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Commentary

Working hypotheses on the meaning of general alarm calls

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General calls are present in the vocal repertoire of a great number of animal species. Because of their lack of context specificity, they are typically argued to possess blurred meaning, or even no meaning at all. Although recent animal cognition studies have demonstrated a growing interest in these vocalizations, there is currently no clear definition of general calls, and their meaning is seldom discussed. Here, we propose a definition of general calls, and review various hypotheses regarding their meaning, focusing on alert contexts. We first discuss the hypothesis that general alarm calls have a general alert meaning. Second, we review an alternative view, that general calls in fact have a specific meaning. With this review, we encourage further research that could help delve into the mechanisms underlying vocal production and comprehension and would improve our understanding of general and specific calls in animals.

The foundational work of Seyfarth, Cheney, and Marler (1980) on the alarm-calling system of vervet monkeys, *Chlorocebus pygerythrus*, gave rise to the production of an abundant literature on the meaning of animal vocalizations. The term 'functional referentiality' was assigned to calls that are produced in response to the presence of specific classes of objects in the environment (production criterion), and that may evoke the presence or imminence of the very object or features of the environment in recipients by triggering adaptive responses (perception criterion; Evans, Evans, & Marler, 1993; Macedonia & Evans, 1993; Townsend & Manser, 2013). The unveiling of functional referential calls has spanned a variety of orders as diverse as primates (e.g. Zuberbühler, 2000), rodents (e.g. Tamura & Yong, 1993) and even bird species (e.g. Evans et al., 1993) with functionally referential calls seemingly present in predator-related contexts, but also in nonpredatory contexts, such as feeding (Bitetti, 2003; Bugnyar, Kijne, & Kotrschal, 2001; Evans & Evans, 1999; Kitzmann & Caine, 2009; Slocombe & Zuberbühler, 2005; but see Clay, Smith, & Blumstein, 2012 for a critical review) or in social contexts (reviewed in Townsend & Manser, 2013).

More recently however, the legitimacy of the functional referentiality framework has come under heavy debate (Scarantino & Clay, 2015; Sievers & Gruber, 2016; Townsend & Manser, 2013; Wheeler & Fischer, 2012). One of the major arguments has been that many of the so-called referential vocalizations may display only vague reference to objects or circumstances in the external world, if any. In other words, a number of animal species show a lack of production specificity for certain calls of their repertoire (Macedonia & Evans, 1993).

Less context-specific vocalizations are sometimes termed 'general' or 'nonspecialized' calls and are found in the vocal repertoire of a great number of animal species, with the typical case being the inclusion of both specific and general calls within vocal repertoires. This seems to be particularly true for many of the calls apparently produced in response to terrestrial predators, which may also occur in nonpredatory contexts, while calls to aerial predators might be produced more specifically (Fichtel & Kappeler, 2002; Kirchhof & Hammerschmidt, 2006; Price et al., 2015; Wheeler & Fischer, 2012). The apparent lack of specificity of these general calls often leads to the conclusion that they only possess blurred meaning compared to specific calls (e.g. Cäsar, Byrne, Hoppitt, Young, & Zuberbühler, 2012) or even no meaning at all (Rendall, Owren, & Ryan, 2009).

As it stands, the status of general calls remains unclear. Yet general calls are particularly important to study as they can help

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shed light on the cognitive mechanisms underlying vocal comprehension in animals. Indeed, results indicate that general calls may require the integration of contextual cues to disambiguate between localized predation and other circumstances (Arnold & Zuberbühler, 2013; Wheeler & Fischer, 2012), providing more general insights into how animals categorize their environment. In this article, our aim is to clarify the meaning of general calls by evaluating the possible theoretical directions. Although we do not possess satisfactory data to choose one hypothesis over the others (most likely, each hypothesis may be appropriate for a given species, but inappropriate for others), we offer empirical directions that may help clarify the debate.

SPECIFIC AND GENERAL ALARM CALLS IN VOCAL REPERTOIRES

What are general calls? As seen above, general calls are found in alarm contexts (Fichtel & Kappeler, 2002), feeding contexts (Clay et al., 2012) and may also be present in social contexts (Townsend & Manser, 2013). For the sake of simplicity, we focus on general alarm calls in the rest of our argumentation. However, the following arguments could also be applied to general calls in other ecologically relevant domains.

Although the concept of general or nonspecialized alarm calls is frequently seen in the literature on animal vocal communication, there is no clear definition. According to Wheeler and Fischer (2012), general alarm calls are calls that can be produced in stressful but nonpredatory contexts, a definition close to that of Fichtel and Kappeler (2002). Similarly, Zuberbühler and Neumann (2017) stated that general alarm calls are alarm calls that are also given in nonpredatory situations (i.e. disturbances). For Townsend and Manser (2013), general calls are produced in more than one context and cannot be used as 'proxies' for external objects. Finally, Scarantino and Clay (2015) assumed that general calls have low stimulus specificity.

More precisely, specific alarm calls exhibit strong and significant correlation with at least one external feature of the predatory event. Features typically include the class of the predator (Manser, Seyfarth, & Cheney, 2002; Seyfarth et al., 1980), the urgency and/or imminence of its attack (Manser et al., 2002), its usual or likely localization, its behaviour and hunting technique (Macedonia & Evans, 1993) or its size or colour (Griesser, 2008; Kiriazis & Slobodchikoff, 2006; Slobodchikoff, Paseka, & Verdolin, 2009). This list is not restrictive: if a given species is predated upon by a predator *P* every time there is a certain distinctive amount of light *y*, then *y* is likely to become a feature of the predation event *P* and be integrated into the meaning of the specific call given exclusively in circumstance *P*. By contrast to specific calls, general calls are only weakly significantly correlated with at least one of the attributes.

This leads to the second part of our definition: general calls are calls that are produced in a set of circumstances that can be relatively greater than, and may often contain, the set of circumstances in which specific calls occur. In what follows, the set of circumstances in which calls occur more than expected by chance will be referred to as their 'semantics' or their 'semantic domain'. In fact, the very concept of semantics and its attribution to animal calls does not at all require that calls denote specific objects in the world (Scarantino & Clay, 2015; Schlenker, Chemla, Schel, et al., 2016). Animal vocalizations possess semantics in the simple sense that one can potentially identify a set of circumstances in which a given call is appropriate or often observed. Thus, calls need not correspond to a natural class of objects in the world (like 'leopard' or 'terrestrial predator') to possess semantics.

Examining the semantics of various calls (and how they may overlap, when certain calls are more 'general' than others) therefore requires evaluating the circumstances in which they are given. It is still an ongoing task in some species. For example, chimpanzees, *Pan troglodytes*, produce 'alarm hoos' to a range of disturbances, including snakes, nonpredatory animals and unusual objects in the environment (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, & Zuberbühler, 2015, 2017; Goodall, 1986; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013) and barked calls in what appear to be more urgent circumstances (Crockford & Boesch, 2003; Goodall, 1986; Schel et al., 2013). Whether this means that barked alarm calls are specific and 'alarm hoos' are general is an empirical question: either 'alarm hoos' and barked alarm calls are semantically distinct (their respective semantic domain does not overlap, i.e. the set of situations where one alarm call is appropriate is exclusive compared to the set of situations where the other alarm call is used) or the semantics of barked alarm calls is a subset of the semantics of 'alarm hoos' (i.e. every situation that could give rise to barked alarm calls could give rise to 'alarm hoos'), or the other way around.

Several species exhibit both specific and general calls, of which a sample is summarized in Table 1. In some cases, more than one alarm call appears to be general in usage, as in dwarf mongooses, *Helogale parvula* (Collier, Radford, Townsend, & Manser, 2017). In these systems, one must specify the semantic extension of the various general and specific alarm calls, with the possibility that certain alarm calls are more general than other general calls. In fact, general calls may only be 'general' relative to other calls. What needs to be explained, though, is how animals select one call over another when both calls share part of their semantic domain and are therefore appropriate in a given situation.

One clear example of a general alarm call is the 'pyow' given by male blue monkeys, *Cercopithecus mitis stuhlmanni*. Blue monkeys produce 'katrain' calls to aerial threats and 'ant' calls to terrestrial threats, but use the general 'pyow' call in a greater variety of contexts, including terrestrial threat, male - male agonism and intergroup encounters (Fuller, 2013, 2014; Fuller & Cords, 2017; Murphy, Lea, & Zuberbühler, 2013; Schlenker, Chemla, Schel, et al., 2016). Therefore, blue monkeys seemingly possess one clear general alarm call ('pyow'), and two alarm calls ('katrain' and 'ant') that are more specific in usage.

Below, we discuss two broad theoretical options on the semantics of general alarm calls: according to theoretical option 1, general alarm calls have a 'general alert' semantics (i.e. they apply to any situation that involves a noteworthy alerting element in the environment). The alternative (theoretical option 2) is that general alarm calls do not possess a 'general alert' semantics. Rather, they could be considered functionally equivalent to specific alarm calls because they possess no semantics at all or because they are calls that are in fact specific and have been misclassified for various reasons. Each theoretical option possesses variants, which may have not been proposed in the literature, but which are a priori reasonable and should be examined.

To evaluate these two broad theoretical options and their variants, we draw our reasoning from observational and empirical data, mainly from blue monkeys. Since blue monkeys seemingly possess an alarm vocal system composed of one general and two specific alarm calls, they are good candidates to illustrate the theoretical options outlined here.

GENERAL ALARM CALLS HAVE A GENERAL ALERT MEANING

General Alarm Calls Mean 'General Alert'

The first theoretical option is that the semantics of general alarm calls is 'general alert'. In other words, general alarm calls can be produced whenever a noteworthy alerting element is detected by the caller, including the circumstances in which specific alarm calls