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Vocal recognition of alarm calls in wild putty-nosed monkeys, *Cercopithecus nictitans*

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Vocal recognition in social contexts is phylogenetically widespread and can be explained by kin and mate recognition or group coordination. It remains unclear why some species evolved alarm calls that also provide cues to signaller identity as the function of these calls is thought to predominantly serve predation avoidance. One hypothesis is that individually distinct alarms facilitate the detection of unreliable callers, which is in line with the idea of reputation-based mate choice. However, it remains unknown whether receivers use provided cues to identify the signaller and, if yes, how vocal signaller recognition impacts on their own behaviour during predation events. In many nonhuman primates, males provide risky antipredator services to the rest of the group while uttering conspicuous alarm calls. In putty-nosed monkeys, some male alarm types have been shown to be individually distinct and females have been shown to vocally recruit males for predation defence. Whether females are sensitive to the identity of the male supporting them in predation defence is unknown. We tested 16 groups of putty-nosed monkeys in the Nouabalé Ndoki National Park (Republic of Congo) with different alarm types from different males. Specifically, we broadcast pyow, hack and kek calls from the group's own male, a neighbouring male and an unknown male, respectively, to each group. Female receivers were sensitive to signaller identity and consistently varied their own antipredator behaviour between different males for two call types but not for eagle-related hacks. We explored different possible explanations for male recognition based on risky male antipredator services and conclude that our results are strongly in line with the reputation-based mate choice hypothesis.

Animal vocalizations can provide information about ongoing external events with different degrees of specificity (Seyfarth et al., 1980; Norcross & Newman, 1993; Randall et al., 2005). For instance, the social context might modify utterances and calls can vary as a function of audience presence and composition (Szipl et al., 2018). Additionally, signaller attributes such as sex (D. T. Blumstein & Munos, 2005; Szipl & Bugnyar, 2014), age (Fischer et al., 2002), kinship (Rendall et al., 1996) and physical condition (Reby & McComb, 2003) can have an impact on the acoustic features of calls. Information about the signaller might thus be provided by involuntarily shaped signal structure by sound production mechanisms, known as the source–filter model of sound production (W. T. Fitch, 2000; Hauser, 1996). In many species, receivers have been shown to be sensitive to perceptual cues and to categorize signallers into classes on the basis of received information (Colombelli-Négrel & Evans, 2017; Zentall et al., 2008). For instance, formant-related features are determined by vocal tract length, a reliable correlate of body size, and there is little control over it (W. T. Fitch, 1997). Hinds have been shown to perceive differences in formant frequencies within male red deer, *Cervus elaphus*, calls and to selectively approach stags that have been judged to be bigger based on acoustic features of their calls (Charlton et al., 2007).

Besides signaller classification based on physical features, receivers might assign signallers to classes that are based on previous experiences (Szipl et al., 2015; Tricarico et al., 2011). Accordingly, signals of members of the same class (e.g. familiar individuals) are physically not more similar than members of another class (e.g. unfamiliar individuals), but it is past encounters of a specific signaller – receiver dyad that constitute signaller recognition and that affect receivers' behaviour. Distinguishing others by familiarity can be beneficial in a variety of contexts including territory defence

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(Levey et al., 2009; Stephan & Zuberbühler, 2016a; Van Dyk & Evans, 2007), group organization (Hopp et al., 2001; Kondo et al., 2012) and reproductive contexts (Charrier et al., 2009; Hemmerich, 2016; Magurran & Ramnarine, 2004). However, sometimes it might be even more beneficial to distinguish between individual familiar signallers (Boeckle et al., 2012; Frommolt et al., 2003; Tibbetts & Dale, 2007). The distinction between familiar conspecifics can be particularly useful for intragroup cohesion, intergroup spacing or the recognition of one's own, dependent kin (Waser, 1977). Indeed, contact calls have been found to be individually distinct in many social species (Maurello et al., 2000; Sproul et al., 2006; Wanker & Fischer, 2001) and receivers are sensitive to these differences (Rendall et al., 1996; Semple, 2001). The function of individually distinct calls in antipredator contexts is less well understood but previous findings in some social mammal species suggest that the recognition of individual alarms might facilitate the detection of unreliable callers, thus allowing receivers to optimize activity budgets (D. T. Blumstein et al., 2004; Cheney & Seyfarth, 1988; Hare & Atkins, 2001). However, this does not seem to generally hold true as signaller identity encoded in alarm calls does not always elicit different behavioural responses in receivers (Schibler & Manser, 2007). It remains unclear whether inferring signaller identity from alarm calls is only beneficial to avoid deceptive callers or whether it might also extend to other functions.

Male nonhuman primates often take over a considerable share of risky antipredator defence (Arlet & Isbell, 2009; Dolotovskaya et al., 2019; Stephan & Zuberbühler, 2016b; van Schaik & van Noordwijk, 1989). First, this phenomenon might be explained by kin protection to ensure the survival of the defender's genes in closely related individuals (Maynard-Smith, 1965; Mehon & Stephan, 2021). Second, benefits from group augmentation (Kokko et al., 2001) are thought to increase the defender's survival through the effects of dilution of predation risk and confusion during antipredator responses (Delm, 1990; Schradin et al., 2019). Males thus have an interest in being part of a group and in maintaining its size as the probability of being attacked decreases for an individual with increasing group size and group cohesion due to stochastic effects and because it is difficult for a predator to focus and follow a single prey individual in a group. Third, the reciprocal provision of benefits, especially between closely bonded individuals could account for male antipredator services if for example females return the favour in other contexts like grooming (Roberts, 2005). Fourth, males might gain reproductive benefits due to female mate choice mediated by the reputation of being a reliably protective male (Sylwester & Roberts, 2013; van Schaik et al., 2022). This might also be relevant in species that form one-male groups if male–male competition is high, for example due to the presence of surrounding, solitary males trying to take females from harem-holding males. If females are sensitive towards different antipredator services provided by males, they might use this assessment to perform some degree of quality assessment and mate choice during encounters between their established male and intruding solitary males. As a result, male tenure length should vary between individual males and be associated with their ability to provide antipredator services for choosy females. Indeed, Samango monkeys, *Cercopithecus mitis labiatus*, a forest guenon forming one-male groups, show prominent differences in male tenure length including two male replacements within 2 years for one group and no male replacement for another group (Macleod et al., 2002). This confirms observations in other forest guenons with male tenure length ranging from less than 1 to 3.5 years (F.G. Mehon, personal observation: diana monkey, *Cercopithecus diana*, putty-nosed monkey). Furthermore, Macleod et al. (2002) confirmed the presence of 14 solitary males in their study area compared to only six males that held a group. This hints to high male–male competition over access to reproduction, especially during the breeding season. However, their observation did not clarify whether females monitor male quality and whether they have any choice in what male establishes itself as the reproductive male of a group. To date, direct evidence for female mate choice in one-male groups is still lacking.

Risky antipredator services are often accompanied by conspicuous alarm calling and some male forest guenons have evolved laryngeal air sacs to utter loud, long-distance calls, which sometimes also function as alarm calls in response to external dangers (J. P. Gautier, 1971; J. P. Gautier & Gautier, 1977; Zuberbühler, 2002). In two forest guenons, putty-nosed and blue, *C. mitis*, monkeys, some of these loud alarm calls, ‘pyows’, convey cues to signaller identity while another call, ‘hack’, does not vary between males (Butynski et al., 1992; Price et al., 2009). This suggests that information about the signaller is shaped not only by the monkeys' vocal system, including the larynx and supralaryngeal vocal tract, but also by the function of different alarm call types.

Putty-nosed monkeys live in harem-structured, one-male groups with several philopatric females and their offspring in tropical rainforests ranging from Liberia to the Democratic Republic of Congo. In the wild, putty-nosed monkeys might live for 20 years (up to 31 years in captivity) (De Magalhaes & Costa, 2009), which indicates that females most likely experience multiple male take-overs during their lives. While females have one general ‘chirp’ alarm uttered in response to all threatening events, males possess three different alarm call types, two loud-calls, ‘pyows’ and ‘hacks’, and a close-range alarm, ‘keks’ (Arnold & Zuberbühler, 2006a; Mehon & Stephan, 2021). Kek calls in our study population in the Nouabalè Ndoki forest resemble calls that were previously classified as ‘short pyows’ in another population (Arnold & Zuberbühler, 2006a), although no unsupervised automated acoustic analysis was conducted and final evidence that keks and short pyows represent the same call type are not yet available.

Male alarms are to some extent indicative of the eliciting context, especially when given at the onset of responses, with pyows uttered mainly to terrestrial threats including leopards, *Panthera pardus*, but also other males' alarms, and hacks produced mostly to crowned hawk-eagles, *Stephanoaetus coronatus*. Additionally, pyows and hacks are frequently incorporated into vocal sequences that are uttered after tree falls (Arnold & Zuberbühler, 2013). The attribution of an exact meaning to both call types remains unclear. In the study population, kek calls have been triggered by terrestrial, moving threats that have been visually spotted. Sometimes, males form pyow—hack sequences that seem to accompany group movement (Arnold & Zuberbühler, 2006b). Females have been recently shown to vocally recruit their group's male with chirps to defend them and their offspring against predators (Mehon & Stephan, 2021). In a population in the Republic of Congo, once the male was recruited, females ceased their own alarm calling and changed to more cryptic behaviour (Mehon & Stephan, 2021), although females from a Nigerian population did not cease their own alarm responses when the male approached a terrestrial threat (Arnold & Zuberbühler, 2013). In the Congolese study population, when hearing female general alarms, males approached their group while uttering pyows, before knowing the nature of the threat. Given that the rest of the group was already informed about leopard presence and that leopards are usually only deterred by close-range mobbing, it remains puzzling why males should start alarm calling when still far from the threat. One possible explanation is that pyow calls might function as ‘signature calls’ that advertise a specific male's commitment to group defence. A link between male antipredator services and reputation-based partner choice has been suggested for other primate species, although systematic investigations are rare (Crofoot, 2012, van Schaik & van Noordwijk, 1989). A crucial prerequisite here is that females vocally recognize different males in dense forest habitats with restricted visibility. A previous study showed that at least some female putty-nosed monkeys approached the sound source after being presented with their male's pyow calls but not when perceiving out-group male calls (Arnold & Zuberbühler, 2008), suggesting that females are able to extract signaller information from male calls. It remains to be systematically tested whether females also distinguish between familiar individuals as well as how male recognition might directly impact on female antipredator behaviour.

We experimentally tested female putty-nosed monkeys with playbacks of different males' alarm calls. First, we evaluated whether male putty-nosed monkeys in our population also provide cues to the caller's identity in their alarm calls, including pyow, kek and hack calls. Second, we presented females of several target groups with calls of their own male, a neighbouring male or an unknown male for all three alarm types. We recorded the females' alarm calling and spatial behaviour to compare female responses to different combinations of alarm call type and male identity. Based on the male's crucial role during predator defence, the previously shown careful monitoring of male antipredator behaviour by females, and the potential to gain social reputation and future reproductive benefits from risky alarm calling and mobbing, we hypothesized that females infer information about male identity from male alarms when available, and that they react differently towards different male signallers giving the same call type.

METHODS

Study Site and Subjects

We tested 16 groups of putty-nosed monkeys in an area of about 60 km^2 of tropical rainforest surrounding a natural forest clearing, Mbeli Baï, in the Nouabalé-Ndoki National Park, Republic of Congo (215.50N, 1624.70E; altitude about 300 m), between March 2020 and April 2021. Groups ranged from seven to 21 individuals (Table A1). None of the groups was habituated to human presence and they could thus not be approached by human observers except when the latter were occluded by dense forest vegetation. All groups have been identified based on group size and individual markings since 2018, when their home range was determined using GPS data and groups started to be followed and continuously monitored. No information is yet available about the genetic relatedness between different groups. However, subadult males that disappeared in their natal group have never been observed in a neighbouring group, suggesting that young males do not usually succeed in taking over the group from an established male neighbouring their natal group. All neighbouring groups shared a peripheral part of their home range, but we never observed two groups (focal and neighbouring) within 150 m of each other.

Playback Stimuli and Data Collection

First, we presented original predator sounds (leopards, $N = 3$; eagle shrieks, $N = 3$) and a moving leopard model to males of target groups and recorded their alarm calls (pyows, hacks, keks). For visual leopard presentations, an assistant, covered in a leopard-print fabric, first hid in dense vegetation and then moved to expose himself to the male of the group while the experimenter recorded the focal male's alarm calls. From these responses, 10 s sequences of male alarms were cut while conserving natural intercall intervals and call order. For some males, alarm calls could not be triggered. We repeated the presentation of predator cues a second time after 2 weeks. If males again did not respond ($N = 10$ trials), their calls were excluded, resulting in a total of 38 different stimuli (pyow: $N_{\text{males}} = 16$; hack: $N_{\text{males}} = 12$; kek: $N_{\text{males}} = 10$). Second, females of a target group were then presented with either hack, pyow or kek sequences from their own male, a neighbouring male or an unfamiliar male. A male was categorized as unfamiliar to a specific target group when he was recorded 5–10 km away from that group. A male that served as the unfamiliar stimulus for one group could provide the neighbour stimulus for another, depending on its territory location. In total, each group was presented with nine playback conditions (three call types × three male signaller classes). The order in which the nine playback conditions were presented to a specific group was randomized. Once the experimenter (D.N.K.) entered the home range of the target group, the latter was located by female contact calls before the male of the group was located and group identity was confirmed. If the male was separated from the rest of the group by at least 30 m, one assistant stayed with him while the experimenter and a second assistant observed the group for about 15 min to exclude any disturbing events. This was indicated by the absence of any alarm calls and scanning behaviour in all observed individuals. After the broadcasting and recording equipment was positioned, the baseline vocal behaviour was recorded for 2–5 min. The majority of females were continuously monitored to ensure that they were neither approaching their male nor showing any vigilant behaviour that might have indicated human detection. We then broadcast the playback stimulus and recorded the females' vocal response (latency to call, call rate) and movements (stay, move to own male, move to speaker) until alarm calling stopped. Humans always stayed hidden and did not expose themselves to the group. Trials were abandoned when responses could have been triggered by other disturbing events, for instance the arrival of chimpanzees, *Pan troglodytes* ($N = 1$), gorillas, *Gorilla gorilla* ($N = 1$) or forest elephants, *Loxodonta cyclotis* ($N = 1$). Only one stimulus was broadcast per day. Groups were revisited after at least 5 days to conduct the next trial, either with the same stimulus when the trial was previously interrupted for the aforementioned reasons, or to present the group with a different stimulus (of the nine conditions per group). We excluded trials from the analysis of nonvocal, behavioural variables if dense vegetation and the necessity for human observers to stay hidden did not allow for clear observations of female behaviour (pyow: $N_{\text{own}} = 7$, $N_{\text{neighbour}} = 5$, $N_{\text{unknown}} = 3$; kek: $N_{\text{own}} = 6$, $N_{\text{neighbour}} = 3$, $N_{\text{unknown}} = 2$; hack: $N_{\text{own}} = 5$, $N_{\text{neighbour}} = 4$, $N_{\text{unknown}} = 3$). This resulted in a total of 122 trials that entered analysis of female vocal, and 105 trials that entered analysis for female nonvocal, behavioural responses (Table A2).

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). Nonvocal behavioural observations of females were conducted using Nikon Monarch 7 binoculars before and after broadcasting different male alarm calls.

Data Analysis

Individuality of male alarms

We evaluated whether males in our population, similar to putty-nosed monkey males in Nigeria (Price et al., 2009), utter alarm calls that contain cues to signaller identity. To this end, we extracted 10 calls of each of the three alarm types from several males (pyow: $N = 5$; kek: $N = 6$; hack: $N = 6$), resulting in 50 pyows, 60 keks and 60 hacks from which we automatically extracted acoustic and temporal features (Table A3). Male calls were only extracted when they were recorded close-range without any overlapping sounds, thus ensuring good recording quality for the optimal extraction of physical features. We then entered these call parameters for each call type separately in a cluster analysis.

Female response to male identity

The latency to call (s) was calculated by measuring the time that elapsed between stimulus presentation and the first female alarm call. The number of female alarms per second (calls/s) was calculated by dividing the total number of female calls by the number of seconds between stimulus presentation and either the end of female responses or the first alarm of the present male. We opted for not considering female alarm calling after the natural onset of male responses to exclude the possibility that their male's alarm calling modified female behaviour. Whether females changed their spatial position was assessed by comparing their position during stimulus presentation with their position 30 s after male alarm call playbacks. Three types of displacement were distinguished, namely no change in position ('stay'), approach to their male ('to male') and approach to the source of the broadcast male alarms ('to speaker').

Male acoustic parameters for the cluster analysis, female call rates and female latencies to call were extracted from these recordings using PRAAT 6.1.16 (Boersma & Weenink, 2003).

Statistical Analysis

Individuality of male alarms

The daisy function in the package 'cluster' (Maechler et al., 2019) was used to calculate physical similarities between single calls. Calls were then iteratively assigned to their closest cluster medoid, using the PAM algorithm (partitioning around medoids) on solutions with 2–10 possible medoids (i.e. cluster). Silhouette widths were plotted to identify the optimal cluster solution (as indicated by highest silhouette scores, S_c) and single calls were assigned to their nearest cluster using the kmeans function (package 'ggpubr', Kassambara, 2020). Results from the cluster analysis entered a principal component analysis (PCA) using the prcomp function ('stats' package) to reduce the original variable set to noncorrelated dimensions. The two dimensions that explained most variation in the data were plotted using the ggscatter function ('factoextra' package, Kassambara & Mundt, 2020).

Female response to male identity

Female latencies to call and call rates in response to different males within a specific call type were compared using the lme function ('nlme' package, Pinheiro et al., 2004) to fit linear mixed-effect models with 'signaller class' as fixed factor and 'group' as random factor. Post hoc pairwise comparisons between different male categories (own, neighbour, unknown) were conducted by calculating estimated marginal means using the function emmeans ('emmeans' package, Lenth, 2022) including adjusted *P* values for multiple testing that were calculated with the Tukey method. This specifically generates confidence intervals for all pairwise differences between factor level means while maintaining the simultaneous error rate at a specified level. Tukey's method adjusts the confidence level for each individual interval so that the resulting simultaneous confidence level is the specified value. A Bonferroni–Holm adjustment of *P* values was applied to account for multiple hypothesis testing (i.e. testing for effects on three different call types).

The homogeneity of proportions of different forms of displacement was compared between responses to different males within each call type using chi-square tests and a Bonferroni–Holm method to correct for multiple hypothesis testing (i.e. testing for effects on three different call types). Statistical analysis was conducted using R v. 3.6.1 (R Development Core Team, 2008).

Ethical Note

All results presented here were obtained by strictly noninvasive methods and with approval by the Institut National de Recherche Forestière within the Ministère de la Recherche Scientifique et de l'Innovation Technologique (research permit no. 270/2020; 051/2021).

RESULTS

Individuality of Male Alarms

The most distinct call categories corresponded to male identity for pyow ($N_{\mathrm{male}} = 5$, $N_{\mathrm{optimal\ cluster}} = 5$, $S_c = 0.6$; Fig. 1a and b) and kek ($N_{\mathrm{male}} = 6$, $N_{\mathrm{optimal\ cluster}} = 6$, $S_c = 0.59$; Fig. 1c and d), but not for hack calls ($N_{\mathrm{male}} = 6$, $N_{\mathrm{optimal\ cluster}} = 9$, $S_c = 0.42$; Fig. 1e and f). Accordingly, pyow and kek calls of the same male were physically more similar than pyow and kek calls of different males. In contrast, hack calls were not found to contain cues to caller identity. The PCA revealed two independent dimensions that explained 57.4% of variance for pyow alarms, 67.1% for kek alarms and 44.7 % for hack alarms. Key variables that distinguished calls from different males were mainly frequency related (Table A4).

Female Response to Male Identity

Female latency to call and alarm calling rates varied considerably between different males for pyow and kek alarms but not for hack calls (Fig. 2a–f, Table 1). Specifically, when perceiving pyow alarms, females started alarm calling fastest with highest calling rates to unknown males and slowest with lowest calling rates to neighbouring males (Fig. 2a and b). Their own male's pyow calls elicited intermediate latencies to call and intermediate calling rates. For male kek alarms, females barely uttered any calls in response to their own male and if they did, it was after considerable delay (Fig. 2c and d). To neighbouring male's keks, they replied moderately quickly with some calls while they produced alarms fast and at the highest rates in response to unknown males' keks. In contrast, for male hack alarms, females consistently started after considerable delay and uttered a few of their own alarms, whether the signaller was their own male, a neighbour or an unknown male (Fig. 2e and f).

Females also differed consistently in their nonvocal behavioural response as a function of male identity for pyow and kek alarms, but not for male hacks (Table 2). Upon perceiving their own and a neighbouring male uttering pyows, females usually did not move ($N_{\mathrm{own}} = 8$ of 9 cases, $N_{\mathrm{neighbour}} = 6$ of 11 cases) or they approached the speaker ($N_{\mathrm{own}} = 1$ of 9 cases, $N_{\mathrm{neighbour}} = 5$ of 11 cases). In contrast, when hearing pyows that were uttered by an unknown male, females often moved towards their own male (7 of 13 cases). Kek calls of their own male never elicited any female displacement (10 of 10 cases). When perceiving kek calls of neighbours or unfamiliar males, females mostly either approached their male ($N_{\mathrm{neighbour}} = 6$ of 13 cases, $N_{\mathrm{unknown}} = 6$ of 14 cases) or they did not move ($N_{\mathrm{neighbour}} = 5$ of 13 cases, $N_{\mathrm{unknown}} = 5$ of 14 cases).

DISCUSSION

The current results show that two of three male alarm call types contain information about signaller identity and that females differ in their antipredator behaviour depending on information about signaller identity. In contrast to pyow and kek calls, hack calls were not found to be individually distinct, thus confirming previous results in another putty-nosed population (Price et al., 2009). Importantly, when females perceived broadcast pyow and kek

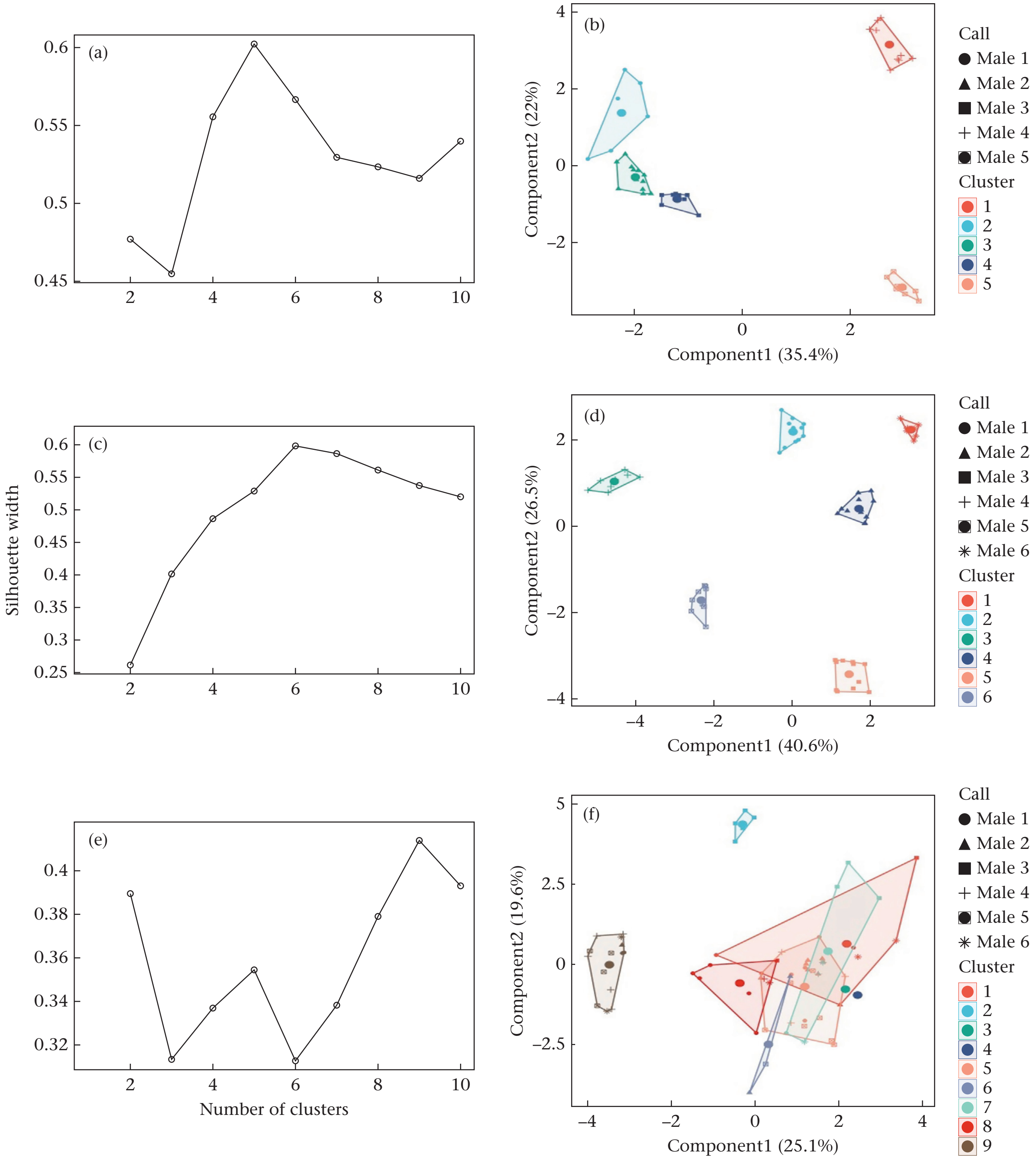

Figure 1. Most distinct cluster solutions and individual males' contribution to each cluster for (a, b) pyows, (c, d) keks and (e, f) hack alarms.

alarms from their own, a neighbouring and an unknown male, they differed consistently in their vocal and nonvocal behavioural responses as a function of male identity. Signaller recognition based on social familiarity seems unlikely as female responses to their own males and neighbours, both known and previously frequently perceived, were considerably different. We thus suggest that female responses might be explained by risk assessments that are based on both inferences from call types that are associated with specific information about the nature of predatory events and inferences about risks related to signaller identity.

Specifically, females did not usually respond to their own male's kek calls, which confirms previous findings in this population, namely that females immediately cease their own alarm calling once the male switches from pyow to kek calls, which usually indicates that he is taking over antipredator defence including leopard mobbing (Mehon & Stephan, 2021). Longer latencies to call and lower call rates than to stranger males suggest that neighbours were perceived as ‘dear enemies’ and not as ‘nasty neighbours’ (Müller & Manser, 2007). For pyow calls, females responded faster and with more calls to their own male's alarms than to a

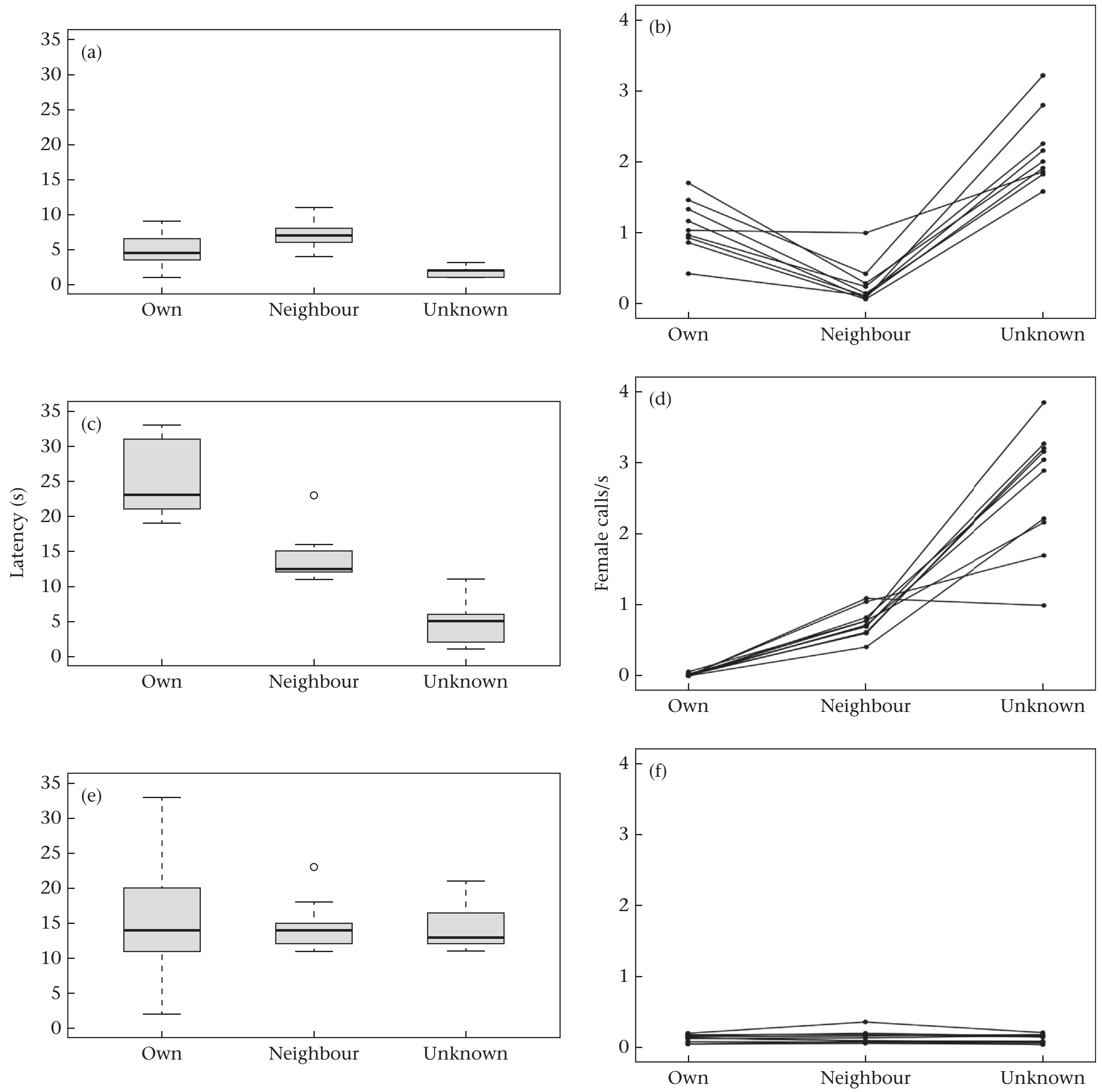

Figure 2. Latency to call and call rates for female responses towards different male classes for (a, b) pyows (N_{own}=12, $N_{\text{neighbour}}$=15, N_{unknown}=14), (c, d) keks (N_{own}=13, $N_{\text{neighbour}}$=14, N_{unknown}=14) and (e, f) hacks (N_{own}=11, $N_{\text{neighbour}}$=12, N_{unknown}=13) calls. For box plots, the box edges indicate the first and third quartiles, the horizontal line within the box represents the median, whiskers include values that amount to 1.5 times the height of the box and circles represent outliers.

neighbour's, which suggests that females might have associated pyows from familiar males with an external risk, which is likely to be closer if pyows are uttered by their own male. However, once females perceived pyows or keks from unknown males, they quickly started intense alarm calling while often moving towards their own male. We hypothesize that the presence of stranger males triggered resource defence rather than antipredator behaviour in females (Stephan & Zuberbühler, 2016a).

Recognition of Male Alarm Calls

There are four main benefits of risky male antipredator behaviour: (1) reciprocally provided services within closely bonded dyads, (2) kin protection, (3) group member protection (group augmentation) and (4) reputation-based access to reproduction, mediated by mate choice preferences for protective males. We consider it unlikely that the reciprocity of services between closely bonded individuals explains our results. First, a male's commitment to risky antipredator defence provides communal benefits for all group members. For instance, despite female nonhuman primates often leading group movements during nonpredatory situations (Fichtel et al., 2011), males have frequently been shown to take over group leadership or to position themselves between group members and a threat (Cibot et al., 2015; Harding, 1977). Second, newly immigrated males that have not yet been able to establish stable social bonds provide antipredator services to the group immediately after group take-overs (F.G. Mehon, personal observation). Our finding that male services are accompanied by female mate recognition is in line with both protection hypotheses (kin and group members) when the possibility that individually distinct

Table 1
Female latency to call and call rates to different male callers

	N_1	N_2	Latency				Call rate			
			M_1	M_2	SE	$P_{corrected}$	M_1	M_2	SE	$P_{corrected}$
Pyow										
Own-neighbour	12	15	4.5	7	0.81	**0.018**	1	0.3	0.16	**0.003**
Own-unknown	12	14	4.5	2	0.81	**0.018**	1	2	0.16	**0.003**
Neighbour-unknown	15	14	7	2	0.85	**0.003**	0.3	2	0.17	**0.003**
Kek										
Own-neighbour	13	14	23	12.5	1.46	**0.003**	0	0.7	0.32	0.084
Own-unknown	13	14	23	5	1.45	**0.003**	0	3	0.32	**0.003**
Neighbour-unknown	14	14	12.5	5	1.46	**0.003**	0.7	3	0.32	**0.003**
Hack										
Own-neighbour	11	12	3.5	3	2.1	>0.999	0.4	0.2	0.06	>0.999
Own-unknown	11	13	3.5	2	2.14	>0.999	0.4	0.2	0.06	>0.999
Neighbour-unknown	11	13	3	2	2.19	>0.999	0.2	0.2	0.06	>0.999

Results of pairwise comparisons of female latency to respond and call rates between different classes of males (calculated using estimated marginal means). M_1 and M_2 refer to the median of each variable. Significant, corrected *P* values are indicated in bold.

Table 2
Female nonvocal, behavioural responses towards different male callers

	N own (N_{total})	*N* neighbour (N_{total})	*N* unknown (N_{total})	Estimateown	Estimate neighbour	Estimate unknown	χ^2	$P_{corrected}$
Pyow								
Stay	8 (9)	6 (11)	2 (13)	0.889	0.545	0.154	11.7	**0.009**
To male	0 (9)	0 (11)	7 (13)	0	0	0.538	13.7	**0.003**
To speaker	1 (9)	5 (11)	4 (13)	0.111	0.455	0.308	2.77	0.753
Kek								
Stay	10 (10)	5 (13)	5 (14)	1	0.385	0.357	11.7	**0.009**
To male	0 (10)	6 (13)	6 (14)	0	0.462	0.429	6.61	0.072
To speaker	0 (10)	2 (13)	3 (14)	0	0.154	0.214	2.35	0.753
Hack								
Stay	5 (11)	6 (12)	5 (13)	0.455	0.5	0.385	0.343	0.842
To male	6 (11)	6 (12)	7 (13)	0.545	0.5	0.538	0.057	0.972
To speaker	0 (11)	0 (12)	1 (13)	0	0	0.0769	1.82	0.753

Comparisons of proportions for behavioural variables in response to the group's, the neighbouring or an unknown male's three alarm call types. Significant, corrected *P* values are indicated in bold.

alarm calls could facilitate group coordination is taken into account (Arnold & Bar-On, 2020). Specifically, if females and their offspring that recognize their own male's pyows selectively approached or coordinated their movements with the signaller, this might increase group cohesion, which in turn could facilitate group defence. However, males that had not yet sired offspring in the group were observed to provide as much predation defence as those that had (F.G. Mehon, personal observation), which gives preference to the group augmentation hypothesis over the parental care hypothesis. To benefit from dilution or confusion effects (Lehtonen & Jaatinen, 2016), one would predict that females would coordinate their position with the male's position by, for example, approaching their male especially after perceiving kek calls, which are uttered by the male when facing a leopard. Although female putty-nosed monkeys vocally recruit their male for predation defence and although they are sensitive to a male's performance in providing antipredator services (Mehon & Stephan, 2021), they did not approach their male or adjust their position after perceiving his kek calls. It remains puzzling how the group augmentation hypothesis could account for the evolution of observed male behaviour in putty-nosed monkeys if females do not approach their male to increase group cohesion although they monitor male antipredator behaviour. Alternatively, pyows and keks might function as signature calls that advertise to females which male has provided risky protective behaviour for them and their offspring. This is in line with the reputation-based mate choice (van Schaik et al., 2022) and the deception detection hypothesis for individually distinct alarm calls (Cheney & Seyfarth, 2013). Accordingly, females and other group members are provided with information that allows them to differentiate males by their reliability in providing protective behaviour. Harem-holding males in our study population are frequently confronted with surrounding solitary males that try to take over their group (D. N'zoulou Kiminou & F.G. Mehon, personal observation) and multiple male take-overs might occur during a female's life span, which is why male–male competition is thought to be high. To confirm that males increase their reputation by providing antipredator services to prolong their tenures, it remains to be shown that females have some say in the outcome of male take-overs and that they base their mate preferences on male performance as a reliable protector.

For hack calls which do not allow for signaller identification, the risk of being predated by eagles and the need to immediately seek safety might exceed the necessity to identify the signaller for females. Eagles have been observed to sometimes chase their prey after they have been detected and to hunt in pairs from different directions (C. Stephan, D. N'zoulou Kiminou & F.G. Mehon, personal observation). Accordingly, previous results showed that another forest guenon, the diana monkey, prioritizes eagle-related information in male alarms over signaller cues to familiarity and male–male competition (Stephan & Zuberbühler, 2016a).

In sum, although we have shown that females have the cognitive means to differentiate between males by their alarm calls and that this assessment is mirrored in female responses towards different calling males, the extent to which reputation-based mate choice explains risky male behaviour remains to be investigated. Crucially, studies that address whether females keep track of how males perform as a protector to form male reputations over time and the possibility that accumulated reputations are used for future mate choice will fully clarify the evolutionary pathways to male antipredator services and female mate recognition in predation contexts.

Author Contributions

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Appendix

Table A1
Group composition of target groups

Group	Male	Females	Subadults	Infants	Total
1	1	7	2	3	13
2	1	8	2	4	15
3	1	8	4	6	19
4	1	3	2	1	7
5	1	6	4	6	17
6	1	11	3	5	20
7	1	8	3	4	16
8	1	11	4	5	21
9	1	10	4	6	21
10	1	6	2	3	12
11	1	7	2	5	15
12	1	5	2	3	11
13	1	7	1	4	13
14	1	11	3	5	20
15	1	6	0	4	11
16	1	5	3	3	12

Table A2
Number of trials that entered the analysis of per male call type and identity

Target group	Pyow			Kek			Hack		
	Own	Neighbour	Unknown	Own	Neighbour	Unknown	Own	Neighbour	Unknown
1	X	X	X		X	X	x	X	
2	X	X	X		X	X	x	X	
3	X	X		X	X	X	x	X	X
4		X	X	X	X	X	x	X	X
5		X	X	X	X	X			
6		X				X			X
7			X			X		X	
8	X	X	X	X	X	X	X		X
9	X	X	X	X	X		X	X	X
10		X	X	X	X	X	X	X	
11	X		X	X	X	X	X	X	X
12	X	X	X			X			X
13	X	X	X	X	X	X			X
14	X	X	X				X	X	X
15	X	X		X	X	X	X		X
16	X	X	X	X	X	X	X		X
N	11	14	13	10	12	14	11	9	11

Table A3
Extracted parameters from male alarm calls

Call parameter	Abbreviation
Acoustic parameter	
Mean fundamental frequency	Mean F0
Maximum fundamental frequency	Max F0
Minimum fundamental frequency	Min F0
Range of fundamental frequency	Range F0
Fundamental frequency at call onset	F0 start
Fundamental frequency at call end	F0 end
Fundamental frequency in middle of call	F0 mid
First formant	F1
Temporal parameter	
Time of maximum fundamental frequency	tF0 max
Time of minimum fundamental frequency	tF0 min
Time of call onset	tF0 start
Time of call end	tF0 end
Call length	-

Table A4
Contributions (%) of original variables to components 1 and 2 for each call type (pyow, hack, kek)

Variables	Component 1	Component 2
Pyows		
Max F0	8.3	3.9
Min F0	13.2	0.1
F0 end	13.2	0.4
F1	0.7	17.6
Total variance explained	35.4	22
Hacks		
Max F0	18.2	0
range F0	10	3.1
F0 start	11.5	0
F0 end	0.2	11.6
Call length	0.7	11.8
Total variance explained	40.6	26.5
Keks		
Mean F0	14.3	0.6
Max F0	8.5	0.1
F1	2.3	8.9
Call length	0	10
Total variance explained	25.1	19.6

Only contributions higher than 7% to at least one component are presented.