                    |                  | <0.05            | <0.001              | <0.001       | n.s.               | n.s.       |
| M2.2  | Latency           | <i>b</i>   | 0.31                     | -2.81           | 1.40                         |            |                         |                    |                  |                  | -0.42               |              | 0.10               | -0.07      |
|       |                   | <i>F</i>   | 10.98                    | 11.91           | 3.12                         |            |                         |                    |                  |                  | 9.25                |              | 13.84              | 9.06       |
|       |                   | <i>p</i>   | <0.01                    | <0.001          | n.s.                         |            |                         |                    |                  |                  | <0.01               |              | <0.001             | <0.01      |
| M2.3  | Duration          | <i>b</i>   | -1.03                    | 2.74            | 0.67                         | 3.38       | -3.07                   |                    |                  | 0.21             | 0.56                | 0.12         |                    | 0.12       |
|       |                   | <i>F</i>   | 2.23                     | 1.75            | 0.08                         | 3.18       | 5.68                    |                    |                  | 5.02             | 10.65               | 14.58        |                    | 16.21      |
|       |                   | <i>p</i>   | 0.14                     | n.s.            | n.s.                         | n.s.       | <0.05                   |                    |                  | <0.05            | <0.001              | <0.001       |                    | <0.00      |
| M2.4  | Speed of          | <i>b</i>   | 0.22                     |                 |                              |            |                         |                    |                  |                  |                     |              |                    |            |
|       | head-lift         | <i>F</i>   | 9.43                     |                 |                              |            |                         |                    |                  |                  |                     |              |                    | 1          |

|      |           |          |       |       |       |       |  |        |
|------|-----------|----------|-------|-------|-------|-------|--|--------|
|      |           | <i>p</i> | 0.01  |       |       |       |  |        |
| M2.5 | Head-ups  | <i>b</i> | -0.11 |       | 0.26  | -0.28 |  | 0.12   |
|      | (number)  | <i>F</i> | 3.03  |       | 5.58  | 0.26  |  | 30.31  |
|      |           | <i>p</i> | n.s.  |       | <0.05 | n.s.  |  | <0.001 |
| M2.6 | Scratches | <i>b</i> | 1.22  | 1.47  | -3.28 |       |  | 0.19   |
|      | (number)  | <i>F</i> | 7.63  | 5.71  | 3.22  |       |  | 7.86   |
|      |           | <i>p</i> | <0.01 | <0.05 | n.s.  |       |  | <0.01  |



