

1 **Persistent females and compliant males coordinate alarm calling in Diana monkeys**

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27 **Summary**

28 Sexual dimorphisms in animal vocal behaviour have been successfully explained by sexual
29 selection theory (e.g. mammals: [1-5]; birds: [6, 7]; anurans: [8, 9]) but this does not usually
30 include alarm calls, which are thought to be the product of kin or individual selection (e.g.
31 [10, 11]). Here, we present the results of playback experiments with wild Diana monkeys, a
32 species with highly dimorphic predator-specific alarms, to investigate the communication
33 strategies of males and females during predator encounters. First, we simulated predator
34 presence by broadcasting vocalisations of their main predators, leopards or eagles. We found
35 that males only produced predator-specific alarms after the females had produced theirs, in
36 response to which the females ceased alarm calling. In a second experiment, we created
37 congruent and incongruent situations, so that the calls of a predator were followed by
38 playbacks of male or female alarms with a matching or mismatching referent. For congruent
39 conditions, results were the same as in the first experiment. For incongruent conditions,
40 however, the males always gave predator-specific alarms that referentially matched the
41 females' calls, regardless of the previously displayed predator. In contrast, females always
42 gave predator-specific alarms that matched the predator type, regardless of their own male's
43 subsequent calls. Moreover, the females persistently continued to alarm call until their own
44 male produced calls with the matching referent. Results show that males and females attend to
45 the informational content of each other's alarm calls but prioritise them differently relative to
46 experienced external event, a likely reflection of different underlying selection pressures.

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50 **Results and Discussion**

51

52 Male primates often play a more active role in predator defence than the rest of the group,
53 hereby taking considerable risks for their own survival. In some primates, males take the
54 threat experienced by other group members into account, independent of their own exposure
55 [12], and adjust their behaviour depending on the presence and awareness of other group
56 members [13, 14]. In Diana monkey groups (*Cercopithecus diana*) the single adult male
57 regularly attacks crowned eagles (*Stephanoaetus coronatus*) and mobs leopards (*Panthera*
58 *pardus*), while directing his loud and conspicuous alarm calls at them [15]. This type of anti-
59 predator behaviour is extremely dangerous and males can suffer considerable mortality, as
60 indicated from remains of male guenons beneath eagle nests [16]. Although male antipredator
61 behaviour is highly efficient in dissuading predators (e.g. [17]) and in distracting attention
62 from vulnerable group members, males often engage in anti-predator behaviour only after
63 considerable delays, typically after the females have started giving alarm calls.

64

65 Here, we were interested in how females and males coordinate their anti-predator and alarm
66 call behaviour. Given the observed delay in male responses, we investigated whether males
67 adjust their anti-predator behaviour to the females' and whether females monitor and
68 influence the male's behaviour.

69

70 Diana monkeys live in stable groups in the dense West African forests with one reproductive
71 male and several adult females with their offspring [18]. Both sexes produce general alert
72 calls and predator-specific alarm calls [19, 15], which are sexually dimorphic ([20-22]; Fig.
73 1). Male vocal behaviour is restricted to responses to threats, usually predators such as
74 leopards or eagles, but also to alarm calls of other species and neighbouring males. Females,
75 in contrast, possess a rich vocal repertoire used in a range of social contexts and to predators.

76 Male alarm calls are much louder and lower-pitched than the females' and carry over
77 considerable distances, suggesting that they also serve in male-male competition, a likely
78 result of sexual selection [23]. Although both females and males usually call in response to
79 predators, the coordination and social dynamics between the two sexes during their alarm call
80 responses have never been analysed.

81

82 We carried out field playback experiments with different wild groups of Diana monkeys by
83 mimicking the presence of one of their main predators, a leopard (simulated by growls) or a
84 crowned eagle (simulated by shrieks). Both sexes responded to both predator models by
85 uttering series of acoustically distinct alarm calls [24] and other call types, in particular alert
86 calls to leopards (males and females) and contact calls to eagles (females only).

87

88 We found that the females consistently started calling before the group's male (LMM, $\beta =$
89 0.41 , $SE = 0.18$, $df = 21$, $t = 2.242$, $p = 0.035$), despite the fact that the predator information
90 was simultaneously available to all individuals (Table S1). Despite this sex difference, there
91 was neither an effect of predator type ($\beta = -0.23$, $SE = 0.167$, $df = 21$, $t = -1.382$, $p = 0.181$)
92 nor an interaction between sex and predator ($\beta = 0.127$, $SE = 0.234$, $df = 21$, $t = 0.544$, $p =$
93 0.592) on response latencies.

94

95 To leopards, females typically first uttered general alarm calls (Fig. 1c), followed by leopard-
96 specific alarm calls. Males showed the same pattern, but this transition only occurred after the
97 first female emitted a leopard alarm, in response to which the male switched from general to
98 leopard alarms (*before vs. after* first female leopard alarm: $N = 11$, $W = 120$, $p < 0.001$). We
99 found the same pattern in response to eagles: as soon as the first female emitted an eagle-
100 specific alarm, the male gave his eagle-specific alarm sequences, but never before (**table 1**).

101 This apparent female-induced change in male calling behaviour had a follow-on effect on the

102 females' own calling behaviour: once the male produced his predator-specific alarm calls, the
103 females' own predator-specific alarm call rates decreased rapidly (*before* vs. *after* male
104 alarms: eagles: N = 11, W = 103, p = 0.004; leopards: N = 11, W = 144, p<0.001).

105

106 One explanation for the observed pattern is that it is a mere by-product of the fact that the
107 average Diana monkey group consists of multiple adult females and one adult male only,
108 suggesting that the probability to first respond to a predator was higher for the females. We
109 consider this an unlikely explanation because male calling was often very delayed, sometimes
110 close to a minute after the predator playback (Table S1). More plausible is that the males
111 monitored the females' alarm calling behaviour and only became active after they produced
112 predator-specific alarm calls.

113

114 To investigate whether the two sexes monitored each other's vocal behaviour, we carried out
115 a second experiment with playbacks of pairs of stimuli. To this end, predator calls (eagle
116 shrieks or leopard growls, S1) were followed by a sequence of predator-specific male or
117 female alarm calls (S2). In each group, the male and the females were tested separately. When
118 focussing on a single male, we played back the calls of a predator first, followed by congruent
119 or incongruent predator-specific alarm calls of his own females (recorded earlier). Similarly,
120 when focussing on a group's females, we played back the calls of a predator, followed by
121 congruent or incongruent predator-specific alarm calls of their own single male (recorded
122 earlier; **table 1**). *Congruent conditions* were predator calls followed by referentially
123 corresponding alarm calls (e.g. leopard growls followed by female leopard alarms) while
124 *incongruent conditions* were predator calls followed by referentially different alarm calls (e.g.
125 leopard growls followed by female eagle alarms).

126

127 Based on results of Experiment 1, we predicted that, if males indeed followed the alarm
128 calling behaviour of their own females, they should always adjust their calls to the females'
129 calls, regardless of the predator type perceived before, in both congruent and incongruent
130 conditions. In contrast, for the females we predicted that they should respond directly to the
131 predator, regardless of subsequent male alarm calls.

132

133 Results showed that males always produced predator-specific alarm calls that matched the
134 females' own predator-specific alarm calls, regardless of prior predator calls (**table 1**). This
135 change in male vocal behaviour may be interpreted as a type of behavioural conformity, as
136 previously described for animals in feeding contexts [25]. Males appear to match the females'
137 alarm calls to advertise their willingness to engage in the anti-predator behaviour requested by
138 the females.

139

140 An alternative interpretation is that males were unable to recognise predator vocalisations and
141 thus followed the females' assessments. We consider this an unlikely explanation since males
142 produce the referentially correct alarm calls rapidly if they detect a predator visually (KZ
143 personal observations) or if they respond to other primate species' alarm calls [26, 27].

144

145 Females, in contrast, always produced predator-specific alarms that matched the predator type
146 presented to them, regardless of the males' responses. Furthermore, females decreased their
147 alarm call rates in congruent conditions (leopard growls → male leopard alarms: N = 13, W =
148 81, $p < 0.001$; eagle shrieks → male eagle alarms: N = 9, W = 36, $p = 0.002$, **table 1**). In
149 contrast, they continued their predator-specific alarm calling in incongruent conditions
150 (leopard growls → male eagle alarms: N = 12, W = 71, $p = 0.504$; eagles shrieks → male
151 leopard alarms: N = 14, W = 12, $p = 0.035$, **table 1**).

152

153 Overall, females decreased call rates more in congruent conditions than they increased call
154 rates in incongruent conditions (LMM, $\beta = -2.172$, $SE = 0.241$, $df = 20$, $t = -9.019$, $p < 0.001$,
155 Fig. 2), suggesting that referential congruence had an effect on the direction and magnitude of
156 female predator-specific alarm call rates.

157

158 In contrast, changes in males' alarm calling rates were unaffected by the referential
159 congruence between predator type and female calls (LMM, $\beta = 0.546$, $SE = 0.259$, $df = 17$, $t =$
160 2.106 , $p = 0.076$). For males, in other words, it seems more important to adjust to the
161 referential content of female alarm calls, overriding the necessity to respond to the predator
162 type perceived. We are not aware of any comparable evidence in the animal communication
163 literature, in which callers prioritise information provided by other individuals over their own
164 assessments [28].

165

166 The females' predator-specific alarm calling can be explained by kin selection as an evolved
167 strategy to inform offspring and other kin about the nature of a threat and, as shown here, to
168 stimulate male anti-predation defence. Although male Diana monkeys are often found at the
169 group's periphery and rarely participate in social interactions [18], the females depend on
170 them to confront predators as 'hired guns' [29, 30], a hypothesis already tested in other
171 primate studies [31]. As a result, females may persist in alarm calling if their male produces
172 calls to a danger they do not perceive as most relevant. However, if a male changes his calls
173 to match the females', they may interpret this as his readiness to engage in the anti-predation
174 behaviour indicated by them. In response, females and other group members switch to more
175 cryptic behaviour, using the male's vocal behaviour as kind of a "stopping rule" [32] and
176 benefiting from the male attracting the predator's attention and driving it away. At the
177 proximate level, females appear to trust their own assessments more than the male's, perhaps
178 because the sex ratio is biased towards females who will therefore identify a predator more

179 rapidly than the single male and because males often respond to the alarm calls of
180 neighbouring males, regardless of local events.

181 In evolutionary terms, it is less clear why males produce alarm calls against their own better
182 knowledge. In particular, such behaviour could be maladaptive if it elicits inappropriate anti-
183 predator behaviour in others. However, because single males often forage away from the
184 group they may often not be aware of local events, and may therefore be willing to accept the
185 females' assessments regardless of their own experience. Moreover, in dense forest habitats, it
186 is usually difficult to unequivocally identify a predator and double predation events are not
187 uncommon, suggesting that males may often perceive situations as ambiguous. Nevertheless,
188 kin selection may also explain why resident males adjust their own responses to the females'
189 if they have sired offspring with them. However, kin selection cannot explain the vocal
190 behaviour of immigrant males who are equally active in their anti-predation behaviour (CS &
191 KZ, unpublished data), before having offspring in the group. As mentioned earlier, males do
192 not benefit directly, as confrontations with both predators are very dangerous for them.

193 An alternative explanation therefore is that male antipredator behaviour has been under
194 additional sexual selection pressure. Females can be attentive to males' acoustic cues to infer
195 and compare the males' physical characteristics and momentary physical conditions [33, 34].
196 It is therefore possible that male antipredator behaviour and calling functions to advertise a
197 commitment to defend the group and that this has evolved in response to sexual selection
198 pressure. A link between anti-predator behaviour and reproductive success has also been
199 suggested for grey-cheeked mangabeys (*Lophocebus albigena*), as the highest-ranking males
200 engaged most in predator mobbing behaviour [35]. To test the sexual selection hypothesis
201 more directly, it would be necessary to investigate whether males that conform to females are
202 more readily accepted during immigration attempts, have longer tenure and produce more
203 surviving offspring than males who prioritise their own assessments of predatory threat, a

204 considerable challenge under field conditions [36-38]. Male replacements are rare events, but
205 if they occur females have been observed to react in hostile ways, suggesting an element of
206 female choice (CS, unpublished data). Likewise, adult females can attack intruding solitary
207 males, with the established male and younger individuals playing a more passive role.

208 In sum, we have shown that female and male Diana monkeys influence each other during
209 predator encounters in their use of predator-specific alarm calls. Females' alarm calls induce
210 male anti-predator behaviour and determine the call types used by males, while male alarm
211 calls appear to signal a commitment to engage in the anti-predator strategy delineated by the
212 females. This pattern has most likely arisen from selection pressures acting differently on the
213 two sexes, with males' being under sexual selection and trying to maximise their tenure by
214 providing anti-predator services and females being predominantly driven by kin selection and
215 trying to minimise predation by engaging males as "hired guns".

216

217 **Experimental procedures**

218 *Subjects and Playback presentation*

219 We collected data from wild Diana monkey groups unhabituated to human presence
220 (Experiment 1: N=22 groups; Experiment 2: N=14 groups) between July 1994, June 1995,
221 July to November 1996, January to June 1997, and February 2000 by KZ (Experiment 1) and
222 August to December 2013 by CS (Experiment 2). We located groups largely by auditory cues
223 throughout a large area of Taï National Park, Ivory Coast, near the 'Station de Recherche en
224 Ecologie de Taï' (Supplemental Experimental Procedures).

225

226 Playback stimuli consisted of 15s of leopard growls (N=3) or eagle shrieks (N=3),
227 respectively, either presented alone (Experiment 1) or followed after 3s by a sequence of N=3
228 male or female predator-specific alarm calls, respectively (Experiment 2). As Diana monkeys

229 recognise familiar individuals by their voices [39] we only used alarm calls previously
230 recorded from the same group (resulting in an overall pool of N=14 sequences of female and
231 male calls, respectively). Each group was tested no more than once in each condition.

232

233 In Experiment 1, the predator sounds were broadcasted with a Sony WM-D6C recorder,
234 connected to a Nagra DSM speaker-amplifier, and vocal responses were recorded with a
235 Sennheiser ME80 microphone and a Sony TCM-3000 cassette recorder. In Experiment 2,
236 playback stimuli (predator sounds and subsequent Diana monkey alarm calls) were presented
237 with an iPod Nano, connected to an AER alpha speaker-amplifier. Vocal responses were
238 recorded with a Sennheiser ME80 microphone and a Marantz PMD 660 solid-state recorder.
239 After each trial, we avoided the surrounding area (radius > 500m) for at least two weeks for
240 experiments with the same stimulus type to avoid habituation.

241

242 *Response analysis*

243 Recordings on analogue cassette tapes were digitised using COOL EDIT 2000 software
244 (Syntrillium Software Corporation, Phoenix, USA). Acoustic analyses were carried out using
245 PRAAT (5.1.29). We analysed the first minute of vocal responses following each playback,
246 the critical time period during which alarm calls were usually emitted. While it was possible
247 to allocate male alarm calls to one specific individual, this was not possible for the adult
248 females who typically forage in the upper forest canopy [40], which makes individual
249 identification impossible for unhabituated groups. Analyses were therefore carried out at the
250 group level. We only analysed groups of similar sizes (approx. 20 individuals, i.e. about 5-8
251 adult females).

252

253 *Statistical analyses*

254 Due to the high number of conditions in Experiment 2 (N=8) with low trial numbers per

255 condition, we opted for an analysis strategy based on non-parametric tests by comparing call
256 rates before and after the simulated conspecific alarms. For consistency, we used two-tailed
257 Wilcoxon signed rank tests in both experiments.

258

259 For Experiment 1, we analysed whether the males changed their calling behaviour in response
260 to females, by comparing the rate of predator-specific calls emitted before and after the first
261 predator-specific female alarm call. The same analysis was conducted for females before and
262 after the male emitted his specific alarms. We also analysed the latencies to call (continuous
263 target variable) using a LMM (linear mixed model, Gaussian error distribution, identity-link
264 function) to identify effects of sex and playback stimulus (fixed factors) on calling behaviour.
265 To control for group differences, we included “group” as a random factor. Corrected Akaike’s
266 information criteria (AICc) values were compared to select the most parsimonious model. To
267 control for normal distribution of residuals, we first conducted a Shapiro Wilk test on the raw
268 data, which revealed a non-normal distribution ($W=0.791$, $p<0.001$). Latencies were thus log
269 – transformed to normally distributed residuals ($W=0.964$, $p=0.279$) and then entered for the
270 LMM.

271

272 For Experiment 2, we compared the number of predator-specific calls for females and males
273 before and after the other sex’ alarm calls (predator-specific male alarms for females,
274 predator-specific female alarms for males) in each condition, including a Bonferroni
275 correction ($\alpha=0.006$). Differences in call rates between congruent and incongruent conditions
276 were compared by means of a LMM (Gaussian error distribution; identity-link function) with
277 “group” as a random factor.

278

279 Statistical analyses were conducted using R v. 13.0.1.

280

281 **Author Contributions**

282 Conceptualisation and Methodology: C.S. and K.Z.; Investigation: C.S. and K.Z.; Formal
283 Analysis, C.S.; Writing – Original Draft, Reviewing & Editing: C.S. and K.Z.; Funding
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285

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295

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	Playback	Target	N	Calls before conspecific alarms			Calls after conspecific alarms		
Predator calls (S1)	Conspecific alarms (S2)			Mean \pm SD	Min	Max	Mean \pm SD	Min	Max
<i>Experiment 1</i>									
Leopard	-	Females	11	2.00 \pm 0.91	1	4	0.01 \pm 0.05	0.00	0.18
		Males		0.09 \pm 0.28	0	1	1.91 \pm 0.66	1.00	3.00
Eagle	-	Females	11	1.45 \pm 0.89	1	4	0.67 \pm 0.86	0.00	3.00
		<u>Males</u>		<u>0.00 \pm 0.00</u>	<u>0</u>	<u>0</u>	<u>1.90 \pm 0.18</u>	<u>0.70</u>	<u>6.00</u>
<i>Experiment 2</i>									
Leopard	Male leopard	Females	13	1.77 \pm 0.79	1	3	0.00 \pm 0.00	0.00	0.00
Leopard	Male eagle	Females	12	1.55 \pm 0.72	1	3	1.20 \pm 1.17	0.30	2.00
Eagle	Male eagle	Females	9	1.66 \pm 0.47	0	1	0.00 \pm 0.00	0.00	0.00
Eagle	Male leopard	Females	14	1.25 \pm 0.80	0	3	2.27 \pm 0.74	1.00	3.80
Leopard	Female leopard	Male	10	0.00 \pm 0.00	0	0	1.92 \pm 1.04	0.80	3.70
Leopard	Female eagle	Male	9	0.00 \pm 0.00	0	0	0.83 \pm 0.54	0.30	1.20
Eagle	Female eagle	Male	8	0.00 \pm 0.00	0	0	1.26 \pm 0.56	0.67	3.67
Eagle	Female leopard	Male	10	0.00 \pm 0.00	0	0	1.27 \pm 0.48	0.67	2.17

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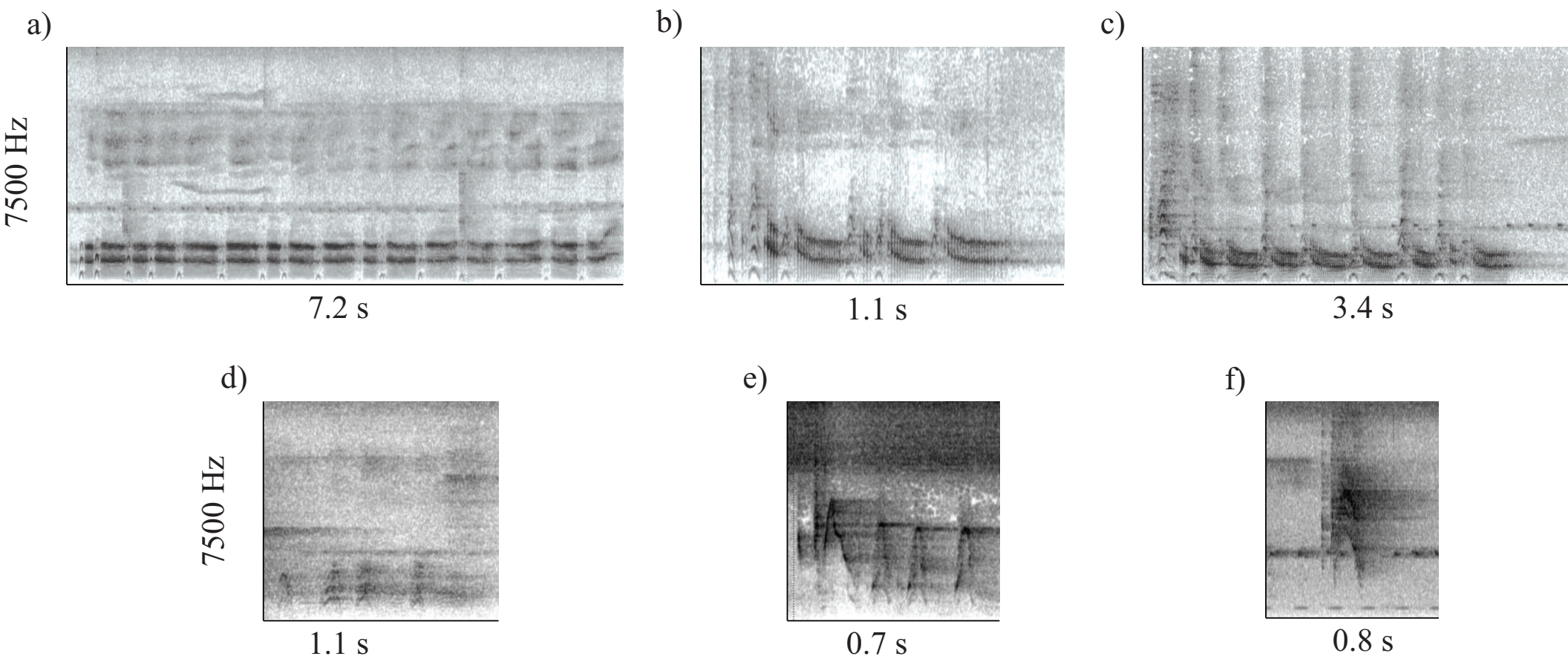
402

Table1. Descriptive statistics of alarm call responses in Experiments 1 & 2. For Experiment 2, incongruent conditions (S1 and S2 with different referents) are indicated in bold.

403 **Fig. 1:** *Spectrographic representations of Diana monkey alarm calls.* Spectrograms illustrate
404 a) male eagle alarm call sequence, b) male leopard alarm call sequence, c) male general alarm
405 call sequence, d) female eagle alarm call sequence, e) female leopard alarm call sequence and
406 f) female general alarm call sequence.

407
408 **Fig. 2:** *Changes in predator-specific alarm calling.* Differences between call rates before and
409 after playbacks of conspecific alarm calls (S2) for congruent (S1 and S2 with same referents)
410 and incongruent (S1 and S2 with different referents) playback conditions in males (grey) and
411 females (white). The horizontal line indicates equal call rates before and after S2 (delta values
412 above the line indicate increased calling after S2, delta values below represent decreased call
413 rates). Box plots indicate the first and third quartiles and the median. Whiskers indicate
414 responses of 1.5 times the height of the box; circles indicate outliers.

Figure



Figure

delta (no. calls after S2 - no. calls before S2)

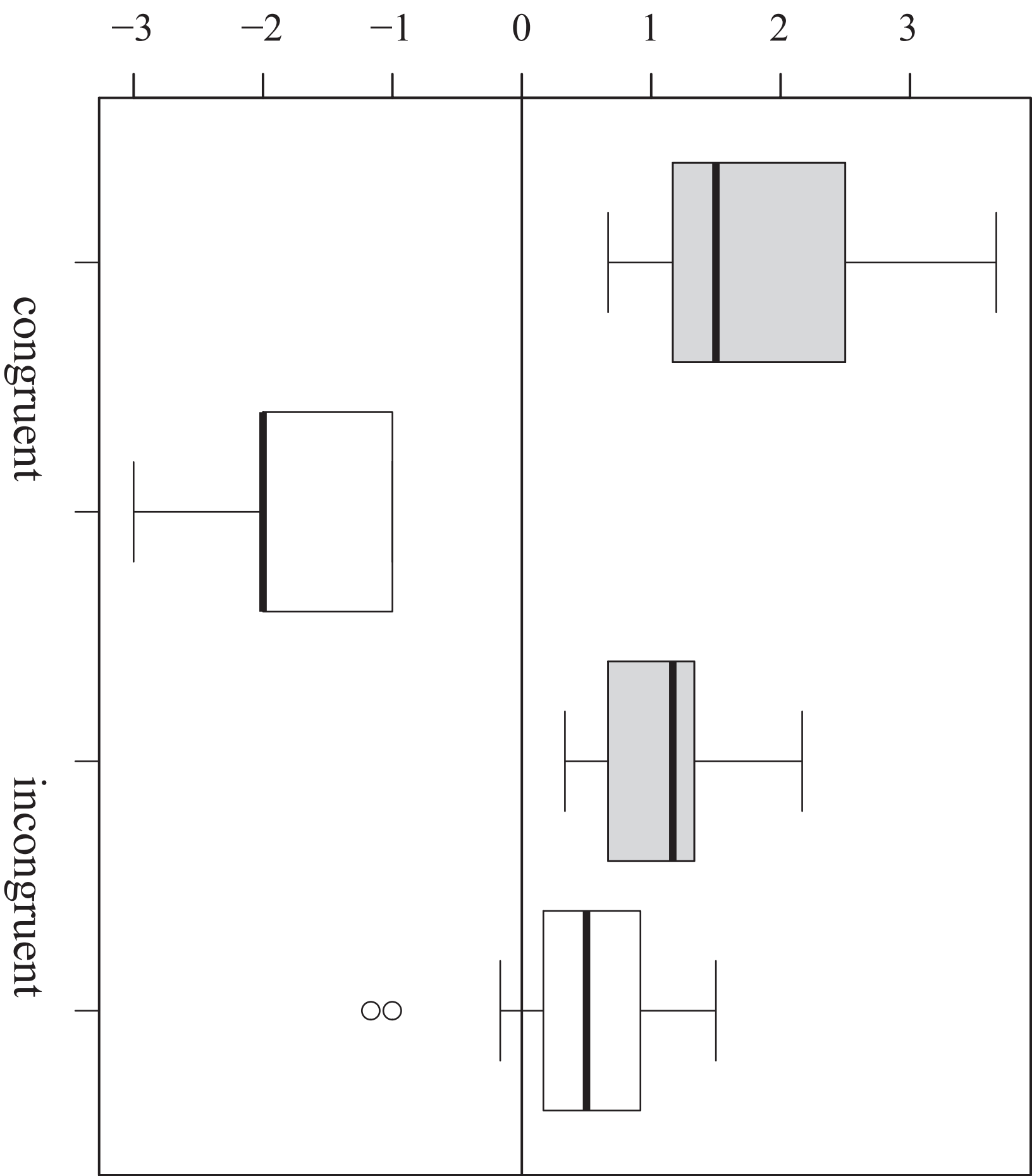


Table S1. Response latencies [s] in Experiment 1

	female leopard alarms	female eagle alarms	male leopard alarms	male eagle alarms
Group 1	4	20	13	38
Group 2	2	1	39	38
Group 3	13	18	19	59
Group 4	2	11	60	11
Group 5	9	21	47	60
Group 6	15	12	27	12
Group 7	8	8	25	9
Group 8	9	12	11	15
Group 9	7	13	10	22
Group 10	4	9	7	31
Group 11	3	11	9	18

Supplemental Experimental Procedures

For Experiment 1, we located groups throughout a 50km² study area, mostly by acoustic cues. We then determined the likely location of the majority of the group members, including the male, before approaching to about 20m in order to broadcast one of two possible predator sounds to all group members. The males' responses obtained by these experiments have been previously analysed under another focus [S1-3].

For Experiment 2, we located groups in the same way, but then approached either the majority of females or the single male (depending on test condition) provided they were at least 50m apart from each other. The target (i.e. the single male or the adult females) was approached from a direction from which no other group members were present. To simulate a spatially plausible situation, we broadcasted the playback stimuli from the general direction of the group (for male targets) or from the general direction of the male (for female targets). This way we were able to prevent the females (or the single male, respectively) from responding to the predator calls before hearing the male's (or the females') alarm calls.

We individually identified groups by their estimated size, location in the study area and the composition of the polyspecific associations. Sometimes it was possible to additionally confirm the identity of a group by the acoustic quality of the male alarm calls, which are individually distinct. If it was not possible to unambiguously identify a group (for example, if a group was encountered in the overlapping zone between two similarly sized neighbouring groups) we postponed the experiment to another day.

After the identity of a group was determined, the experimenter positioned the equipment and then conducted an observational period of at least 10 min to describe the group's general behaviour. Trials were not carried out in case of any unusual event, such as the appearance of another mammal (e.g., bushbuck, duiker), an encounter with a neighbouring group, naturally occurring alarm calling, or the presence of chimpanzees or other predators. We additionally monitored the behaviour of any associated monkey species and the approximate distance of the male from the group. We then started the pre-playback recording period, which lasted between 3-5min during which the group's baseline vocal behaviour was recorded. We then broadcasted the playback stimulus and recorded the monkeys' vocal responses for at least 5min or until the group returned to baseline behaviour, indicated by cessation of alarm calls and resumption of female social calls. This was typically combined with a decrease in vigilant behaviour (scanning) and a return to foraging or resting behaviour.

We excluded trials from further analysis if the monkeys' responses were elicited by an external disturbance, such as a real predator (N=5), a neighbouring group (N=7), other monkey species' alarm vocalisations, including

during experiments before the target called (N=13), or a terrestrial mammal (N=3). On a few occasions we failed to obtain recordings of sufficient quality due to technical problems or noisy external conditions (N=8).

Supplemental References

- S1. Zuberbühler, K., Noë, R. and Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* *53*, 589–604.
- S2. Zuberbühler, K., Jenny, D. and Bshary, R. (1999a). The Predator Deterrence Function of Primate Alarm Calls. *Ethology* *105*, 477–490.
- S3. Zuberbühler, K., Cheney, D. L. and Seyfarth, R. M. (1999b). Conceptual semantics in a nonhuman primate. *J. Comp. Psych.* *113*, 33-42.