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

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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 (A*cinonyx 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^2. 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 ± s.e. = 9.05 ± 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    $$L(i,j) = \sum_{x=1}^{n} I_{xj}\varepsilon_{ix}A_x,$$

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

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 3rd 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 ± s.e. =

168   17.7 ± 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, $X^2_{11,510}$ = 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, $X^2_{11,2322}$ = 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 2*B*),

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 2*A*), 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 2*E*), 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 2*C*), 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 2*D*), 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 2*F*), 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

350	**Acknowledgements**

356

357

358	**Funding**

361

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.

379

380

381   **References**

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Hypothesis	Predictions	References
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) H3.1: Receivers respond more strongly to alarm calls from more consistent informants 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 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	[47]
	Responsiveness decreases with proximity to cover	
	Responsiveness increases with wind speed	
	Responsiveness decreases with distance to caller	
	Responsiveness decreases with group size	

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

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