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Vervet monkeys greet adult males during high-risk situations

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Many animal species produce ritualized signals during dyadic encounters but the functions of such 'greeting' behaviour vary considerably, or are often unknown. One established function is to acknowledge existing dominance relationships. At the same time, call rates often increase during social tension, suggesting additional functions, such as to appease higher-ranking individuals, or to maintain spatial proximity and friendly relations. For vervet monkeys, *Chlorocebus pygerythrus*, vocal behaviour has been studied extensively, but little research has been devoted to calls given during encounters between two individuals, i.e. grunts. Here, we examined how individual and relationship features affected the vocal greeting behaviour of wild vervet monkeys in different ecological and social situations. We used an information theory approach to investigate the functional hypotheses of vervet monkeys' vocal greeting signals. We found little support for the main functions proposed in the literature, that is, to signal submission, to avoid conflicts, to test social bonds or to coordinate group activity. Results supported the use of grunts to signal benign intent, and we found that grunts were mostly given to closely bonded males near rivers, suggesting that vervet monkeys use vocal greeting signals to recruit individuals in situations of danger to reduce predation risk.

Living in groups involves both costs and benefits. Benefits can be derived from decreased predation risk, for example due to safety in numbers, predator confusion, decreased vigilance costs or cooperative defence (Krause & Ruxton, 2002). Costs can emerge due to competition and increased time demands for social activities, such as the maintenance of social bonds, to the detriment of other essential activities, such as foraging (Lehmann, Korstjens, & Dunbar, 2007; Majolo, de Bortoli Vizioli, & Schino, 2008). Animals thus have to balance the costs incurred from living in groups and the benefits from their interactions with other group members.

One way by which group-living animals can manage their social relations is by performing ritualized behaviours during close encounters, which have been termed greetings (Brown, 1967; Hall, 1962). Greeting signals appear in various modalities, which include vocalizations (e.g. red-bellied woodpeckers, *Centurus carolinus*: Kilham, 1961; bottlenose dolphins, *Tursiops truncatus*: Quick & Janik, 2012; African wild dogs, *Lycaon pictus*: Estes & Goddard, 1967; African elephants, *Loxodonta africana*: Poole, 2011; mantled howlers, *Alouatta palliata*: Dias, Rodriguez Luna, & Canales Espinosa, 2008; chimpanzees, *Pan troglodytes*: Laporte & Zuberbühler, 2010), but also facial expressions, affiliative gestures and a variety of postures (e.g. lesser black-backed gulls, *Larus fuscus*: Brown, 1967; wild boars and warthogs, *Sus scrofa* and *Phacochoerus aethiopicus*: Frädrich, 1974; spotted hyaenas, *Crocuta crocuta*: East, Hofer, & Wickler, 1993; baboons, *Papio* sp.: Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003; spider monkeys, *Ateles geoffroyi*: Aureli & Schaffner, 2007).

Although greeting signals are relatively widespread in group-living animals, their exact function has remained mostly unclear. The current literature suggests five main functions to explain why animals signal to each other during close-range encounters. First, the 'benign intent hypothesis' posits that individuals use greeting signals in socially tense situations (e.g. around food resources or when outcomes of interactions are unpredictable) to signal

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willingness to interact in a friendly way (Bauers, 1993; Katsu, Yamada, & Nakamichi, 2014; Silk, 1996, 2000; Silk, Cheney, & Seyfarth, 1996). For instance, wild female baboons use vocal signals to communicate benign intent when approaching mothers to increase the likelihood of affiliative contacts, especially with infants (Silk, Seyfarth, & Cheney, 2016).

Second, the 'conflict management hypothesis' posits that individuals use greeting signals to avoid conflicts and repair their relationships after agonistic interactions (de Waal & Roosmalen, 1979). Reconciliatory grunts, for example, are produced by female baboons to encourage friendly approaches between former opponents (Cheney & Seyfarth, 1997). During fusion events, spider monkeys and mantled howlers also use greeting signals, such as embraces, sniffs, throat rumbles, clucks or a variety of postures, presumably as a strategy to avoid conflicts (Aureli & Schaffner, 2007; Dias et al., 2008).

Third, according to the 'signal submission hypothesis' individuals use greeting signals to acknowledge existing dominance relationships by advertising their inferior social status, which then increases social tolerance from higher-ranking individuals (de Waal, 1986). This has been documented in wolves and dogs, *Canis lupus* sp. (Schenkel, 1967), spotted hyaenas (East et al., 1993) and rhesus macaques, *Macaca mulatta* (de Waal & Luttrell, 1985). Another well-studied example is the pant-grunt of chimpanzees, produced by low-ranking individuals when encountering higher-ranking ones (Laporte & Zuberbühler, 2010).

Fourth, the 'social coordination hypothesis' posits that individuals use greeting signals to increase group cohesion and to coordinate joint activities, which can have fitness benefits in terms of reducing predation risk (e.g. synchronized swimming of long-finned pilot whales, *Globicephala melas*: Senigaglia, de Stephanis, Verborgh, & Lusseau, 2012 or cooperative hunting of African wild dogs: Estes & Goddard, 1967. Similarly, male capuchins, *Cebus apella*, produce 'sirena' screams to increase social coordination with allies when encountering other groups (Lynch Alfaro, 2008) and Hamadryas baboons, *Papio hamadryas*, use a ritualized form of presenting to recruit males to cooperate with them against rivals in getting access to females (Abegglen, 1984). Observations on wild chimpanzees and crested macaques, *Macaca nigra*, showed that individuals produce lip-smacks, a nonvocal but audible behaviour in which the lips moved repeatedly during face-to-face encounters, when approaching other group members to elicit affiliative interactions, such as grooming (Fedurek, Slocombe, Hartel, & Zuberbühler, 2015; Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013).

Fifth, the 'social bond testing hypothesis' posits that individuals use greeting signals to assess the quality of their social relationships. Here, the idea is that greeting behaviour can vary in terms of completeness, reciprocity and symmetry depending on the strength of the interacting individuals' social bond, and thus serves as a proxy to assess their mutual affiliation (Whitham & Maestripieri, 2003). Signals are often intimate or risky, such as kissing, embracing, sniffing or, for males, inspecting and touching genitals (Wang & Milton, 2003), as if males are 'literally placing their future reproductive success in the trust of another male' (Smuts & Watanabe, 1990, p. 169). Generally, these kinds of greetings are often between closely bonded individuals (e.g. spotted hyaenas: Smith et al., 2011; spider monkeys: Schaffner & Aureli, 2005; Tonkean macaques, *Macaca tonkeana*: De Marco, Sanna, Cozzolino, & Thierry, 2014; capuchin monkeys: Matheson, Johnson, & Feuerstein, 1996; chimpanzees: Okamoto, Agetsuma, & Kojima, 2001). Such potentially dangerous signals thus appear to strengthen their existing bonds.

Vervet monkeys, *Chlorocebus pygerythrus*, live in multimale/multifemale groups and various studies on their communication system have generated insights concerning their social cognition. For example, playback experiments of screams have demonstrated that mothers distinguish their own offspring from unrelated juveniles, while bystander females can allocate juveniles to their respective mothers (Cheney & Seyfarth, 1980). Other work has shown that some call types convey relatively specific meanings to recipients, as demonstrated by the monkeys' reactions to playbacks of predator-specific alarm calls (Seyfarth, Cheney, & Marler, 1980 but see Price et al., 2015) and different grunt variants (Cheney & Seyfarth, 1982).

Grunts are an acoustically heterogeneous soft call type, produced in a range of situations, which includes group progressions, as well as intra- and intergroup encounters (Struhsaker, 1967). During intragroup encounters, grunts appear to function as a greeting signal, and it has been proposed that the calls signal submission and inhibit aggressive behaviours from higher-ranking group members (Struhsaker, 1967). Although vervet monkeys have been studied extensively, we are not aware of any systematic research on greeting behaviour. During pilot observations, we noted that adults often produced grunts while approaching males near rivers, where predation risk is high (see Appendix 1). Therefore, we generated a new functional hypothesis, the 'risk reduction hypothesis', which posits that greeting signals are produced in dangerous situations to group members who are most valuable in situations of danger (Krause & Ruxton, 2002). In vervet monkeys, adult males are most vigilant and play the most active role in predation defence (Baldellou & Henzi, 1992), but individuals should also greet closely bonded individuals who are also likely to provide support in risky situations (e.g. macaques: Berghänel, Ostner, Schröder, & Schülke, 2011; Micheletta et al., 2012 or dwarf mongooses, *Helogale parvula*: Kern & Radford, 2016).

The goal of our study was to describe the general patterns of greeting behaviours of wild vervet monkeys and examine the function of vocal signals produced in this context. To this end, we first examined individual, dyadic and ecological factors that triggered grunts during close encounters in an intragroup context. Specifically, we investigated the influence of sex, relative rank difference and strength of social bonds between interacting partners, as well as the influence of visibility (habitat type) and predation risk (i.e. close to rivers, high-risk areas where most natural predator encounters occur in our study site; Appendix 1).

Following this analysis, we used multimodel inference to explore the function of grunts produced during dyadic encounters in male vervet monkeys. We identified five predictor variables to test the six hypotheses outlined before. Two predictors described the social relationship between the interacting individuals, that is, relative rank differences ('signal submission hypothesis') and social bonds strength ('social bond testing hypothesis'). Two further predictors described the ecological situation when signalling occurred. First, being close to rivers may require coordinating movement ('social coordination hypothesis') and support by valuable group members, that is, adult males ('risk reduction hypothesis'), since predation risk is high near rivers (Appendix 1). Another predictor was the presence of contestable food ('conflict management hypothesis') which is likely to increase aggression (Isbell, 1991). A final predictor described whether calls were given by the approaching individual ('benign intent hypothesis'), to signal its willingness for a peaceful interaction.

We used an information theory approach to compare a set of six competing, nonexclusive models, representing the six described functional hypotheses of greeting behaviour in animals (Table 1). This approach allowed us to compare and rank our models in terms of how well they fit the existing data (Burnham & Anderson, 2003; Burnham, Anderson, & Huyvaert, 2011). Information theory is a viable alternative to more traditional falsification-based hypothesis