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

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Summary

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

Results and Discussion

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

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

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

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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.

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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, ß =

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 (ß = -0.23, SE = 0.167, df = 21, t = -1.382, p = 0.181)

92　　nor an interaction between sex and predator (ß = 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: $N = 11$, $W = 144$, $p<0.001$).

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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, ß = -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, ß = 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

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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

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

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

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

Statistical analyses were conducted using R v. 13.0.1.

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Author Contributions

Conceptualisation and Methodology: C.S. and K.Z.; Investigation: C.S. and K.Z.; Formal

Analysis, C.S.; Writing – Original Draft, Reviewing & Editing: C.S. and K.Z.; Funding

Acquisition: K.Z.

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

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.

17

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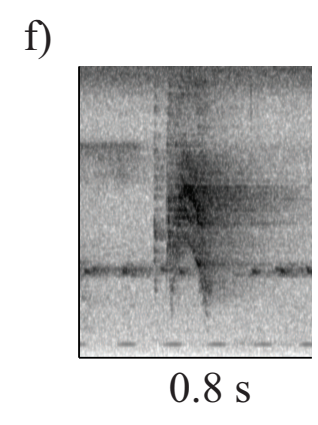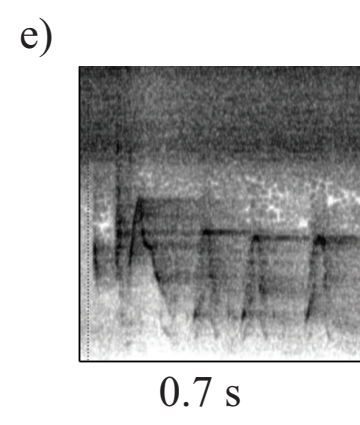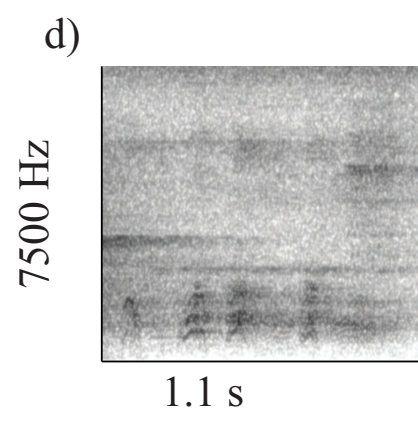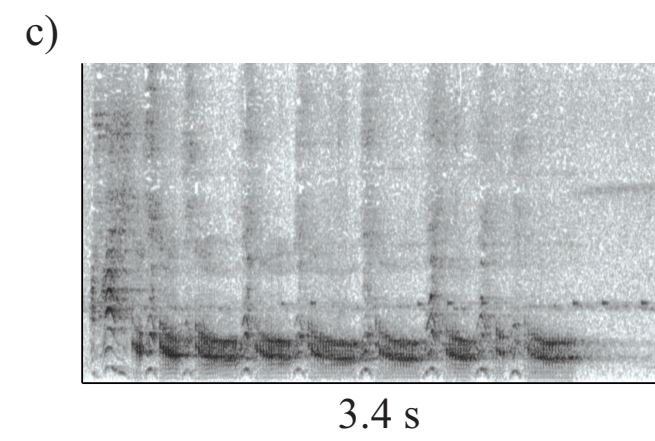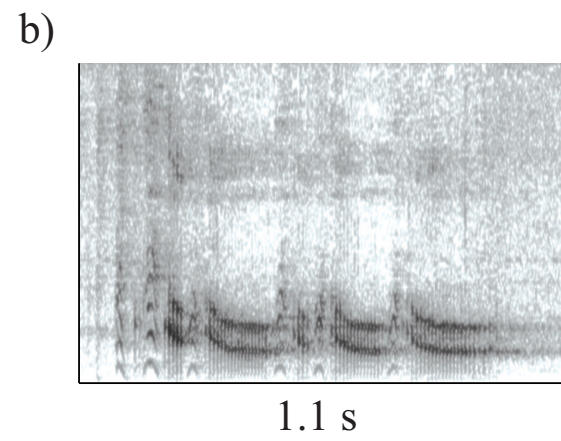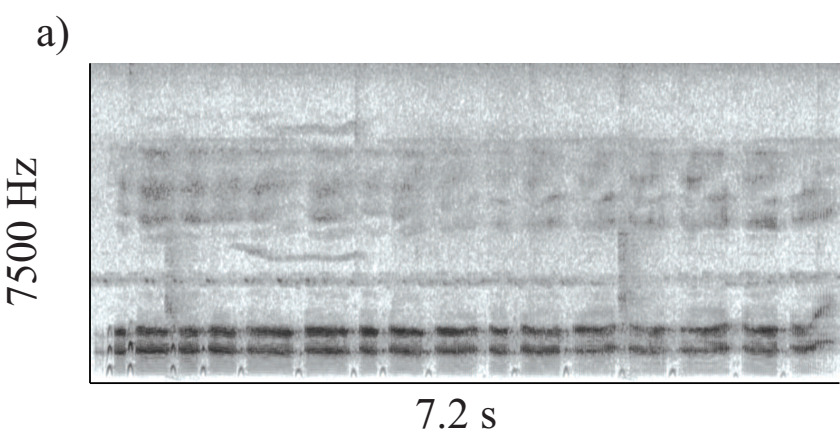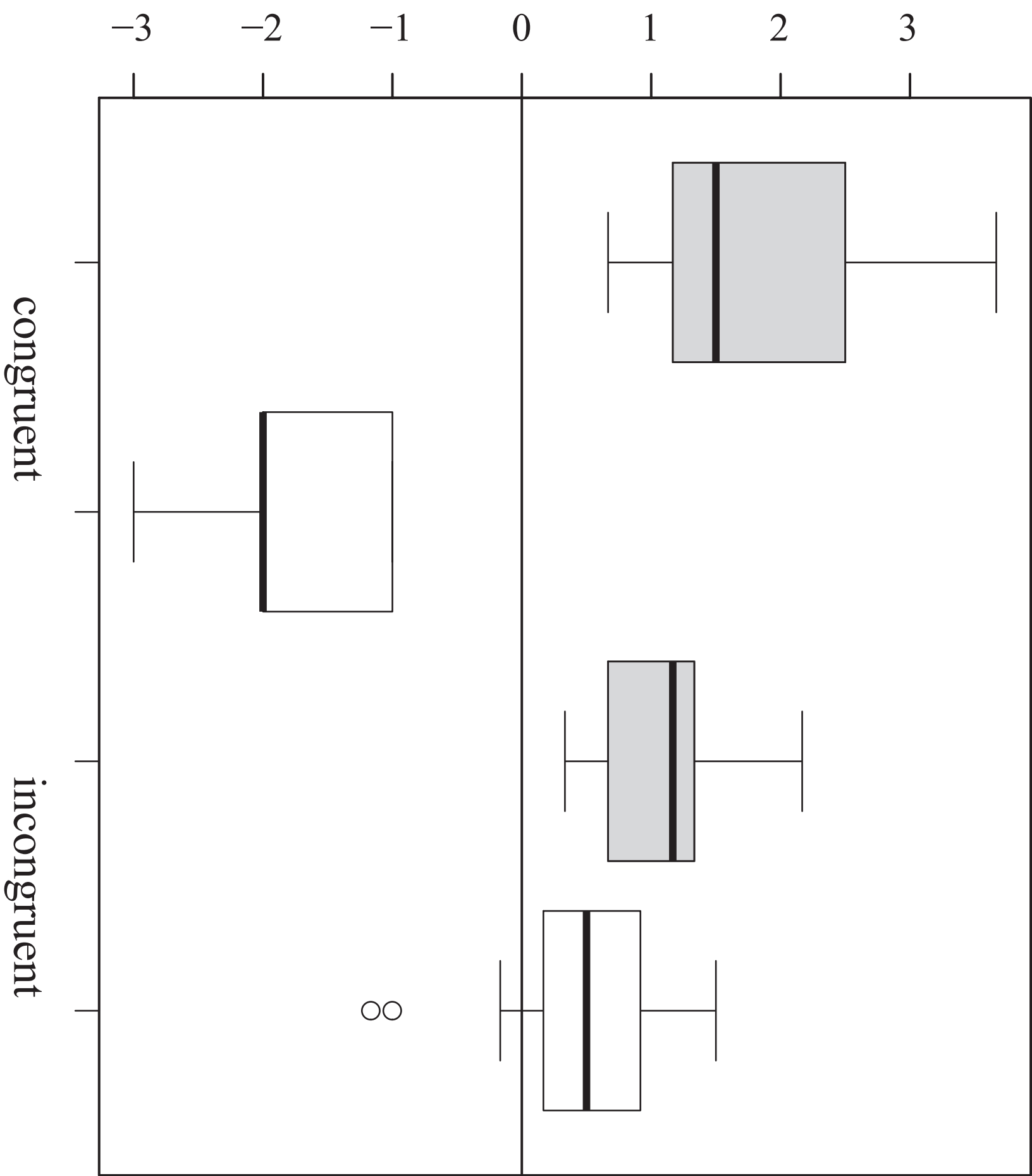
delta (no. calls after S2 - no. calls before S2)

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 50km^2 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.