Current Biology

Report

Persistent Females and Compliant Males Coordinate Alarm Calling in Diana Monkeys

Highlights

- Female and male monkeys attend to the predator specificity of each other's alarms
- Male alarms are determined by female alarms, regardless of own predator experience
- Female predator-specific alarms are determined by predator type, not male calls
- Selection pressures underlying alarm call evolution seem to be sexually dimorphic

Authors

Claudia Stephan, Klaus Zuberbühler

Correspondence

clamoretgaudium@gmx.net

In Brief

Stephan and Zuberbühler show that wild Diana monkeys coordinate predator alarm calls in sex-specific ways. Regardless of own experience, males always reiterated predator information provided by females, while females only responded to perceived predator, regardless of male alarms, and terminated calling when males conformed to their assessment.

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Persistent Females and Compliant Males Coordinate Alarm Calling in Diana Monkeys

Claudia Stephan[1,2,4,*] and Klaus Zuberbühler[1,2,3]
[1]Institute of Biology, Department of Comparative Cognition, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchatel, Switzerland
[2]Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, KM 17 Route de Dabou, Adiopodoumé Yopougon, Abidjan 01 B.P. 1303, Côte d'Ivoire
[3]School of Psychology & Neuroscience, University of St Andrews, St Mary's Quad, South Street, St Andrews, Fife KY16 9JP, Scotland, UK
[4]Lead Contact
*Correspondence: clamoretgaudium@gmx.net
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SUMMARY

Sexual dimorphisms in animal vocal behavior 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 vocalizations 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 prioritize them differently relative to an experienced external event, a likely reflection of different underlying selection pressures.

RESULTS AND DISCUSSION

Male primates often play a more active role in predator defense 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 behavior 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 behavior is extremely dangerous, and males can suffer considerable mortality, as indicated from remains of male guenons beneath eagle nests [16]. Although male anti-predator behavior is highly efficient in dissuading predators (e.g., [17]) and in distracting attention from vulnerable group members, males often engage in anti-predator behavior 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 behavior. Given the observed delay in male responses, we investigated whether males adjust their anti-predator behavior to the females' and whether females monitor and influence the male's behavior.

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 [15, 19], which are sexually dimorphic ([20–22]; Figure 1). Male vocal behavior is restricted to responses to threats, usually predators such as leopards or eagles, but also to alarm calls of other species and neighboring males. Females, in contrast, possess a rich vocal repertoire used in a range of social contexts and to predators. Male alarm calls are much louder and lower-pitched than the females' and carry over considerable distances, suggesting that they also serve in male-male competition, a likely result of sexual selection [23]. Although both females and males usually call in response to predators, the coordination and social dynamics between the two sexes during their alarm call responses have never been analyzed.

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

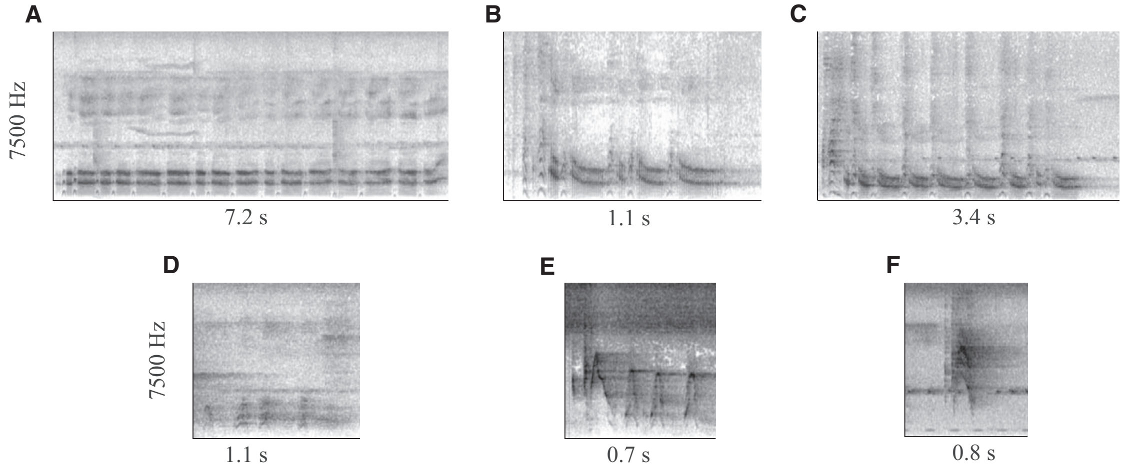

Figure 1. Spectrographic Representations of Diana Monkey Alarm Calls

(A–F) Spectrograms illustrate male eagle alarm call sequence (A), male leopard alarm call sequence (B), male general alarm call sequence (C), female eagle alarm call sequence (D), female leopard alarm call sequence (E), and female general alarm call sequence (F).

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

To leopards, females typically first uttered general alarm calls (Figure 1C), followed by leopard-specific alarm calls. Males showed the same pattern, but this transition only occurred after the first female emitted a leopard alarm, in response to which the male switched from general to leopard alarms (before versus after first female leopard alarm: $n = 11$, $W = 120$, $p < 0.001$). We found the same pattern in response to eagles: as soon as the first female emitted an eagle-specific alarm, the male gave his eagle-specific alarm sequences, but never before (Table 1). This apparent female-induced change in male calling behavior had a follow-on effect on the females' own calling behavior: once the male produced his predator-specific alarm calls, the females' own predator-specific alarm call rates decreased rapidly (before versus after male alarms: eagles: $n = 11$, $W = 103$, $p = 0.004$; leopards: $n = 11$, $W = 144$, $p < 0.001$).

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

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

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

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

An alternative interpretation is that males were unable to recognize predator vocalizations and thus followed the females' assessments. We consider this an unlikely explanation since males produce the referentially correct alarm calls rapidly if they detect a predator visually (K.Z., unpublished data) or if they respond to other primate species' alarm calls [26, 27].

Females, in contrast, always produced predator-specific alarms that matched the predator type presented to them,

Table 1. Descriptive Statistics of Alarm Call Responses in Experiments 1 and 2

Playback		Target	n	Calls before Conspecific Alarms			Calls after Conspecific Alarms		
Predator Calls (S1)	Conspecific Alarms (S2)			Mean ± SD	Minimum	Maximum	Mean ± SD	Minimum	Maximum
Experiment 1									
Leopard	–	females	11	2.00 ± 0.91	1	4	0.01 ± 0.05	0.00	0.18
		males		0.09 ± 0.28	0	1	1.91 ± 0.66	1.00	3.00
Eagle	–	females	11	1.45 ± 0.89	1	4	0.67 ± 0.86	0.00	3.00
		males		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[a]	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[a]	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[a]	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[a]	female leopard	male	10	0.00 ± 0.00	0	0	1.27 ± 0.48	0.67	2.17

[a] Row shows incongruent condition (S1 and S2 with different referents) for experiment 2

regardless of the males' responses. Furthermore, females decreased their alarm call rates in congruent conditions (leopard growls → male leopard alarms: $n = 13$, $W = 81$, $p < 0.001$; eagle shrieks → male eagle alarms: $n = 9$, $W = 36$, $p = 0.002$; Table 1). In contrast, they continued their predator-specific alarm calling in incongruent conditions (leopard growls → male eagle alarms: $n = 12$, $W = 71$, $p = 0.504$; eagles shrieks → male leopard alarms: $n = 14$, $W = 12$, $p = 0.035$; Table 1).

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

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

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

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

An alternative explanation therefore is that male anti-predator behavior has been under additional sexual selection pressure. Females can be attentive to males' acoustic cues to infer and compare the males' physical characteristics and momentary physical conditions [33, 34]. It is therefore possible that male anti-predator behavior and calling functions to advertise a commitment to defend the group and that this has evolved in response to sexual selection pressure. A link between anti-predator behavior and reproductive success has also been suggested for gray-cheeked mangabeys (*Lophocebus albigena*),

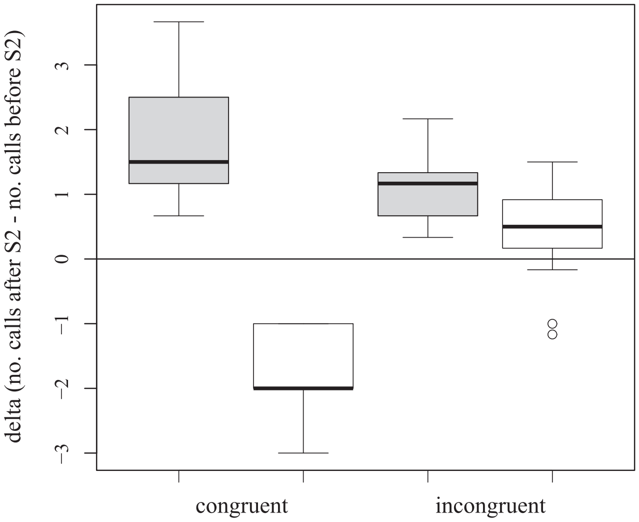

Figure 2. Changes in Predator-Specific Alarm Calling

Differences between call rates before and after playbacks of conspecific alarm calls (S2) for congruent (S1 and S2 with same referents) and incongruent (S1 and S2 with different referents) playback conditions in males (gray) and females (white). The horizontal line indicates equal call rates before and after S2 (delta values above the line indicate increased calling after S2; delta values below represent decreased call rates). Boxplots indicate the first and third quartiles and the median. Whiskers indicate responses of 1.5 times the height of the box; circles indicate outliers.

as the highest-ranking males engaged most in predator mobbing behavior [35]. To test the sexual selection hypothesis more directly, researchers will need to investigate whether males that conform to females are more readily accepted during immigration attempts, have longer tenure, and produce more surviving offspring than males who prioritize their own assessments of predatory threat, a considerable challenge under field conditions [36–38]. Male replacements are rare events, but if they occur, females have been observed to react in hostile ways, suggesting an element of female choice (C.S., unpublished data). Likewise, adult females can attack intruding solitary males, with the established male and younger individuals playing a more passive role.

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

EXPERIMENTAL PROCEDURES

Subjects and Playback Presentation

We collected data from wild Diana monkey groups unhabituated to human presence (experiment 1: n = 22 groups; experiment 2: n = 14 groups) between July 1994, June 1995, July 1996 to November 1996, January 1997 to June 1997, and February 2000 (by K.Z.; experiment 1) and August 2013 to December 2013 (by C.S.; experiment 2). We located groups largely by auditory cues throughout a large area of Taï National Park, Ivory Coast, near the Station de Recherche en Ecologie de Taï (Supplemental Experimental Procedures).

Playback stimuli consisted of 15 s of leopard growls (n = 3) or eagle shrieks (n = 3), respectively, either presented alone (experiment 1) or followed after 3 s by a sequence of n = 3 male or female predator-specific alarm calls, respectively (experiment 2). As Diana monkeys recognize familiar individuals by their voices [39], we only used alarm calls previously recorded from the same group (resulting in an overall pool of n = 14 sequences of female and male calls, respectively). Each group was tested no more than once in each condition.

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

Response Analysis

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

Statistical Analyses

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 analyzed whether the males changed their calling behavior 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 analyzed the latencies to call (continuous target variable) using an LMM (Gaussian error distribution; identity-link function) to identify effects of sex and playback stimulus (fixed factors) on calling behavior. 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 alarm calls of the other sex (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 an LMM (Gaussian error distribution; identity-link function) with "group" as a random factor.

Statistical analyses were conducted using R v.13.0.1.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.08.033.

AUTHOR CONTRIBUTIONS

Conceptualization, C.S. and K.Z.; Methodology, C.S. and K.Z.; Investigation, C.S. and K.Z.; Formal Analysis, C.S.; Writing – Original Draft, C.S.; Writing – Reviewing & Editing, C.S. and K.Z.; Funding Acquisition, K.Z.

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