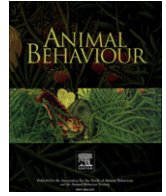




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Greetings promote cooperation and reinforce social bonds among spotted hyaenas

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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.

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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 nigrilus*: 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 & König 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 (Conrad & 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 & Maestriperi 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 matrilineal lines 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 non-conciliatory greetings among adult female spotted hyaenas. Non-conciliatory 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 & Pruett 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 (Kruuk

1972; Frank 1986; Mills 1990; Smith et al. 2008). Feeding competition is reduced seasonally when migratory ungulates are present with resident herds (Holekamp et al. 1996; Höner et al. 2005; Smith et al. 2008). Thus, if greetings reduce tensions over food, then females should greet most often per opportunity when kills are immediately present, especially during those months when prey are locally scarce. Finally, if greetings reduce tensions or substitute for aggression in tense situations, then greeting partners should direct less aggression towards one another in the minutes directly after reunions than dyads that fail to greet at reunions.

Predictions Based on the Social Bonding Hypothesis

The social bonding hypothesis posits that group-living animals should use risky interactions to routinely reinforce affiliative relationships (Zahavi 1977b; Smuts 2002). Specifically, senders and receivers should theoretically use costly signals to exchange honest information about social bonds (Zahavi 1977a; Gintis et al. 2001), defined here as close and enduring affiliative relationships (Silk et al. 2003, 2006). Hyaena greetings may result in severe genital wounding (Kruuk 1972) and may therefore represent potentially costly signals that function to reinforce, and thus maintain, existing social bonds among adult female hyaenas. If greetings reflect affiliative ties, then hyaenas should greet their preferred social partners most often, and these greetings should be the most symmetric. Furthermore, if greetings reinforce bonds, then they should occur most often in contexts in which tensions are low between greeting partners (Smuts & Watanabe 1990), as in the absence of direct feeding competition. Moreover, the social bonding hypothesis predicts that the immediate act of greeting should facilitate cooperation among greeting partners (Smuts 2002). Hyaenas are highly cooperative (Holekamp et al. 2007; Drea & Carter 2009), so if this hypothesis is correct, then greetings might promote coalition formation among adult female hyaenas during group hunting, territory defence or intragroup disputes.

METHODS

Study Subjects

During June 1988–December 2004, we monitored spotted hyaenas from a large clan that defended a stable group territory in the Masai Mara National Reserve (Boydston et al. 2001). In total, we recorded 15 852 greetings involving 414 individual hyaenas of various age and sex categories during 15 288 observation hours. Thus, the specific numbers of greetings and subjects used for each analysis represent a subset of these data, reflecting each particular goal of the study.

We identified each subject individually based upon its unique spots, and sexed hyaenas based on the morphology of the erect phallus (Frank et al. 1990). Mother–offspring relationships were established based on nursing associations (Holekamp et al. 1993). Paternal kinship was determined based on genotyping (Engh et al. 2002; Van Horn et al. 2004). We estimated (to ± 7 days) the ages of cubs upon first observing them above ground at dens (Holekamp et al. 1996). We considered cubs to be den-independent when they were found more than 200 m from the den on at least four consecutive occasions; this occurred when cubs were 8–9 months old (Boydston et al. 2005). Den-dwelling cubs and den-independent subadults were considered juveniles because hyaenas at both life history stages are sexually immature. We classified females as adults at 36 months of age, or at their first known date of conception, whichever occurred first. We considered all immigrant males to be adults (Van Horn et al. 2003).

Here we determined the social rank of each individual based on the occurrence of submissive behaviour during dyadic agonistic interactions; adult females were dominant to adult males (Holekamp & Smale 1993; Smale et al. 1993). We ranked adult males and females in separate hierarchies, with the highest rank in each being one. Following Smith et al. (2007), rank distance was indicated as a positive integer, calculated as the absolute value of the difference in intrasexual ranks between the members of each dyad.

Behavioural Data Collection

Using our field vehicles as mobile blinds, we observed hyaenas daily around dawn and dusk, between 0530 and 0900 hours and between 1700 and 2000 hours. We initiated an observation session each time we encountered one or more hyaenas separated from other clan members by at least 200 m; hyaenas in different sessions were typically separated by at least 1 km (Smith et al. 2008). Upon arrival at each session, and during subsequent scans (performed every 15–20 min), we recorded the identity and activity of every hyaena in that focal subgroup. We recorded, as critical incidents (Altmann 1974), all occurrences of agonistic interactions, greetings and hunting. Aggressive behaviours included head waves, lunges, chasing, displacements, standing over, biting, pushing and aggressive postures. Following Wahaj et al. (2001), we considered a greeting to serve a conciliatory function between former opponents if it occurred within 10 min immediately after a fight between those opponents. Based on this definition, we categorized each greeting as either conciliatory or nonconciliatory. We also recorded all well-recognized submissive signals (e.g. head-bobbing, submissive posture, carpal crawling and open-mouth appeasement), including unsolicited appeasements, and whenever possible, all affiliative behaviours (e.g. nuzzling, rubbing against, presenting, sniffing or friendly approaches) performed by hyaenas during greetings.

Initiation, Duration and Rates of Greetings

Kruuk (1972) identified the initiator of each greeting based on the role of each partner in the leg-lifting part of the display. East et al. (1993) extended this definition to identify a hyaena as initiating a greeting if it lifted its leg first, approached first, or erected its phallus first. East et al. (1993) generally found equivalent results for all three measures, and, in some cases, rank-related asymmetries in leg lifting were even more pronounced than those based on phallic erections. To confirm that Kruuk's (1972) leg-lifting measure provides equivalent information to that conveyed by the erect phallus in our study population, we recorded the characteristics of erections for a subset of greetings ($N = 855$ greetings). As in East et al. (1993), we found high concordance between leg lifting and phallic erections. When a focal hyaena ($N = 135$) initiated a greeting by lifting its leg first, it was also significantly more likely to erect its phallus first ($88 \pm 1.7\%$, Wilcoxon signed-ranks test: $Z = 9.518$, $P < 0.00001$). Thus, in the current study, we used the leg-lifting display to identify the initiators of greetings. This measure was the most conspicuous to human observers and was consistently used in both earlier studies (Kruuk 1972; East et al. 1993). Here we defined symmetric and asymmetric greetings as those greetings during which both members, or only one member, respectively, engaged in leg lifting.

We timed a subset of greetings ($N = 283$) using a stopwatch to understand whether sex, age or rank influenced the duration of conciliatory and nonconciliatory greetings. Each greeting started when the initiator lifted its hindleg and ended when the terminating hyaena put its hindleg back down on the ground (East et al.

1993). Most greetings were timed during 1997, but additional greetings were recorded in 2005 to supplement the original data set. Because we found no year effects, we pooled all data together to evaluate the extent to which our predictor variables explained the duration of greetings. From these data, we calculated the duration of each greeting for which a clear initiator, start time and end time could be discerned.

Following Van Meter (2009), we calculated the hourly rate of greetings for each hyaena while controlling for variation among sessions with respect to opportunities for each hyaena to greet other clan members. Thus, we calculated an hourly rate of greeting for each individual present in a given observation session with at least one potential partner as follows: (number of greeting interactions involving that individual/number of potential greeting partners present/number of hours in that observation session). We then averaged the rate per session for each individual throughout the entire period during which that animal belonged to a particular age class.

Testing the Submission Hypothesis

We first confirmed that using the nonparametric approaches employed by earlier workers produced equivalent results to those found in Serengeti hyaenas with respect to age and rank relationships; that is, we confirmed that juveniles and lower-ranking members of hyaena dyads in our study clan initiate greetings most often, as do hyaenas in the Serengeti (Kruuk 1972; East et al. 1993). Then we tested whether the hierarchical orders of winning fights and receiving greetings were equivalent (de Vries et al. 1993).

Directional consistency (DC)

We calculated the DC index (van Hooff & Wensing 1987) for dominance and greeting matrices constructed for the same adult females, all of which interacted with each other as adults, both at and away from kills. DC is the number of times that a behaviour was performed in the direction of higher frequency within each dyad (H) minus the number of times it occurred in the direction of lower frequency within each dyad (L), divided by the number of times it was performed by all individuals: $DC = (H - L)/(H + L)$. DC ranges from zero, for completely bidirectional exchanges, to one for completely unidirectional exchanges (van Hooff & Wensing 1987). Because this measure is a proportion, it allows for meaningful comparisons between matrices containing unequal numbers of interactions. It also provides information comparable to that included in indices used by previous authors (e.g. Rowell 1966; Noë et al. 1980).

Linearity of dominance and nonconciliatory greeting matrices

We evaluated the linearity and transitive properties of both dominance and greeting matrices. First, linearity measures how consistently each individual outranks subordinates ranked lower than themselves in the hierarchy (Whitehead 2008). If such relationships are transitive, then when A outranks B, and B outranks C, A must also outrank C. We used an improved version of Landau's (1951) h index of linearity, called h' (de Vries 1995), to correct for unknown relationships. This corrected measure allowed for comparisons between matrices in which relationships within some dyads were unknown. This measure ranges from zero, for a completely nonlinear system, to one for a completely linear system (de Vries 1995). Second, we calculated K to assess the significance of linearity based on the transitivity of triads within each matrix (Appleby 1983).

Testing the Tension Reduction and Social Bonding Hypotheses

Greetings may occur either at subgroup fusion when individuals reunite after being separated, or among hyaenas that have been

present together in a subgroup for several hours (Kruuk 1972), so we first quantified the distribution of greetings over time after reunions. Because the vast majority of greetings occurred within the first 10 min after subgroup fusion events (see Results), we constructed statistical models to assess the effects of social and ecological variables on the propensity for adult females to greet, given the opportunity to do so, within 10 min after fusion. Models based on greetings occurring within 5 min after fusion produced equivalent results, but for the sake of brevity, we report only the former results. Focal pairs of hyaenas greeted less often at fusions occurring in large subgroups, so we entered subgroup size at fusion (number of possible greeting partners available to each arriving female) as a covariate in our model to account for greeting queues forming in large subgroups.

Kin have the most secure social bonds (Holekamp et al. 1997a; Wahaj et al. 2001); therefore, we modelled the effects of kinship on greeting interactions by entering two measures of relatedness directly into our models as continuous predictor variables. First, following Wahaj et al. (2001), we assigned coefficients of relatedness based only on maternal kinship. Second, following Smith et al. (2010), we assigned coefficients of relatedness to female pairs based on maternal pedigrees and genetic assignment of paternal relationships.

Patterns of association represent how often pairs of hyaenas spend time with each other, thus, reflecting the strength of social bonds among hyaenas (Holekamp et al. 1997a; Wahaj et al. 2004; Smith et al. 2007). Here we calculated the twice-weight association index (AI) of Cairns & Schwager (1987) for each pair of females, hyaenas A and B, during which they were concurrently present in the clan as adults. We calculated $AI_{A,B}$ as follows: $(A + B_{together}) / ((A_{without B}) + (B_{without A}) + (A + B_{together}))$, where $(A + B_{together})$ is the number of sessions in which A and B present together, $(A_{without B})$ is the number of sessions in which A was present without B, and $(B_{without A})$ is the number of sessions in which B was present without A.

To test whether greetings promote cooperation, we recorded the tendency for greeting dyads of females to subsequently: (1) form at least one aggressive coalition directed towards another clanmate, (2) join forces to attack alien hyaenas during intergroup conflicts at territory boundaries, called clan wars, (3) cooperatively attack lions, or (4) chase a selected prey animal for at least 50 m, regardless of the outcome of the hunting attempt (Kruuk 1972; Zabel et al. 1992; Holekamp et al. 1997b; Smith et al. 2010). Within a session, each pair could potentially cooperate in up to four ways; as intragroup coalition partners, as participants in a clan war, as coalition partners directing joint attacks towards lions, or as hunting partners. To test whether greetings protect hyaenas from fighting, we examined whether pairs of hyaenas that had greeted, but that had not previously fought before greeting, were less likely to fight after greeting than were hyaenas that failed to greet after fusion.

Although data on greeting symmetry were available throughout our longitudinal study (1988–2004), we limited our statistical models explaining symmetry to those greetings observed from 1988 to 2000 to ensure that social ranks were stable; our study clan permanently split into two clans in 2001 (J. E. Smith, C. C. Strelhoff & K. E. Holekamp, unpublished data). Statistical models explaining the tendency to greet at fusion were based on all fusion events ($N = 4895$) involving pairs of adult females from 1996 to 2000.

Statistical Analyses

We implemented all matrix analyses in MatMan 1.0 (Noldus Information Technology, Wageningen, The Netherlands). For measures of linearity, we used a two-step permutation test with 10 000 randomizations (de Vries 1995). Matrix analyses were based

on one-tailed probabilities because these hypotheses make clear, directional predictions (Hemelrijk 1990; de Vries 1993). All other tests were based on two-tailed probabilities. Differences were considered significant at alpha less than 0.05. We applied the sequential Bonferroni adjustment to correct for multiple testing, and report all *P* values in their corrected form (Rice 1989). For binomial trials, we report means ± 1 SE and sample proportions ± 1 SD (Agresti & Coull 1998).

We built generalized linear mixed models (GLMM) using lme4 (Bates & Maechler 2010) in R v.2.6.2 (The R Foundation for Statistical Computing, Vienna, Austria). We modelled the duration data assuming a Gaussian family because these data were normally distributed. We implemented the binomial family to model female decisions to (1) greet with potential adult female partners within 10 min after fusion events and (2) engage in symmetric gestures when greeting. We entered the identity of each hyaena as a random effect to avoid potential pseudoreplication, and tested the significance of its inclusion in each model using likelihood ratio tests (Pinheiro & Bates 2000). For each data set, we sequentially entered and dropped all potential explanatory terms, including all two-way interactions, and deemed the candidate model with the smallest Akaike's information criterion (AIC) to be the best (Burnham & Anderson 2002). No strongly intercorrelated variables were retained in the final models ($r^2 \leq 0.15$). We obtained statistics for terms removed from our best model by adding each term individually to the minimal model.

We used Statistica v.6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.) to analyse data failing to meet assumptions of normality and/or homoscedasticity of variances. We compared means for two, or more than two, independent groups using Mann–Whitney *U* and Kruskal–Wallis tests, respectively. We compared means from dependent groups using Wilcoxon signed-ranks tests and tested correlations using Spearman's rank correlation.

RESULTS

Distribution and Patterning of Conciliatory and Nonconciliatory Greetings

Only 0.3% ($N = 52$) of the 15 852 greetings observed in our study involved more than two partners, such that the mean number of hyaenas involved in each greeting was 2.0 ± 0.0 hyaenas (range 2–7 partners). Greetings were generally spontaneous, and rarely occurred in response to overt aggression. In fact, only 8.9% of greetings were conciliatory (occurring between former opponents within 10 min immediately after a fight) and the rest (91.1%) were nonconciliatory. Initiating hyaenas ($N = 387$) were almost twice as likely to engage in one or more affiliative behaviours ($35.9 \pm 2.0\%$ of greetings) than to display submissive signals when soliciting greetings ($18.2 \pm 1.0\%$ of greetings; Wilcoxon signed-ranks test: $Z = 11.00$, $P < 0.00001$). Similarly, recipients ($N = 395$) of invitations to greet were twice as likely to engage in affiliative behaviours ($21.9 \pm 1.1\%$ of greetings) than to display submissive signals ($10.6 \pm 0.9\%$ of greetings; Wilcoxon signed-ranks test: $Z = 10.13$, $P < 0.00001$). Hyaenas never attempted to greet heterospecifics, and natal hyaenas only greeted clan members. On only seven occasions did immigrant males greet males from neighbouring clans; it is possible that the males involved in these immigrant dyads previously belonged to the same clan.

Duration of Conciliatory and Nonconciliatory Greetings

For the subset of greetings timed here, we found that greetings were similar in duration to those measured by East et al. (1993), lasting, on average, 20.9 ± 0.7 s (range 1–95 s, $N = 283$ greetings). We first used

Table 1

Independent variables predicting the duration of greetings in which focal hyaenas participated

Coefficients	Estimate \pm SE	Z	P
(Intercept)	18.517 \pm 0.807	22.947	<0.000001
Age (adult)	2.584 \pm 1.122	2.303	0.022
Sex (female)	1.720 \pm 1.144	1.503	0.134

Effects of age and sex were additive (interaction: -0.769 ± 2.344 , $Z = -0.328$, $P = 0.743$). Although the main effect of sex was not statistically significant, its inclusion improved the overall fit of our best model. Neither the main effect of social rank (-0.005 ± 0.032 , $Z = -0.141$, $P = 0.888$), nor its interaction with age (0.052 ± 0.063 , $Z = 0.828$, $P = 0.409$) or sex (-0.056 ± 0.064 , $Z = -0.877$, $P = 0.382$) improved the fit of the model. Including the random effect of hyaena identity improved the best model (likelihood ratio test: $\chi^2_1 = 4.3$, $P = 0.038$), which was based on 283 greetings involving 32 juvenile males, 18 adult males, 20 juvenile females and 31 adult females.

the methods of East et al. (1993) to confirm that intrasexual greetings were longer between adult females (24.6 ± 1.1 s) than between adult males (18.7 ± 2.0 s, $N_F = 27$, $N_M = 17$; Mann–Whitney *U* test: $Z = 2.194$, $P = 0.028$). We then extended this result by modelling factors that might influence the duration of greetings within dyads containing different age–sex classes. In general, adult females ($N = 31$, 22.8 ± 1.0 s) tended to participate in greetings that lasted longer than those involving adult males ($N = 18$, 19.4 ± 2.0 s; Table 1) or juveniles ($N_M = 32$, 17.4 ± 1.1 s, $N_F = 20$, 21.0 ± 1.1 s).

The duration of the 283 timed greetings was also influenced by the relationships between the hyaenas involved. Intriguingly, on average, conciliatory greetings lasted roughly 50% longer (30.7 ± 4.8 s, $N = 19$) than those between partners that had not fought during the minutes directly before greeting (20.2 ± 0.7 s, $N = 264$; Table 2). Greetings between adults (24.7 ± 1.4 s, $N = 89$) also lasted longer than those in which one or more participants were juveniles (19.2 ± 1.4 s, $N = 194$; age: Table 2). Furthermore, sex of the hyaena initiating the greeting was retained in our best model, suggesting that greetings initiated by females (23.4 ± 1.1 s, $N = 141$ greetings) generally lasted longer than those initiated by males (18.4 ± 0.9 s, $N = 142$ greetings; Table 2). Finally, greetings initiated by dominants (22.4 ± 1.4 s, $N = 98$) lasted longer than those initiated by subordinates (20.1 ± 0.8 s, $N = 185$; initiator outranks recipient: Table 2).

Hourly Rates of Greetings Vary with Life History Stage and Context

We extend earlier results of East et al. (1993), who reported only on the frequencies of greetings (but not hourly rates) among

Table 2

Independent variables predicting greeting duration in hyaenas based on the relationships between initiators and recipients of greetings

Coefficients	Estimate \pm SE	Z	P
(Intercept)	16.706 \pm 1.100	15.193	<0.0000001
Conciliatory greetings	10.254 \pm 2.667	3.844	0.0001
Age composition (both adults)	3.793 \pm 1.589	2.388	0.018
Sex of initiator (female)	2.820 \pm 1.478	1.908	0.058
Initiator outranks recipient	2.770 \pm 1.412	1.962	0.051

All factors listed above were retained in our best model because they improved its overall fit, but the inclusion of the following additional factors as predictors of the duration of greetings failed to further improve the fit of our best model: kinship (0.876 ± 1.4980 ; $Z = 0.585$, $P = 0.559$), rank distance (-0.045 ± 0.065 ; $Z = -0.697$, $P = 0.487$), absolute rank of initiator (0.026 ± 0.047 ; $Z = 0.546$, $P = 0.586$) and absolute rank of recipient (-0.007 ± 0.047 ; $Z = -0.159$, $P = 0.874$). Including the random effect of hyaena identity improved the model (likelihood ratio test: $\chi^2_1 = 15.1$, $P = 0.0001$), which was based on 283 greetings involving 32 juvenile males, 18 adult males, 20 juvenile females and 31 adult females. Age composition of pairs influenced duration; greetings between adults lasted longer than greetings involving one or more juveniles.

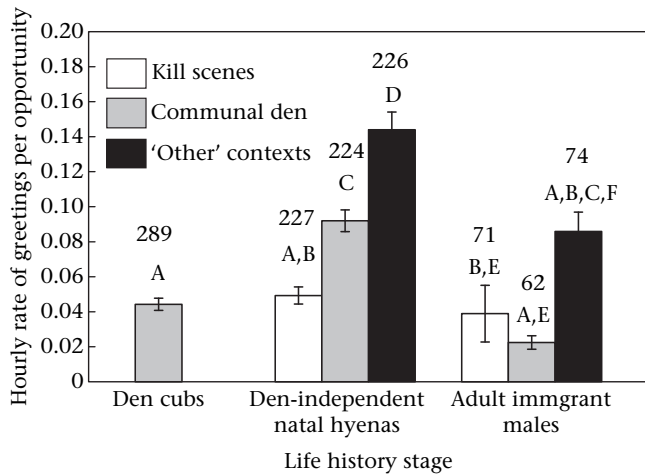


Figure 1. Mean \pm SE hourly rates at which hyaenas in each life history stage participated in greeting ceremonies at kills and dens, and in 'other' contexts (away from kills and dens). Because we detected no sex differences in the rates at which greetings occurred among den cubs or den-independent natal animals, we pooled the values for males and females within each life history stage. Sample sizes shown above each bar represent numbers of individuals. Letters above bars indicate statistically significant differences after correcting for multiple testing at $P < 0.05$.

different age and sex categories in a single context (e.g. observed exclusively at the communal den). Here, by contrast, for the first time we report the hourly rates at which various classes of hyaenas participated in greetings in multiple contexts: at dens, at kills, and at locations (called 'other' contexts) away from both kills and dens. We combined subadults and adult females into a single category, called den-independent hyaenas, because these natal hyaenas participated in greetings at indistinguishable rates within each context (see Appendix). Den cubs were only observed at dens, but we compared rates at which den-independent natal hyaenas ($N = 232$) and immigrant males ($N = 76$) greeted in all three contexts. Overall, the hourly rates at which hyaenas participated in greetings with clan members varied significantly among life history stages and among contexts (Kruskal–Wallis test: $F_{6,1299} = 234.3$, $P < 0.0001$; Fig. 1, for details see Appendix).

Initiation of Greetings by Juveniles and Subordinates

Adopting the methods of East et al. (1993), we analysed patterns of initiation for all greetings such that our initial analysis included both conciliatory and nonconciliatory greetings. As found by East et al. (1993), the younger or socially subordinate of the two partners typically solicited greetings by lifting its leg first. In general, the extent to which juveniles initiated greetings with adults depended on the sexes of the partners involved (Kruskal–Wallis ANOVA: $H_{3,610} = 10.873$, $P = 0.0124$; Fig. 2). When we used the same methods as those of East et al. (1993), we observed the same patterns they did (for details see Appendix).

Testing Hypotheses Explaining Nonconciliatory Greetings Among Adult Females

Linearity and directional consistency among adult females

Although the results reported thus far are consistent with those obtained by East et al. (1993), if nonconciliatory greetings function as formal status indicators, they should exhibit a degree of linearity and directional consistency similar to that produced by fight outcomes. To test the submission hypothesis, we focused on 8 years of pairwise interactions among a subset of adult females ($N = 19$),

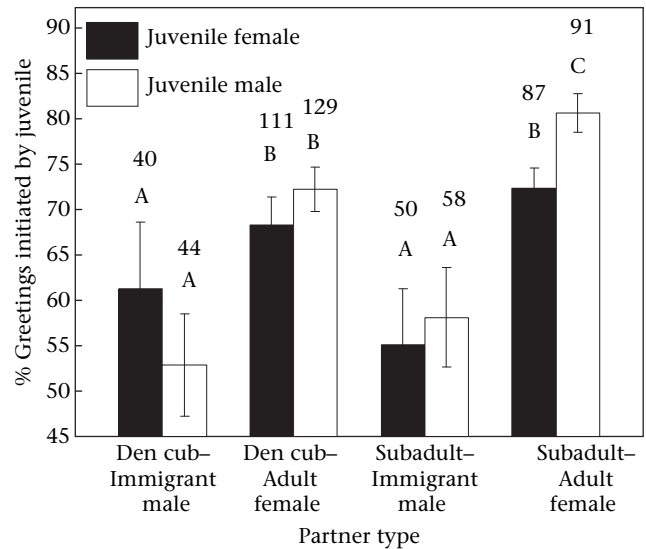


Figure 2. Percentage of greetings with adults that were initiated by juveniles. Den cubs were juveniles still residing at the den, whereas subadults were juveniles that were independent of the den. Sample sizes shown above each bar represent numbers of individuals involved in greetings with partners in each adult category. Letters above bars indicate statistically significant differences after correcting for multiple testing.

all of which interacted as adults, both at kills and away from kills. A dominance matrix (Fig. 3a) containing these 19 females was generated based on outcomes of dyadic fights; the 'winner' was the hyaena being appeased and the 'loser' displayed appeasement when the fight ended (Engh et al. 2005). A nonconciliatory greeting matrix (Fig. 3b) involving the same females was based on interactions in which the 'initiator' lifted her leg first to solicit greeting from a 'recipient'.

After correcting for the number of interactions observed for each dyad ($TauK_r = 0.329$), a partial row-wise matrix correlation revealed a weak, but significant, tendency for losers of fights to also be the member of each dyad responsible for initiating nonconciliatory greetings ($TauK_r = 0.186$, $P < 0.05$; Fig. 3). Nevertheless, in contrast to the results predicted by the submission hypothesis, we found multiple striking discrepancies between dominance and greeting matrices. First, only 15.8% of the rankings generated by fight outcomes and by the initiation of greetings were in agreement. Second, the directional consistency of fight outcomes was high overall and nearly perfectly unidirectional, indicating an extreme imbalance in competitive ability within dyads of adult females ($DC = 0.97$). This value remained virtually the same when calculated for these 19 adult females at food ($DC = 0.98$) and away from food ($DC = 0.97$). In stark contrast, the directional consistency of greeting interactions was relatively low overall ($DC = 0.65$) and varied among contexts. Although greetings were generally rare at kills, when they did occur, the DC (0.83) at kills was greater than the DC (0.66) away from kills. Thus, contrary to the predictions of the submission hypothesis, the initiation of greetings was not unidirectional, nor was the directional nature of the initiation of greetings 'context-free'.

We confirmed that the observed difference between DCs based on fight outcomes and greeting initiations was statistically different from zero by bootstrapping each matrix 10 000 times and calculating 95% confidence intervals (CI) using two methods. First, bootstrapping observed events yielded differences in DCs that were significantly greater than zero (95% CI = 0.19–0.33; median = 0.26). Second, we added a count of 1 event to each cell of the two original matrices, which permitted us to resample all possible pairs within each matrix despite incomplete data on all

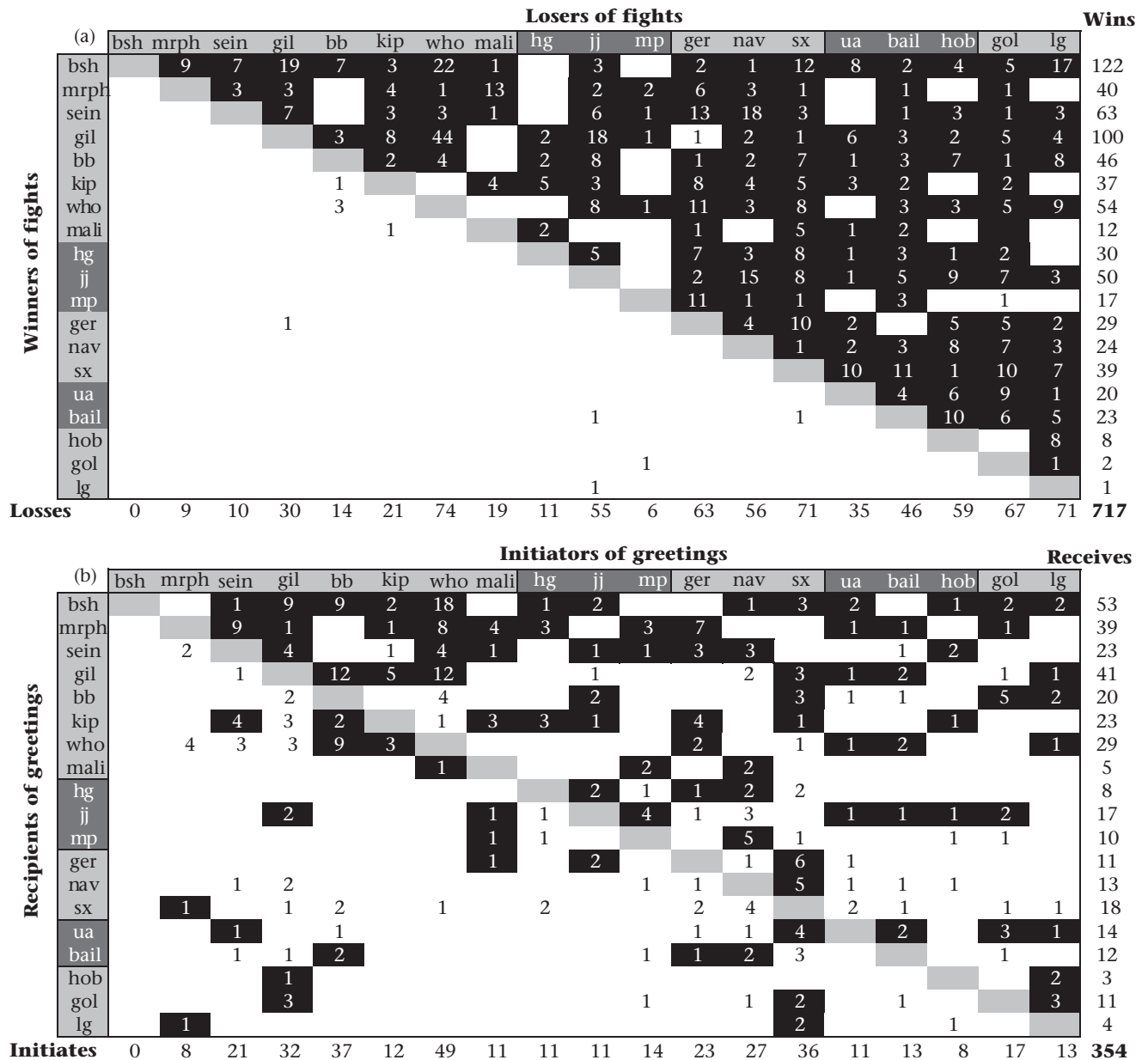


Figure 3. (a) Dominance matrix based on the outcomes of 717 dyadic fights, each of which had a clear winner and loser (see text). Each row of the matrix represents a different adult female ($N = 19$), all of which were present together as adults both at food and away from food. At the intersection of each row (the winner) and column (the loser), a cell shows the number of fights won against the loser. We listed individuals based on their rank order, with the alpha female (bsh) represented in the top row and the leftmost column of the matrix. Similarly shaded adjacent cells within the first row and the leftmost column represent adult females belonging to the same matriline. For example, the alpha matriline contains bsh, mrph, sein, gil, bb, kip, who and mali. A total of five matriline members are represented within the matrix. Dyadic relationships were either unidirectional (71.9%, $N = 123$), bidirectional (4.1%, $N = 7$), or unknown (24.0%, $N = 41$). Black squares indicate that one adult female member of the dyad won the majority of fights within that dyad. White squares indicate dyads for which an equal number of agonistic interactions or no agonistic interactions were observed. (b) Greeting interaction matrix based on 354 greetings, each of which had a clear initiator and recipient (see text). Because the individuals included here were the same as in (a), and because the act of initiating greetings failed to produce a significantly nonrandom ordering of relationships, we ranked females based on the dominance rank order established in (a). At the intersection of each row (the recipient of greetings) and column (the solicitor of greetings), a cell shows the number of greetings received by a particular individual from the initiating hyaena. Dyadic relationships were either unidirectional (39.7%, $N = 68$), bidirectional (21.1%, $N = 36$), or unknown (39.2%, $N = 67$). Black squares indicate that one member of the dyad preferentially received greetings more often than it initiated greetings with the other adult female within that dyad. White squares indicate dyads for which an equal number of greetings or no initiations were observed.

pairwise interactions. As before, bootstrapped differences between DCs did not include zero (95% CI = 0.05–0.22; median = 0.14).

We also found another striking discrepancy between the two matrices. Fight outcomes produced a rigid and significantly transitive linear dominance hierarchy (improved linearity test: $h' = 0.59$, $P = 0.0001$; Fig. 3a). This structure remained statistically significant when based on fights occurring only over food ($h' = 0.35$, $P = 0.014$) or only in nonfood contexts ($h' = 0.47$,

$P = 0.0001$). In contrast, greeting initiation failed to produce a linear rank order ($P = 0.136$; Fig. 3b), with a linearity index ($h' = 0.26$) that was less than half of that produced by fight outcomes. Moreover, greeting interactions failed to produce a linear structure within a single context (food: $h' = 0.18$, $P = 0.967$; nonfood: $h' = 0.23$, $P = 0.397$). Kendall's coefficient of linearity further confirmed these results; fight outcomes (overall: $K = 0.55$, $\chi^2_{25,8} = 87.2$; food: $K = 0.27$, $\chi^2_{25,8} = 44.5$; nonfood: $K = 0.42$,

$\chi^2_{25.8} = 67.4$, $P \leq 0.022$ in all cases), but not greeting interactions (overall: $K = 0.20$, $\chi^2_{25.8} = 34.1$; food: $K = 0.08$, $\chi^2_{25.8} = 14.9$; nonfood: $K = 0.16$, $\chi^2_{25.8} = 27.6$, $P \geq 0.201$ in all cases), produced significant, transitive rank relationships. Whereas all dyads in which one member won the majority of fights (Fig. 3a, black squares) were above the diagonal in the dominance matrix, the greeting matrix contained multiple dyads for which the member of the dyad that received the most greetings (Fig. 3b, black squares) was the female situated below the diagonal. Overall, the majority of these data failed to support the submission hypothesis.

Most greetings occur directly after fusion events

Timing of conciliatory ($N = 1315$) and nonconciliatory ($N = 11759$) greetings relative to a preceding fusion event was known for greetings involving 449 different hyaenas. In general, hyaenas initiated greetings immediately after reuniting with individuals from whom they had been separated. The modal number of minutes to pass between fusion and greeting onset was one. On average, hyaenas greeted within 6.3 ± 0.2 min after fusion (range 1–137 min postfusion). Interestingly, however, focal hyaenas ($N = 267$) engaged in conciliatory greetings significantly later during the postfusion interval (7.4 ± 0.4 min) than they engaged in nonconciliatory greetings (5.9 ± 0.1 min; Wilcoxon signed-ranks test: $Z = 2.866$, $P = 0.004$). Because our main goal here was to explain the function of nonconciliatory greetings, we next characterized the timing of only nonconciliatory greetings; these typically occurred within 5.8 ± 0.2 min after fusion ($N = 448$ hyaenas), and became less frequent as time passed after fusion (Spearman rank correlation: $r_s = -0.958$, $P < 0.00001$; Fig. 4). More than half of these nonconciliatory greetings (57.7%) occurred within 1 min, 77.7% within 5 min, and 86.6% within 10 min after fusion.

Females are selective when greeting after fusion events

Away from kills, focal adult females ($N = 33$) that had previously initiated fusion were significantly more likely to initiate nonconciliatory greetings ($58.2 \pm 4.0\%$) than were focal adult females that were joined by another female ($41.8 \pm 4.0\%$; Wilcoxon signed-ranks test: $Z = 2.16$, $P = 0.031$). In contrast, the initiation of greetings at kills was less structured; focal females ($N = 24$) were no more likely to initiate greetings upon arriving at subgroups ($47.9 \pm 8.3\%$) than they were when they were joined by other females ($52.1 \pm 8.3\%$; Wilcoxon signed-ranks test: $Z = 0.355$, $P = 0.723$). Adult females ($N = 37$) typically joined subgroups after

travelling alone. On average, females arrived with less than one (0.8 ± 0.1) companion and joined subgroups containing 7.9 ± 0.2 hyaenas, of which 2.8 ± 0.5 were also adult females. Upon arrival, adult females were selective with respect to their decisions to greet clanmates, and, on average, greeted only $7.1 \pm 0.6\%$ of the adult females available to them after fusion events.

Modelling Factors to Explain Decisions to Greet After Fusion Events

Next we identified the subset of candidate predictor variables that significantly explained decisions by adult females to participate in nonconciliatory greetings with other adult females after fusion. In contrast to the predictions of the submission hypothesis, neither the relative social rank nor the rank distance of the arriving female to potential greeting partners explained whether females greeted after fusion (Table 3). Also contrary to the predictions of the tension reduction hypothesis, females were actually least likely to greet per opportunity at kills, where social tensions should theoretically be high (Table 3, Fig. 5). Moreover, the act of greeting in nonconciliatory contexts failed to protect hyaenas from receiving aggression immediately after fusion (Table 3). Specifically, females greeting clanmates with whom they had not previously fought in a session were just as likely to fight with them after participating in nonconciliatory greetings as were females that failed to greet after fusion. Nevertheless, arriving females greeted high-ranking females most often per opportunity (Table 3). This final result suggests that, irrespective of their rank relative to potential partners, females prefer to greet high-ranking social allies.

As predicted by the social bonding hypothesis, but in direct contrast to the predictions of the tension reduction hypothesis, our best model indicated that adult females preferentially greeted kin (Table 3, Fig. 5) and closely associating nonkin (Table 3, Fig. 6) most often per opportunity after each fusion event. After controlling for the influence of kinship, close associates greeted significantly more often at fusion events than did distant associates, regardless of local prey abundance (association*prey abundance: -2.048 ± 3.138 ; $Z = -0.737$, $P = 0.461$). However, the effect of kinship significantly

Table 3

Independent variables predicting whether adult female hyaenas that joined a group greeted particular females within that group

Coefficients	Estimate \pm SE	Z	P
(Intercept)	-1.747 \pm 0.233	-7.495	<0.000001
Subgroup size (at fusion)	-0.086 \pm 0.013	-6.609	<0.000001
Intragroup coalition partners	1.038 \pm 0.258	4.023	0.00006
Food present (kill scene)	-0.556 \pm 0.150	-3.713	0.0002
Clan war participants	2.477 \pm 0.843	2.939	0.003
Absolute rank of partner	-0.030 \pm 0.011	-2.681	0.007
Association index	3.605 \pm 1.925	1.873	0.061
Cooperatively attacked lions	0.795 \pm 0.451	1.765	0.078
Coefficient of relatedness	1.926 \pm 0.558	3.453	0.0006
Prey abundance	0.096 \pm 0.151	0.636	0.525
Relatedness*prey abundance	-2.502 \pm 0.752	-3.326	0.0009

All factors listed above were retained in our best model because they improved its overall fit, but the following additional factors failed to improve the fit of the best model predicting whether females greeted after fusion events: maternal kinship (0.341 ± 0.270 ; $Z = 1.262$, $P = 0.207$), relative rank (arriving female subordinate to potential partner: 0.174 ± 0.142 ; $Z = 1.231$, $P = 0.218$), rank distance between potential partners (-0.020 ± 0.017 ; $Z = -1.172$, $P = 0.241$), absolute social rank of the arriving female (0.003 ± 0.011 ; $Z = 0.305$, $P = 0.761$), whether females cooperatively hunted (-0.467 ± 0.635 ; $Z = -0.735$, $P = 0.462$) or fought each other after fusion (0.035 ± 0.186 ; $Z = 0.190$, $P = 0.850$). Including hyaena identity as a random effect improved the fit of our best model (likelihood ratio test: $\chi^2_1 = 14.6$, $P = 0.0001$), which was based on a total of 433 possible greeting pairs of adult females. Adult females ($N = 37$) only participated in a total of 369 nonconciliatory greetings out of 4448 potential opportunities after fusion. The negative relationship between the absolute rank of available partners and greetings per opportunity reflects a preference by adult females to greet high-ranking females.

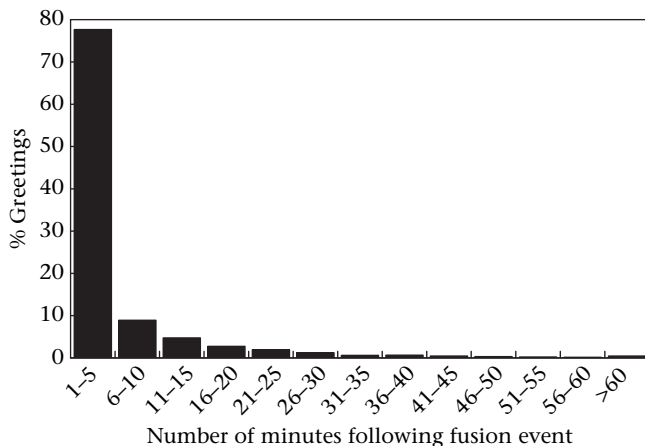


Figure 4. Percentage of all nonconciliatory greetings ($N = 11759$) that occurred among spotted hyaenas within the 5 min intervals directly after subgroup reunions ('fusion events') throughout our longitudinal study.

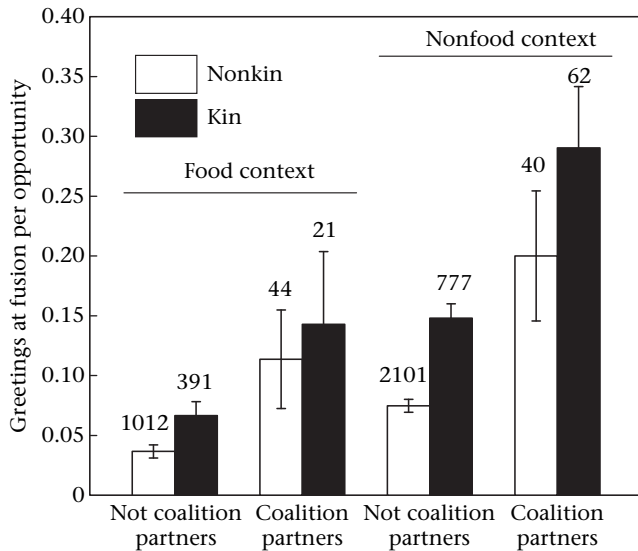


Figure 5. Proportion of fusion events in which adult females greeted within 10 min of subgroup fusion, out of all opportunities to do so, at kills (food context) and away from kills (nonfood context). Coalition partners formed at least one aggressive coalition directed towards another hyaena or towards a lion during the minutes after fusion; noncoalition partners failed to form a coalition during the minutes after a fusion event. We entered the coefficient of relatedness (r) for each dyad as a continuous variable in our statistical model (Table 2). For the purposes of visual representation, bar colour here indicates whether members of each dyad were nonkin (white, $r = 0.00$) or kin (black, $0.125 \leq r \leq 0.5$). Sample sizes over each bar indicate the number of opportunities available to arriving females to greet potential female partners. Error bars represent ± 1 SD for binomial trials.

interacted with the effect of local prey abundance (Table 3). Whereas nonkin greeted at similarly low rates throughout the year (prey abundance: 0.030 ± 0.154 ; $Z = 0.197$, $P = 0.844$), kin were most likely to greet per opportunity during months when prey were scarce (prey abundance: -0.562 ± 0.185 ; $Z = -3.041$, $P = 0.004$). Nevertheless, kin were generally more likely than nonkin to greet during months of both low prey (0.642 ± 0.198 ; $Z = 3.241$, $P = 0.002$) and high prey (0.362 ± 0.219 ; $Z = 1.656$,

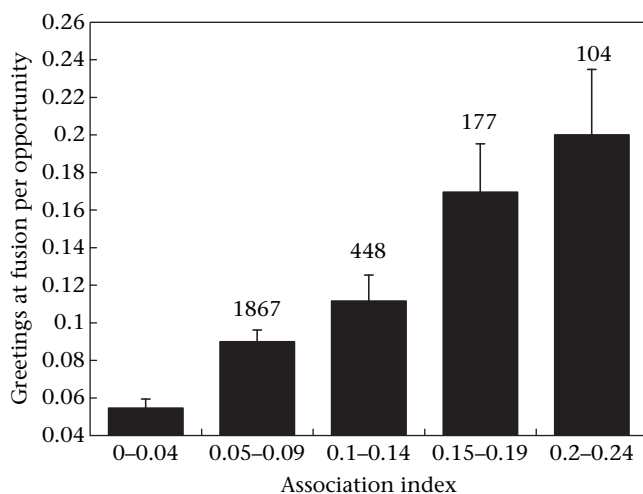


Figure 6. Proportion of fusion events in which adult females greeted within 10 min of subgroup fusion, out of all opportunities to do so, as a function of how often pairs of adult females associated with each other. For the purposes of visual representation only, we present patterns of association binned into discrete categories, but entered values as a continuous variable into our statistical model (Table 3). Sample sizes over each bar indicate the number of opportunities available to arriving adult females to greet potential adult female partners at fusion events. Error bars represent ± 1 SD for binomial trials.

$P = 0.098$) abundance. Overall, females greeted kin most often per opportunity during those times of year when prey are most scarce.

After controlling for the effects of kinship and patterns of association, females that joined forces to form aggressive coalitions after fusion were significantly more likely to greet per opportunity than were noncoalition partners (Table 3, Fig. 5). This was the case when adult females directed intragroup coalitions towards other clan members and when females cooperatively attacked alien intruders at clan wars or attacked lions during defence of food. We detected no relationship between the acts of greeting and cooperative hunting, but this might be attributed to our small sample size ($N = 15$ cooperative hunts by adult females after fusion events; Table 3).

When females formed aggressive coalitions with greeting partners after fusion (Fig. 5), they were roughly four times more likely to do so in the minutes immediately after greeting than in the minutes directly before greeting (Wilcoxon signed-ranks test: $Z = 2.520$, $N = 21$ females, $P = 0.012$; Fig. 7). On average, when these females formed coalitions to attack another hyaena, they did so within 2.7 ± 0.9 min of greeting initiation. The tendency for females to preferentially form coalitions with greeting partners was not explained simply by the amount of time that females were observed with social partners. Females remained in subgroups for similar amounts of time after fusion, regardless of whether or not they formed a coalition (35.7 ± 2.7 min versus 31.4 ± 0.5 min; Wilcoxon signed-ranks test: $Z = 1.547$, $N = 21$ females, $P = 0.123$).

Adult females that greeted at reunions were more likely to form coalitions than females that failed to greet, but coalition formation was not restricted to greeting partners. On average, for those adult females ($N = 25$) that formed coalitions within 10 min after fusion, they greeted their coalitionary allies prior to forming a coalition in $23.0 \pm 6\%$ of the coalitions formed.

Modelling Factors to Explain the Symmetry of Nonconciliatory Greetings

Following East et al. (1993), a single univariate analysis of all greetings (e.g. conciliatory and nonconciliatory combined) indicated that the asymmetry of leg lifting increased as the rank distance between adult females increased (Spearman rank

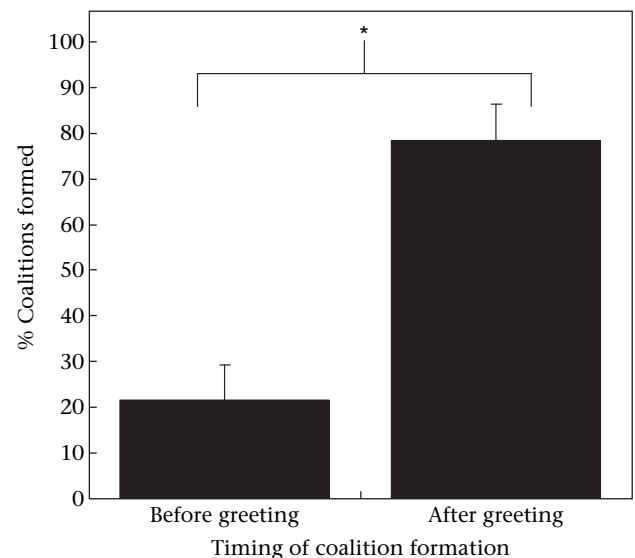


Figure 7. Mean \pm SE percentage of aggressive coalitions in which focal adult females ($N = 22$) greeted allies in the minutes before or after forming coalitions with those same allies within 10 min of subgroup fusion.

Table 4
Independent variables predicting the symmetry of nonconciliatory greetings among adult female hyaenas

Coefficients	Estimate±SE	Z	P
(Intercept)	-0.246±0.115	-2.142	0.032
Association index (AI)	4.037±1.472	2.742	0.006
Coefficient of relatedness	-1.108±0.418	-2.650	0.008

All factors listed above were retained in our best model because they improved its overall fit, but the additional predictor variables failed to improve the fit of our best model: rank distance (-0.016 ± 0.014 ; $Z = -1.106$, $P = 0.269$); maternal kinship (-0.255 ± 0.267 ; $Z = -0.955$, $P = 0.339$); cooperative hunting (0.701 ± 0.463 ; $Z = 1.514$, $P = 0.130$); intragroup coalition partners (-0.137 ± 0.232 ; $Z = -0.592$, $P = 0.554$); clan war participants (0.878 ± 0.894 ; $Z = 0.982$, $P = 0.326$); cooperatively attacked lions (0.133 ± 0.726 ; $Z = 0.184$, $P = 0.854$); prey abundance (-0.093 ± 0.105 ; $Z = -0.885$, $P = 0.376$); food (-0.051 ± 0.130 ; $Z = -0.396$, $P = 0.692$). The interaction between association and kinship (AI*kinship: -7.657 ± 7.153 ; $Z = -1.070$, $P = 0.284$), or that of any other terms, failed to improve the fit our model. A likelihood ratio test confirmed that the inclusion of the random effect, 'hyaena identity', improved the model's fit ($\chi^2 = 11.6$, $P = 0.0007$), which included 1750 nonconciliatory greetings involving 456 different pairs of adult females from 1988 to 2000 ($N = 58$ adult females).

correlation: $r_s = 0.553$, $N = 22$ rank distances, $P = 0.007$). Interestingly, conciliatory greetings involving focal females ($N = 52$) were significantly more asymmetric ($63.3 \pm 4.3\%$) than were nonconciliatory greetings ($48.3 \pm 2.7\%$; Wilcoxon signed-ranks test: $Z = 4.049$, $P = 0.00005$). After we accounted for association indices and relatedness, in contrast to predictions of the submission hypothesis, rank distance was excluded from our best model explaining the symmetry of nonconciliatory greetings (Table 4). In contrast to the tension reduction hypothesis, but in support of the social bonding hypothesis, females that associated closely engaged in the most symmetric greetings. Among close associates, kin engaged in less symmetric greetings than nonkin (-0.975 ± 0.494 ; $Z = -1.974$, $N = 58$ adult females, $P = 0.048$), suggesting that socially bonded nonkin might rely most heavily upon reciprocal greetings to reinforce social bonds. Kinship failed to predict greeting symmetry among distant associates (-1.033 ± 0.7144 ; $Z = -1.448$, $N = 58$ adult females, $P = 0.148$). Taken together, our findings are generally most consistent with predictions of the social bonding hypothesis.

DISCUSSION

Differences Between Conciliatory and Nonconciliatory Greetings

Our findings reveal that greetings represent complex multimodal signals. First, as found in early studies, here the vast majority of greetings served a nonconciliatory function (East et al. 1993; Hofer & East 2000). The low frequency of conciliatory greeting (e.g. occurring immediately after fights) is presumably because hyaenas rely most heavily upon dispersive conflict resolution to settle disputes (Wahaj et al. 2001; Smith et al. 2008). Second, whereas conciliatory greetings transpire primarily among nonkin and are initiated mostly by losers of fights (Wahaj et al. 2001), we found here that nonconciliatory greetings mainly involved kin, even after correcting for opportunities to greet. Third, nonconciliatory greetings were more symmetric and occurred more immediately after fusion events than did conciliatory greetings. Finally, conciliatory greetings lasted longer than nonconciliatory greetings, a finding consistent with the idea that it takes more time to renegotiate damaged relationships than to reinforce existing social bonds (Aureli et al. 2002).

Nonconciliatory Greetings Fail to Signal Submission

Although spotted hyaena greetings are still cited as one of the key examples of 'reliable ritualized expressions of formal rank'

(Cafazzo et al. 2010, page 444), our critical test of the submission hypothesis revealed that this does not in fact appear to be the case. In general, the results of our study are consistent with data obtained earlier when we used the same methods as those used in earlier studies (Kruuk 1972; East et al. 1993). That is, younger or subordinate spotted hyaenas generally initiated greetings more often than did older or socially dominant hyaenas. However, when we focused on nonconciliatory greetings and simultaneously accounted for potential confounding factors using a modelling approach not yet widely available when the earlier studies were conducted, we obtained results that differed from those of East et al. (1993). Importantly, our work revealed that social bond strength predicts patterns of nonconciliatory greetings better than do rank relationships, a finding consistent with the social bonding hypothesis originally proposed by Kruuk (1972).

The availability of new matrix permutation tools also allowed us to quantify the linearity of greeting initiation and fight outcomes while explicitly correcting for unknown relationships (e.g. de Vries 1995). These analyses revealed that fight outcomes clearly adhered to the expectations of a linear dominance hierarchy (sensu Drews 1993), but that greetings failed to do so. Here the initiation of greetings was far more balanced within dyads than were fight outcomes. Moreover, although fight outcomes were always unidirectional, the DC of greeting initiation differed between food and nonfood contexts.

DC is the most informative measure for comparing the strength of competition among taxonomic groups (Isbell & Pruettz 1998; Isbell & Young 2002; Archie et al. 2006a). Interestingly, our findings indicate that the dominance hierarchies of spotted hyaenas are extremely linear and rigid. For instance, Table 5 reveals that the DC for hyaena fights outcomes was similar to or exceeded values reported for most female mammals. Given this, our results represent particularly strong evidence against the submission hypothesis because despite the high DC for fight outcomes among adult female hyaenas, the DC for hyaena greetings was more akin to DC values based on affiliative behaviours, such as allogrooming, than to those based on fight outcomes for most species reviewed here (Table 5). Whereas these findings might seem surprising, use of these new quantitative methods has similarly revealed misconceptions about signalling in other species (reviewed by Kutsukake 2009).

Although allogrooming among primates is often preferentially directed towards higher and adjacently ranked coalition partners (Seyfarth 1977; Seyfarth & Cheney 1984; Schino 2001), grooming clearly does not signal submission. In addition to its hygienic and hedonistic values, it provides important 'political' information (Dunbar & Sharman 1984; Cheney et al. 1986; Dunbar 1991). The pivotal role of grooming in social bond maintenance is well documented among primates living in cohesive groups (e.g. Matheson & Bernstein 2000; Lazaro-Perea et al. 2004; Silk et al. 2006; Gomes et al. 2009), especially when the value of social partners changes dynamically with time and circumstances (e.g. Barrett et al. 2002, 2003). Adult female hyaenas rarely allogroom, but our results are consistent with the idea that greetings might function to quickly update social bonds. Similarly, spider monkeys, *Ateles geoffroyi*, also exchange greetings, but not allogrooming, at fusion (Schaffner & Aureli 2005). In fact, Aureli & Schaffner (2007) theorized that individuals living in fission–fusion societies should quickly update relationships at reunions. As predicted, friendly greetings among hyaenas were very brief and occurred immediately after fusion.

Nonconciliatory Greetings Fail to Reduce Tension

Our results generally failed to support the hypothesis that nonconciliatory greetings reduce social tensions. Specifically,

Table 5
Directional consistency (DC) of behavioural interactions among gregarious adult female mammals

Species	Interaction type	DC±SE (N)	Subject no. ^{Type}	Source
Black-and-white colobus, <i>Colobus guereza</i>	Allogrooming	0.26	4 ^C	Kutsukake et al. 2006
Wedge-capped capuchins, <i>Cebus olivaceus</i>	Allogrooming	0.43	9 ^W	O'Brien 1993
Vervet monkeys, <i>Cercopithecus aethiops</i>	Allogrooming	0.33±0.03 (3)	7–8/group ^W	Seyfarth 1980
Spider monkeys, <i>Ateles belzebuth hybridus</i> *	Allogrooming	0.51	6 ^C	Leiva et al. 2008
Chimpanzees, <i>Pan troglodytes schweinfurthii</i>	Friendly approaches	0.57	18 ^W	Murray 2007
Bonobos, <i>Pan paniscus</i>	Feeding ability	0.53	3 ^C	Vervaecke et al. 1999
Black-and-white colobus, <i>C. guereza</i>	Greeting initiation	0.60	4 ^C	Kutsukake et al. 2006
Spotted hyaenas, <i>Crocuta crocuta</i>	Greeting initiation	0.65	19^W	Current study
Wolves, <i>Canis lupus</i> *	Tail wagging	0.66	15 ^C	van Hooff & Wensing 1987
Domestic cows, <i>Bos taurus</i>	Allogrooming	0.68±0.06 (6)	8/group ^C	Val-Laillet et al. 2009
Domestic cows	Feeding ability	0.71±0.03 (6)	8/group ^C	Val-Laillet et al. 2009
Wolves*	Genital sniffing	0.72	15 ^C	van Hooff & Wensing 1987
European badgers, <i>Meles meles</i> †	Allogrooming	0.75±0.04 (3)	3–7/group ^W	H. Dugdale & D.W. Macdonald, unpublished data
Feral domestic dogs, <i>Canis familiaris</i> ‡	Fight outcomes	0.75	4 ^W	Cafazzo et al. 2010
Patas monkeys, <i>Erythrocebus pata</i>	Fight outcomes	0.78	17 ^W	Isbell & Pruettz 1998
European badgers	Directed aggression	0.86±0.08 (3)	3–7/group ^W	Hewitt et al. 2009
Olive baboons, <i>Papio anubis</i>	Fight outcomes	0.89	10 ^C	McMahan & Morris 1984
Grey-cheeked mangabeys, <i>Lophocebus albigena</i>	Fight outcomes	0.89±0.03 (5)	4–7/group ^W	Chancellor & Isbell 2009
Feral domestic cats, <i>Felis catus</i> ‡	Fight outcomes	0.90	5 ^W	Bonanni et al. 2007
Hanuman langurs, <i>Semnopithecus entellus</i>	Fight outcomes	0.90	13 ^W	Lu et al. 2008
Hanuman langurs	Presenting	0.91	13 ^W	Lu et al. 2008
Pigs, <i>Sus domestica</i>	Fight outcomes	0.92±0.04 (9)	8/group ^C	Hoy & the 2005
American bison, <i>Bison bison</i>	Fight outcomes	0.94	42 ^C	Vervaecke et al. 2005
African elephants, <i>Loxodonta africana</i>	Fight outcomes	0.94±0.03 (2)	47–82/group ^W	Archie et al. 2006a
Olive baboons	Fight outcomes	0.96	26 ^W	Barton & Whiten 1993
Orang-utans, <i>Pongo borneo</i>	Fight outcomes	0.97	7 ^W	de Vries 1995
Chimpanzees	Fight outcomes	0.97	18 ^W	Murray 2007
Spotted hyaenas	Fight outcomes	0.97	19^W	Current study
Hamadryas baboon, <i>Papio hamadryas hamadryas</i>	Fight outcomes	0.98	13 ^C	Leinfelder et al. 2001
Mountain goats, <i>Oreamnos americanus</i>	Fight outcomes	0.98	45 ^W	Côté 2000
Vervet monkeys	Fight outcomes	1.00	9 ^W	Isbell & Pruettz 1998
Bonobos	Peering	1.00	3 ^C	Vervaecke et al. 1999

Some DC values were calculated based on data extracted from published matrices. Because DC is measured at the group level, we only report means ± SE and number of groups (N) for those studies with multiple groups. Subject number represents the number of adult females observed in each study. Subject type denotes whether subjects were wild (W) or captive (C).

* Based on interactions among male and female subjects.

† Based on counts of unreciprocated allogrooming.

‡ Based on submissive signals, including those occurring outside of aggression. Note: Although DC values are unavailable, the unidirectional nature of play within dyads of domestic dogs increases across ontogeny and most closely resembles the dominance relationships within adult pairs (see Bauer & Smuts 2007; Ward et al. 2008).

females were least likely to greet when meeting up after fusion events with distant associates, the individuals with whom they had the least secure social relationships (Wahaj et al. 2001). Moreover, most greetings occurred in neutral contexts in which tensions were low compared to situations in which resource competition was likely to enhance tension (Frank 1986). Finally, the act of greeting in nonaggressive contexts failed to protect hyaenas from immediately receiving aggression. This last finding is consistent with earlier studies, including those involving many species of primates (reviewed by Widdig 2007). Therefore, even though kin represent the best allies, hyaenas are just as likely to direct aggressive attacks towards relatives as they are towards nonrelatives.

Like hyaena greetings, genital contacts among adult female bonobos (*P. paniscus*) serve multiple functions, and are sometimes used to reconcile fights (Hohmann & Fruth 2000). Nonconciliatory genital contacts reduce tensions over food, thus facilitating food sharing within the egalitarian societies of bonobos (Hohmann & Fruth 2000). In contrast, nonconciliatory greetings here occurred most often away from food, and these greetings promoted the formation of intragroup coalitions, which mainly function to reinforce existing dominance relationships among adult females (Smith et al. 2010).

Nonconciliatory Greetings Reinforce Bonds and Promote Cooperation

Overall, our results were most consistent with the social bonding hypothesis. Indeed, adult females exchanged greetings

with a small subset of the adult females present after each subgroup reunion. They selectively directed these gestures towards preferred social companions, including coalitionary allies, relatives and close associates. Thus, the finding that females often initiate greetings with high-ranking females (East et al. 1993; Table 3) probably reflects social preferences for powerful allies, rather than simply signalling submission to dominants. Here, high-ranking adult females received the most greetings. As in many primates (Schino 2001), high-ranking hyaenas are the most attractive social companions (Smith et al. 2007); adult females, especially high-ranking ones, lead the most attacks during clan wars and intra-group coalitions (Boydston et al. 2001; Smith et al. 2010).

Although mutual inspection of the highly vulnerable genitalia might improve the efficacy of gestures signalling bond strength (Zahavi 1977b; Smuts 2002), hyaenas generally minimized the risk involved in greetings by selecting partners unlikely to harm them, and by greeting these partners most often away from contexts in which aggression is common. First, because the reproductive careers of relatives are closely linked to one another through direct and indirect fitness benefits (Hamilton 1964), females should theoretically be disinclined to damage the reproductive organs of their kin. Second, we found here that hyaenas generally greeted in neutral contexts. Similarly, male baboons (*Papio cynocephalus anubis*) and domestic dogs (*Canis familiaris*) greet most often when there are no immediate resources at stake (Smuts & Watanabe 1990; Smuts 2002). Thus, greetings appear to offer a mechanism by which animals can assess the cooperative tendencies of potential allies in contexts in which risk of injury is reduced.

Whereas greetings failed to play an important role in preparing hyaenas for cooperative hunting, African wild dogs, *Lycaon pictus*, almost always engage in greetings prior to hunting and increase their per capita energy intake by hunting in large groups (Creel 1997; Creel & Creel 2002). In contrast, because hyaenas often hunt alone to avoid feeding competition resulting from hunting cooperatively (Smith et al. 2008), opposing selection pressures might contraindicate the use of greetings to coordinate group hunting in this species.

Importantly, we found strong evidence that greetings facilitate intragroup coalition formation, participation in clan wars and cooperative mobbing of lions; this was true even after controlling for effects of kinship, association patterns and immediate ecological context. Although many workers theorize that greetings promote coalition formation, direct empirical evidence for this is limited. Smuts (2002) noted that a cooperating pair of male olive baboons, *Papio anubis*, engaged in more risky and more symmetric genital touching than did noncoalition partners. Ritualized embracing and mutual genital inspection also appear to mediate social relationships in many nonhuman primates (Smuts & Watanabe 1990; Colmenares 1991; Matheson et al. 1996; Perry 1998; Okamoto et al. 2001; Perry et al. 2003; Wang & Milton 2003; Whitham & Maestripietri 2003; Alfaro 2008). However, our work demonstrates for the first time a temporal link between the patterning of greetings and coalition formation.

Cognitive Demands of Bond Maintenance in Complex, Dispersed Societies

Whereas shifting ecological conditions are known to favour enhanced cognitive abilities in animals (e.g. Braithwaite & Salvanes 2005; Kotrschal & Taborsky 2010), variation in social group composition attributed to fission–fusion dynamics might also impose cognitive demands upon species in which individuals recognize the relationships among groupmates from whom they are often separated (Barrett et al. 2003; Connor 2007; Amici et al. 2008; Aureli et al. 2008). This prediction stems from the social brain (or Machiavellian intelligence) hypothesis, a theory proposed to explain the evolution of large brains in response to the demands of life in complex societies (Byrne & Whiten 1988; Dunbar 1998; Dunbar & Shultz 2007).

Because resource competition often forces members of fission–fusion societies to spend time in fragmented subgroups (reviewed by: Wrangham et al. 1993; Aureli et al. 2008), many social animals, including spotted hyaenas (East & Hofer 1991; Theis et al. 2007), use contact calls to ‘stay in touch’ over long distances (e.g. Smolker et al. 1993; McComb et al. 2003; Ramos-Fernandez 2005; Spillmann et al. 2010). Moreover, hyaenas maintain cohesion within their social network by depositing individually distinct scent marks (Drea et al. 2002; Theis 2008; Burgener et al. 2009). Although vocal and olfactory cues effectively communicate individual identity when clan members are spatially separated, and although spotted hyaenas recognize third-party relationships among groupmates (Engh et al. 2005), experiments suggest that contact calls fail to communicate information about third-party relationships (Holekamp et al. 1999). Our findings suggest that greetings represent reliable signals with which hyaenas can quickly update social alliances in a society in which group members spend much of their time apart. These signals appear to be especially important in maintaining bonds among kin during those times of year when resource limitation most strongly constrains social cohesion (Smith et al. 2008). That is, the dynamic nature of greeting interactions among kin suggests that hyaenas greet relatives most often during periods when reinforcement of social bonds is needed most.

Natural selection should theoretically favour efficient signalling that coordinates collective behaviours when those behaviours confer an evolutionary advantage (reviewed by: Conradt & Roper 2005; Noë 2006). Here greetings signalled a hyaena’s immediate commitment to social allies within a continuously shifting social milieu. Thus, our findings elucidate the fundamental role of multimodal signalling in coordinating cooperation among social partners within spatially and temporally dynamic social landscapes. More broadly, our findings extend a growing body of literature suggesting that ritualized signals are centrally important to the maintenance of cooperative partnerships in complex societies (e.g. Flack & de Waal 2007; Rossano 2009).

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APPENDIX

Age and Sex Structuring of Greetings

The hourly rate at which hyaenas participated in greetings with any member of the clan varied among life history stages

(Kruskal–Wallis test: $H_{2,649} = 102.7$, $P < 0.0001$). In general, adult females ($N = 75$) and subadults ($N = 209$) participated in greetings at similarly high hourly rates (Mann–Whitney U test: $Z = 0.276$, $P = 1.0000$). Both adult females and subadults greeted clan members at higher rates than did den cubs ($Z \geq 8.101$, $N = 289$ cubs, $P \leq 0.000001$). We detected no sex differences in the rates at which den cubs ($Z = -0.690$, $N_F = 137$, $N_M = 152$, $P = 1.0000$) or subadults ($Z = 0.270$, $N_F = 97$, $N_M = 112$, $P = 1.0000$) greeted members of the clan. Immigrant males ($N = 76$) greeted clan members at lower rates than did subadults or adult females ($Z \geq 2.979$, $P \leq 0.014$), but at rates similar to those of den cubs ($Z = 0.702$, $P = 1.0000$). When greeting partners differed in age, the younger hyaena lifted its leg first significantly more often ($76.6 \pm 2.2\%$) than did the older partner (Wilcoxon signed-ranks test: $Z = 8.25$, $N = 304$ focal hyaenas, $P < 0.000001$). Both den cubs ($N = 259$) and subadults ($N = 178$) initiated a significant majority of their greetings with adult females ($Z \geq 6.921$, $P \leq 0.000001$). However, the initiation of greeting was bidirectional between den cubs ($N = 85$) or subadults ($N = 108$) and adult males ($Z \leq 0.856$, $P \geq 0.398$). Focal den cubs ($N = 79$) and subadults ($N = 103$) initiated a greater proportion of greetings involving adult females than they did when greeting adult males ($Z < 3.922$, $P \leq 0.007$). We found no sex difference in the extent to which den cubs initiated greetings with adult females ($N_F = 111$, $N_M = 129$) or males (Mann–Whitney U test: $Z \leq 0.994$, $N_F = 40$, $N_M = 44$, $P \geq 0.960$ for both). Strikingly, although both sexes of subadults ($N_M = 58$, $N_F = 50$) initiated greetings with adult males to similar extents (Mann–Whitney U test: $Z = -0.231$, $P = 1.000$), male subadults ($N = 91$) were significantly more likely than female subadults ($N = 87$) to initiate greetings with adult females ($Z = -2.903$, $P = 0.0185$). Among same-sexed dyads of adults, the subordinate partner was significantly more likely to lift its leg first in both sexes than was the dominant greeting partner ($75.1 \pm 4.9\%$ and $73.7 \pm 3.2\%$; $Z \geq 4.19$, $N_M = 42$, $N_F = 59$, $P \leq 0.00003$).