

## Male blue monkey alarm calls encode predator type and distance

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There is considerable controversy about what is encoded when primates produce alarm calls to an external event. Results are often compatible with multiple explanations, such as differences in a caller's perceived level of threat, direction of attack or category of predator. Using acoustic predator models, we investigated how male blue monkeys', *Cercopithecus mitis stuhlmani*, alarm calls were affected by predator type, distance, and elevation. We found that individuals produced two types of acoustically distinct alarm calls, 'pyows' and 'hacks'. Males produced these calls in predator-specific ways, but call rates were also affected by the distance and location of the predator. We discuss these findings in relation to the different predator hunting techniques and two common antipredator strategies pursued by monkeys, predator deterrence and conspecific warning.

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Despite profound differences between human speech and nonhuman primate calls, a number of shared features have emerged in these two communication systems. For example, primate communication is based on a collection of acoustically distinct signals that can refer to external objects or social events (e.g. Zuberbühler 2012). Such signals have sometimes been termed 'functionally referential' (Marler et al. 1992) to acknowledge the fact they are often highly stimulus class specific and can be interpreted by listeners without reliance on context. In many animals aerial danger consistently elicits acoustically distinct alarm calls in response to which listeners show adaptive behaviour, even in the absence of any real danger (Blumstein 2001).

Seyfarth et al.'s (1980) pioneering research suggested that vervet monkeys, *Chlorocebus aethiops*, categorized predators into different classes and responded to them with acoustically distinct, functionally referential signals. More recently, Blumstein (1999) found that, while marmots seem to use their alarm calls to communicate relative predation risk, some species vary their rate of alarm calling and (in the case of Vancouver Island marmots,

*Marmota vancouverensis*) call types, depending on whether they encountered an aerial or terrestrial predator. Manser et al. (2002) also found that suricates', *Suricata suricatta*, alarm calls conveyed both information about the class of predator (aerial or terrestrial) and urgency of the threat perceived by the caller. Similar results have been found in other groups of animals, such as chickens, *Gallus gallus domesticus* (Gyger et al. 1987) and different species of primates (e.g. Zuberbühler 2001; Schel et al. 2009).

Some primates combine discrete signals systematically into combinations that are apparently meaningful to receivers. Arnold & Zuberbühler (2006) found that male putty-nosed monkeys, *Cercopithecus nictitans* (which, like most male forest guenons, produce two basic loud calls, 'pyows' and 'hacks', in response to a range of disturbances) combine different calls into sequences that have more or less distinct meanings, such as 'eagle' (a series of 'hacks'), terrestrial disturbances (a series of 'pyows') and a combined sequence ('pyows' followed by 'hacks') that initiates group movements. Social factors may also be reflected in such call sequences. Papworth et al. (2008) found that adult male blue monkeys, *Cercopithecus mitis stuhlmani*, produced more alarms in response to a neighbouring male's eagle alarm calls, if the neighbouring male was close to the focal male's group members, but this was independent of the focal male's own position. This difference was found

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in the structure of the males' alarm-calling sequences and, in particular, in the number of calls given, where males produced more calls when his group mates were in more danger.

Like putty-nosed monkeys, adult male blue monkeys produce two loud, acoustically distinct alarm calls, known as 'hacks' and 'pyows', in response to predators (Papworth et al. 2008). In other studies, 'hacks' have also been referred to as 'ka-trains' (e.g. Marler 1973; Rudran 1978). They are short, low-pitched, loud, tonal calls that can be produced singly or as a cluster in quick succession (Fig. 1a). 'Pyows' are also short (but slightly longer than 'hacks'), high-pitched, loud, tonal calls that are typically produced as single utterances (Butynski et al. 1992; Fig. 1b). In blue monkeys and other closely related guenons, 'pyows' are usually produced spontaneously or to terrestrial disturbances, while 'hacks' are mainly produced to aerial danger (Arnold & Zuberbühler 2006; Papworth et al. 2008). Males almost always produce series of calls, which can comprise (1) 'pyows' only, (2) 'hacks' only, (3) 'hack' series containing some 'pyows', or (d) 'hacks' followed by 'pyows'.

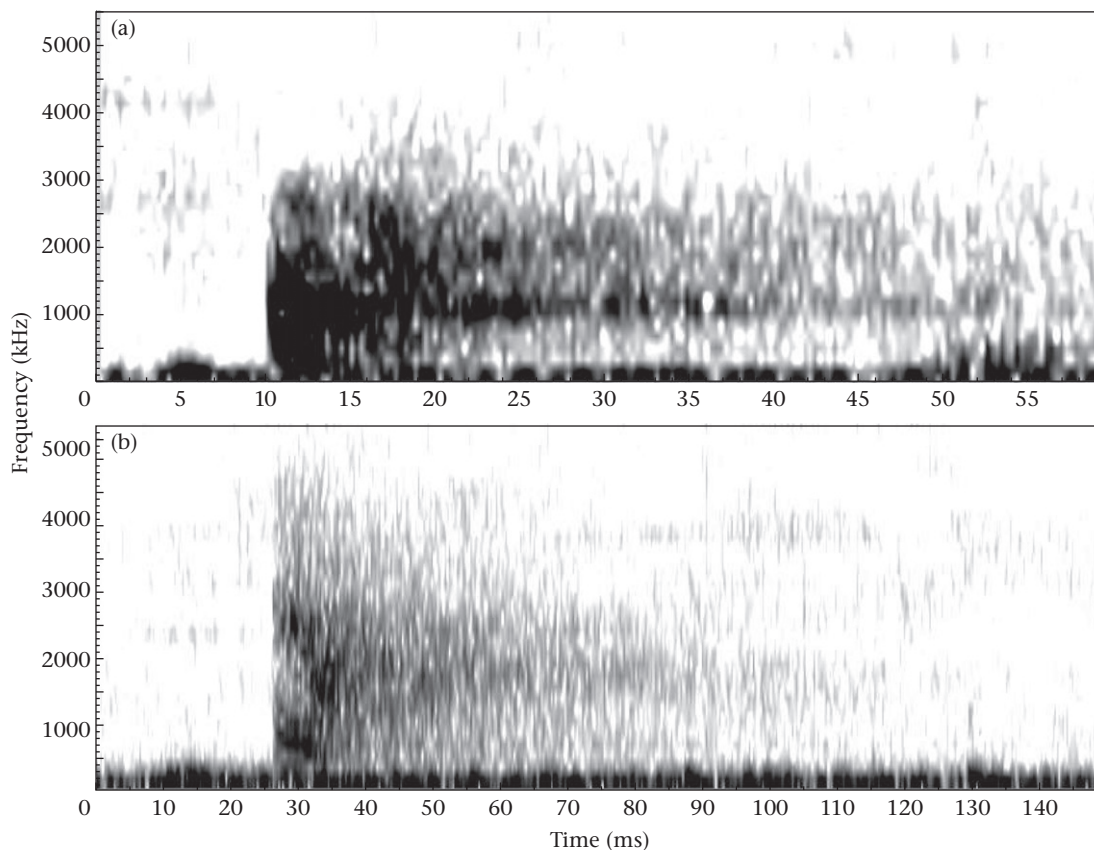
In the current study, we examined how blue monkey alarm calls are affected by predator class and distance. We predicted that male blue monkeys will produce acoustically distinct alarm calls in response to aerial and terrestrial predator vocalizations, and that the structure of the alarm-calling response will differ reflecting the degree of threat to the group, where a nearby predator poses a greater threat than one far away. Furthermore, although leopards, *Panthera pardus*, typically attack from the ground and eagles from above or within the canopy, both predators can attack from both directions, which adds an additional complexity for an alarm-calling individual. Thus, the main purpose of our study was to investigate how predator elevation, type and distance affect the calling behaviour of the monkeys.

## METHODS

### Study Site and Species

The study was conducted in the Sonso area of the Budongo Forest Reserve, Uganda, from June to August, 2011, with permission from the Uganda Wildlife Authority and the Uganda National Council for Science and Technology, and with ethical approval from the Psychology Ethics Committee at the University of Exeter. Budongo Forest is a moist, semideciduous tropical rainforest with roughly 435 km<sup>2</sup> of continuous canopy, located in western Uganda between 1°37'N–2°03'N and 31°22'E–31°46'E (Reynolds 2005). Data were collected in the Sonso area, a roughly 9 km<sup>2</sup> patch of secondary forest (1°43'N, 31°32'E) divided into a grid system consisting of north–south and east–west transect lines at regular intervals of about 100 m (see Appendix). Budongo Forest is home to chimpanzees, *Pan troglodytes*, baboons, *Papio anubis*, Guereza colobus monkeys, *Colobus guereza occidentalis*, red-tailed monkeys, *Cercoptes ascanius*, blue monkeys and crowned eagles, *Stephanoaetus coronatus* (Reynolds 2005). Leopards are thought to have been locally extinct in the Sonso area for some decades (Reynolds 2005). Thus, while eagles still pose a severe threat to most monkeys, it is unlikely that individuals will have had any experience with leopards.

Blue monkeys typically live in groups comprising one adult male with several adult females and juveniles, ranging from 10 to 40 individuals (Ghiglieri 1988). Females usually remain in their natal group all their life, while males leave when they reach sexual maturity in order to join another group (Förster & Cords 2005). Resident adult males thus have a strong biological interest in protecting group members from predators and rival males (Zuberbühler et al. 2009). Possibly in response to predation pressure, blue monkeys



**Figure 1.** Spectrograms depicting (a) a male blue monkey's 'hack' in response to an eagle shriek and (b) a male blue monkey's 'pyow' in response to a leopard growl. Spectrograms were generated using Raven Lite 1.0 (<http://www.birds.cornell.edu/brp/raven/RavenVersions.html>).

frequently form mixed-species groups with other primates (Rudran 1978). At Sonso, we observed that they frequently feed in the same tree as red-tailed monkeys and guereza colobus monkeys, and occasionally even chimpanzees. Home range sizes of blue monkey groups in the Budongo forest range from 5.1 to 11.7 ha (Aldrich-Blake 1970, cited in Rudran 1978), but reach even higher densities in the Sonso study area (Plumptre & Reynolds 1994; Papworth et al. 2008).

### Mapping

Before beginning any trials, the experimenter and a field assistant systematically searched the study area for blue monkey groups. Groups were mostly located by the sound of their movements within the canopy, by their vocalizations and occasionally by sight alone. Groups were found in 43 locations within the 9 km<sup>2</sup> study area. Once a group was located, we determined its position using a Garmin GPSMAP 76 and a map. As monkeys were not habituated to human presence nor individually known, we considered all individuals within a roughly 100 m radius as members of the same group, with no other monkeys within 100 m of the outermost monkey in the group. On a few occasions we identified two separate groups close together (<200 m) by hearing two different males calling simultaneously nearby. In such cases, neither group was tested. Although all groups were tested with the experimental stimuli, they were not part of any systematic observations.

### Experimental Stimuli

Male alarm calling was experimentally elicited using 15 s playbacks of continuous, typical predator vocalizations. These were obtained from the National Sound Archive, London, U.K. (leopard growls,  $N = 2$ ) or recorded in the Tai National Park, Ivory Coast (eagle shrieks,  $N = 3$ ). All playback stimuli were edited using Praat version 5.2.25 (Boersma & Weenink 2011) to include a 5 min period of silence prior to a predator vocalization. The amplitude of each stimulus was adjusted using a 'Radio Shack Sound Level Meter' at 1 m from the source, in the natural environment in which the experiments took place, to a natural amplitude range (leopard growls 70–90 dB, eagle shrieks 80–100 dB; Schel & Zuberbühler 2009). Although crowned eagles typically rely on stealth when hunting monkeys (Mitani et al. 2001), previous studies used recordings of eagle vocalizations to elicit alarm calls successfully in blue monkeys (e.g. Papworth et al. 2008) and other arboreal primates (e.g. Campbell's monkeys: Ouattara et al. 2009a, b; Guereza colobus monkeys: Schel & Zuberbühler 2009).

### Experimental Protocol

Once a group was located, it was randomly assigned to one of eight possible experimental conditions, based on the variables 'predator' (eagle or leopard), 'elevation' (high or low), and 'distance' (near or far). We then set up the audio equipment: an Apple iPod Touch 1G connected to a powered Bose 151 speaker. For each predator type, the following trials were conducted: near–high, near–low, far–high and far–low. Each group was tested only once in one of these experimental conditions.

(1) Distance: in the 'near' condition, the speaker was placed within 15.5 m of the focal monkeys (mean = 12.1 m, range 2.8–15.2 m), while in the 'far' condition the speaker was placed at least 22.0 m away (mean = 28.8 m, range 22.3–38.7 m).

(2) Elevation: in the 'low' condition, the speaker was placed on the ground, while in the 'high' condition, it was placed at least 7.0 m above ground in a tree (mean = 8.9 m, range 7.3–11.8 m). To position the speaker, a small weighted bullet, tied to a fishing line, was

fired over a suitable branch using a catapult and then tied to a thicker rope, which was used to hoist the speaker into the canopy.

Although only data collected from the adult male of the group were analysed, it was not possible to locate and determine which animal was the adult male before he called. Focal animals were, therefore, opportunistically selected and observed for at least 5 min to ensure they were unaffected by our presence. The audio equipment was then adjusted so that the speaker was directed towards the focal monkeys, while the rest of the equipment was placed on the ground out of sight and as far away as possible. A trial was aborted if the group reacted to the presence of the experimenter, if a natural predator was observed in the area, or if the male gave an alarm call before the presentation of the predator stimulus. No data were collected from the focal animal (unless this happened to be the adult male).

Once the equipment was set up, the field assistant moved away from the speaker, to where he could see the focal animal without being detected. Once he was in place, the experimenter initiated a playback trial and also moved away from the speaker. The field assistant filmed the focal monkeys from a covert location using a Sony Camcorder. Filming began roughly 1 min before a playback stimulus was broadcast and continued until the focal monkeys moved out of sight. At the same time, the experimenter recorded the vocal behaviour of all monkeys using a Marantz PMD660 portable solid-state recorder with a Sennheiser ME66-K6 directional microphone. Recording also began about 1 min before each playback and continued for about 5 min or until the male stopped giving alarm calls.

After each trial, the experimenter noted the location, time and date, and measured the distance between the speaker and the base of the tree where the focal monkeys were located. The height of the speaker above ground was estimated with a Leica DISTO laser range finder, which reported distance to the nearest centimetre. The behavioural responses of the focal monkeys, based on the experimenter's and field assistant's own observations, were also noted, as were other details such as the presence of other species.

Groups within 200 m of each other were not tested on the same day, and typically not tested within a week of each other. Males sometimes foraged at considerable distances from the main group, in which case they could probably not hear the playback stimulus. In such cases, the group was sometimes tested for a second time, but only after a gap of at least 2 weeks, and never with the same stimulus.

### Analyses

As we were not primarily interested in the response rate to the different experimental conditions but in the structure of the utterances produced by callers, we did not include trials in the analysis in which there was no response from the male. A  $2 \times 2 \times 2$  (predator [eagle or leopard]  $\times$  distance [near or far]  $\times$  elevation [high or low]) independent measures design was used for the analysis. For each calling series produced by a male, the following structural and temporal acoustic parameters were determined using spectrograms generated by Praat version 5.2.25 (Boersma & Weenink 2011) and through experimenter coding of the audio recordings: (1) number of calls in the calling series; (2) number of pyows per series; (3) number of hacks per series, (4) duration of series (s) and (5) latency to first call after the onset of playback (s). Data were not normally distributed and thus violated the assumptions for parametric testing. Zwick (1985) outlined a nonparametric alternative to the parametric MANOVA based on the Pillai–Bartlett trace. Following this procedure, data were rank-transformed and analysed using a MANOVA (alpha levels were set at 0.05 and Pillai's trace test statistic is reported in each case), which was followed up by a number of univariate ANOVAs. Results are reported with a Bonferroni correction in each case.

## RESULTS

We conducted 83 trials (eagle shrieks:  $N = 37$ ; leopard growls:  $N = 43$ ), of which three had to be rejected owing to equipment malfunctioning. The groups' single males produced alarm vocalizations in 10 eagle trials (response rate = 27%) and in 10 leopard trials (response rate = 23%). One leopard trial was discounted as an outlier. The remaining 19 trials were distributed across eight experimental conditions as follows: two trials each in the leopard – high–near, leopard – high–far, leopard – low–near, eagle – high–near and eagle – high–far conditions, and three trials each in the leopard – low–far, eagle – low–near and eagle – low–far conditions.

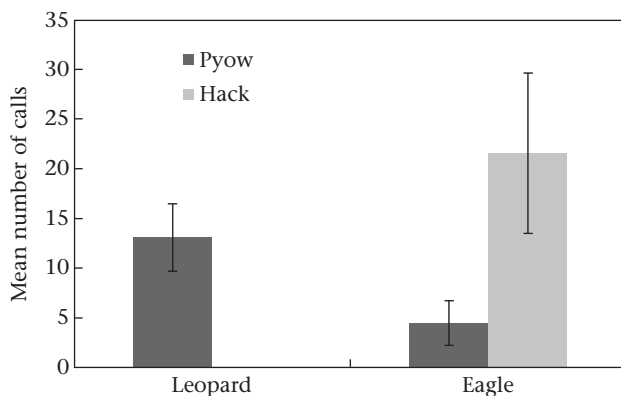
### Predator Class

There was a significant main effect of predator class on male alarm calling (MANOVA:  $F_{5,7} = 8.66$ ,  $P = 0.007$ ). This effect was due to males giving significantly more 'hacks' in response to eagle shrieks (mean = 21.6, SD = 25.5, median = 10) than to leopard growls (mean = 0, SD = 0, median = 0; univariate ANOVA:  $F_{1,11} = 33.10$ ,  $P < 0.001$ ) and giving significantly more 'pyows' to leopard growls (mean = 13.1, SD = 10.2, median = 12) than eagle shrieks (mean = 4.5, SD = 7.1, median = 2.5; univariate ANOVA:  $F_{1,11} = 10.01$ ,  $P = 0.009$ ; Fig. 2).

### Predator Distance

We found no main effect of predator distance (MANOVA:  $F_{5,7} = 1.92$ , NS), but a significant interaction effect between predator class and distance (MANOVA:  $F_{5,7} = 4.77$ ,  $P = 0.032$ ). To eagle shrieks, males gave more 'pyows' when the speaker was near (mean = 8.0, SD = 9.0, median = 4.0) compared to far away (mean = 1.0, SD = 1.4, median = 0), while to leopard growls, males gave more 'pyows' when the speaker was far away (mean = 15.6, SD = 11.3, median = 17) than when it was near (mean = 10.0, SD = 9.1, median = 8; univariate ANOVA:  $F_{1,11} = 7.26$ ,  $P = 0.021$ ; Fig. 3a). To eagle shrieks, males gave more 'hacks' when the predator was far away (mean = 34.0, SD = 30.2, median = 47.0) than when it was near (mean = 9.2, SD = 13.1, median = 0), while to leopard growls, males never responded with 'hacks' (univariate ANOVA:  $F_{1,11} = 8.62$ ,  $P = 0.014$ ; Fig. 3b).

To eagle shrieks, the latency to the first call was greater if the speaker was near (mean = 105.1 s, SD = 101.3, median = 69.6 s) than far away (mean = 19.6 s, SD = 12.0, median = 12.2 s), whereas to leopard growls, the latency to the first call was greater if the speaker was far away (mean = 62.2 s, SD = 45.4, median = 45.8 s) than near (mean = 38.7 s, SD = 18.8, median = 40.7 s; univariate ANOVA:  $F_{1,11} = 9.79$ ,  $P = 0.01$ ; Fig. 3c).



**Figure 2.** Average number of 'pyows' and 'hacks' in male blue monkey alarm call series in response to eagle and leopard vocalizations (means  $\pm$  SE).

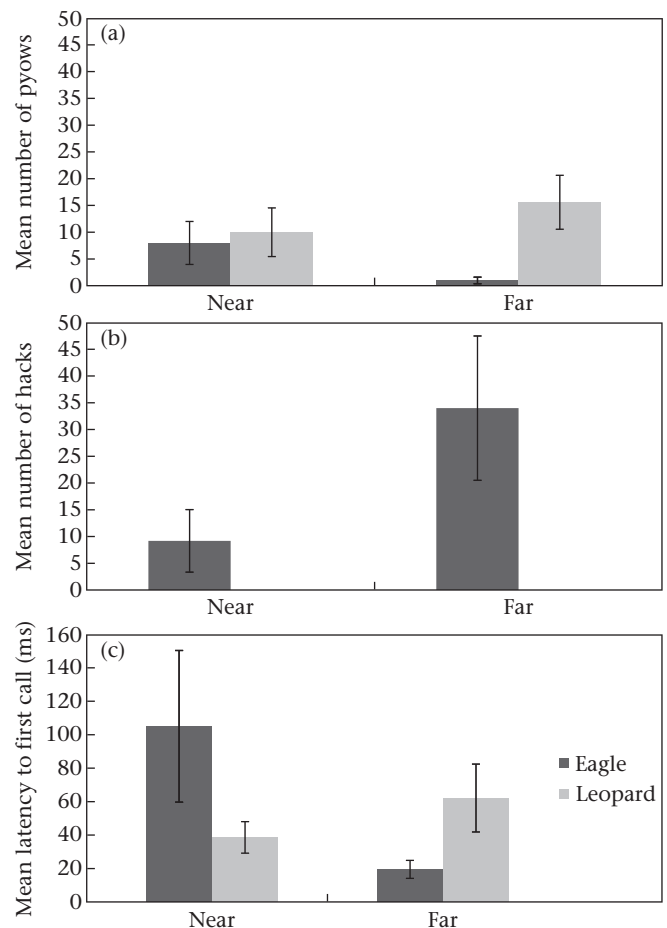
### Predator Location

There was no main effect of predator elevation (MANOVA:  $F_{5,7} = 1.67$ , NS), but we found a significant interaction effect between predator class and elevation (MANOVA:  $F_{5,7} = 4.23$ ,  $P = 0.043$ ), owing to the overall number of calls (univariate ANOVA:  $F_{1,11} = 21.95$ ,  $P = 0.001$ ) and the number of 'hacks' (univariate ANOVA:  $F_{1,11} = 6.08$ ,  $P = 0.031$ ), but not 'pyows' (Fig. 4).

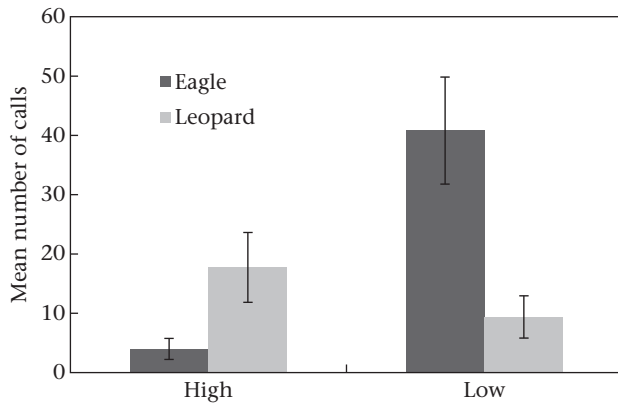
To eagle shrieks, males gave more calls if the speaker was on the ground (mean = 40.8, SD = 22.1, median = 45) compared to the canopy (mean = 4, SD = 3.6, median = 3). Specifically, males gave more 'hacks' when it was on the ground (mean = 35.5, SD = 24.3, median = 37.5) than in the canopy (mean = 0.8, SD = 1, median = 0.5). To leopard growls, males gave more calls if the speaker was in the canopy (mean = 17.8, SD = 11.8, median = 17) compared to on the ground (mean = 9.4, SD = 8, median = 5). Males never responded to leopard growls with 'hacks', regardless of location.

### Combined Effects of Distance and Elevation

There was a significant interaction between the main effects of predator distance and elevation (MANOVA:  $F_{5,7} = 4.01$ ,  $P = 0.049$ ) on the overall number of calls given in response to predator vocalizations. When the speaker was placed far away, males gave more calls if it was on the ground (mean = 35.5, SD = 24.8, median = 34) than if it was in the canopy (mean = 10.0, SD = 14.8, median = 3.5; univariate ANOVA:  $F_{5,7} = 8.26$ ,  $P = 0.015$ ).



**Figure 3.** Significant interactions between the effects of predator class and distance: (a) the number of 'pyows', (b) the number of 'hacks' and (c) the latency to the first call (in ms) given by male blue monkeys in response to eagle and leopard vocalizations at near and far distances (means  $\pm$  SE).



**Figure 4.** Significant interactions between the effects of predator class and elevation: the number of calls given by male blue monkeys in response to eagle and leopard predator models when presented from the ground (low) and from within the canopy (high) (means  $\pm$  SE).

### Call Patterns

In response to eagle shrieks, the default response was a 'hack' series typically composed of clusters of calls produced in quick succession. However, males also responded with a 'transitional' series, that is, a 'hack' series that included a number of 'pyows' or a 'hack' series followed by a 'pyow' series.

With regards to distance, males produced 'hack' clusters in two out of five 'near' trials (10% of all trials), and in three out of five 'far' trials (15% of all trials). Males produced more 'hack' clusters per call series if the predator was far than if it was near. With regard to elevation, males only produced 'hack' clusters in five out of six 'low' trials (25% of all trials) and never in 'high' trials.

Males produced 'hack' clusters with a larger number of calls if the predator was far than near. Notably, in call series with the highest number of 'hack' clusters, each cluster was composed of only a few calls.

Males produced 'pyow' series to three eagle trials (15% of all trials), 'hack' series to four eagle trials (20% of all trials), and transitional series to three eagle trials (15% of all trials). Although both 'pyow' and 'hack' series were produced in both 'high' and 'low' trials, 'transitional' series were only ever given if the eagle stimulus was played from the ground, and not from within the canopy. Although 'transitional' and 'hack' series were given in both 'near' and 'far' conditions, males only produced 'pyow' series to the eagle calls when they were near, and never when they were far (Table 1).

## DISCUSSION

### Behavioural Responses

Whenever possible, we noted the behavioural responses of focal individuals although systematic analyses were not possible because of small sample sizes. From these observations we noted that in response to eagle shrieks, monkeys typically ran into cover or down from the canopy, while in response to leopards, monkeys ran into cover or up into the canopy. One exception was when the leopard stimulus was high up in the canopy and near the group, in which case the monkeys ran downwards. Overall, the monkeys' responses were similar to those reported by Papworth et al. (2008), suggesting that acoustic predator models elicit adaptive responses and are thus suitable for investigating alarm-calling behaviour in these primates. Although the males responded vocally in only 25% of trials, such low response rates are not uncommon in these types of playback experiments (e.g. Papworth et al. 2008; Schel & Zuberbühler 2009; Schel et al. 2009).

**Table 1**

Number of eagle trials in which the male responded with pure pyow, pure hack and transitional series

		Pyow	Hack	Transitional
Distance	Near	3	1	1
	Far	0	3	2
Elevation	Low	1	2	3
	High	2	2	0

### Vocal Responses

Group members often responded to the predator vocalization before their own male began to call, suggesting that the male's alarm calls were not necessary to elicit appropriate antipredator behaviour in other group members, although male calls can have the same effect in blue monkeys (Papworth et al. 2008) and other primate species (e.g. Seyfarth et al. 1980; Zuberbühler et al. 1997; Arnold & Zuberbühler 2008).

For the males, response rates were relatively low to both predators. 'Pyows' appear to function as relatively unspecific alert calls since, under natural conditions, monkeys produce 'pyows' to a range of disturbances. 'Hacks', on the other hand, are highly predator-specific and appear to be given only in response to crowned eagles (Papworth et al. 2008). The fact that monkeys produced 'pyows' to leopards and eagles on the ground and within the canopy further suggests that 'pyows' are not even specific to terrestrial disturbances.

This pattern is relatively often observed in primates. Many species appear to produce one call type for a narrow range of aerial predators and another more general call type for other disturbances, often on the ground (e.g. white-faced capuchins, *Cebus capucinus*: Digweed et al. 2005; lemurs, *Eulemur fulvus rufus*, and white sifakas, *Propithecus verreauxi verreauxi*: Fichtel & Kappeler 2002).

Our results further suggest that additional contextually relevant information may be contained in the structure of the call series. First, both the latency to call and the number of calls per series ('pyows' and 'hacks') were affected by the distance and elevation of a suspected eagle. To eagles that were far away, males produced few 'pyows' and many 'hacks', while the opposite was observed to nearby eagles. To leopards that were far away, males produced fewer pyows than when the predator was near. Call sequences thus contain information about the distance of the predator, and by extension the threat it poses to the group. Similarly, to nearby eagles, males waited for longer before they began to call than when the predator was far away, while the opposite pattern was found for leopards.

As mentioned, the local monkey population has no experience with leopards, suggesting that their vocal responses to leopard growls may have been driven by a mechanism not specific to this predator. Although previous work has shown that Guereza colobus monkeys in leopard-free and leopard-infested areas respond in similar ways (Schel & Zuberbühler 2009), it is unlikely that anti-predator behaviour to leopards is completely hardwired. Leopard playbacks, thus, may be representative of an unfamiliar disturbance, which may be more relevant if nearby. Eagles, however, are a real threat and most monkeys will have had personal experiences with this predator. It is thus likely that males perceive nearby eagles as more dangerous than far away ones, which may explain their relative reluctance to call to nearby eagles.

Predator elevation also affected the structure of males' alarm call series. To eagles on the ground, males gave more 'hacks' (and more calls overall) than to eagles in the canopy, whereas to a leopard on the ground, males gave fewer 'pyows' (no 'hacks' given) than to leopards in the canopy. Although both predators have been observed to attack from both above and below (Zuberbühler 2001), leopards typically attack from the ground (Zuberbühler et al. 1999) and eagles typically attack from above the

canopy (Gautier-Hion & Tutin 1988). An eagle calling from the ground may not be regarded as so great a threat as one calling from the canopy, and thus the male can afford to give more calls to warn his group members of the potential danger without fear of being attacked. In line with this argument is the more general finding that, when the predator was on the ground and far away, males generally gave more calls than when it was within the canopy. Again, this result may be due to the male giving more calls when the threat of predation is lower.

The males' responses to predator stimuli presented at different distances and levels of elevation indicate that, regardless of the urgency of the threat or the direction of a possible attack, the class of predator was reliably labelled with different alarm call types. Similar results have also been found for Diana monkeys (Zuberbühler 2000). However, Fichtel & Kappeler (2002) suggested that variation in a single call type, as found in the current study, may reflect both a referential- and urgency-based system. In the current study, we found that male blue monkeys gave fewer calls, or a lower proportion of predator-specific calls (pyows to leopards, hacks to eagles), when the threat was greater. This is contrary to the earlier finding that high levels of urgency are reflected in higher proportions of predator-specific call types in the alarm calls of male Campbell's monkeys (Ouattara et al. 2009a) and blue monkeys (Papworth et al. 2008). The pattern found in the current study might indicate that blue monkey alarm calls have been shaped by the hunting strategies of predators, and that males can inhibit their alarm calling in high-risk situations. It is not possible to conclude from these results that callers intend to inform others about the location and distance of a predator, although this does not preclude the possibility that listeners can extract such information from the perceived calling patterns.

As mentioned, males produced 'hacks' both singly and in clusters of different call rates. Rapid clusters were only given to an eagle on the ground, while slow clusters (with more hacks per cluster, and more clusters per call) were given to far away eagles. Structural differences at the cluster level, in other words, may inform recipients about the distance and location of an eagle, a hypothesis that can be tested empirically. Additionally, males sometimes produced transitional call series, beginning with 'hacks' but including or ending with 'pyows'. In putty-nosed monkeys, 'pyow-hack' sequences ('pyows' followed by 'hacks') function to initiate group movement while 'transitional series' ('hacks' followed by 'pyows') are given in less dangerous eagle encounters (Arnold & Zuberbühler 2006). The blue monkeys in the current study never produced 'pyow-hack' sequences. Although we did find 'transitional series', the pattern was different, as 'transitional series' were only produced in response to eagle shrieks presented from the ground. These findings are tentative and future research will have to address this finding more systematically.

In previous research, male blue monkeys have been found to take into account the threat predators pose to their groups (Papworth et al. 2008), a pattern also found in other primate species (e.g. Thomas's langurs, *Presbytis thomasi*: Wich & de Vries 2006). Similar findings have been reported in Campbell's monkeys, *Cercopithecus campbelli*, which vary call rates depending on perceived threat (Ouattara et al. 2009a). By including information about the location and distance in the structure of a call sequence, blue monkeys can increase the range of messages they can communicate to other group members with a limited number of distinct calls.

The findings of this and similar studies suggest that the ability to combine discrete signals to provide additional information in a call series is common to all forest-living guenons, and may have been present in their common ancestor. It is not known yet whether this ability is present in all primate communication systems, although Ouattara et al. (2009a) speculated that it may be. Indeed, similar findings have been found in apes (e.g. white-handed gibbons, *Hylabates lar*: Clarke et al. 2006). Our results suggest that the ability to

combine existing signals to produce new messages has evolved independently in forest-living guenons and may be latently available in all higher primates to have acted as a precursor to the evolution of vocal productivity, which is particularly evident in human language.

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Appendix

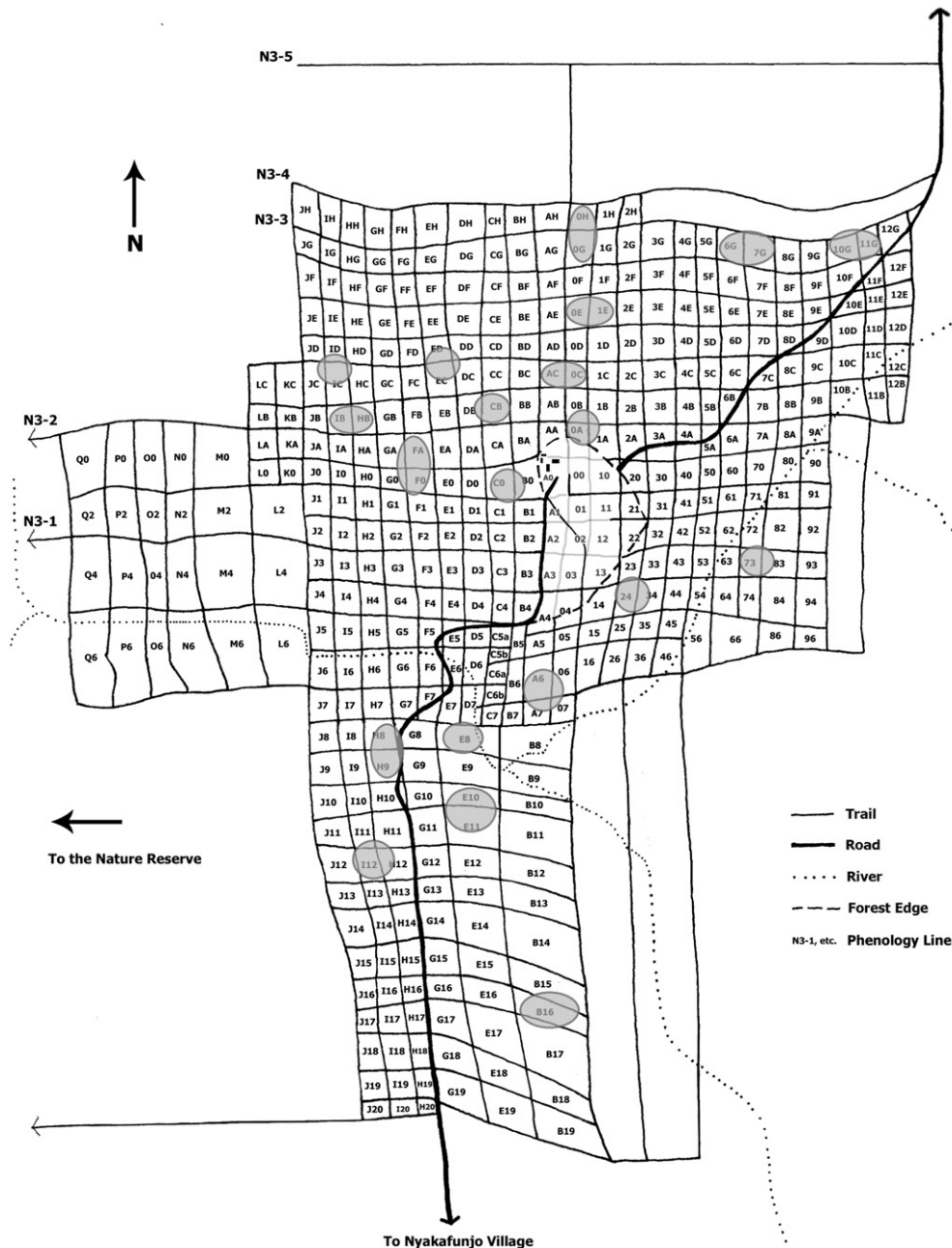


Figure A1. A map of the Sonso grid of the Budongo forest, showing labelled grid transects. Grey circles indicate the locations of the blue monkey groups used in the current study.