



Graded or discrete? A quantitative analysis of Campbell's monkey alarm calls

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A standard way of describing the vocal behaviour of nonhuman primates is to classify the vocal repertoire as either graded or discrete. We analysed a large database of calls given by adult males of a primate considered a typical example for discrete vocal behaviour, the forest-dwelling Campbell's monkeys, *Cercopithecus campbelli*. We recorded vocal responses from several dozen individuals to their main predators, crowned eagles and leopards. Using cluster analysis techniques, we found two main call types, which were modified further by optional affixation of an inflexible vocal structure. It was possible to force the four call types into eight subtypes, with various degrees of gradedness. When taking context into account, we found that acoustically discrete and nonaffixed calls tended to be given right after discovering a predator, while acoustically graded and affixed calls were given during later parts of a predator encounter and to nonpredatory disturbances. In sum, our results suggest that classifications of primate vocal repertoires as either discrete or graded are likely to be meaningless, as communicatively relevant acoustic variation can be present within seemingly discrete call types.

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One way of classifying primate vocal systems is to determine whether the calls within a species' repertoire are acoustically graded or discrete (Hammerschmidt & Fischer 1998). In graded systems the acoustic structures of vocalizations form a continuum, lacking distinct boundaries between call types. Although some structures may be more common than others, a graded system is characterized by the presence of intermediate forms, which makes classification of call types difficult (Marler 1975, 1976; Hammerschmidt & Fischer 1998; Fischer, in press). In discrete signal systems, call types are acoustically distinct from one another and are easily discriminated, mainly because intermediate forms are uncommon (Marler 1975, 1976; Cheney & Seyfarth 1990; Hammerschmidt & Fischer 1998). At the same time there is good evidence that animals are capable of classifying vocalizations, regardless of whether their vocal repertoire is classified as graded or discrete (Cheney & Seyfarth 1990; Fischer et al. 2001b; Fitch 2010).

The evolution of graded and discrete signalling systems is not well understood. Early theories suggested that the discreteness of a vocal repertoire was determined by a species' habitat and social

structure (Marler 1975). Species that lived in visually or auditorily difficult habitats, such as dense rainforests, with limited visual ranges and noisy environments, were thought to have evolved discrete call systems so that messages were less likely to be misinterpreted. Alternatively, species living in more open habitats, such as savannah or forest edges, were thought to be able to combine vocal communication with visual signals and should therefore evolve acoustically graded call types. In terms of social structure, Marler (1976) argued that discrete signals were more likely to evolve in species with single- than multimale groups, for example because single males required loud, unambiguous signals to defend and influence their group. Predation has also been identified as a factor, as animals that require predator-specific defence strategies should evolve acoustically distinct alarm calls to reduce ambiguity to recipient conspecifics (Cheney & Seyfarth 1990; Fischer et al. 2001a).

Although the distinction between graded and discrete vocal systems is intuitively attractive, there are a limited number of studies that have addressed the topic in a quantitative way. Nevertheless, graded vocal repertoires have been allocated to rhesus macaques, *Macaca mulatta* (Rowell & Hinde 1962), Japanese macaques, *Macaca fuscata* (Green 1975), red colobus monkeys, *Procolobus badius* (Marler 1970), chimpanzees, *Pan troglodytes* (Marler 1976) and bonobos, *Pan paniscus* (de Waal 1988). In contrast, many forest

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monkey species are said to have discrete vocal systems, such as Diana monkeys, *Cercopithecus diana* (Zuberbühler et al. 1997), putty-nosed monkeys, *Cercopithecus nictitans* (Arnold & Zuberbühler 2006) and blue monkeys, *Cercopithecus mitis* (Papworth et al. 2008).

More recent research has shown that different primate species can demonstrate varying amounts of acoustic gradation in call types employed for different functions. In chimpanzees, for instance, 'barks' or 'screams' are highly graded, whereas 'laughters' or copulation calls are much more discrete (Marler 1976; Crockford & Boesch 2003; Slocombe et al. 2009; Townsend & Zuberbühler 2009). Other research has shown that, in red-capped mangabeys, *Cercocebus torquatus*, contact and threat calls show more acoustic variability than long-distance and alarm calls (Bouchet et al. 2012). Similar attempts to quantify acoustic variability across a primate species' repertoire have been made for lemurs, *Microcebus murinus* (Leliveld et al. 2011), baboons, *Papio hamadryas ursinus* (Rendall et al. 2009) and Campbell's monkeys, *Cercopithecus campbelli* (Lemasson & Hausberger 2004). In Campbell's monkeys, the alarm call system of the males is composed of seemingly discrete call types (Ouattara et al. 2009a), while the contact calls of the females have revealed high levels of socially determined acoustical variability (Lemasson & Hausberger 2004, 2011; Lemasson et al. 2011). Based on these findings it is unlikely that 'graded' or 'discrete' are suitable labels to describe a species' entire vocal behaviour or repertoire. More likely, the level of gradedness/discreteness varies across call types, most likely in relation to the calls' functions (Lemasson & Hausberger 2011; Bouchet et al. 2012).

In this study, we focused on a classic example of discreteness, the predator alarm calls of male Campbell's monkeys, a forest-dwelling primate that forms single male groups. The male alarm calls are interesting because they are given in reference to a number of external disturbances, a pattern also found in many other guenon species (Cercopithecines; Seyfarth et al. 1980; Zuberbühler et al. 1999; Arnold & Zuberbühler 2008; Papworth et al. 2008; Ouattara et al. 2009a). Other research has concluded that their alarm calls demonstrate a rudimentary syntax in the form of semantically meaningful call combinations and affixation: the addition of an acoustic element, a suffix or affix, that can occur only as a subpart of an utterance and cannot function independently (Zuberbühler 2001, 2002; Ouattara et al. 2009a, b). Previous studies on the alarm calling of male Campbell's monkeys have largely been based on classifications of call types by ear.

To test the assumption of discreteness, we carried out a standard set of acoustic analyses followed by clustering techniques, to establish a classification scheme based solely on acoustic structure. We then explored whether or not any gradation was homogeneously distributed across the vocal repertoire. To this end, we analysed recordings of calls in different contexts, given by an unusually large number of free-ranging individuals in one of their natural habitats, the Taï Forest, Côte d'Ivoire.

METHODS

Study Site and Subjects

Field playback experiments were conducted in the Taï National Park, Côte d'Ivoire, between 1994 and 2000. The study area consisted of approximately 50 km² of primary rainforest close to the Centre de Recherche en Ecologie (5°50'N, 7°21'W). Campbell's monkeys live in social groups containing a single adult male and multiple adult females with their offspring and occupy geographically stable home ranges at densities of 1–2 groups/km² (McGraw et al. 2007). The species is highly territorial and will defend their home range against members of neighbouring groups (Cords 1987; Buzzard & Eckardt 2007). At the time of data collection at least 50

different Campbell's monkey groups were living within the study area (Zuberbühler 2001). None of the subjects were habituated to the presence of human observers.

Playback Stimuli

The following four stimulus types were used in the experiments: shrieks of a crowned eagle, *Stephanoaetus coronatus*, growls of a leopard, *Panthera pardus*, male Campbell's alarm calls to an eagle, and male Campbell's alarm calls to a leopard. Eagle vocalizations and Campbell's alarm calls were recorded at the study site at the beginning of the study; leopard growls were obtained from the National Sound Archive, London, now part of the British Library. Playback amplitude ranged between 88 and 110 dB for predator calls and between 90 and 100 dB for Campbell's alarm calls. Campbell's alarm calls consisted of series of natural 'hok' calls (responses to eagle) and 'krak' calls (responses to leopard; Ouattara et al. 2009a), and were recorded only from individuals that were unknown to the subjects. All playback stimuli were edited so that they contained between three and five equally spaced alarm calls. All stimuli were played on a Nagra DSM speaker-amplifier connected to a Sony WMD6C Professional Walkman.

Data Collection

Campbell's monkey groups are very cryptic and difficult to locate without being detected by them first. They spend much of their time in association with Diana monkeys (Wolters & Zuberbühler 2003; Buzzard 2010), a highly conspicuous species whose contact calls can be heard from over a few hundred metres. We thus systematically searched the 50 km² study area until a Diana monkey group was located, typically by hearing their vocalizations. When a group was located, the speaker was hidden in an elevated position, roughly 1.5 m from the ground, and 20–50 m away from the target group. The experimenter (K.Z.) then waited for 30 min before initiating a playback trial.

Unhabituated monkeys respond with strong antipredator behaviour to the presence of humans, typically by alarm calling and flight. Therefore, a playback experiment was discarded if the experimenter was detected in the 30 min before the start of or during a trial. The group's geographical location was noted using a map and a Magellan Pioneer Global Positioning System receiver. The monkeys' vocal responses were recorded from an average distance of 50 m on analogue tape with a Sony TCM5000EV recorder and a Sennheiser ME67 or ME88 directional microphone. Playback trials contained either one or two playback stimuli, separated by a 5 min period of silence. In some trials a Campbell's monkey responded to the second playback stimulus but not the first; these were excluded because it was impossible to ensure that the group's male was present during the first stimulus (and thus whether they had simply not heard the stimulus or whether they had selected not to respond). If multiple Campbell's males responded with alarm calls the trial was also excluded, as distinguishing between individuals was not reliable. This occurrence was rare (only six of 91 trials) as the single male groups occupy geographically stable home ranges that are territorially defended. Lastly, trials were excluded if spectrographic analysis was not possible owing to poor recording quality. In the primary analysis we were interested in the degree of acoustic gradation present in Campbell's monkeys' alarm calls, based on an empirical call classification scheme. In total, 85 playback trials were carried out, which yielded a total of 142 trials that were retained for analysis (leopard growl trials: $N = 58$; eagle shriek trials: $N = 49$; Campbell's eagle alarm call trials: $N = 19$; Campbell's leopard alarm call trials: $N = 16$).

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