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Greetings promote cooperation and reinforce social bonds among spotted hyaenas

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Societies characterized by fission–fusion dynamics consist of subgroups that frequently change in size and composition. Although this flexible lifestyle permits individuals to reduce conflicts of interest, it simultaneously imposes a unique set of challenges on group members that are regularly subject to prolonged separation. Theory predicts animals should evolve ritualized and risky displays to quickly update relationships at reunions. Here we investigated the function of nonconciliatory greetings among adult female spotted hyaenas, *Crocuta crocuta*, belonging to a single, large female-dominated social group in Kenya. We tested three hypotheses forwarded to explain the occurrence of these multimodal signals: formal submission, tension reduction and social bonding hypotheses. In contrast to predictions of the formal submission hypothesis, rank distance and relative rank were excluded from our best model predicting greetings among adult females. Moreover, directional consistency of greetings was low (0.65) compared to that of submissive behaviours during dyadic agonistic interactions (0.97). Instead, our data revealed that adult females greeted coalition partners and close associates, including kin, most often per opportunity, and they did so in neutral contexts more frequently than in situations characterized by social tension. Although these findings are in direct contrast to the predictions of the tension reduction and formal submission hypotheses, they strongly support the social bonding hypothesis. Importantly, the immediate act of greeting promoted cooperation among allies during intragroup and intergroup coalition formation. Thus, these risky, multimodal signals permit hyaenas to effectively communicate cooperative affiliations within a continuously shifting social milieu.

Societies characterized by fission–fusion dynamics consist of subgroups of variable size and composition in which group members regularly join (fusion) or separate from (fission) one another (Kummer 1971). This flexible lifestyle characterizes societies of humans and other apes (e.g. chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*: Symington 1990; Rodseth et al. 1991; de Waal 1997; Lehmann & Boesch 2004), some monkeys (e.g. spider monkeys, *Ateles* spp., and tufted capuchins, *Cebus apella nigritus*: Chapman et al. 1995; Alfaro 2007; Asensio et al. 2009), elephants (*Loxodonta* spp.: Wittemyer et al. 2005; Archie et al. 2006b), many cetaceans (e.g. bottlenose dolphins, *Tursiops* spp.: Connor et al. 2001; Lusseau 2003) and bats (see Kerth & Konig 1999; Willis & Brigham 2004; Metheny et al. 2008), as well as most gregarious carnivores (reviewed by Gittleman 1989). This social structure permits individuals to separate temporarily from one another when costs of grouping are high, and to aggregate when costs of grouping are low or benefits of sociality are high (reviewed by Wrangham et al. 1993; Aureli et al. 2008). Although this lifestyle permits individuals to reduce conflicts of interest (Conradt & Roper 2005), it also imposes a unique set of challenges upon group members that often experience long separations from one another (Aureli et al. 2008). Importantly, these individuals must cope with uncertain relationship status after such separations (Barrett et al. 2003).

When relationship status is uncertain, theory predicts that ritualized signals should evolve that quickly communicate the intent of senders to receivers (Maynard Smith & Price 1973; Zahavi 1980; Endler 1993). Consistent with this prediction, many animals use ritualized multimodal signals to communicate their intentions to conspecifics. For example, greetings, or meeting ceremonies, are important nonaggressive displays involving risky and intimate contact. Ritualized greetings can function to reconcile fights (Aureli et al. 2002), signal acknowledgment of dominance status (de Waal & Luttrell 1985; de Waal 1986; Preuschoft 1999), reduce tension among individuals with insecure social relationships (Kutsukake

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et al. 2006; Aureli & Schaffner 2007; Dias et al. 2008), or reinforce social bonds (Smuts & Watanabe 1990; Smuts 2002; Whitham & Maestripieri 2003).

In the present study, we investigated greetings between spotted hyaenas, *Crocuta crocuta*, which are long-lived carnivores that reside in complex societies, called clans, containing up to 90 individuals that together defend a common territory (Kruuk 1972). Clans are fission–fusion societies in which individual members travel, rest and forage in subgroups that change membership roughly every hour (Kruuk 1972; Mills 1990; Smith et al. 2008). Clans are structured by linear dominance hierarchies (Frank 1986) and contain one to several matrilines of adult females and their offspring, as well as multiple adult immigrant males. Virtually all males permanently disperse from their natal clans after puberty, but females are philopatric (Mills 1990; Smale et al. 1997; East & Hofer 2001; Höner et al. 2007).

Spotted hyaenas engage in greetings when two partners stand parallel to one another and face in opposite directions to sniff each other's anogenital region (Kruuk 1972; East et al. 1993; Glickman et al. 1997). The importance of the erect phallus for both sexes makes these greetings particularly intriguing. During greetings, females erect their penile clitoris, and males erect their penis. Although both partners of either sex may erect their phalluses during a greeting, usually one partner erects its phallus before the other partner does (East et al. 1993). Symmetric greetings occur when both members engage in the same set of behaviours, such as both lifting their leg during mutual investigation of the genitalia (East et al. 1993). In asymmetric greetings, one partner shows the behaviour, but the other partner does not.

Although conciliatory greetings are useful in preventing escalated aggression between former opponents (Hofer & East 2000; Wahaj et al. 2001), the vast majority of greetings occur in contexts unrelated to aggression. Specifically, only 8–9% of hyaena greetings serve as a form of reconciliation (East et al. 1993), suggesting that greetings also serve other important functions. Two earlier studies found that hyaenas in the Serengeti National Park, Tanzania typically initiate greetings with social partners dominant to, or older than, themselves (Kruuk 1972; East et al. 1993). Whereas both studies agreed that low-ranking hyaenas were most likely to initiate greetings, the interpretation of these results differed. Kruuk (1972) hypothesized that greetings might serve the 'function of keeping two individuals close together…[and] facilitate the reestablishment of social bonds' (page 229). In contrast, East et al. (1993) concluded that 'greetings are a ritualized, active form of submission' (page 364), and referred to the first phallus erected during a greeting as a 'flag of submission'. Whereas greetings might signal submission, East et al. (1993) failed to rule out alternative hypotheses that appeared in the literature after 1993 and failed to use contemporary multivariate statistics to account for correlations among potential predictor variables.

Our main goal here was to investigate the function of nonconciliatory greetings among adult female spotted hyaenas. Nonconciliatory greetings are defined as greetings between partners that had not previously fought in the 10 min directly before greeting each other (Hofer & East 2000; Wahaj et al. 2001). We focused in particular on adult female hyaenas because they greet each other at the highest frequencies relative to other age–sex classes (East et al. 1993). Moreover, rank relationships are extremely stable among adult females (Engh et al. 2000), whereas those of juveniles are often not yet firmly established (Holekamp & Smale 1993; Smale et al. 1993). Furthermore, whereas adult females maintain long-term social bonds (Holekamp et al. 1997a), associations among adult males are often weak (Smith et al. 2007) or short-lived (Van Horn et al. 2003). Adult female hyaenas make decisions to join temporary subgroups containing their kin (Holekamp et al. 1997a). Among nonkin, adult females associate most often with females ranked directly above them in the dominance hierarchy and, by doing so, gain enhanced tolerance from dominants (Smith et al. 2007).

Here, we take advantage of modern conceptual frameworks and quantitative methods to extend earlier work, and to resolve discrepancies in the interpretation of early studies. Adopting the methods of East et al. (1993), we first replicate their work by documenting the occurrence of greetings among members of a single, large social group of spotted hyaenas in the Masai Mara National Reserve, Kenya. Next, we confirm that reconciliation only accounts for a small fraction of greetings in our population and, for the first time, reveal how conciliatory and nonconciliatory greetings differ. Finally, we test the formal submission hypothesis (hereafter called the 'submission hypothesis'), tension reduction hypothesis and social bonding hypothesis, each of which proposes a potential function of nonconciliatory greeting behaviour among adult female hyaenas.

Predictions Based on the Submission Hypothesis

To minimize the costs of competition, dominance hierarchies structure societies in which individuals use signals to communicate their knowledge of power asymmetries among group members (Drews 1993; Preuschoft 1999). Because spotted hyaenas use multiple status indicators to reliably signal submission in a variety of contexts (Kruuk 1972; Frank 1986), the initiation of greetings might represent another formalized status signal (East et al. 1993). The submission hypothesis predicts that low-ranking females should initiate greetings more often than high-ranking females, as found by East et al. (1993). Importantly, it further predicts that initiation of greetings should be strictly unidirectional within dyads across ecological contexts for species in which rank relationships are stable among contexts (de Waal & Luttrell 1985). Directional consistency (DC) is a reliable measure of the presence and direction of a hierarchical ordering of behavioural interactions for species in which some group members interact at relatively low rates (Isbell & Pruetz 1998; Isbell & Young 2002; Archie et al. 2006a). Thus, the degree of DC and transitive properties of greeting initiation should match those found in dominance relationships based on fight outcomes. Moreover, because animals closest in rank possess the greatest need to clarify dominance relationships (de Waal 1991), females should greet most often and engage in the most asymmetric greetings (in which only one greeting partner lifts its leg) with females holding ranks similar to their own.

Predictions Based on the Tension Reduction Hypothesis

The tension reduction hypothesis posits that natural selection should favour the evolution of ritualized signals indicating peaceful intent, and thus preventing potentially costly physiological responses in contexts in which tensions might otherwise be elevated, as during resource competition or reunions between group members with insecure social relationships (Colmenares et al. 2000; Hohmann & Fruth 2000; Kutsukake et al. 2006; Aureli & Schaffner 2007; Dias et al. 2008). Indeed, social tensions elevate glucocorticoid concentrations in spotted hyaenas (Van Meter et al. 2009). Thus, if greetings evolved to reduce social tensions, then adult females should greet most often and engage in the most symmetric greetings (both partners lift their legs) with the females with whom their social relationships are least secure, such as nonkin or hyaenas with whom they rarely form coalitions. Additionally, feeding competition is intense in this species; hyaenas feed at kills that are energetically rich and highly ephemeral