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Twenty-five years of primate research in the Ndoki Forest

# Population differences in putty-nosed monkey (*Cercopithecus nictitans*) call order

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## Abstract

Non-human primates generally lack the ability to learn new call structures or to substantially modify existing ones, suggesting that callers need alternative mechanisms to convey information. One way to escape the constraints of limited vocal control is by assembling calls into variable sequences, as has been documented in various animal species. Here, we were interested in the flexibility with which different calls might be assembled in a species known for its meaningful call order, putty-nosed monkeys (*Cercopithecus nictitans*). Since most information comes from studies conducted at Gashaka Gumti National Park (Nigeria), we tested two further populations in the Nouabalé-Ndoki National Park (Republic of the Congo) and Taï National Park (Côte d'Ivoire) in how males responded to common threats, leopards, and crowned eagles. As predicted, callers produced the same basic call types as seen elsewhere—long 'pyow', short 'pyow' ('kek'), 'hack'—but populations differed in how males assembled calls. To leopards, males from both populations started with 'pyows' and 'keks', with occasional hacks later, as already reported from Gashaka. To crowned eagle, however, Nouabalé-Ndoki males consistently initiated their responses with 'pyows', whereas neither Taï nor Gashaka males ever did, demonstrating that nonhuman primates have some control over sequence production. We discuss possible mechanisms to account for the population differences, predation pressure, and male–male competition, and address implications for linguistic theories of animal call order, notably the Urgency and Informativity Principles.

**Keywords** Alarm calls · Forest guenons · Call compositions · Informativity Principle

## Introduction

Non-human primates (hereafter: primates), including all great apes, are surprisingly limited in their vocal repertoires, with no compelling evidence for human-like vocal learning or vocal control (e.g., Egnor and Hauser 2004; Fischer et al. 2015). Nevertheless, various studies have shown that limited information transfer is possible with only a few call types (Fedurek and Slocombe 2011; Fischer and Hammerschmidt 2020), including references to external events or information about the signaler's identity and current psychological state (Laidre and Johnstone 2013). If callers use their repertoires in context-specific ways, which is often the case, listeners can learn the corresponding associations

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and make predictions about ongoing or future events (e.g., lemurs (*Lemur catta*): Pereira and Macedonia 1991; Diana monkeys (*Cercopithecus diana*): Zuberbühler 2000, tamarins (*Saguinus oedipus*): Elowson et al. 1991; chimpanzees (*Pan troglodytes*): Slocombe and Zuberbühler 2006). The majority of such evidence is from the predation context, but some other calls used in daily social interactions function to maintain group cohesion, refer to food or resolve conflicts (e.g., Eckhardt et al. 2015; Fedurek et al. 2016).

While primates other than humans undoubtedly have limited vocal control, various studies have observed flexibility at other levels, such as during call use. Many call types can be inhibited (Townsend et al. 2008), output rates can be adjusted depending on the situation (Zuberbühler et al. 1999; Bshary 2001; Stephan and Zuberbühler 2008) or depending on the composition and/or knowledge of the audience (e.g., Wich and de Vries 2006; Slocombe and Zuberbühler 2007; Zuberbühler 2008; Crockford et al. 2012; Schel et al. 2013; Coye et al. 2022). Flexibility has also been seen in how some species produce sequences of calls. For instance, Campbell's monkeys (*C. campbelli*) use 'boom' calls at response onsets to modify the urgency of perceived threats from high to low (Zuberbühler 2002). Another example comes from putty-nosed monkeys (*C. nictitans*) who announce group travel in sequences in which 'pyow' calls precede 'hack' calls (Arnold and Zuberbühler 2006a).

Putty-nosed monkeys are common in the sub-Saharan rainforest belt with populations found in Equatorial Guinea (Bioko Island), from Liberia to Ivory Coast and between Nigeria and the Democratic Republic of Congo (Oates 2011). Their taxonomy is debated, with West Africa populations sometimes categorized as a distinct subspecies *C. nictitans stampflii* (Jentink 1888), while other authors group all populations as *C. nictitans nictitans,* apart from the Bioko Island population *C. nictitans martini* (Wilson and Reeder 2005). The species forms one-male groups with several females and their offspring (Buzzard and Eckardt 2007). In Nouabalé-Ndoki, a habitat with high population densities, groups are often surrounded by solitary males who presumably try to take over groups from established males (CS, unpublished data). Females and their offspring form cohesive social units, with the groups' single males often living in the periphery, 20–100 m away from the others.

When exposed to danger, females vocally recruit their male with specific 'chirp' alarms, in response to which the male approaches the eventual predator by producing loud alarm calls (Mehon and Stephan 2021). Thus, male alarm calling is suspected to function to refer to the type of danger, but also to indicate the male's intention to engage with the predator (Mehon and Stephan 2022), something also reported from Diana monkeys (Stephan & Zuberbühler 2016). The males produce three distinct calls in response to danger, 'hacks', 'pyows', and 'keks' (i.e., short pyows; Arnold and Zuberbühler 2006b; Mehon and Stephan 2021, ESM 1). 'Hack' calls are predominantly uttered in response to crowned eagles (*Stephanoaetus coronatus*), a major primate predator throughout Africa (Mitani et al. 2001; Shultz 2002), or they are assembled into 'pyow-hack' sequences, which in Gashaka Gumti, Nigeria, is predictive of group displacements (Arnold and Zuberbühler 2006a). 'Pyow' calls are less context-specific and are emitted to a broader range of events, including leopards (*Panthera pardus*), tree falls, other male alarm calls, and as part of 'pyow-hack' sequences (Arnold and Zuberbühler 2006a, b; Mehon and Stephan 2021). 'Pyows', thus, appear to function as attention-getters that provide only very general contextual information (Arnold and Bar-On 2020). 'Kek' calls (short pyows), finally, have been recorded to moving leopard models and humans (Mehon and Stephan 2021; K. Arnold, personal communication), comparable to the acoustically very similar 'ant' calls in blue monkeys (*C. mitis*, Fuller 2014). Importantly, 'pyow' and 'kek' calls are acoustically individually distinct, allowing females to recognize the male by his calls (N'zoulou Kiminou et al. 2022), which is not the case for the 'hack' calls (Price et al. 2009; Mehon and Stephan 2021; N'zoulou Kiminou et al. 2022).

Whether primates possess flexibility in the order with which they arrange call types is largely unclear. Equally unclear is the nature of the underlying cognition, which could range from evolved propensities to basic associative learning, to conscious decision-making. Here, we were interested in these problems, which we addressed with a population comparison. If members of the same species differed in how they ordered calls to the same events, this would reveal a socio-ecological impact on call ordering and the communicative flexibility available to callers. To address this, we compared populations in Taï National Park, Ivory Coast, and in Nouabalé-Ndoki National Park, Republic of Congo, in how males assemble calls in response to standardized events. We elicited male vocal responses by broadcasting crowned eagle shrieks and leopard growls to several groups. We first investigated the acoustic features of male calls to see whether the different call types were distinguishable in both populations. Second, we tested whether males of both populations arranged the different call types in similar or different ways when responding to the same events, using response rates and latencies as proxies of perceived threat.

## Methods

### Study sites, subjects, and playback stimuli

We conducted playback experiments on $N = 6$ groups of unhabituated putty-nosed monkeys in the primary, mixed rain forest of Taï National Park (5° 50′ N, 7° 21′ W;

average altitude 200 m) from September to November 2013 (65 days), and from April to May 2016 (21 days). Another $N = 19$ groups of unhabituated putty-nosed monkeys were tested in the primary, mono-dominant *Gilbertiodendron dewevrei* forest in the Nouabalé-Ndoki National Park in the Republic of Congo (2° 16′ N 16°25′ E; altitude about 300 m) from January to June 2019 (126 days). Prior to any data collection, all groups have been monitored and followed to document home ranges using GPS data, individual marks, and group composition (Taï groups: 2 months in 2013, Nouabalé-Ndoki groups: 6 months in 2018). There were no male takeovers in the study groups during the study period. Groups in both populations had the same social organization with one reproductive male and 3–11 adult females and their offspring (ESM 2). However, densities differed drastically with around 1.5 groups km$^{-2}$ in Nouabalé-Ndoki (FGM, CS, unpublished data) and around 0.02 groups km$^{-2}$ in Taï (Zuberbühler and Jenny 2002; Eckardt and Zuberbühler 2004). In Taï forest, putty-nosed monkeys are thought to compete with Diana monkeys, a species that occupies a very similar ecological niche and is not present in Nouabalé-Ndoki (Oates 2011), nor in Gashaka Gumti. Stimuli consisted of 15 s of recordings of leopard growls ($N = 3$ recordings) or crowned eagle shrieks ($N = 3$ recordings).

## Data collection

First, the experimenter (CS or FGM) located target groups by auditory cues within their estimated home ranges. Groups were identified using a combination of factors, such as location of home range as assessed with GPS data, group composition, and characteristic features of individuals (e.g., broken tails or permanent scars). Once a group was identified, the experimenter, in collaboration with local assistants, approached the female—offspring cluster, which constitutes the majority of the group, to about 30 m (ground distance to the tree(s) females and offspring were in). We then monitored individuals for 15–30 min to exclude alarm responses to naturally occurring events. Using ground vegetation and natural obstacles, the group was further approached to about 15 m, to set up the equipment and to start recording their vocal behavior. To monitor whether human presence was detected by the group, one assistant monitored individuals' vocal and non-vocal behavior. If observations suggested that humans were detected (e.g., by female 'chirp' alarms), the entire team retreated and no trial was initiated (Taï: $N = 2$, Nouabalé-Ndoki: $N = 6$). If observations did not indicate the detection of human presence, we initiated an experimental trial by recording baseline vocal behavior for 3–5 min. Baseline (undisturbed) behavior was characterized by the absence of any alarm call utterance and usually comprised contact calls, resting, or feeding behavior. After baseline recording of undisturbed vocal behavior of target groups, we either broadcasted leopard growls or eagle shrieks from 0.5 to 2 m from the ground. Prior to experiments, the experimenter measured the amplitude of predator sounds at a distance of 1 m from the speaker amplifier in the groups' natural forest habitat using a Radio Shack Sound Pressure Level Meter and adjusted it to natural amplitude ranges for leopard growls (70–90 dB) and eagle shriek (80–100 dB). Recordings continued until male alarm calling stopped for at least 1 min. The order of stimulus presentation was balanced, such that each group contributed with only one trial per condition (i.e., eagle or leopard playbacks). In some instances, the males did not respond with alarm calls, so the trial was repeated after a period of about 4 weeks. If a male did not respond in the second trial, the group was excluded (ESM 3). None of the study groups were habituated to human presence and experimenters stayed concealed throughout experiments. On some occasions, trials had to be excluded from further analysis: Taï: problems with the recording equipment ($N = 1$); natural eagle attack during an initiated trial ($N = 1$); Nouabalé-Ndoki: retreat from arriving forest elephants (*Loxodonta cyclotis*; $N = 3$) or gorillas (*Gorilla gorilla gorilla*; $N = 5$).

All abovementioned acoustic stimuli were broadcasted using an Apple iPod digital player connected to an AER alpha speaker amplifier. Vocal responses were recorded with a Sennheiser ME67 directional microphone, connected to a Marantz PMD 660 solid-state recorder in Taï and to a Zoom H4n recorder in Nouabalé-Ndoki (both recorders: 44.1 kHz sampling rate, 16 bits amplitude resolution and stored in.wav format).

## Data analysis

### Call production: acoustic structure of call types

We selected high-quality calls that did not overlap with other calls from recorded responses, resulting in 293 calls from 6 different groups in Taï and 444 calls from 19 different groups in Nouabalé-Ndoki (Table 1). From these calls, we extracted eight spectral and three temporal parameters (PRAAT DSP package, settings: time step: 0.03 s; expected

**Table 1** Sample size of calls per call type that entered analysis for both populations

| | $N_{\text{males}}$ | pyow | $N_{\text{males}}$ | hack | $N_{\text{males}}$ | kek |
|---|---|---|---|---|---|---|
| Taï | 6 | 139 | 6 | 40 | 6 | 114 |
| Nouabalé-Ndoki | 15 | 268 | 12 | 101 | 13 | 75 |

F0 frequency range: 500–2000 Hz, with an automatic logger in an output file; ESM 4).

(1) Are call types shared between both populations?

All parameters entered an unsupervised cluster analysis to test whether calls from both populations cluster by call types (‘pyow’, ‘hack’, ‘kek’). We calculated acoustic similarities between calls, using the daisy function in the package “cluster” (Maechler et al. 2019). We iteratively assigned calls to their closest cluster medoid (i.e., cluster), using the PAM algorithm (partitioning around medoids) on solutions with 2 to 10 possible medoids. Medoids determine the center of a cluster by calculating minimal distances between a given point and all other data points (calls) loading on a specific cluster. Cluster centers represented actual data points, in contrast to means that represent the average distance between data points within a specific cluster. Silhouette widths were plotted for solutions with 2 to 10 medoids, using the plot function to identify the optimal cluster solution based on the highest silhouette width (most distinctive cluster with highest distances between single clusters, $S_c$). Results from the optimal cluster solution entered a Principal Component Analysis (PCA) using the prcomp function (“stats” package) to reduce the original variable set to non-correlated dimensions. The two dimensions that explained most of the variation in the data have been plotted using the ggscatter function (package “ggpubr”, Kassambara 2020).

(2) Are vocal repertoires similarly distinctive in Taï and in Nouabalé-Ndoki (are all three call types distinguishable in both populations)?

We replicated analytic steps as under (1) but divided the original data set by population to investigate if male alarm calls (‘pyow’, ‘hack’, ‘kek’) are equally distinctive in Taï and in Nouabalé-Ndoki.

(3) Do single call types provide acoustic features that systematically differ between both populations (i.e., can calls of one call type be classified by population)?

We replicated analytic steps as under (1) but divided the original data set by call type, containing calls of both populations, to elucidate population-specific differences for ‘pyow’, ‘hack’, and ‘kek’ calls.

### Call usage: call order in alarm responses, response probability, and latency

To address whether males prioritize different information, we analyzed call type selection at response onset for eagle and leopard playbacks in Taï and in Nouabalé-Ndoki. We compared the expected proportions with observed proportions using *z* tests (two-tailed, function “binom.test”, package “stats”). We assumed that call type selection on response onset is based on predatory information alone, based on previous findings in a third population (Arnold and Zuberbühler 2006b; Schlenker et al. 2016a, b). We attributed a probability of utterance as first call of 100% to ‘hack’ calls for eagle trials and 50% to ‘pyow’ and ‘kek’ calls, respectively, for leopard trials as both have been shown to initiate male alarm calling to terrestrial threats (Arnold and Zuberbühler 2006b).

We calculated overall percentages of vocal responses in both populations (ESM 5) and conducted Fisher’s exact tests to test for differences in the likelihood to respond. For latencies to respond, we used the lme function of the lme4 package (Bates et al. 2015) with “stimulus” and “habitat” as fixed factors and “group” as the random factor. Corrected Akaike’s Information Criteria (AICc) were evaluated to identify the most parsimonious model (ESM 6).

Acoustic analysis was conducted using PRAAT 6.2.03 (Boersma and Weenink 2003] and statistical analysis was performed in R vs. 4.1.2 (R Core Team 2021). All tests were two-tailed.

## Results

### Call production: acoustic structure of call types

(1) Are call types shared between both populations?

To clarify whether males in Taï and in Nouabalé-Ndoki produce the same alarm call types, we first investigated whether calls from both populations together could be classified into the three call types that correspond to the three known male call types. Calls were best assigned to two clusters ($S_c = 0.75$) with one cluster containing ‘pyow’ calls from both the Taï and the Nouabalé-Ndoki population and the second cluster containing ‘hack’ and ‘kek’ calls from Taï and Nouabalé-Ndoki. The second-best categorization ($S_c = 0.64$) further split the second cluster in “kek” calls from Taï and Nouabalé-Ndoki and predominantly ‘hack’ calls from Taï and Nouabalé-Ndoki, thus forming one cluster for each of the three call types. Interestingly, some “kek” calls from Taï were clustered together with ‘hack’ calls from both populations. Male putty-nosed monkeys in Taï and Nouabalé-Ndoki, thus, possess similar alarm call repertoires showing that they share ‘pyow’, ‘hack’, and ‘kek’ calls with ‘pyows’ being more distinct from ‘hack’ and ‘kek’ calls than the latter two call types from each other.

(2) Are vocal repertoires similarly distinctive in Taï and in Nouabalé-Ndoki (i.e., are all three call types distinguishable in both populations)?

The clear distinction of ‘pyows’ and higher physical similarity between ‘kek’ and ‘hack’ calls was found in Taï where the optimal cluster solution distinguished again only two clusters—‘pyows’ from ‘kek’ and ‘hack’ calls ($S_c = 0.79$, Fig. 1a, b) The second-best solution again separated ‘kek’ and ‘hack’ calls ($S_c = 0.75$, Fig. 1a), providing three clusters that corresponded to the three call types. In Nouabalé-Ndoki,

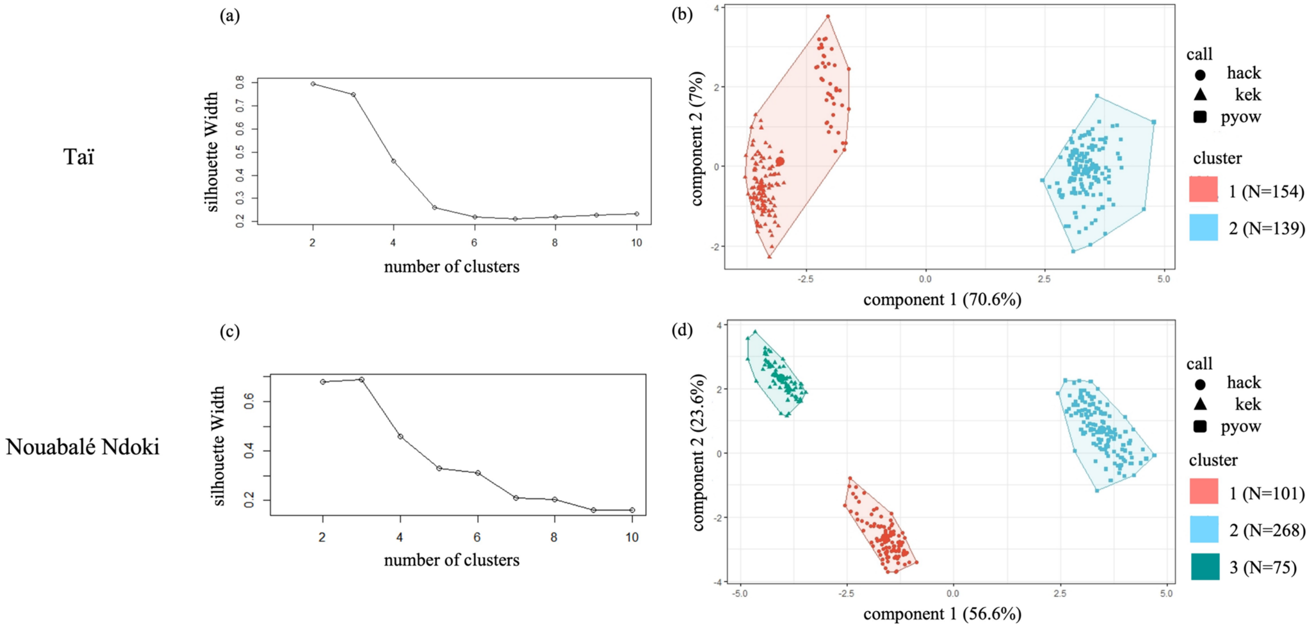

**Fig. 1** Cluster analysis of the distinctiveness of male alarm calls for the Nouabalé-Ndoki and the Taï population separately. Most distinct cluster solutions for male alarm call repertoires as indicated by silhouette widths for Taï (**a**) and for Nouabalé-Ndoki (**c**), and scatter plots showing call types loading on most distinct clusters for Taï (**b**) and for Nouabalé-Ndoki (**d**). Colors in cluster plots indicate unsupervised automatic assignment to clusters, symbols indicate the call type that loaded on each automatically generated cluster. The big circle within each cluster represents the respective cluster medoid

the optimal solution already distinguished three clusters representing ‘pyows’, ‘hacks’, and ‘keks’, separately ($S_c = 0.68$, Fig. 1c, d), showing that males in Nouabalé-Ndoki produced ‘kek’ and ‘hack’ calls that showed greater physical difference than ‘kek’ and ‘hack’ calls produced by Taï males.

(3) Do single call types provide acoustic features that systematically differ between both populations (i.e., can calls of one call type be classified by population)?

Optimal cluster solutions for each call type indicate two clusters (‘pyows’: $S_c = 0.62$, “hack”: $S_c = 0.84$, ‘kek’: $S_c = 0.68$). Cluster plots confirm that calls from the same population loaded on the same cluster for all call types. In other words, all three call types were more coherent within than between populations (Fig. 2; ESM 4).

## Call usage: call order in alarm responses, response probability, and latency

In Taï, 6 of 6 males started with ‘hacks’ and never with ‘kek’ or single ‘pyow’ calls to eagle playbacks (followed by ‘pyow-hack’ sequences), which corresponded to expected probabilities ($z$-test, $N = 6$, $p = 1$, Fig. 3). To leopard playbacks, male responses started with ‘pyows’ or ‘keks’ ($z$-test, $N = 6$, “pyow”: 4 of 6, $p = 0.6875$; ‘kek’: 2 of 6, $p = 0.3471$). In Nouabalé-Ndoki, only 2 of 13 males started with ‘hack’ calls to eagle playbacks, which was considerably below expectation ($z$-test, $N = 13$, $p > 0.001$). As in Taï, no ‘kek’ calls were given. To leopard playbacks, 7 of 12 males started with ‘pyows’ ($N = 12$, $p = 0.774$) and 3 of 12 males started alarm calling with ‘kek’ calls ($N = 12$, $p = 0.146$). Two males uttered ‘pyow-hack’ sequences at response onsets (Fig. 3).

Male putty-nosed monkeys from Nouabalé-Ndoki were generally more likely to alarm call to eagles than males from Taï Forest (Fisher ‘s exact test, $p = 0.02$), but not to leopards ($p = 0.43$, ESM 5). Moreover, Nouabalé-Ndoki males started alarm calling earlier than Taï males to both predators (LMM latency, fixed factor habitat: $F = 19.8$, $df = 1$, $p > 0.001$; ESM 5). In contrast, predator type and the interaction between habitat and predator type only had little impact on the variation in the latency to call (predator type: $F = 4.13$, $df = 1$, $p = 0.065$; habitat*stimulus: $F = 0.21$, $df = 1$, $p = 0.654$).

## Discussion

We here show that adult males of two wild, geographically separated populations of putty-nosed monkeys, produce the same three basic alarm call types, with only minor differences. Alarm call types in the Nouabalé-Ndoki were acoustically slightly more distinctive than those in Taï forest, and calls were acoustically more similar within than between populations. Overall, however, we confirmed that male alarm call repertoires are very similar in both populations. In contrast, the way in which males assembled these call types

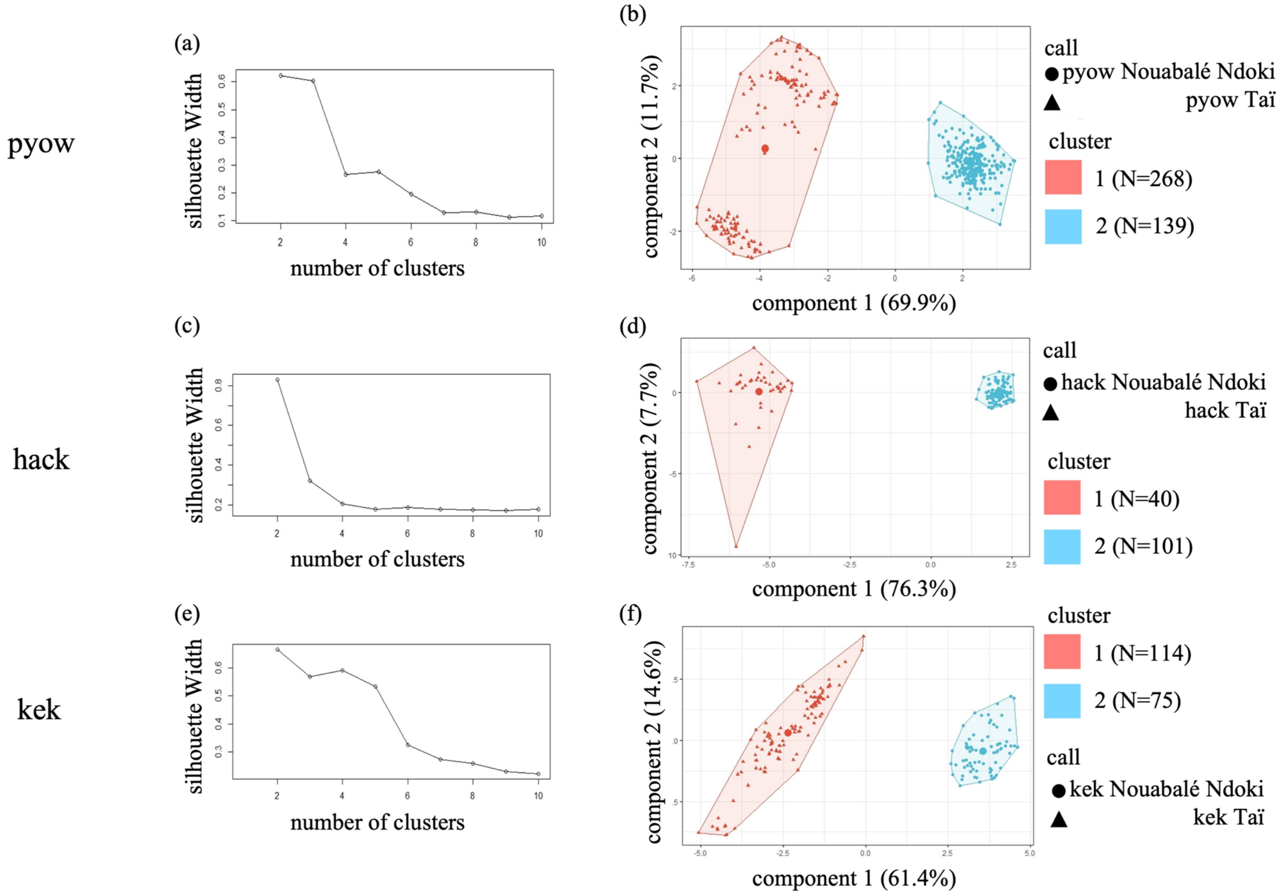

**Fig. 2** Cluster analysis for inter-population acoustic differences within each male alarm call type. 'Pyow' calls: (**a**, **b**), 'Hack' calls: (**c**, **d**) 'Kek' calls: (**e**, **f**). Colors in cluster plots indicate unsupervised automatic assignment to clusters, symbols indicate the call type that loaded on each automatically generated cluster. The big circle within each cluster represents the respective cluster medoid

to simulated eagle and leopard threats differed systematically between Nouabalé-Ndoki and Taï. Crowned eagle playbacks elicited eagle-typic 'hack' calls in Taï males, while Nouabalé-Ndoki males first uttered individually distinct general 'pyow' calls subsequently followed by eagle-typical 'hack' calls. To leopard playbacks, males in Taï and in Nouabalé-Ndoki started their alarm responses with 'pyow' and 'kek' calls, which refer to non-eagle threats and contain information about signaler identity. When comparing this to the Gashaka Gumti males, the call repertoire was again the same, while call order patterns corresponded to Taï (and not Nouabalé-Ndoki) responses (Arnold and Zuberbühler 2006b).

Acoustic similarities in call type structure are consistent with previous primate studies showing that geographically separated populations often possess acoustically similar repertoires (Mitani et al. 1999; Delgado 2007; Price et al. 2014, 2015). For putty-nosed monkeys, only little variation was found in the acoustic structure of call types even in comparison with phylogenetically close blue monkeys (Guschanski et al. 2013). Specifically, "pyow", "ka", and "ant" calls in blue monkeys correspond in both acoustic structure and contextual usage to "pyow", "kek", and "hack" calls in putty-nosed monkeys (Fuller 2014; Fuller and Cords 2017; Arnold and Zuberbühler 2006b; Mehon and Stephan 2021). Whether the repertoire is genetically hardwired and modified by social learning or accommodation cannot be decided with our data (Fischer et al. 2000, 2015; Nieder and Mooney 2020; Fischer 2002). Through vocal accommodation (in contrast to lexical learning), genetically determined calls are slightly modified in structure by matching own calls to perceived template calls. Due to a low putty-nosed monkey density in Taï, males certainly have fewer occasions to encounter other adult male vocal models during vocal development, which may lead to different outcomes compared to Nouabalé-Ndoki males. Future investigations are needed to distinguish between both explanations.

More relevant here is the striking population difference in call arrangement, which requires an explanation. Leopards and eagles are present in both habitats. Predator density is high in Taï (leopards: 0.07–0.11 Ind/km$^{-2}$, eagles: 0.30–0.46 Ind/km$^{-2}$; Jenny 1996, Shultz 2002), but

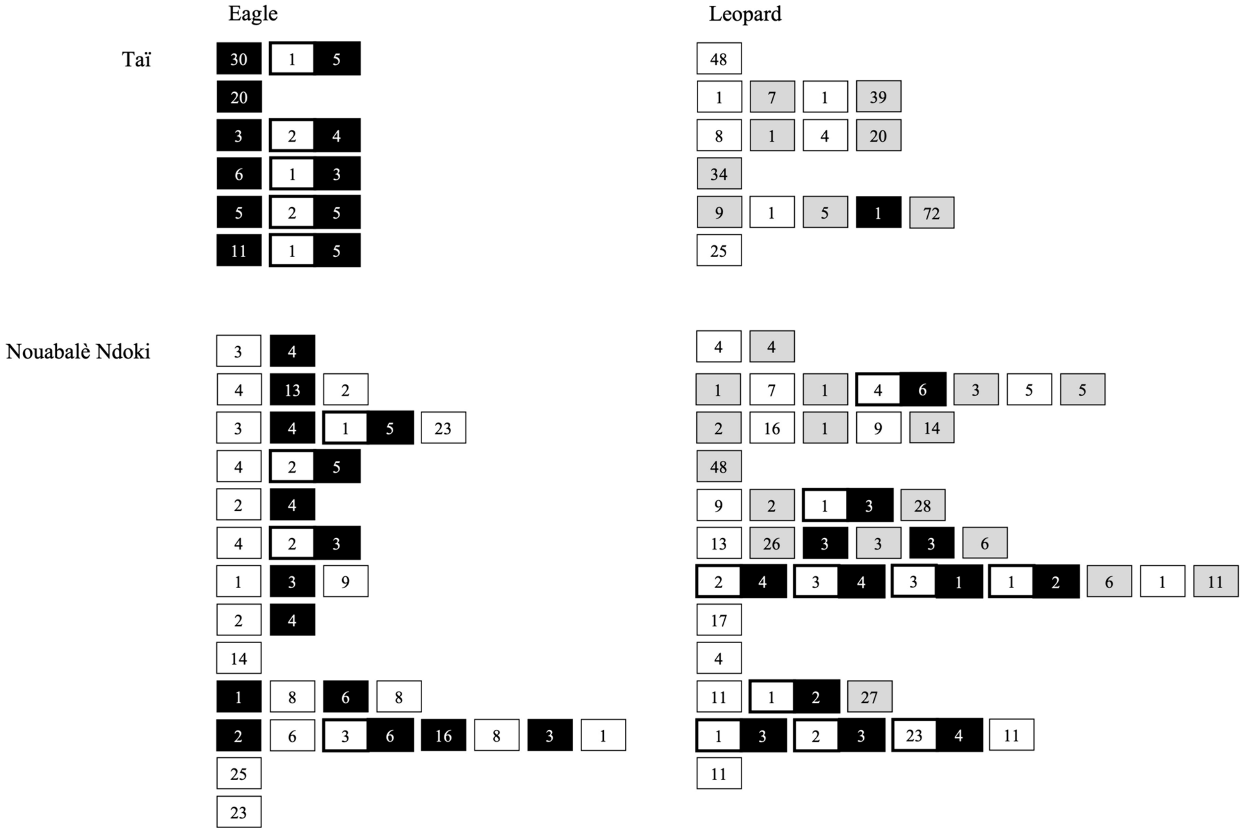

**Fig. 3** Raw data of alarm call sequences to eagle and leopard playbacks in Taï and in Nouabalé-Ndoki males. Squares indicate call type (black: 'hack', white: 'pyow', grey: 'kek') and numbers in squares indicate the number of emitted calls for the respective call type. Please note that 'Pyow-hack' sequences are indicated by white–black square combinations without space in between and framed in bold. 'Pyow-hack' sequences have shorter inter-call intervals than separate 'pyows' followed by separate 'hacks' and usually indicate movement. Each line represents the response of the reproductive male of a specific group and squares are chronologically ordered (from left to right)

comparable data for leopards and eagles do not exist for Nouabalé-Ndoki, although both predators are present and cues are frequently seen (Henschel 2009; Mavinga 2018; FGM, CS personal observation). If predation pressure by eagles was lower in Nouabalé-Ndoki, males might find it less urgent to immediately produce eagle-specific 'hack' sequences, compared to Tai and Gashaka. However, regardless of densities, eagle attacks are uniformly dangerous that require immediate action. Despite this, Nouabalé-Ndoki males started eagle-related responses with 'pyows', hereby drawing attention to their location and identity, before giving eagle-specific 'hack' sequences. Also important is that Nouabalé-Ndoki males responded faster and more reliably to eagles than Taï males, suggesting that eagle playbacks had strong eliciting power on signalers (Egnor et al. 2004).

One explanation for differences in call arrangement might be that the link between predator type and call type differs between populations (i.e., "hack" calls are more indicative for eagles in Taï whereas "pyow" calls more reliably refer to eagles in Nouabalé-Ndoki). Observed alarm call usage does not promote this possibility. Stand-alone "hack" calls predominantly occurred in responses to eagles but not to leopards in both populations. "Pyow-hack" sequences were also uttered to leopards in Nouabalé-Ndoki but they usually indicate group movement and not eagle presence (Arnold and Zuberbühler 2006a). Furthermore, "pyows" in Nouabalé-Ndoki were uttered to both eagles and leopards, thus not allowing any inferences about the nature of the threat. This renders the associative link between "hack" calls and eagle presence similarly likely in both populations.

Male primates often play a special role in protecting the group from predation, and this capacity may even be a factor in mate choice (Manson 2005; Van Hooff et al. 2005; Bshary et al. 2022). It has been suggested that access to females might be reputation-based and biased toward males that provide reliable anti-predation defense (van Schaik et al. 2022). In line with this, female Diana monkeys monitor their male's alarm call behavior and interfere if their own assessment of a threat conflicts with the male's assessment (Stephan and Zuberbühler 2016). In putty-nosed monkeys, females vocally recruit their male for costly predator deterrence (Mehon and Stephan 2021). If female putty-nosed monkeys indeed possess some degree of mate choice, this could lead to male–male competition in anti-predator behavior. Some support for the importance of reputation building for reproduction comes from phylogenetically more distant species. Several bird species show sex-specific audience effects with males engaging more fiercely in predator mobbing with more females in the audience while there was no effect of increasing male bystanders (da Cunha et al. 2017). In the primate lineage, male baboon alarm call rates (*Papio cynocephalus ursinus*) are correlated with the dominance status of signalers, which is probably also linked to male–male competition over reproduction (Kitchen et al. 2003). With a higher number of competing rivals, also male–male competition for reproduction should increase. Although group size and composition are similar in both populations (ESM 2), group density is considerably higher in Nouabalé-Ndoki (unpublished data) than in Taï (Zuberbühler and Jenny 2002; Eckardt and Zuberbühler 2004) and possibly also in Gashaka Gumti. The reliable and fast responses of Nouabalé-Ndoki males, with identity communicated first, suggests that males are primarily concerned that their anti-predator efforts are recognized by others.

Putty-monkey studies have previously made contributions to theories of animal communication (Schlenker et al 2016a, b; Zuberbühler et al 2011), mainly from data collected at the Gashaka Gumti study site. Two paradigms have been previously suggested to underpin call order—the Informativity and the Urgency Principle (Schlenker et al. 2016a, b). According to the Informativity Principle, calls that contain more information than others should be prioritized, i.e., if $C'$ is more informative than $C$ and both are true, use $C'$. For example, Gashaka males usually start responses by referring to the external events first (e.g., 'hack' calls when spotting an eagle), followed by more general 'pyow' calls or 'pyow-hack' sequences (Arnold and Zuberbühler 2006b). The Urgency Principle states that callers should prioritize more urgent over less urgent information. So far, the Urgency Principle was limited to information about the nature/location of a threat.

One problem in applying both principles to the current results is their focus on external, predation-related information. Generally, 'hacks' are more informative than 'pyows' in a predatory context. However, 'pyows' are more informative than 'hacks' in a social context. Depending on socio-ecological factors and fitness consequences, males might weigh one context over the other and pragmatically infer what information provides them with more benefits when communicated first—information about external threats or information about their individual commitment to provide anti-predation services to the group. Hence, Informativity and Urgency can relate to both, the nature of events and signaler-related information. Applied to our findings, this suggests that providing caller identity information is more relevant in Nouabalé-Ndoki, than in Tai or Gashaka, where male densities are lower and individual identities clear. The findings also suggest that, for the Nouabalé-Ndoki males, providing identity information is more urgent than providing predator information (or the commitment to attack the eagle). This might be at least partly due to competitive solitary males maneuvering around groups, but more data are needed to confirm any causal link between male-male competition and call order.

Clearly, these interpretations require more data on females, specifically, whether they prefer males that provide anti-predation services (van Schaik et al. 2022). Second, it also needs to be checked whether the alleged higher population density in Nouabalé-Ndoki leads to increased male densities and male–male competition (Cords 2000). Third, due to low putty-nosed monkeys' density in Taï, sample size for this population could compromise the generalizability of results. Finally, systematic assessments of habitat-specific predator visibility and hunting strategies provide promising ground for future research.

In sum, we showed that although alarm call repertoires are highly similar, call order differs between putty-nosed monkey populations. The arrangement of calls, therefore, is more flexible than modifying the acoustic structure of individual calls. Our results also pose an interesting challenge to the Informativity and Urgency Principles, which may require modifications. Whether male alarm calling is driven by reproductive interests, not just to protect genetic relatives but also to remain attractive for sexual partners, provides promising ground for future research.

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**Author contributions** The study was conceived by CS, FGM, and KZ. FGM and CS conducted playback experiments and recorded vocalizations. FGM and CS analyzed the data. CS wrote the first draft of the manuscript with input from FGM and KZ. KZ and CS acquired funding. All authors approved the final version of the manuscript.

**Data availability statement** Data are available on request to the corresponding author.

## Declarations

**Conflict of interest** The authors declare that they do not have any competing interests. The research presented here utilizes data from the Mbeli Baï Study of the Wildlife Conservation Society (WCS)—Congo Program. The views expressed here are those of the authors and do not necessarily represent the views of WCS. Any errors are attributable to the authors.

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