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Predator and non-predator long-distance calls in Guereza colobus monkeys

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ABSTRACT

East African Guereza colobus monkey males are known for their conspicuous roaring behaviour; a spectacle that can dominate the predawn hours of African forests. Recent research has shown that these monkeys also produce roars during daytime hours in response to predators. While roars to leopards and eagles differ in how roaring phrases are assembled into sequences, there are no obvious structural differences between predawn roars and roars to eagles. Although recipients could use daytime information to disambiguate between the two contexts, this may be a risky strategy because eagles can be active before dawn. We carried out acoustic analyses, which showed that the duration of the first roaring phrase was significantly longer in predawn roars compared to eagle roars. Furthermore, the initial call repetition rate was faster in response to eagle roars compared to predawn roars. Apart from these two differences, all other acoustic characteristics were identical between the two contexts. Although these monkeys exhibit some of the most basic vocal behaviour found in non-human primates, callers are able to provide reliable contextual information by varying the duration and assemblage of individual vocal units. Playback experiments are needed to confirm whether recipients relate these acoustic differences to different contexts.

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1. Introduction

Many animals rely on vocal signals for their social interactions with each other. A typical finding is that different biological functions, such as mating (e.g. Clay and Zuberbühler, 2011; Poole et al., 1988; Townsend et al., 2008), feeding (reviewed in Clay et al., 2012), predation (e.g. Manser et al., 2001; Owings and Virginia, 1978; Struhsaker, 1967; Seyfarth et al., 1980; Zuberbühler et al., 1997), or group cohesion (e.g. Arnold and Zuberbühler, 2008; Rendall et al., 1999), trigger acoustically distinct vocalisations that are easily discriminated by recipients. In some species, it is more difficult to identify discrete call types, but instead the acoustic features of vocalisations gradually change across contexts. Although a potential source of confusion, there is evidence that recipients can perceive graded information in categorical and context-specific ways (e.g. Byrne, 1982; Fischer et al., 2001; Kitchen et al., 2003). For example, chacma baboons' barks grade from tonal, harmonically rich to noisy, harsh variants, depending on whether the call is given in association with issues of group cohesion or predation (Fischer et al., 2001). Playback experiments have shown that recipients of these graded vocalisations differentiate between the call variants in context-specific ways (Fischer et al., 2001). One interpretation has been that such acoustic differences are related to different internal states of the callers (Owren and Rendall, 1997). For example, baboons encountering a predator may experience high levels of arousal (causing the production of harsh variants), whereas unsatisfactory levels of group cohesion may be experienced as less arousing (causing the production of more tonal variants). Recipients may be able to infer something about the callers' inner states, provided the acoustic structures are reliably produced in context-specific ways.

Another source of flexibility in primate communication is based on variation in the calls' temporal features. Some primates produce acoustically identical vocalisations in different contexts, which nevertheless can be disambiguated by temporal differences or differences in how individual calls are assembled into higher units. For example, male Thomas langurs (*Presbytis thomasi*) produce the same types of loud calls during intergroup encounters, spontaneously before predawn, and to predators, but calls differ in their temporal structure depending on the production context (Wich et al., 2003). Putty-nosed monkeys (*Cercopithecus nictitans*) and white-handed gibbons (*Hylobates lar*) produce the same types of

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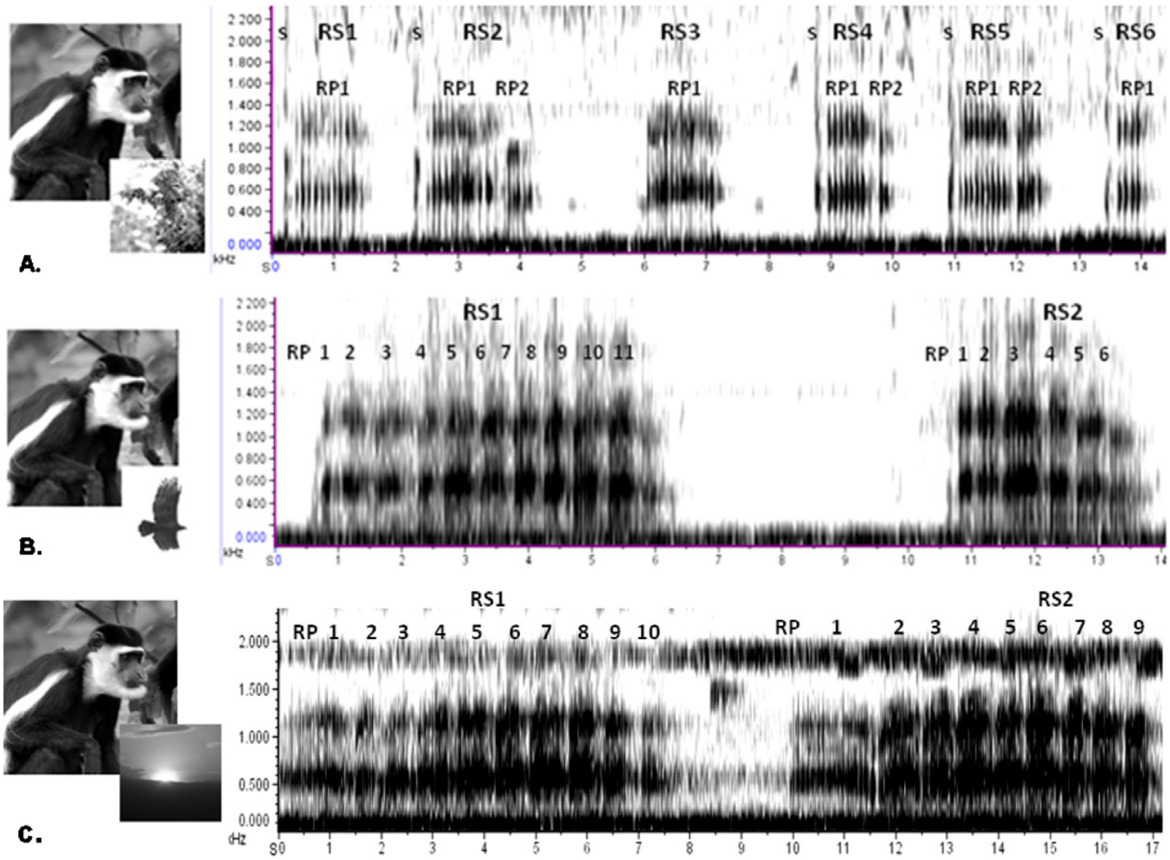

Fig. 1. Spectrographic representation of the structural characteristics of Guereza's leopard- (A), eagle- (B) and predawn chorusing (C) roars. The *x*-axis represents time in seconds, the *y*-axis represents frequency in kHz. 'RS' stands for roaring sequence, 'RP' stands for roaring phrase, and 's' stands for snort.

vocalisations in predation and non-predation contexts (e.g. pair-bonding or group movement), but callers combine individual calls into context-specific sequences that may be meaningful to conspecifics (Arnold and Zuberbühler, 2008; Clarke et al., 2006).

Male Guereza colobus monkeys produce a specific type of vocalisation, the 'roar', in both predatory and non-predatory contexts, i.e. to leopards, chimpanzees and eagles, as well as before dawn (Marler, 1972; Oates, 1977; Schel et al., 2009; Schel and Zuberbühler, 2011). The basic vocal unit of these roars is an acoustically invariable 'roaring phrase', which is repeated to form a 'roaring sequence' (Schel et al., 2009). To ground predators, callers produce a small number of roaring phrases per roaring sequence (usually preceded by noisy 'snorts'), although the number of roaring sequences is large. In response to eagles, they produce a small number of roaring sequences, but each one is composed of many roaring phrases (usually not preceded by snorts; Fig. 1; Schel et al., 2009). Playback experiments conducted during a previous study (Schel et al., 2010) revealed that these differences in sequencing are meaningful to conspecific recipients: when analysing the Guerezas' gaze directions in response to conspecific playback stimuli, it was found that recipients immediately looked upwards in a significantly higher proportion of trials if they heard roars referring to an eagle compared to roars referring to a leopard. For downward looks, the pattern was correspondingly reversed, despite the fact that playbacks were always broadcasted from below (Schel et al., 2010). Preliminary observations further revealed that listeners responded with appropriate gaze directions about 1–2 s following a playback. This suggests that a median processing time between 1 s and 2 s is needed to extract the meaning of a conspecific signal and to respond adaptively.

Interestingly, Guereza males also produce roars before dawn in the absence of predators. This behaviour is usually initiated by one male in some part of the forest, but then often spreads to neighbouring groups until a large part of the forest is covered by calling monkeys (Schel and Zuberbühler, 2011). Remarkably, these predawn roars appear to be structurally and acoustically identical to the roars produced during eagle encounters (Fig. 1). However, in two separate playback studies, we have made observations to suggest that, despite these acoustic similarities, the behavioural responses of listeners are distinctly different. In particular, when 15 s of 'eagle roars' were played back to recipients during daytime, the usual response was to look skywards and to approach the presumed caller without counter-calling (Schel et al., 2010). In contrast, the usual response to a 'loop' of predawn roars played back in the early morning was to counter-call and to remain stationary (Schel and Zuberbühler, 2011). One explanation for these response differences is that there are subtle acoustic differences in the two roar types that listeners can differentiate. Counter-calling when hearing conspecific predawn roars is an adaptive strategy, because predawn roars are likely to function in male–male competition (Schel and Zuberbühler, 2011). However, counter-calling when hearing conspecific eagle roars would be maladaptive, because these roars are likely to function in predator-deterrence, and hearing these calls indicates that someone else is already engaged in chasing this predator. Instead, silently approaching the caller and scanning the surroundings to locate the predator are more adaptive responses in this context (Schel et al., 2010). A more conservative explanation for the observed difference in response rates in the previous studies is that stimulus duration ('loop' vs. '15s' of playback) drove the Guerezas' decision to counter-call, with

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