Intentional Alarm Calling in Wild Female Putty-Nosed Monkeys (*Cercopithecus nictitans*)

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Abstract – The intentionality that characterizes human language currently still lacks conclusive evidence for precursors in animal vocal communication. Complex intersubjectivity as in language is usually supposed to be either evolutionary rooted in gestural communication or unique to humans. Here we systematically tested various groups of wild putty-nosed monkeys (*Cercopithecus nictitans*) for female first-order intentional alarm calling using a recently suggested framework to comparatively test for intentionality in animal communication. Specifically, we used a leopard model to elicit female alarm calls that usually trigger the group's male alarm calls and further recruit that male to mob and deter the nearby predator. We experimentally disentangled male alarm calling from male predator mobbing to test for female goal directedness in recruiting males for predator defense, voluntary alarm call usage, and the successful manipulation of male behavior. Females monitored male behavior and immediately ceased own alarm calling once the group's male took over group defense but not after perceiving the male's typical alarm calls. Unsuccessful male recruitments and the absence of male predator mobbing resulted in persistent and considerably longer female alarm calling. We discuss different communicative functions of female alarms and conclude that our results are most likely explained by the intentional use of female alarms in order to recruit males as 'hired guns.'

Keywords – First-order intentionality, Manipulation, Reputation-based mate choice, Alarm calls

Animal vocalizations have been heavily debated with regards to their potential to be (first-order) intentional signals, uttered to manipulate the behavior of others (Dennett, 1983). To unravel the possibility that animal calls might be tactically used to achieve a certain goal is essential to understand potential animal precursors to the evolution of intersubjectivity in human language (Grice, 1982; Scott-Phillips, 2015). Among various criteria proposed (e.g., Rodrigues & Froehlich, 2021), we tested the following three criteria systematically in order to assume intention in animal communication, including vocalizations (Schel et al., 2013) and gesture production (Cartmill & Byrne, 2007; Schel et al., 2022). First, a signal has to be uttered in order to achieve a specific goal (goal directedness). Second, signalers have some control over signal production and adjust their communication to recipient behavior; i.e., they persist until achieving their goal (voluntary signal usage). Third, recipients actually change their behavior, which means signalers achieved their goal (goal achievement). To date, hints to intentionality in animal vocal communication are mainly restricted to great apes (Byrne, 2016; Crockford et al., 2012; Leavens & Hopkins, 1998; Zuberbühler & Gomez, 2018), which nourishes theories on the gestural evolutionary roots of language (Tomasello, 2008). For instance, chimpanzees have been shown to produce alarm calls, 'travel hoos' and 'rest hoos' depending on audience presence and composition, which suggests voluntary signal use (Bouchard & Zuberbühler,

2022; Crockford et al., 2015; Gruber & Zuberbühler, 2013). However, it remains unclear whether receivers change their behavior due to signal perception and whether signalers stop calling because they achieved behavioral changes in receivers, although, at least for alarm calls, signal use ceased once receivers were safe from a nearby snake (Schel et al., 2013). One difficulty in order to satisfactorily fulfil criteria for intentional communication is thus to demonstrate the interactive feedback loop between behavioral changes in recipients and signalers that ultimately leads to goal achievement.

Putty-nosed monkeys (*Cercopithecus nictitans*) are mainly arboreal forest guenons living in one-male groups with various females and their offspring (Buzzard & Eckardt, 2007). The reproductive male is often found isolated at the group's periphery and does not engage much in social interaction. During threatening events, the male takes over major group defense while females engage far less in predator mobbing and usually retreat with more vulnerable offspring. Males utter different alarm calls that denote external events with varying degree of context specificity while females only possess one general alarm, "chirp", that is emitted in response to all threats (Arnold & Zuberbühler, 2006). Male short-range "kek" alarms are often heard at the onset of responses towards leopards (*Panthera pardus*) and usually advertise male predator mobbing (Mehon & Stephan, 2021; Mehon et al., in review). Recent findings showed that females use their chirps to recruit males for costly anti-predation services (Mehon & Stephan, 2021) and that females are sensitive to male signaler identity (N'zoulou Kiminou et al., 2022). In the majority of cases, the group's male approached females and started predator-specific mobbing behavior, to which females reliably stopped own alarm calling and retreated with their offspring in dense vegetation for cover. Because both the utterance of kek calls and male anti-predator behavior naturally occur simultaneously, it remains unclear if females ceased own alarm calling in response to male calls or in response to male predator-mobbing and group defense. The question whether females use their alarm calls strategically with the intention to manipulate male behavior could thus not be clarified.

Here, we experimentally disentangled male kek calls from male anti-predation behavior and recorded changes in female alarm calling throughout four stages of a simulated predation event. First, we recorded baseline female vocal behavior without disturbance. Second, we presented a leopard model to the females of a target group, which elicits female alarm calling. Third, after females started alarm calling to the leopard model, we broadcasted the group's male kek calls to females and recorded any changes in female alarm calling. Importantly to note, we constantly monitored the male's position and only broadcasted the group's male kek calls to females when the male of the group was at least 60 m away from the females and offspring. Fourth, we waited until the male of the group naturally approached the rest of the group in response to female alarms ("male recruitments") and recorded female alarm calling after their male started mobbing behavior towards the presented leopard model. In cases in which males did not approach the rest of the group, we kept recording female alarm calling until it ceased without male anti-predation intervention. To assess females' intentionality to modify male behavior, we tested female alarm calling against criteria that were recently summarized for comparative approaches to animals' intentional use of signals (Townsend et al., 2017). If females use their alarms intentionally to change male behavior, they should continue alarm calling after receiving their male's kek calls until the male approaches the group and provides anti-predation services like predator mobbing (criterion 1: goal-directedness). In cases in which the group's male could not be recruited for predation defense, we expect females to alarm call considerably longer and more than after male recruitments in order to persist in changing male behavior towards the provision of services in group protection (criterion 2: voluntary signal usage towards a recipient in order to achieve a goal). We expect most of the males to follow female recruitments in order to advertise their quality as reliable providers of anti-predation services and, in turn, females to cease own alarm calling once their male engages in predator mobbing (criterion 3: goal achievement).

Method

Ethics Statement

The work conducted during the current study received approval by the Congolese Ministère de l'Economie Forestière, the Agence Congolaise de la Faune et des Aires Protégées (ACFAP), and the Institut en Recherche Forestière within the Ministère de la Recherche Scientifique et de l'Innovation Technologique (research permit no. 270/2020; 001/2021), and it complies with guidelines for the work with animals as provided by the Association of the Study of Animal Behaviour.

Subjects, Site, and Stimuli

The study was conducted with 13 groups of wild putty-nosed monkeys (consisting of 7 to 22 individuals, Table 1) in the Nouabalé-Ndoki National Park, northern Republic of Congo (2°15.50 N 16°24.70 E) in a mono-dominant *Gilbertiodendron dewevrei* forest and mixed species forest on *terra firma* soil. Data were collected between March 2020 and June 2021. Since 2018, home ranges have been determined for all groups using GPS data, and specific individual markings have been documented. Both main, natural predators, crowned eagles (*Stephanoetus coronatus*) and leopards (*Panthera pardus*), are present in the study area. We opted to use a moving, leopard-print fabric to simulate leopard presence (Figure 1) instead of an eagle model because the latter's natural movements would have been harder to mimic. For this purpose, an assistant completely covered himself with the fabric in a hidden location and subsequently presented himself moving on four limbs to target subjects. Each group's male 'kek' calls were elicited and recorded between May 2019 and May 2020 in the framework of another study (N'zoulou Kiminou et al., 2022) by selectively presenting the leopard model to the male of the group. Sequences of 10 – 15 s of male kek calls were then created while conserving natural inter-call intervals and call order. Before the onset of data collection, we confirmed that present males were the same males from whom kek calls were previously recorded and that no male take-over took place in one of the study groups. Groups were not habituated to human presence and experimenters stayed concealed throughout the experiment.

Table 1

Group Composition of Target Groups

Group	Male	Females	Subadults & Infants	Total
1	1	3	5	9
2	1	8	5	14
3	1	10	7	18
4	1	4	2	7
5	1	8	5	14
6	1	9	6	16
7	1	9	12	22
8	1	11	9	21
9	1	11	8	20
10	1	6	4	11
11	1	7	8	16
12	1	7	5	13
13	1	6	6	13

Figure 1

Leopard Model
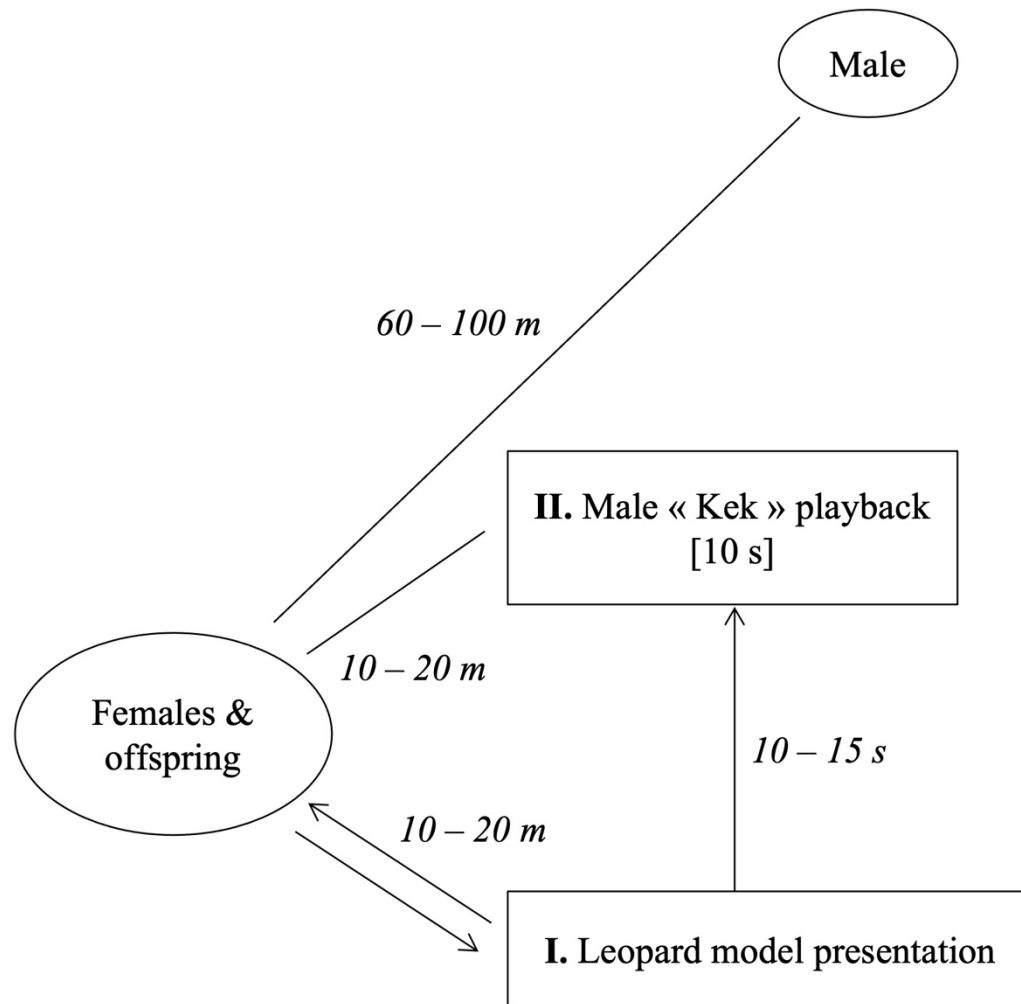

Data Collection Protocol

Groups were located by female contact calls within known home ranges. Target groups were then identified by characteristics of specific individuals (e.g., broken tails and scars) and group composition. First, it was confirmed that the group was not associated with any other monkey species to prevent interferences with other species' anti-predation behavior and to reassure good acoustic recording quality. Second, the male was localized and an assistant (assistant 1) stayed hidden with the group's male and confirmed to the experimenter (FGM) once the male was 60 – 100 m away from the rest of the group using Motorola walkie talkies (Figure 2). A second assistant (assistant 2) always stayed with the females and confirmed that no other disturbing events occurred. Once the separated position of females and the male was confirmed, the experimenter positioned all broadcasting and recording equipment in 10 – 20 m from the females in the direction of their group's male and recorded baseline vocal behavior for 5 min. Hidden by dense vegetation, assistant 2 completely covered himself in the leopard-printed fabric and started moving from a distance of 10 – 20 m on four limbs towards females and their offspring and moved beneath the tree where they were located. After the first female alarm, the experimenter waited another 10 – 15 s before launching the playback of the same group's male kek alarm sequence. Vocal responses were recorded until females ceased alarm calling. To account for differences between groups in the distance that a group's male was away from the rest of the group, we categorized male recruitments by females as successful if the male arrived with its females within 5 min after the first female alarm call. Because of the urgency to apply anti-predation strategy immediately during predation events, we classified male recruitments as unsuccessful if the group's male did not start mobbing behavior within 5 min after the first female alarm. For successful male recruitments, the onset of male mobbing towards the leopard model was noted. After the male engaged for 15 – 30 s in predator mobbing, the leopard model (assistant 2) retreated in dense vegetation to mimic natural predator deterrence. Trials in which responses could have been modified by other events were excluded from final analysis (a solitary male surrounding the target group detected the leopard model before females and started alarm calling: $n = 3$; nearby chimpanzee (*Pan troglodytes troglodytes*) vocalizations: $n = 4$; gorilla (*Gorilla gorilla gorilla*) arrival: $n = 1$; forest elephant (*Loxodonta cyclotis*) arrival: $n = 2$). All

disturbances occurred before male kek playbacks, i.e., during baseline recording and before females saw the leopard model. Trials that had to be cancelled due to beforementioned reasons were initiated again at least two weeks after the first attempt. Each target group was only presented once with the leopard model and thereafter with one kek alarm sequence of the same group's male.

Male alarm calls were broadcasted using an Apple iPod touch connected to an AER alpha speaker-amplifier. Vocal responses were recorded with a Sennheiser ME67 directional microphone and a Zoom H4n recorder (44.1 kHz sampling rate, 16 bits amplitude resolution and stored in .wav format). Observations of the target group were made using Nikon Monarch 7 binoculars.

Figure 2

Schematic Experimental Set Up

Note. Circles represent putty-nosed monkeys, squares represent experimental phases and lines indicate the distance between monkeys and presentations as well as the time that elapsed between both experimental phases.

Data Analysis

To evaluate any changes in female alarm calling, we calculated call rates by dividing the number of female alarm calls that were emitted during a specific phase of the experiment by the duration of the respective response phase (calls/s). Different phases of the experiment included: 1) vocal baseline behavior

(5 min undisturbed vocal behavior before leopard model presentation), 2) leopard model presentation until male kek playback ("leopard model detection"), 3) male kek playback until male arrival with group ("male 'kek' call perception") 4) male arrival with group until last female alarm call ("male arrival & predator mobbing") or, in case the male did not approach his group and was not successfully recruited, average duration until male approach until last female call ("NO male arrival & NO predator mobbing"). We investigated differences in female alarm calling in different experimental phases within groups using Kruskal Walis tests and subsequent Wilcoxon signed rank tests including a Bonferroni holm correction to control for multiple hypotheses testing. Female response lengths were compared between different groups for trials with and without male approaches and anti-predation services using Mann-Whitney-U-tests. Pearson's correlation coefficient was calculated to link call rate differences between groups to the number of females in each group to exclude other group-specific peculiarities that might account for between-group differences in alarm calling.

Acoustic analysis was conducted using PRAAT 6.1.16 (Boersma & Weenink, 2003) and statistical analysis was conducted by means of R vs. 4.0.2 (R Core Team, 2022). All tests were two-sided.

Results

Comparison of female alarm calling rates during different phases of simulated leopard encounters revealed consistent differences both in trials during which males were successfully recruited to take over anti-predator services (Kruskal-Wallis test, $H(3) = 22.67$, $p < .001$) and in trials in which males remained at a distance without approaching the rest of the group ($H(3) = 17.56$, $p < .001$).

Females reliably started alarm calling upon detection of the leopard model (13 out of 13 groups). Upon hearing playbacks of their male's kek calls, females only showed slight decreases in alarm calling (Table 2, Figure 3). If a male approached the rest of its group, mobbing behavior was immediately started. Males arrived with the group in these cases on average after 183 s after the first female alarm call, thus considerably faster than our criterion for successful male recruitments. If males did not arrive during 5 min after the first female alarm, they also did not approach their group afterwards. Crucially, for trials in which males approached their group and started predator mobbing, females stopped alarm calling once the male took over defensive behavior ($N = 7$, Figure 3a, Table 2). In contrast, when their male did not approach them, and did not engage in anti-predation behavior, females did not change alarm calling rates ($N = 6$, Figure 3b, Table 2). In these cases of unsuccessful male recruitments, females also consistently alarm called longer (Mann-Whitney U test, $W = 5$, $p = .022$).
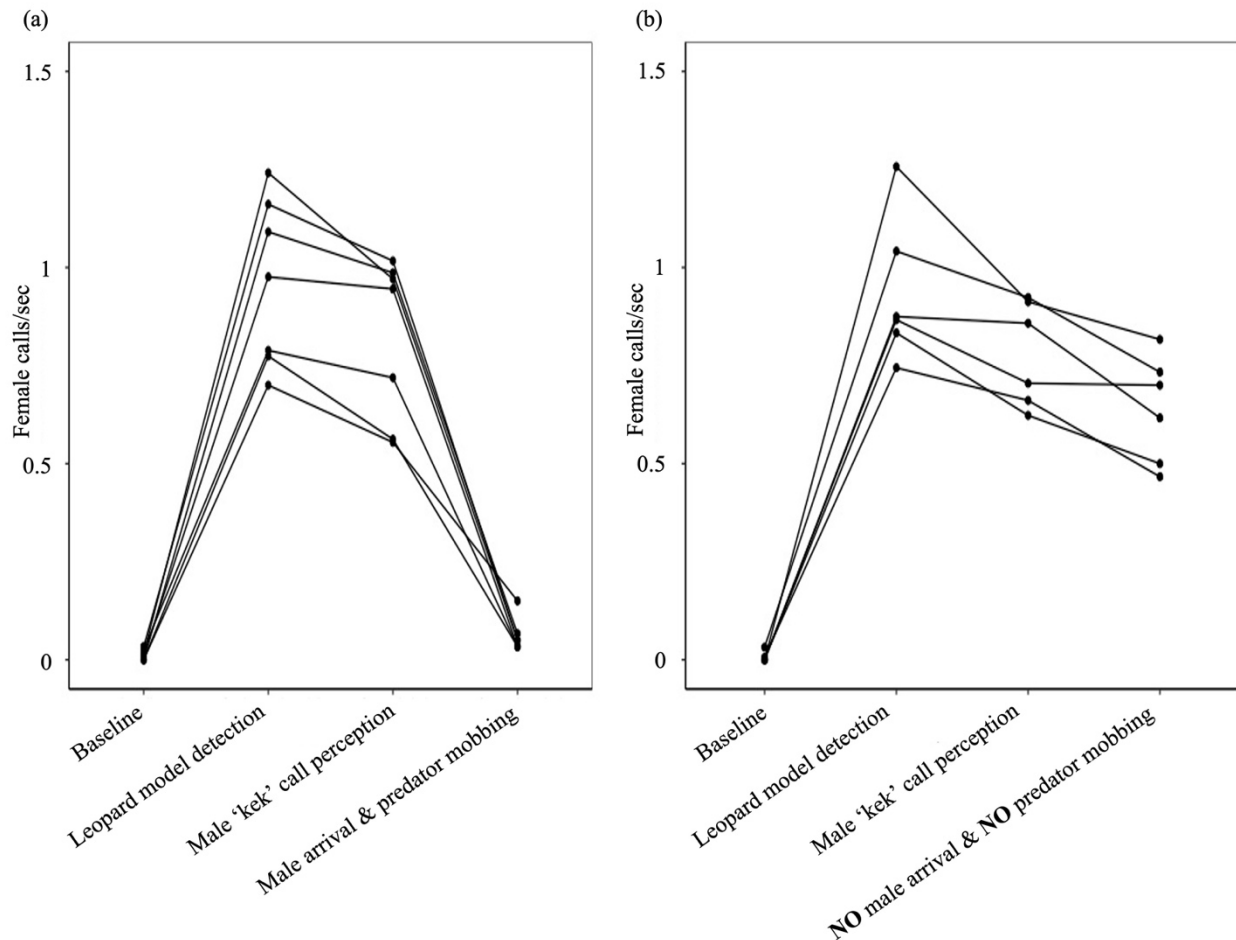
Group differences in calling rates were best explained by group composition, with groups comprising more females also uttering a higher number of calls per sec (Figure 4).

Table 2

Female Calling Rates

Pairwise comparison of female alarm calling rates	p-value$_{corrected}$	Relative change in alarm calling
Male provides anti-predation service		
Before vs. after detection of leopard model	**.0093**	+ 7824 %
Before vs. after male kek call	.2593	- 14 %
Before vs. after male arrival	**.0093**	- 92 %
Male does not provide anti-predation service		
Before vs. after detection of leopard model	**.0195**	+ 14625 %
Before vs. after male kek call	.3168	- 16 %
Before vs. after median male arrival	.3168	- 18 %

Note. Pairwise comparisons of female alarm calling rates for trials with successful male recruitments for predator mobbing and trials in which males could not be recruited for group defense. Significant p-values are indicated in bold.

Figure 3

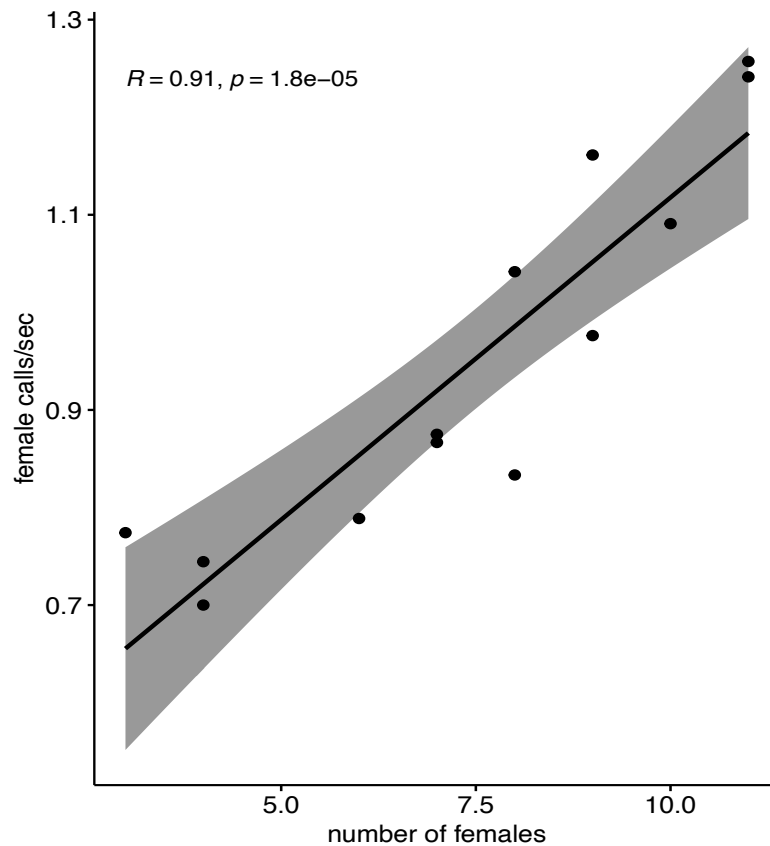*Female Call Rates During Different Experimental Stages*

Note. (a) Trials with successful male recruitments for mobbing behavior. (b) Trials without male predator mobbing behavior.

Discussion

Female putty-nosed monkeys monitored male anti-predation behavior and only ceased their own alarm calling once their male engaged in anti-predation defense (i.e., goal-directedness). Male's individually distinctive kek alarms, which usually accompany predator mobbing, were not sufficient to lead to the cessation of female alarm calling. In cases in which males could not be recruited, and males did not take over anti-predation services, females persisted considerably longer in alarm calling (i.e., voluntary signal usage). More than half of the males responded to female recruitments, and approached and started predator mobbing after perceiving female general alarms (i.e., goal achievement). We argue that with this interactive exchange of alarm calls and associated behavioral changes in both females and males in response to each other's alarms, all three criteria for female first-order intentional communication are fulfilled. Furthermore, that females and males flexibly aligned and vocally mediated their anti-predation behavior shows that they were aware of each other's behavior and that both sexes responded accordingly to the behavior of the other sex. The social engagement with each other and the mutual awareness leading to own behavioral responses are often seen as the foundation of intersubjectivity as seen in human language (Terrace et al., 2022).

Figure 4

Relationship between number of females and female alarm calling rate

$R = 0.91$, $p = 1.8e{-}05$

Note. Correlation plot between the number of females in a group and the number of female alarm calls for each group including Pearson's rank coefficient. The grey shaded area represents the confidence interval set at 95%.

What communicative function is served through females' socio-cognitive abilities of using alarm calls intentionally? We consider it unlikely that females inform ignorant group members because first, female general alarm calls do not allow receivers to infer any detailed information about the nature of the threat and to adapt their anti-predation behavioral strategies. Second, females and offspring usually form a cohesive cluster and other group members except for the peripheral male likely have visual access to ongoing events. We suggest that female alarms are neither declarative nor informative but interrogative instead, representing imperative demands for defense towards males. It has been previously suggested that males follow female recruitments for anti-predation services in order to increase their reputation as "hired guns" and to reassure future access to reproduction (Rubenstein, 1986), mediated by "reputation-based mate choice" (van Schaik et al., 2022). Similarly, males of several non-human primates have been shown to take over predation defense (Gautier-Hion & Tutin, 1988) as well as the lion's share of agonistic interactions during intergroup conflicts (Bshary et al., 2022), which further promotes the idea that males provide defense services to females. Additional empirical support for male anti-predation behavior in the context of mate quality advertisement comes from a study investigating audience effects in 19 different bird species (da Cunha et al., 2017). Results show that predator mobbing in males increased with an increasing number of bystander females, but not with an increasing number of males in the audience. Importantly, female non-human primates have been shown to possess some control over mate choice (Arlet et al., 2007) and to monitor and persist if the male's assessment of a threat is not in line with their own judgement of the situation (Stephan & Zuberbühler, 2016). Male recognition by alarm calls alone additionally provides

females with the cognitive means to keep track of individual male performances in the provision of anti-predation services and to build male reputation in group defense over time (Butynski et al., 1992; N'zoulou Kiminou et al., 2022). Finally, male inter-individual variability in the provision of anti-predation services as indicated by males not following female recruitments provide the ground for the inter-sexual selection for reliably defensive mates (Darwin, 1871). Results presented here confirm that females sensitively monitor and respond to male inter-individual differences in predation defense.

In sum, our results are in line with the idea that female monkeys intentionally use their general alarm calls to recruit their group's male as a hired gun to defend them and their offspring against a predator. Our results further suggest that there might be a sex-specific disparity in the cognitive mechanisms that underpin female and male alarm call usage that might be the result of different alarm call functions in females and males. It seems likely that alarm calls evolved under sexual selection in addition to natural selection (Delgado, 2006; Zuberbühler, 2004) through female mating preferences for good male protectors. The level of intentionality that is involved in alarm call usage remains an interesting topic for future investigation. In how far females and males attribute mental states and inferentially communicate (Warren & Call, 2021) during the flexible and interactive coordination of anti-predation strategies remains another topic for future investigations. Despite notorious difficulties to obtain long-term data on wild, habituated groups, data on differences in male tenures as a function of different males' anti-predation service provision to females are highly suitable to shed further light on the evolution of alarm calling and its potential to elucidate language evolution.

Acknowledgments

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