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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.

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 stuhlmanni*, 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^2 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^2 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, *Cercopithecus 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

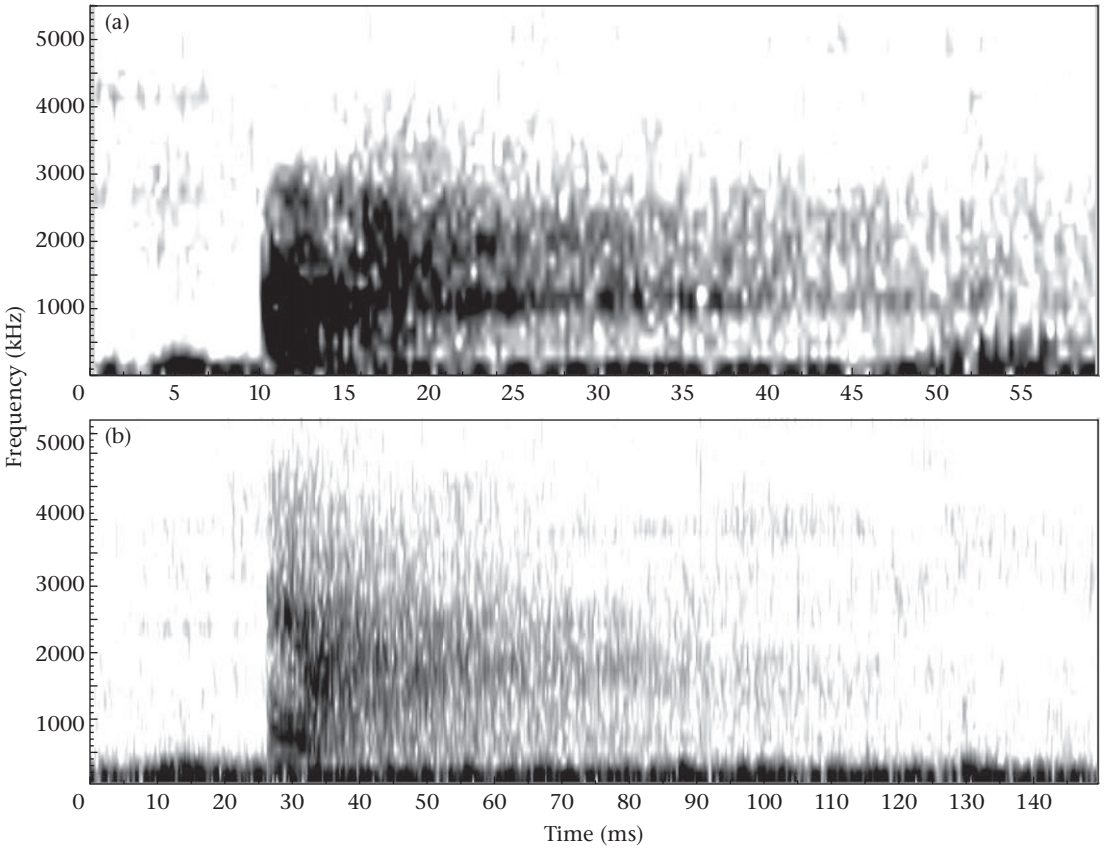

Figure 1. Spectrograms depicting (a) a male blue monkey's 'hack' in response to an eagle shriek and (b) a male blue monkey's 'pyow' in response to a leopard growl. Spectrograms were generated using Raven Lite 1.0 (http://www.birds.cornell.edu/brp/raven/RavenVersions.html).