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

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Abstract

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

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

Introduction

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

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

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

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

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

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

Methods

Study system

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

Ecological and morphological species characteristics

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

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).

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

Results

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

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

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

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

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

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

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

These findings show that the responses of African savanna herbivores to heterospecific alarm calls are shaped by a range of factors which are partly adaptive, as indicated by the effects of 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.

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

Our findings also suggest that herbivores adjust their alarm responses to environmental factors increasing predation risk [47] (H6). Stronger responses were found to alarm calls when heard on plains with longer grass. This is likely an adaptive precaution since stalking predators are 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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357

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361

362

Table captions

Table 1: Hypothetical framework.

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

Figure labels

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

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

References

1. Bradbury J.W., Vehrencamp S.L. 2011 *Principles of animal communication*. Sunderland, Mass., Sinauer Associates.
2. Nowicki S., Searcy W.A. 2005 *The evolution of animal communication: reliability and deception in signaling systems*. Princeton, N.J., Princeton University Press.
3. Schmidt K.A., Dall S.R.X., van Gils J.A. 2010 The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* **119**(2), 304-316. (doi:10.1111/j.1600-0706.2009.17573.x).
4. Farine D.R., Aplin L.M., Sheldon B.C., Hoppitt W. 2015 Interspecific social networks promote information transmission in wild songbirds. *Proc Roy Soc B* **282**(1803), 20142804. (doi:10.1098/rspb.2014.2804).
5. Goodale E., Ruxton G.D., Beauchamp G. 2017 *Mixed-species groups of animals : behavior, community structure, and conservation*.
6. Seppanen J.T. 2007 Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**(11), 2950-2950. (doi:10.1890/06-1757.1).
7. Magrath R.D., Haff T.M., Fallow P.M., Radford A.N. 2015 Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol Rev Camb Philos* **90**(2), 560-586. (doi:10.1111/brv.12122).
8. Dehn M.M. 1990 Vigilance for predators- detection and dilution benefits. *Behav Ecol Sociobiol* **26**(5), 337-342. (doi:10.1007/BF00171099).
9. Clutton-Brock T. 2009 Cooperation between non-kin in animal societies. *Nature* **462**(7269), 51-57. (doi:10.1038/nature08366).
10. Goodale E., Beauchamp G., Magrath R.D., Nieh J.C., Ruxton G.D. 2010 Interspecific information transfer influences animal community structure. *Trends Ecol Evol* **25**(6), 354-361. (doi:10.1016/j.tree.2010.01.002).

406 11. Templeton C.N., Greene E. 2007 Nuthatches eavesdrop on variations in heterospecific
407 chickadee mobbing alarm calls. *Proc Natl Acad Sci USA* **104**(13), 5479-5482.
408 (doi:10.1073/pnas.0605183104).
409 12. Carrasco M.F., Blumstein D.T. 2012 Mule deer (Odocoileus hemionus) respond to yellow-
410 bellied marmot (Marmota flaviventris) alarm calls. *Ethology* **118**(3), 243-250. (doi:10.1111/j.1439-
411 0310.2011.02002.x).
412 13. Magrath R.D., Pitcher B.J., Gardner J.L. 2009 An avian eavesdropping network: alarm signal
413 reliability and heterospecific response. *Behav Ecol* **20**(4), 745-752. (doi:10.1093/beheco/arp055).
414 14. Munoz N.E., Brandstetter G., Esgro L., Greene W., Blumstein D.T. 2015 Asymmetric
415 eavesdropping between common mynas and red-vented bulbuls. *Behav Ecol* **26**(3), 689-696.
416 (doi:10.1093/beheco/aru206).
417 15. Hare J., Atkins B. 2001 The squirrel that cried wolf: reliability detection by juvenile
418 Richardson's ground squirrels (Spermophilus richardsonii). *Behav Ecol Sociobiol* **51**(1), 108-112.
419 (doi:10.1007/s002650100414).
420 16. Blumstein D.T., Verneyre L., Daniel J.C. 2004 Reliability and the adaptive utility of
421 discrimination among alarm callers. *Proc Roy Soc B* **271**(1550), 1851-1857.
422 (doi:10.1098/rspb.2004.2808).
423 17. Fallow P.M., Pitcher B.J., Magrath R.D. 2013 Alarming features: birds use specific acoustic
424 properties to identify heterospecific alarm calls. *Proc Roy Soc B* **280**(1754), 20122539.
425 (doi:10.1098/rspb.2012.2539).
426 18. Getschow C.M., Rivers P., Sterman S., Lumpkin D.C., Tarvin K.A. 2013 Does Gray Squirrel
427 (Sciurus carolinensis) Response to Heterospecific Alarm Calls Depend on Familiarity or Acoustic
428 Similarity? *Ethology* **119**(11), 983-992. (doi:10.1111/eth.12145).
429 19. Ramakrishnan U., Coss R.G. 2000 Recognition of heterospecific alarm vocalization by Bonnet
430 Macaques (Macaca radiata). *J Comp Psychol* **114**(1), 3-12. (doi:10.1037//0735-7036.114.1.3).

431 20. Magrath R.D., Pitcher B.J., Gardner J.L. 2009 Recognition of other species' aerial alarm calls:
432 speaking the same language or learning another? *Proc Roy Soc B* **276**(1657), 769-774.
433 (doi:10.1098/rspb.2008.1368).
434 21. Magrath R.D., Haff T.M., McLachlan J.R., Igic B. 2015 Wild birds learn to eavesdrop on
435 heterospecific alarm calls. *Curr Biol* **25**(15), 2047-2050. (doi:10.1016/j.cub.2015.06.028).
436 22. Fitzgibbon C.D. 1990 Why do Hunting cheetahs prefer male gazelles. *Anim Behav* **40**, 837-
437 845. (doi:10.1016/s0003-3472(05)80984-4).
438 23. Kiffner C., Kioko J., Leweri C., Krause S. 2014 Seasonal patterns of mixed species groups in
439 large East African mammals. *PLoS One* **9**(12), e113446. (doi:10.1371/journal.pone.0113446).
440 24. Estes R. 1991 *The behavior guide to African mammals : including hoofed mammals,*
441 *carnivores, primates*. Berkeley, University of California Press.
442 25. Ogutu J.O., Owen-Smith N., Piepho H.P., Said M.Y. 2011 Continuing wildlife population
443 declines and range contraction in the Mara region of Kenya during 1977-2009. *J Zool* **285**(2), 99-109.
444 (doi:10.1111/j.1469-7998.2011.00818.x).
445 26. Creel S., Schuette P., Christianson D. 2014 Effects of predation risk on group size, vigilance,
446 and foraging behavior in an African ungulate community. *Behav Ecol* **25**(4), 773-784.
447 (doi:10.1093/beheco/aru050).
448 27. Broekhuis F. 2016 Mara cheetah project- annual report. *Kenya Wildlife Trust*.
449 28. Hayward M.W., Kerley G.I.H. 2005 Prey preferences of the lion (Panthera leo). *J Zool* **267**(03),
450 309-322. (doi:10.1017/S0952836905007508).
451 29. Hayward M.W. 2006 Prey preferences of the spotted hyaena (Crocuta crocuta) and degree
452 of dietary overlap with the lion (Panthera leo). *J Zool* **270**(4), 606-614. (doi:10.1111/j.1469-
453 7998.2006.00183.x).
454 30. Hayward M.W., Henschel P., O'Brien J., Hofmeyr M., Balme G., Kerley G.I.H. 2006 Prey
455 preferences of the leopard (Panthera pardus). *J Zool* **270**(2), 298-313. (doi:10.1111/j.1469-
456 7998.2006.00139.x).

457 31. Hayward M.W., Hofmeyr M., O'Brien J., Kerley G.I.H. 2006 Prey preferences of the cheetah
458 (Acinonyx jubatus) (Felidae : Carnivora): morphological limitations or the need to capture rapidly
459 consumable prey before kleptoparasites arrive? *J Zool* **270**(4), 615-627. (doi:DOI 10.1111/j.1469-
460 7998.2006.00184.x).
461 32. Hayward M.W., Porter L., Lanszki J., Kamler J.F., Beck J.M., Kerley G.I.H., Macdonald D.W.,
462 Montgomery R.A., Parker D.M., Scott D.M., et al. 2017 Factors affecting the prey preferences of
463 jackals (Canidae). *Mamm Biol* **85**, 70-82. (doi:10.1016/j.mambio.2017.02.005).
464 33. Deeming D.C., Sibly R.M., Magole I.L. 1996 Estimation of the weight and body condition of
465 ostriches (Struthio camelus) from body measurements. *Vet Rec* **139**(9), 210-213.
466 34. Lovich J.E., Gibbons J.W. 1992 A review of techniques for quantifying sexual size
467 dimorphism. *Growth Dev Aging* **56**(4), 269-281.
468 35. Bro-Jørgensen J., Beeston J. 2015 Multimodal signalling in an antelope: fluctuating
469 facemasks and knee-clicks reveal the social status of eland bulls. *Anim Behav* **102**, 231-239.
470 (doi:10.1016/j.anbehav.2015.01.027).
471 36. Friard O., Gamba M., Fitzjohn R. 2016 BORIS: a free, versatile open-source event-logging
472 software for video/audio coding and live observations. *Methods Ecol Evol* **7**(11), 1325-1330.
473 (doi:10.1111/2041-210x.12584).
474 37. R Development Core Team. 2017 R: A language and environment for statistical computing
475 (Vienna, Austria, R Foundation for Statistical Computing.
476 38. Barton K. 2016 MuMIn: Multi-Model Inference. R package version 1.15.6.
477 39. Singmann H., Bolker B., Westfall J., Aust F. 2017 Afex: Analysis of factorial experiments. R
478 package version 0.18-0.
479 40. Bates D., Mächler M., Bolker B., Walker S. 2015 Fitting linear mixed-effects models using
480 lme4. *J Stat Softw* **67**(1). (doi:10.18637/jss.v067.i01).

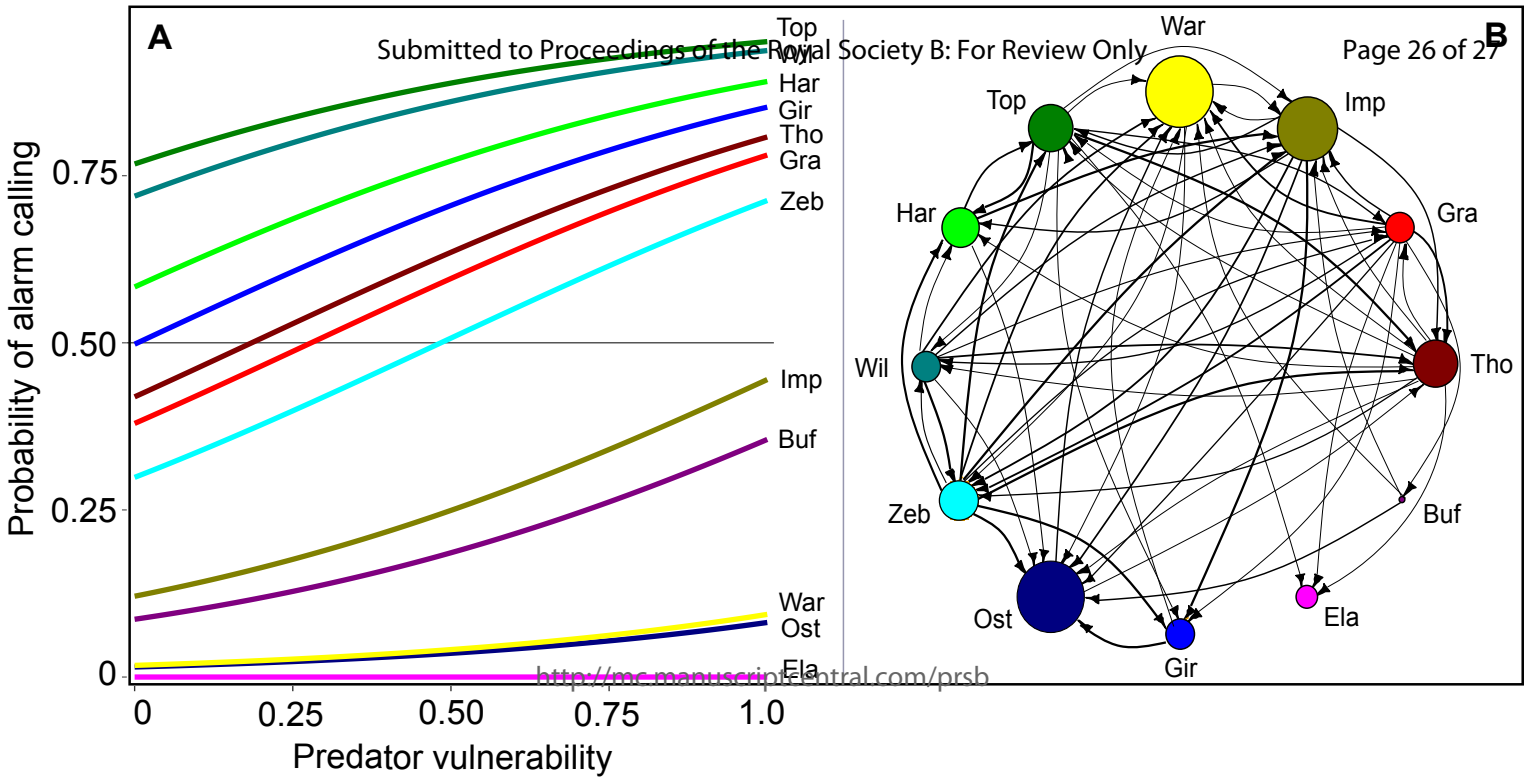
481 41. Hopcraft J.G., Olff H., Sinclair A.R. 2010 Herbivores, resources and risks: alternating
482 regulation along primary environmental gradients in savannas. *Trends Ecol Evol* **25**(2), 119-128.
483 (doi:10.1016/j.tree.2009.08.001).
484 42. Lima S.L., Dill L.M. 1990 Behavioral decision under the risk of predation: a review and
485 prospectus. *Can J Zool* **68**, 619-640. (doi:10.1139/z90-092).
486 43. Beauchamp G., Ruxton G.D. 2007 False alarms and the evolution of antipredator vigilance.
487 *Anim Behav* **74**(5), 1199-1206. (doi:10.1016/j.anbehav.2007.02.014).
488 44. Haff T.M., Magrath R.D. 2013 Eavesdropping on the neighbours: fledglings learn to respond
489 to heterospecific alarm calls. *Anim Behav* **85**(2), 411-418. (doi:10.1016/j.anbehav.2012.11.016).
490 45. Magrath R.D., Bennett T.H. 2012 A micro-geography of fear: learning to eavesdrop on alarm
491 calls of neighbouring heterospecifics. *Proc Roy Soc B* **279**(1730), 902-909.
492 (doi:10.1098/rspb.2011.1362).
493 46. Russ J., Jones G., Mackie I., Racey P. 2004 Interspecific responses to distress calls in bats
494 (Chiroptera: Vespertilionidae): a function for convergence in call design? *Anim Behav* **67**(6), 1005-
495 1014. (doi:10.1016/j.anbehav.2003.09.003).
496 47. Stankowich T., Blumstein D.T. 2005 Fear in animals: a meta-analysis and review of risk
497 assessment. *Proc Roy Soc B* **272**(1581), 2627-2634. (doi:10.1098/rspb.2005.3251).
498 48. Caro T.M. 2005 *Antipredator defenses in birds and mammals*. Chicago, University of Chicago
499 Press.
500 49. Cherry M.J., Barton B.T. 2017 Effects of wind on predator-prey interactions. *Food Webs*.
501 (doi:10.1016/j.fooweb.2017.02.005).
502 50. Bowyer R.T., Kie J.G. 2009 Thermal landscapes and resource selection by black-tailed deer:
503 implications for large herbivores. *Calif Fish Game* **95**(3), 128-139.
504
505

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 Responsiveness decreases with proximity to cover Responsiveness increases with wind speed Responsiveness decreases with distance to caller 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^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



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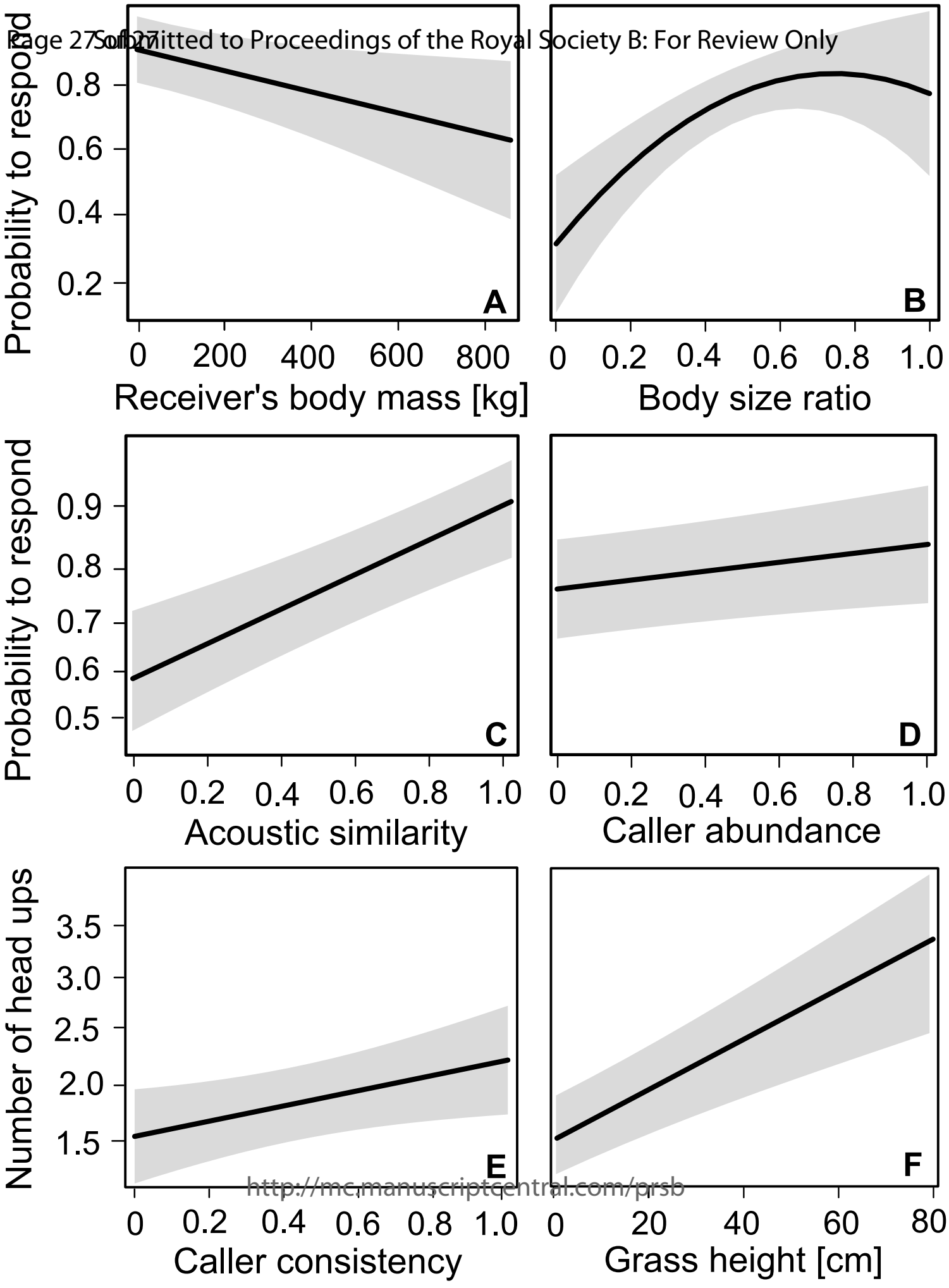

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