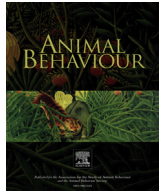




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Call concatenation in wild meerkats

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Repertoire size, frequently determined by the number of discrete call types, has been used to assess vocal complexity in animals. However, species can also increase their communicative complexity by using graded signals or by combining individual calls. Animal call sequences can be divided into two main categories, each subdivided into two classes: repetitions, with either an unlimited or finite number of iterations of the same call type, and mixed call combinations, composed of two or more graded or discrete call types. Social contexts involve a wide range of behaviours and, unlike predation contexts, can be associated with both positive and negative emotions. Therefore, interactions linked to social contexts may place additional demands on an animal's communicative system and lead to the use of call combinations. We systematically documented call combinations produced by wild meerkats, *Suricata suricatta*, a highly social carnivore, in social contexts in their natural habitat. We observed 12 distinct call combinations belonging to all four classes of combination, produced in all the observed behavioural contexts. Four combinations were each produced in a specific context whereas the remaining eight were produced in several contexts, albeit in different proportions. The broad use of combinations suggests that they represent a non-negligible part of meerkat social communication and that they can be used in flexible ways across various behavioural contexts. Comparison with combinations produced in predation contexts indicated that social call combinations are more varied in number of classes and structural complexity than the former, perhaps due to the greater variety of social contexts. However, in meerkats, combinations of functionally referential calls have been documented in predation but not social contexts, suggesting that both social and predation pressures may play a role in the evolution of combinatoriality in animal communication.

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Communicative complexity related to signal diversity can be measured in two main ways: by the number of distinct signals produced or by calculating the bits of information contained in the system (Freeberg, Dunbar, & Ord, 2012). Acoustic communicative complexity has mostly been assessed using vocal repertoire size (Oller & Griebel, 2008). However, most vocal repertoires only list the acoustically discrete call types the species produce and, for the majority of species, the number of these call types is physically constrained, limiting the size of their repertoire (Fitch, 2000). To achieve a higher communicative flexibility despite this limitation, some animal species produce intermediate call types, leading to a graded call system (Marler, 1976). An additional way to increase communicative flexibility is to combine individual calls (Arnold &

Zuberbühler, 2006; Engesser, Crane, Savage, Russell, & Townsend, 2015). Combining calls has frequently been argued to be a more efficient way of conveying new messages than creating new calls (Jackendoff, 1999; Nowak, Plotkin, & Jansen, 2000) and may reduce the risk of perception errors from the receiver's side (Nowak & Krakauer, 1999; Nowak, Krakauer, & Dress, 1999).

By dividing call combinations described in the literature into categories based on the number of component call types, we can identify two main groups: repetitions and mixed call combinations. Repetitions are combinations composed of only one call type and can be subdivided into two classes: unlimited and finite. Unlimited repetitions are combinations that are not characterized by the number of times the call is repeated. Examples of such combinations are the aggression calls of corncrakes, *Crex crex* (Rek, 2013) and alarm calls produced repeatedly in many species (nonprimate mammals: Blumstein & Armitage, 1997; Manser, 2001; nonhuman primates: Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Macedonia, 1990; Schel, Candiotti, & Zuberbühler, 2010). In

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contrast, finite repetitions are always composed of the same number of calls, for example the double calls of Bulwer's petrels, *Bulweria bulwerii*, are always composed of two calls (James & Robertson, 1985).

Here we define mixed call combinations as sequences that include at least two different call types and can be either graded or discrete or both. Graded call combinations are sequences of calls that grade along a structural or temporal continuum between two discrete call types (Keenan, Lemasson, & Zuberbühler, 2013). Gradation can occur in the frequency parameters (e.g. peak frequency, frequency range), amplitude or duration of the call. Examples of such combinations can be found in diverse taxa from amphibians to nonhuman primates (hereafter primates). One case of such a graded sequence is the aggression call of the Blanchard's cricket frog, *Acris crepitans blanchardi*. These calls become more aggressive with the approach of a simulated intruder (Wagner, 1989), as expressed by an increase in length and number of pulses. In another case, when excited, the Senegal bushbaby, *Galago senegalensis senegalensis*, produces sequences of calls that grade from one call type to another as the caller gets more aroused (Zimmermann, 1985). Moreover, combinations may contain graded calls that are not graded into each other during the sequence, as seen in sequences of calls produced by banded mongooses, *Mungos mungo*, in the context of being separated from the group: these sequences contain both close calls and lost calls, which are two distinct graded calls (Jansen, 2013). Discrete mixed call combinations are composed of several discrete call types with no intermediate forms. For example, male Túngara frogs, *Physalaemus pustulosus*, produce calls composed of two distinct components, a whine followed by up to six chucks to attract females (Ryan, 1980). In primates, female Diana monkeys, *Cercopithecus diana*, produce several social calls, used to communicate over short distances with other group members in nonpredatory contexts, in combinations integrating two distinct call types (Candiotti, Zuberbühler, & Lemasson, 2012). Examples of discrete mixed call combinations include the assembly of functionally referential acoustic units resulting in a new or related meaning, as seen in the alarm call systems of some forest guenon species (putty-nosed monkeys, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2006; Campbell monkeys, *Cercopithecus campbelli*: Ouattara, Lemasson, & Zuberbühler, 2009).

Recent attention has focused on call combination production in non vocal-learning species. Unlike vocal learning species such as songbirds, hummingbirds, and parrots in birds, and humans, some marine mammals, and bats in mammals (Slater & Janik, 2010), non vocal-learners cannot expand their vocal repertoire by learning to produce new sounds. Hence non vocal-learning species could be expected to use call combinations as a means to increase their communicative output (Nowak & Krakauer, 1999; Nowak et al., 1999). Many studies on call combinations in animal communication systems have focused on nonhuman primates, in particular their alarm or long calls (black-fronted titi monkeys, *Callicebus nigrifrons*: César, Byrne, Young, & Zuberbühler, 2012; Bornean orang-utans, *Pongo pygmaeus wurmbii*: Spillmann et al., 2010; Campbell monkeys: Ouattara et al., 2009; putty-nosed monkeys: Arnold & Zuberbühler, 2006; white-handed gibbons, *Hylobates lar*: Clarke, Reichard, & Zuberbühler, 2006). However, an emerging body of data suggests quieter social calls may represent a suite of calls also open to combinatorial operations (chimpanzees, *Pan troglodytes*: Crockford & Boesch, 2005; bonobos, *Pan paniscus*: Clay & Zuberbühler, 2009; red-capped mangabeys, *Cercocebus torquatus*: Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Diana monkeys: Candiotti et al., 2012).

It has been hypothesized that, unlike most predation contexts where an immediate change in behaviour in response to a call is

adaptive, in most social situations, latency to respond is not necessarily crucial for survival. Therefore both the caller and the receiver should have more time to produce and process longer strings of acoustic units in social contexts (Collier, Bickel, van Schaik, Manser, & Townsend, 2014). Moreover, social contexts can involve a highly variable range of behaviours and, unlike predation contexts, they can be associated with both positive and negative emotions. Thus, interactions during social contexts may place additional demands on the communication system that could promote combinatoriality. Data from primates seem to support this (Bouchet et al., 2010; Candiotti et al., 2012; Clay & Zuberbühler, 2009; Crockford & Boesch, 2005), and some nonprimate species have also been described as producing call combinations in non-predation contexts (banded mongooses: Jansen, Cant, & Manser, 2012; corncrakes: Rejk, 2013; chestnut-crowned babblers, *Pomatostomus ruficeps*: Engesser et al., 2015). However, a systematic documentation of the presence and extent of combinatorial communication within a species' repertoire is rarely undertaken (but see Crockford & Boesch, 2005 for a study on wild chimpanzees and Bouchet et al., 2010 for a study on captive red-capped mangabeys). Quantifying the extent and use of combinations within a species' communication system is key to understanding both the diversity of combinations produced in animal communication and the extent to which they result from different combinatorial production mechanisms. Furthermore, elucidating the variance in distribution of combination types between social and predation contexts in different species could shed light on interspecies differences and subsequently on the contexts promoting communicative complexity. This could ultimately lead to a better understanding of the factors influencing the evolution of combinatoriality more generally.

Some animal calls have been termed functionally referential due to their high context specificity and link to an external object or event (Macedonia & Evans, 1993), while other calls seem to mainly reflect the animal's internal state and are referred to as motivational/emotional calls (Darwin, 1872; Morton, 1977). An animal's internal state includes both motivation, which is the behavioural state the animal experiences adjusted to its external environment and internal physiological state, and emotion, a short but intense affective reaction to a stimulus which can be measured along two dimensions: arousal (high or low) and valence (positive or negative) (Briefer, 2012). It is now recognized that the same call can encode both types of information, functional reference and internal state (Manser, Seyfarth, & Cheney, 2002). Given that call combinations are built from several different calls, the combinations themselves have the potential to carry similar types of information, pertaining to the internal state or external event experienced by the signaller. Furthermore, as they comprise several calls, combinations could also inform receivers about mixed motivations/emotions, more than one external event or even combine the two types of information expressing both the caller's internal state and an external event.

Here, by investigating the combinatorial vocal behaviour of meerkats, *Suricata suricatta*, we aimed to test the hypothesis that social contexts promote the production of call combinations in animal communication. In line with previous work in primates showing broad usage of call combinations in social situations, we expected call combinations to be widely used in social situations. Furthermore, if social contexts represent an additional relevant pressure favourable to the production of call combinations, we would expect meerkats to produce at least the same combinatorial structures with the same relative frequency in social as in predation contexts.

Meerkats are a highly social species of cooperative breeding mongoose, living in groups of 3–50 individuals (Clutton-Brock

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