Animal Behaviour 78 (2009) 35–44

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

The alarm call system of female Campbell's monkeys

Karim Ouattara [a,b,c,d,1], Klaus Zuberbühler [b,e,*], Eliezer K. N'goran [c,2], Jean-Emile Gombert [d,3], Alban Lemasson [a,1]

[a] Ethologie animale et humaine, U.M.R. 6552-C.N.R.S., Université de Rennes 1
[b] Centre Suisse de Recherches Scientifiques, Taï Monkey Project, Côte d'Ivoire
[c] Laboratoire de zoologie et de biologie animale, Université de Cocody
[d] Centre de Recherche en Psychologie, Cognition et Communication, Université de Rennes 2
[e] School of Psychology, University of St Andrews

ARTICLE INFO

Article history:
Received 3 November 2008
Initial acceptance 23 December 2008
Final acceptance 12 March 2009
Published online 9 May 2009
MS. number: 08-00712R

Keywords:
alarm call
Campbell's monkey
Cercopithecus campbelli
evolution of language
predation
referential
semantic

Field studies on male forest guenon alarm-calling behaviour have revealed a number of intricacies about how these primates use vocalizations to protect themselves from predation. In these species, the vocal behaviour of adult females is often different from that of the males, but little systematic work has been done. Here, we describe the alarm call system of female Campbell's monkeys, *Cercopithecus campbelli*, in their natural forest habitat in western Ivory Coast. We found that in response to disturbing events, females produced three basic alarm call types, 'wak-oos', 'hoks' and acoustically variable 'trill' calls, consisting of repeated and rapidly ascending (RRA) pulses, which varied systematically in the temporal and frequency domains. Using observational and experimental data we were able to demonstrate that the RRA calls consisted of four acoustic variants, which could be associated with specific contexts, allowing listeners to draw inferences about the type of disturbance experienced by the caller. We also compared the alarm call behaviour of free-ranging individuals with published results from captivity. As predicted, captive individuals failed to produce predator-specific alarm calls, but they also produced an RRA variant in response to humans that was absent in the wild. We discuss the relevance of these findings in terms of their broader potential impact on evolutionary theories of primate communication.

Most forest guenons show a marked age–sex difference in their vocal behaviour (Gautier & Gautier 1977). Adult females and their subadult offspring typically produce a diverse repertoire of close-range vocal signals, which serve various functions during their daily activities (see Gautier 1975, 1978 for examples in the wild and Lemasson et al. 2004; Lemasson & Hausberger 2004 for captive Campbell's monkeys, *Cercopithecus campbelli campbelli*). The single adult males of forest guenon groups, in contrast, behave in markedly different ways. They rarely participate in any of these vocal interactions, but instead produce a small range of low-pitched and high-amplitude calls that carry over considerable distances through the dense forest vegetation. These male loud calls are typically given in response to disturbances, but sometimes also without any apparent reason. The calls tend to affect the locomotor behaviour of conspecifics, and a range of studies has shown that they can convey something about the call-eliciting external referent, usually some sort of a disturbance such as the presence of a predator (Zuberbühler 2000c, 2001; Arnold & Zuberbühler 2006a, 2008; Arnold et al. 2008).

While the vocal behaviour of guenon males is relatively well studied for a number of species, comparably little progress has been made with the females and subadults. In most species, female calls are soft low-amplitude signals, audible only over relatively short distances. This makes systematic recording difficult, unless the animals are well habituated to the presence of human observers and regularly forage in the lower forest canopy. Studies on captive Campbell's monkeys have reported considerable acoustic diversity in the vocal behaviour of adult females, with much of the observed variation caused by changes in the social and ecological environment (Lemasson et al. 2003, 2004, 2005; Lemasson & Hausberger 2004). Similarly, studies on Diana monkeys, *Cercopithecus diana diana*, in the Taï Forest of Ivory Coast demonstrated that adult females produced acoustically distinct alarm calls to different

* Correspondence: K. Zuberbühler, School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JP, U.K.
E-mail address: kz3@st-andrews.ac.uk (K. Zuberbühler).
[1] K. Ouattara and A. Lemasson are at Ethologie animale et humaine, U.M.R. 6552-C.N.R.S., Université de Rennes 1, 35380 Paimpont, France.
[2] E. K. N'goran is at Laboratoire de zoologie et de biologie animale, Université de Cocody, 22 BP 770, Abidjan 22, Côte d'Ivoire.
[3] J.-E. Gombert is at the Centre de Recherche en Psychologie, Cognition et Communication, Université de Rennes 2, 6 Av G. Berger, 35043 Rennes cedex, France.

0003-3472/$38.00
doi:10.1016/j.anbehav.2009.03.014

predators (Zuberbühler et al. 1997), while their contact calls varied acoustically depending on context (Uster & Zuberbühler 2001).

In this study, we investigated the alarm-calling behaviour of free-ranging Campbell's monkey females of Taï Forest, Ivory Coast. The species has already been investigated before, although the attention has been on the adult males (Zuberbühler et al. 1999; Zuberbühler 2000b, 2001, 2002; Wolters & Zuberbühler 2003). Adult males produce a range of basic call types in response to external events, such as falling trees, leopards, *Panthera pardus,* and crowned eagles, *Stephanoaetus coronatus* (Zuberbühler 2003). These calls are meaningful in the sense that nearby listeners respond to them as if they had witnessed the call-eliciting event themselves, a phenomenon that also crosses species barriers (Zuberbühler 2000c; Rainey et al. 2004a, b). Another relevant finding was that Campbell's monkey males combine different call types into structured sequences that can function as carriers of meaning (Zuberbühler 2002; K. Ouattara A. Lemasson & K. Zuberbühler, unpublished data), a behaviour also seen in wild putty-nosed monkeys, *Cercopithecus nictitans* (Arnold & Zuberbühler 2006a, b, 2008; Arnold et al. 2008).

Given the general significance that vocal signals have for primates when interacting with their predators (e.g. Seyfarth et al. 1980) and in light of previous results from captivity and the wild, we predicted that female Campbell's monkeys produced predator-specific alarm calls, even though previous research efforts have not revealed any interesting patterns (Zuberbühler 2001). We were also interested in how the vocal behaviour of free-ranging monkeys compared to what has already been described in captivity (Lemasson 2003; Lemasson et al. 2004).

To address these points, we monitored the adult females of six Campbell's monkey groups in the Taï Forest, two of which were fully habituated to human observers. Data were collected both during the females' responses to naturally occurring disturbances and by simulating the presence of natural predators with customized visual and acoustic predator models.

METHODS

Study Groups

Data were collected in the Taï National Park of western Ivory Coast in a study area adjacent to the Taï Monkey Project Research Station (5° 50′N, 7° 21′W) between January 2006 and September 2007. Two Campbell's monkey groups had been followed by researchers and field assistants for more than 10 years. Group members were fully habituated to the presence of observers and individually known. The responses of some females of four additional semihabituated groups to predator models were added to the database. Study groups consisted of one adult male and three to seven adult females with their offspring.

Natural Calling Behaviour

Natural calling events were recorded from the two habituated groups. For this purpose, a focal animal was selected by the observer (K.O.) and subsequently monitored for a 15 min period between 0800 and 1700 hours GMT. During each period, all her vocalizations, as well as her general behaviour (travel, forage, rest, groom, aggression), and any unusual event immediately preceding a vocalization were recorded. If an unusual and relevant event occurred at other times, such as detection of a predator, calls from all group members were collected using ad libitum sampling (Altmann 1974). The total observation time was about 2000 h. Focal animal samples amounted to a total of 193 h, during which we also recorded three leopard encounters (0.016/h) and 11 crowned eagle encounters (0.057/h). In addition, a field assistant also observed the monkeys independently for an additional 800 h during which he recorded six eagle and two leopard encounters.

Recordings were made with a Sony TCD D100 stereo cassette recorder and a Sennheiser ME88 microphone. If necessary, spoken comments were made simultaneously, using a Lavallier microphone, and later transcribed. With this protocol, about 2000 alarm calls were recorded from the different females of all groups. A large majority of alarm calls were given in response to one of the following events: (1) presence of a predator (leopard, crowned eagle), (2) male Diana monkey alarm call to a predator, (3) sudden appearance of a flying animal (e.g. bird, flying squirrel), (4) sudden movements by the observer, (5) risky locomotion by the caller within the canopy (descending from tree; jumping to another branch).

Predator Experiments

We studied the females' alarm call behaviour more systematically by presenting visual predator models (leopard, crowned eagle and Gaboon viper, *Bitis gabonica*) and acoustic predator models (leopard and crowned eagle), five types of stimuli in total, which allowed us to investigate the monkeys' natural response to these predators more systematically. Each stimulus type was presented once to six of seven different groups. From the moment of detection, we determined the first call uttered by an adult female and we monitored the vocal response of all adult females for the first 3 min. Both acoustic and visual predator models have been used successfully before in primate alarm call studies, and these studies have shown that both modalities work equally well to simulate predator presence (Cheney & Seyfarth 1985; Hauser & Wrangham 1990; Zuberbühler 2003; Coss et al. 2007; Arnold et al. 2008).

The following conditions had to be met before an experiment could be conducted. First, the observer had to establish contact with the group for at least 30 min during which no alarm calls were produced by any group members. Second, focal animals had to be less than 10 m off the ground to ensure sufficient recording quality, although the usual recording distance from the habituated individuals was typically 5 m or less. Third, in visual trials, the predator model had to be positioned by a field assistant on the projected travelling route so that only a member of the study group detected the model first. Campbell's monkeys often associate with other monkey species, and if a member of another primate species detected the model first, the trial was discounted.

For eagle trials, the model was positioned in the canopy at an elevation of 2–3 m; for leopard and snake trials, the model was presented on the ground. Eagle shrieks were recorded in the study area by K.Z.; leopard growls were purchased from the National Sound Archive, London (see Zuberbühler et al. 1997 for spectrographic representations of the playback stimuli). All acoustic stimuli were broadcast with a Sony WMD6C professional Walkman connected to a Nagra DSM speaker-amplifier. Stimulus amplitude was adjusted so that the calls sounded natural to a human observer at a distance of about 20 m. Previous research has shown that the amplitude of predator vocalizations had no effect on the monkeys' alarm call responses, provided they were presented within a natural range (Zuberbühler 2000a).

Acoustic Analyses

Pilot observations indicated that adult female Campbell's monkeys produced at least three basic and acoustically distinct alarm calls to external disturbances, and these calls could be