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The irrelevance of individual discrimination in meerkat alarm calls

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Individual discrimination is an important element in the evolution of social behaviour and is particularly important in social living species which show intense intragroup interactions. Numerous previous studies, particularly with nonhuman primates, ground squirrels and marmots, demonstrate the widespread ability of various species to signal and perceive individual identity from vocalizations. The function of individually different alarm calls is thought to assist in the detection of unreliable individuals. This would allow individuals to optimize the benefits of antipredator behaviour by self-assessing the relative predation risk, and responding selectively to reliable callers. In this study we investigated whether meerkats, *Suricata suricatta*, a social mongoose, discriminated among alarm callers individually, and adjusted their response accordingly. Several parameters of the acoustic structure of meerkat alarm calls were measured and analysed with multivariate statistics. Within groups, the 10-fold cross-validation of a multinomial regression yielded, on average, 90% correct assignment. This strongly suggests that meerkats have individually distinct alarm calls. With a habituation–dishabituation playback experiment, we then tested whether meerkats use this information to discriminate between individual callers. Receivers did not distinguish between different individuals in the playback experiments. In meerkats, unreliable callers appear to be uncommon, and the cost of being predated might exceed the costs of responding to an unreliable caller, thus rendering a reliability-based discrimination mechanism unnecessary. Although meerkat alarm calls contain information on individual identity, this information does not appear to be important to the receivers in this context.

Keywords: alarm call; acoustic structure; habituation–dishabituation playback; individual discrimination; meerkat; reliability; *Suricata suricatta*

The signalling and perception of identity are of major importance in the evolution of social behaviour (Hamilton 1963; Trivers 1971; Wilson 1979) and may be the basic requirement for complex mechanisms of social communication (Beecher 1982; Cheney & Seyfarth 1990). Hence, we might expect to find such recognition abilities especially in systems where coalitions or subgroups are present and where the interactions within and between such social categories are essential. Above all, nonhuman primates, with their complex social behaviour, have received most attention in regard to individual recognition mechanisms. Many of the calls emitted in various social contexts show acoustic properties that differ between individuals (Hauser 1991), and based on these individual differences, many nonhuman primates are able to differentiate between callers (Snowdon & Cleveland 1980; Rendall et al. 1996; Semple 2001; Weiss et al. 2001; Ceugniet & Izumi 2004).

The function of individual differences in alarm calls is less clear. Cheney & Seyfarth (1988) proposed the concept of signal reliability to explain such differences. They reasoned that in systems where individuals give deceptive alarm calls, 'selection should favour the ability of recipients to compare signals on the basis of their meaning and to transfer information about the reliability of a signaller's calls from one context to another'. The same selective pressure should apply in systems where variable thresholds for emitting such calls occur, that is high and low false alarm rates (Blumstein et al. 2004). In both cases,

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individuals experience a severe fitness cost when responding to unreliable callers, compared with a situation where they only respond to reliable callers. Therefore, animals that are able to recognize unreliable individuals on the basis of their alarm calls may benefit by optimizing their antipredator behaviour and so allocate more time to other important activities. In yellow-bellied marmots, *Marmota flaviventris*, this leads to an increase in vigilance behaviour after being exposed to artificially created unreliable callers (Blumstein et al. 2004); that is, individuals respond to reliable callers, but make their own independent assessment of relative risk after hearing alarm calls by unreliable callers, thereby optimizing their foraging efficiency. Additionally, both Richardson's ground squirrels, *Spermophilus richardsonii*, which are thought to benefit socially through reciprocal altruism (Hare & Atkins 2001), and vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth 1988) show an ability to discriminate between unreliable and reliable callers based on an association with their previous antipredator behaviour.

In this study, we investigated whether consistent differences exist between the alarm calls of individual meerkats, *Suricata suricatta*, and if so whether they were important in determining an individual's response to them. Meerkats are highly cooperative small mammals, which inhabit the drier, open regions of southern Africa (Estes 1991), and live in groups up to 50 individuals (Clutton-Brock et al. 2005). They typically forage for 5–8 h a day, digging for invertebrates and small vertebrates in the sand (Doolan & Macdonald 1996), and while doing so they are unable to detect predators, and annual mortality rate is high (Clutton-Brock et al. 1999a). Their main aerial predators are martial eagles, *Polemaetus bellicosus*, and pale chanting goshawks, *Melierax canorus*. Group members alternate in guarding from a raised position (Manser 1999; Clutton-Brock et al. 1999b), alerting other group members by emitting a variety of alarm calls (Manser 2001), and foraging animals frequently scan their surroundings for predators, and warn other group members, in the same manner. Meerkat alarm calls not only encode information about the predator type, but also about the relative risk that the calling individual is exposed to (Manser 2001). Therefore, it is likely that variable thresholds for emitting alarm calls exist, and hence the potential for discrimination between individuals arises (Blumstein et al. 2004).

To investigate whether individual discrimination is of importance in meerkat alarm calling and response behaviour, we first determined whether they emit individually distinctive alarm calls using a multinomial discriminant function. Secondly, we conducted a modified habituation–dishabituation playback experiment (Cheney & Seyfarth 1988; Johnston & Jernigan 1994; Gheusi et al. 1997; Hauser 1998; Weiss et al. 2001; Blumstein & Daniel 2004), to investigate whether receivers use the information on individuality to differentiate amongst each other. We focused on 'medium-urgent aerial alarm calls' (see Fig. 1a), which are usually emitted when aerial predators approach (Manser 2001). On hearing this call, meerkats immediately stop foraging, and either stand up on their rear legs, or run to the nearest shelter (Manser et al. 2001).

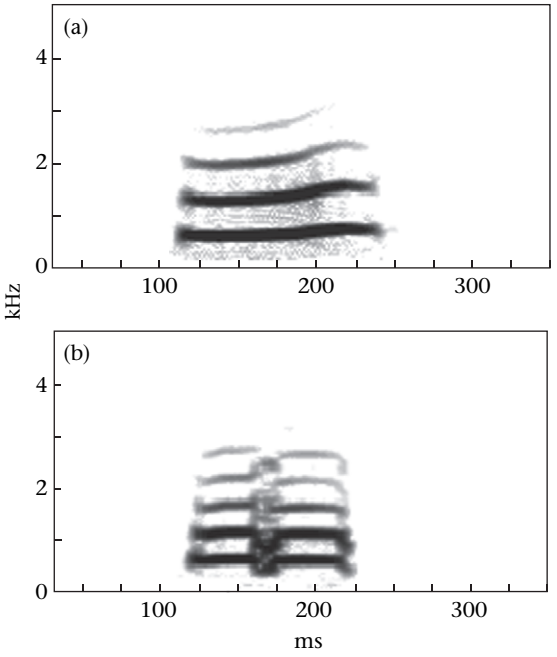

Figure 1. Spectrogram of one call out of an alarm call sequence: (a) medium-urgent aerial alarm; (b) medium-urgent terrestrial alarm.

METHODS

Study Site and Animals

Recordings and playbacks were conducted on nine groups of free-living meerkats at the Kuruman River Reserve, which lies about 30 km east of Van Zylsrus along the dry riverbed of the Kuruman River (26°58′S, 21°49′E) (Clutton-Brock et al. 1998). Groups consisted of six to 23 individuals, resulting in a total of approximately 144 individuals, all of whose genealogy is known as they have been marked and observed since emergence. We focused on adult subordinate individuals, preferably from the same sex within the same group. As part of the Kalahari Meerkat Project's long-term study, all animals in every group were marked with a subcutaneous transponder (Clutton-Brock et al. 2001) and with superficial dye spots for individual identification (details see Jordan et al. 2007), and were habituated to a level that allowed recordings and observations within 0.5 m.

Acoustic Analysis

Audio recordings

Recordings of medium-urgent aerial alarm calls were performed between February and August 2005 throughout the day, with a Sennheiser microphone ME66/K6 connected to a portable Marantz PMD670 digital professional solid state recorder (D&M Professional, IL, U.S.A.). The majority of all recorded calls were obtained during naturally occurring predator encounters. For three test groups call sequences were insufficient in numbers, and we therefore presented a model kite painted in black in a distance of 200 m and a height of up to 50 m, to elicit alarm calls. The kite resembled a hovering aerial predator