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Flexible use of simple and combined calls in female Campbell's monkeys

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Call combinations allow animals to expand the communicative power of small repertoires with acoustically inflexible elements. In Campbell's monkeys, *Cercopithecus campbelli*, males possess a small repertoire of calls that can be merged to an acoustically invariable suffix and which are concatenated into various sequences, mainly in response to external disturbances. The vocal repertoire of adult females has been less well studied although it is much richer, containing both alarm and various social calls. In particular, females possess a low-pitched contact call, produced either alone or merged with a high-pitched, arched unit. Combined contact calls are identity-richer and easier to detect than simple calls. Here, we investigated the socioecological factors that determined the production of single and combined utterances and found that combined utterances were more common when identity was relevant such as in mixed-species associations and during socially important vocal exchanges. In contrast, single calls were used mainly when predation risk was high, as part of this species' generally cryptic antipredator strategy. We discuss these finding in the light of current theories regarding the evolution of combinatorial signalling.

Living in groups provides antipredation benefits but also requires coordination and communication between group members (Gautier & Gautier-Hion, 1977; Lehmann, Korstjens, & Dunbar, 2007; Oda, 1996; Uster & Zuberbühler, 2001; see Bennett & Cuthill, 1994; Osorio & Vorobyev, 2008; Wyatt, 2003 and Liebal, Waller, Slocombe, & Burrows, 2013 for reviews). As a result, interactions with predators and conspecifics are likely to act as two major forces in the evolution of animal communication (McComb & Semple, 2005; Pollard & Blumstein, 2012; Stephan & Zuberbühler, 2008). First, predation is the likely driver for alarm call evolution (Hauser, 1996), especially to encode different levels of urgency or predator types (Furrer & Manser, 2009; Manser, 2001; Pereira & Macedonia, 1991). Second, the daily challenge of social coordination is the likely driver for social call evolution, with callers generally benefiting from advertising their ongoing activity, identity and location to other group members (Bouchet, Blois-Heulin, & Lemasson, 2013; Manser et al., 2014).

As a general pattern, increasing social complexity, for example, via group size or diversification of social roles, is thought to select for more complexity in communication, for example, via larger repertoire size or more informative signals (Freeberg, Dunbar, & Ord, 2012; Manser et al., 2014; McComb & Semple, 2005). This is mainly because individuals are faced by more complex coordination problems resulting from increasingly complex social networks (Freeberg et al., 2012; McComb & Semple, 2005; Seyfarth, Cheney, & Bergman, 2005). However, most mammals, and particularly nonhuman primates, are constrained in how much motor control they have over their vocal tracts (Lameira, Maddieson, & Zuberbühler, 2014). As a result, vocal repertoires tend to be small with only limited numbers of call types (Hammerschmidt &

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Fischer, 2008). Enlarging the repertoire by generating new acoustic structures, in other words, may simply not be possible for most species.

One way to enhance the communicative power of such limited systems is to evolve the ability to produce acoustic variants within the main vocal classes, a persistent finding in many species (Bouchet et al., 2013; Gustison, le Roux, & Bergman, 2012; Knotkova, Veitl, Sumbera, Sedlacek, & Burda, 2009; Le Roux, Cherry, & Manser, 2009). Another way is to merge existing vocal units into combined calls consisting of different acoustic elements uttered in close succession (Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Coye, Zuberbühler, & Lemasson, 2016; Lemasson & Hausberger, 2011). A third way to overcome limited vocal control is to combine calls with existing meaning into longer sequences, with sometimes modified meanings (Arnold & Zuberbühler, 2008; Engesser, Ridley, & Townsend, 2016; Lemasson, 2011; Schlenker et al., 2016; Zuberbühler & Lemasson, 2014) In this case, the relevant vocal units are single calls separated by intercall intervals (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Bohn, Schmidt-French, Ma, & Pollak, 2008; ten Cate & Okanoya, 2012). The latter two mechanisms are of particular interest because of possible similarities with human phonology and syntax (Collier, Bickel, Schaik, van Manser, & Townsend, 2014). Whether or not they result from the same phenomenon, or should be considered distinct processes, is currently unknown and requires further research.

There has been a recent surge in studies with evidence for combinatorial structures in birds (Engesser, Crane, Savage, Russell, & Townsend, 2015; Engesser et al., 2016; Suzuki, Wheatcroft, & Griesser, 2016), but also terrestrial mammals (Jansen, Cant, & Manser, 2012; Kershenbaum, Ilany, Blaustein, & Geffen, 2012) and primates (Cäsar, Byrne, Young, & Zuberbühler, 2012; Clarke, Reichard, & Zuberbühler, 2006; Clay & Zuberbühler, 2011; Crockford & Boesch, 2005; Hedwig, Mundry, Robbins, & Boesch, 2015). Among the latter, combinatorial systems have been identified in alarm calls of male Campbell's monkeys, *Cercopithecus campbelli* (Coye, Ouattara, Zuberbühler, & Lemasson, 2015; Ouattara, Lemasson, & Zuberbühler, 2009a,b; Zuberbühler, 2002) and putty-nosed monkeys, *Cercopithecus nictitans* (Arnold & Zuberbühler, 2008, 2012) and social calls of female Diana monkeys, *Cercopithecus diana* (Candiotti, Zuberbühler, & Lemasson, 2012a; Coye et al., 2016). Although it is evident that callers can increase the number of acoustic structures by producing combinations of limited sets, the communicative function of such combinations is not so self-evident, especially for social calls.

Animals living in societies with individualized relationships, as is the case for primates, need to recognize each other individually (Arlet, Jubin, Masataka, & Lemasson, 2015; Candiotti, Zuberbühler, & Lemasson, 2013; Kondo & Watanabe, 2009; Rendall, Rodman, & Emond, 1996), especially if they live in visually dense habitats (Candiotti et al., 2013; Lemasson & Hausberger, 2011). Unsurprisingly, individually distinctive calls have been described in many group-living animals (Jansen et al., 2012; Kondo & Watanabe, 2009; Le Roux et al., 2009; Palombit, Seyfarth, & Cheney, 1997) but not all call types seem to be affected in the same way (Bouchet, Blois-Heulin, Pellier, Zuberbühler, & Lemasson, 2012; Lemasson & Hausberger, 2011). As a general pattern, social calls tend to contain higher degrees of individual signatures than alarm calls (Bouchet et al., 2012, 2013; Lemasson & Hausberger, 2011). Furthermore, there is also evidence that, within different social calls, identity is encoded flexibly and to various degrees, depending on context or audience composition (e.g. starling, *Sturnus vulgaris*, Adret-Hausberger, 1982, 1989; Henry & Hausberger, 2001; zebra finch, *Taeniopygia guttata*, Vignal, Mathevon, & Mottin, 2004; grey mouse lemur, *Microcebus murinus*, Leliveld, Scheumann, & Zimmermann, 2011; Diana monkey, Candiotti, Zuberbühler, & Lemasson, 2012b).

Here, we focus on Campbell's monkeys, a species for which combinatorial capacities have been described in male calls (Coye et al., 2015; Ouattara, Lemasson, & Zuberbühler, 2009a, 2009b). Campbell's monkeys are territorial, arboreal guenons living in West African tropical forests, often in association with other primate species (McGraw, Zuberbühler, & Noë, 2007). They form harem groups with a single adult male and several adult females with their offspring (Candiotti et al., 2015). The adult male does not interact much with other group members and, probably as a result, his vocal repertoire is limited to a few acoustically stereotyped alarm calls, given in different sequence compositions according to external events (Coye et al., 2015; Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Ouattara et al., 2009a). Three basic alarm calls have been distinguished (Keenan, Lemasson, & Zuberbühler, 2013), which can be further modified by an acoustic affixation principle (Ouattara et al., 2009a) to express differences in perceived urgency. Affixation is meaningful for listeners, as recently demonstrated experimentally with wild Diana monkeys from a population sympatric with Campbell's monkeys (Coye et al., 2015). In Campbell's monkeys, the adult females constitute the social core of the group and form stable social bonds of variable strength with each other (Candiotti et al., 2015; Lemasson, Gandon, & Hausberger, 2010; Lemasson & Hausberger, 2004). They produce a range of alarm and social calls, to navigate in a visually restricted habitat (Brown, Gomez, & Waser, 1995; Marler, 1965; Waser & Brown, 1986). The most common calls are contact calls, which appear in three types (Lemasson & Hausberger, 2011): SH (short harmonic), CHb (combined harmonic broken) and CHf (combined harmonic full). SH types are low pitched and can be uttered alone or combined with an arched frequency modulation to form broken or full CH types (i.e. which involve, respectively, a partial or complete arched-shaped frequency modulation merged after the 'SH' part, Fig. 1). The main alarm call is the repetitive rapid ascending (RRA) call (Fig. 1).

The combinatorial structure of Campbell's monkeys' contact call system needs to be verified experimentally (e.g. by testing the relevance of recombined calls to receivers). Yet, its marked resemblance to the call system of Diana monkeys strongly suggests that both rely on a similar combinatorial mechanism. Female Diana monkeys possess calls very similar to the calls of Campbell's monkeys (e.g. with calls structurally homologous to RRA, SH, CHb and CHf calls, Candiotti et al., 2012a,b; Lemasson & Hausberger, 2011). In contrast to Campbell's monkeys, however, Diana monkeys can form combined calls by merging an arched unit to distinct calls relating to the emotional context (e.g. to RRA-like calls in negative contexts or to SH-like calls in neutral contexts). Observational and playback studies on wild Diana monkeys demonstrated that combined calls are meaningful to receivers and that their meaning depends on the vocal units involved (Coye et al., 2016b).

While the context of production and likely function of call combination has been elucidated in Diana monkeys, they remain unclear in Campbell's monkeys. In particular, the possible advantage of this very limited system (i.e. which only allows the combination of arches in SH calls) and its possible functions (i.e. why would females use three distinct calls for the same apparent purpose?) are obscure. One possible explanation for this pattern lies in the calls' potential for identity coding which varies with the presence and completeness of an arched unit (Lemasson & Hausberger, 2011). This is so because the potential for identity coding of Campbell's monkeys' contact calls gradually increases between SH, CHb and CHf calls with the latter encoding identity most strongly (Lemasson & Hausberger, 2011).