UNPACKING THE PROXIMATE FUNCTIONS OF FUNCTIONALLY REFERENTIAL SIGNALS: A TEST OF 3 HYPOTHESES

Stuart K Watson[*1,2,3], Andrea Müller[3], and Marta Manser[2,3]

[*]Corresponding Author: swatso88@gmail.com

[1] Department of Comparative Language Science, University of Zurich, Switzerland

[2] Center for the Interdisciplinary Study of Language Evolution, University of Zurich, Switzerland

[3] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

Decades of research have demonstrated a broad range of species possess vocal signals which are produced only in the presence of specific stimuli, such as a particular predator type. Crucially, conspecific receivers are able to decode these stimulus-specific associations and use them to choose an appropriate behavioural response to the eliciting cause (Arnold & Zuberbühler, 2013; Dawson Pell et al., 2018; R. Seyfarth et al., 1980). Because of the surface-level resemblance of these call-types to referential language, these have been termed "functionally referential" vocalisations, and have been argued to present a likely evolutionary precursor to semantics (R. M. Seyfarth & Cheney, 2017). However, plausible competing explanations for the underlying function of these calls have also been presented. For example, stimulus-specific calls may be a reflexive expression of the internal arousal state brought about by a particular stimulus, which receivers have simply learned to associate with the eliciting cause (Wheeler & Fischer, 2012). Alternatively, they may be more akin to 'imperative' statements in language, functioning primarily to direct a specific behavioural change in receivers (Schamberg et al., 2018). Determining the proximate function of these signals is therefore key to understanding both animal communication systems and the evolutionary foundations of language. Unfortunately, the underlying function of these calls from a producer perspective is not trivial to determine. Playback experiments are a powerful tool for revealing how receivers interpret and extract information from a given call, but cannot directly inform us about the motivation of callers themselves. Here, we use a novel model predator demonstration experiment to shed light on the proximate function of aerial-specific alarm call production in meerkats (*Suricata suricatta*), a cooperatively breeding species of mongoose with a complex communication system (Manser et al., 2014).

Meerkats have an expansive vocal repertoire, one item of which is a functionally referential alarm call produced only in response to aerial predators (typically martial eagles) (Manser et al., 2002). In the Kalahari Desert, we simulated predation events for 7 groups of wild meerkats (4-22 individuals per group) using a model predator, a kite painted to imitate a martial eagle. Demonstrations took place in two behavioural contexts: i) while the majority of the group was safe and close (<5m) to their burrows (N = 3 trials per group), and ii) while the majority of the group was vulnerable, foraging at a distance (>10m) from their burrows (N = 3 trials per group). All trials elicited strong predator-avoidance response behaviours from the meerkats. We recorded all calling bouts produced in response to these predator demonstrations and coded whether they contained an aerial alarm call. Contextual information was also recorded, including: the distance of the caller to shelter, the proportion of the group who were close to shelter, and the distance of the kite from the group. The association between contextual variables and the production of aerial alarm calls was then used to test three hypotheses regarding the underlying function of these calls (Table 1).

Table 1. Summary of hypotheses for the underlying function of meerkat aerial alarm calls and their corresponding empirical predictions.

Hypothesis		**Predictions**
Referential	Produced to share contextual information with receivers	Production will not vary according to the relative danger towards the caller or group
Imperative	Produced to elicit a specific behaviour in receivers	Production is more likely when the group (i.e. receivers) are further from safety
Emotional	Produced reflexively as a product of arousal state	Production is more likely when the caller is further from safety / closer to danger

To determine which of these three hypotheses best explained the observed data, we fit a suite of Bayesian generalised linear mixed-effects models with effect structures corresponding to each of these hypotheses. The out-of-sample predictive power of each of these models was then compared using Watanabe-Akaike information criterion. We found that the model which best fit the data was one in which no fixed effects corresponding to the relative safety of the caller or group influenced the likelihood of an individual producing an aerial alarm call, supporting the referential hypothesis.

This finding indicates that the production of aerial alarm calls in meerkats primarily serves a referential function, i.e., to inform receivers about the presence of a particular predator type in their immediate surroundings. This novel approach provides the first insights into the cognition and motivations underlying the production of these functionally referential signals Broader application of this approach to the functionally referential signals of other species will determine whether this is a general feature of this class of signal, or if there is variation within and between species.

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