

Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals

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Coalitional support in agonistic interactions represents cooperation because intervening in a fight is potentially costly to the donor of support but benefits the recipient. Here, we first review the characteristics of, and evolutionary forces favoring, intragroup coalitions in 49 species and find that patterns of intragroup coalition formation are remarkably similar between primates and nonprimates. We then test hypotheses suggesting kin selection, reciprocal altruism, and direct benefits as adaptive explanations for coalitionary interventions among adult female spotted hyenas (*Crocuta crocuta*) belonging to a large social group in Kenya. As predicted by kin selection theory, females supported close kin most often, and the density (connectedness) of cooperation networks increased with genetic relatedness. Nevertheless, kinship failed to protect females from coalitionary attacks. We found no evidence of enduring alliances based on reciprocal support among unrelated adult females. Instead, donors generally minimized costs to themselves, intervening most often during low-intensity fights and when feeding opportunities were unavailable. Females also gained direct benefits from directing coalitionary attacks toward subordinates. Finally, females monitored the number of dominant bystanders in the “audience” at fights and modified their level of cooperation based on this knowledge. Overall, hyenas made flexible decisions regarding whether or not to intervene in fights, modifying their tendency to cooperate based on multiple types of information about their immediate social and ecological environments. Taken together, these findings indicate that the combined evolutionary forces of kin selection and direct benefits derived from reinforcing the status quo drive coalitionary interventions among adult female spotted hyenas. *Key words:* agonistic support, audience effect, cooperation network, direct benefits, kin selection, reciprocal altruism, review. [Behav Ecol 21:284–303 (2010)]

As originally proposed by Charles Darwin (1859), the theory of natural selection fails to explain seemingly altruistic acts in which animals reduce their individual fitness to help increase the fitness of others. In light of this problem, behavioral ecologists have invoked the theoretical constructs of kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971), direct benefits (also called by-product mutualisms, West-Eberhard 1975; Brown 1983; Connor 1995), and group selection (Wilson 1975a; Wilson DS and Wilson EO 2007) to explain the evolution of cooperation (reviewed by Queller 1985; Dugatkin 2002; Sachs et al. 2004; Noë 2006; Nowak 2006; West et al. 2007a, 2007b; Clutton-Brock 2009). Agonistic aiding, also called intervention or coalition formation, represents a cooperative act; intervening in a fight is potentially costly to the donor, who risks physical injury, expends energy fighting, and allocates time to this behavior that might otherwise be devoted to other activities. Agonistic aiding is beneficial to the recipient because it increases the recipient’s likelihood of winning the fight.

Agonistic aiding occurs when group members join forces to attack either members of their own social group (intragroup coalitions) or members of a different group (intergroup coalitions). A social group is “any set of organisms belonging to the same species that remain together, . . . interacting with one another to a distinctly greater degree than with other conspecific organisms” (Wilson 1975b, p. 8). Although researchers have investigated patterns of intergroup coalition

formation in many taxa (reviewed by Harcourt 1992; Creel and Macdonald 1995; Fashing 2001), research on intragroup coalitions has historically focused on nonhuman primates. In fact, early workers suggested that complex patterns of intragroup coalition formation might be unique to primates. For example, Harcourt (1992) proposed that primate coalitions are more complex than nonprimate coalitions. Specifically, he posited that intragroup coalitions among primates might occur at higher frequencies, involve larger numbers of coalition partners, and involve adult beneficiaries of support more often than do nonprimate coalitions. Further, because the outcomes of coalitions can affect the social ranks of individual group members, and because rank often influences reproductive success, agonistic aiding should theoretically have profound fitness consequences for all participants (Seyfarth 1977; Wrangham 1980; Sterck et al. 1997; Isbell and Young 2002). Nonetheless, most studies have investigated adult male coalitions or interventions by adult females on behalf of their immature offspring (reviewed by de Waal and Harcourt 1992; Olson and Blumstein 2009). As a result, we currently understand little about the evolutionary forces promoting intragroup coalitions among adult females, especially in nonprimates (Silk 2007a, 2007b).

In light of recent advances in our understanding of social complexity among nonprimates, we first perform a comprehensive review of 49 species to evaluate the notion that intragroup coalitions formed by primates differ from those formed by nonprimates. We then conduct a detailed investigation documenting patterns of coalition formation in a nonprimate, the spotted hyena (*Crocuta crocuta*). Spotted hyenas are gregarious carnivores that live in female-bonded groups (Holekamp, Cooper, et al. 1997; Smith et al. 2007), called clans (Kruuk 1972).

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Because hyena clans are strikingly similar in size and hierarchical structure to troops of cercopithecine primates (Drea and Frank 2003; Holekamp et al. 2007), this provides a unique opportunity to compare the evolutionary forces favoring coalition formation in primates and carnivores, taxonomic groups that last shared a common ancestor 90–100 Ma (Springer et al. 2003). Specifically, here we describe patterns of coalition formation among various age-sex classes of spotted hyenas belonging to a single, large social group. We then explain these patterns by inquiring in particular why natural selection favors coalitionary support among adult female spotted hyenas.

Like troops of cercopithecine monkeys (Drea and Frank 2003; Holekamp et al. 2007), hyena clans are multigenerational groups that usually contain multiple matrilines of adult females and their offspring, as well as multiple adult immigrant males born elsewhere (Kruuk 1972). Further, as in many cercopithecines (Chapais 1992), adult female spotted hyenas provide coalitionary support to their juvenile offspring to aid them in rank acquisition (Smale et al. 1993; Engh et al. 2000; East et al. 2009). Although it has been shown that hyena siblings generally form coalitions at higher hourly rates than do unrelated individuals (Wahaj et al. 2004), it is unknown to what extent kinship and other factors influence aiding decisions made by adult spotted hyenas. Because the ultimate goal of this investigation is to elucidate the evolutionary forces shaping this decision-making process, here we test hypotheses suggesting that kin selection, reciprocal altruism, and direct benefits, respectively, drive intragroup coalition formation among adult female spotted hyenas, as detailed below.

Predictions based on kin selection

Kin selection theory (Hamilton 1964) predicts that, if individuals possess the ability to discriminate on the basis of kinship, then they should gain inclusive fitness benefits by biasing helpful behavior toward relatives, and harmful behavior away from them. Because spotted hyenas can discriminate among conspecifics based on both maternal and paternal kinship (Van Horn, Wahaj, and Holekamp 2004; Wahaj et al. 2004), kin selection theory may explain patterns of coalition formation among adult females. If this theory is correct, then females should intervene to support females to which they are most closely related, and direct coalitionary attacks at lower frequencies or intensities toward relatives than toward nonrelatives. Moreover, when individual fitness costs associated with fighting are context dependent (Maynard Smith and Price 1973), Hamilton's rule (1964) predicts females should help kin most often when costs to donors are low, or when benefits to beneficiaries are high. Because clans are fission–fusion societies in which individual members travel, rest, and forage in subgroups that frequently change composition (Kruuk 1972; Mills 1990; Smith et al. 2008), the immediate social environment in which cooperation occurs is variable. Therefore, because hyenas typically direct attacks toward subordinates (Frank 1986), the number of dominant bystanders present at any particular fight should represent a proxy for the risk of retaliation for joining that fight. Thus, if females act to minimize their own risks, then they should intervene most often when fight intensity is low or when few dominant bystanders are present. However, if hyenas base decisions solely on the projected benefits to kin, then donors should intervene most often during fights of high intensity when kin are most at risk.

Predictions based on reciprocal altruism

Natural selection might favor interventions on behalf of nonkin via reciprocal altruism if the projected future benefits to

the donor outweigh the immediate costs (Trivers 1971). Although firm evidence of reciprocal altruism among nonkin in animal societies is rare (Clutton-Brock 2009), reciprocity is most likely to evolve in long-lived animals with low dispersal rates, frequent social interactions, and cognitive abilities permitting individuals to remember earlier interactions (Ridley et al. 2005). Female spotted hyenas satisfy these conditions. They live up to 19 years in the wild (Drea and Frank 2003), they are philopatric (Smale et al. 1997) and highly gregarious (Holekamp, Cooper, et al. 1997; Smith et al. 2007), and they demonstrate many of the same cognitive abilities as monkeys (Holekamp et al. 2007).

If the reciprocal altruism hypothesis is correct, then female hyenas should offer other females either immediate coalitionary support (direct reciprocity) or access to other commodities (interchange trading) in exchange for future coalitionary support from nonkin (Hemelrijk and Ek 1991). However, partner choice mechanisms (Schino and Aureli 2009) based on the threat of switching partners within the “biological marketplace” (Noë and Hammerstein 1994) failed to explain patterns of coalition formation among unrelated adult female hyenas in our previous study (Smith et al. 2007). Nonetheless, it remains possible that females might exchange coalitionary support within a “service economy” (e.g., de Waal 1997) for access to commodities such as help during hunting, affiliative greetings, social tolerance, or establishment and maintenance of stable alliances. Aid during hunting is valuable because pairs of hyenas are 19% more likely to capture prey than are lone hunters, and because hyenas can only capture some species of prey when hunting in groups (Kruuk 1972; Holekamp, Smale, et al. 1997). Greetings occur when 2 females stand parallel to each other and sniff each other's anogenital region, each exposing its fully erect “pseudopenis” (Kruuk 1972; East et al. 1993; Wahaj et al. 2001). Greetings are valuable in that they reinforce social bonds, but they involve risk of genital injury. Social tolerance occurs when one female receives low rates of dyadic aggression from another, thus permitting the former better access to resources (Smith et al. 2007).

Females might maintain alliances based on repeated acts of support. Whereas coalitionary support indicates short-term cooperation, alliances are relationships between 2 individuals who repeatedly join forces over long time periods (Seyfarth 1977; Noë 1992). Therefore, if unrelated adult females form stable alliances, then donors should intervene repeatedly on behalf of the same beneficiaries.

Finally, indirect reciprocity might explain patterns of support if members of the audience observe a donor behaving altruistically and later help that same donor even though the audience members themselves were not direct beneficiaries of the original support (Nowak and Sigmund 1998, 2005). Because high-ranking adult female hyenas provide the most effective support (Smith et al. 2007), if females intervene to improve their own reputation, then we should detect an “audience effect” (Zuberbühler 2008) in which females donate the most support when large numbers of higher-ranking group members are present in the audience.

Predictions based on direct benefits

Direct benefits result from cooperative acts in which a donor gains immediate individual fitness benefits by helping, and the recipient benefits as a by-product of his or her partner's selfish behavior (West-Eberhard 1975; Brown 1983; Connor 1995). We tested 2 hypotheses suggesting direct benefits that females might gain by intervening in fights.

Food access hypothesis

Feeding competition is intense among spotted hyenas; these animals typically feed at fresh carcasses that are energetically rich but highly ephemeral, often persisting for only a few minutes (Kruuk 1972; Frank 1986; Mills 1990; Smith et al. 2008). Thus, adult female hyenas might directly benefit from joining fights if doing so provides them with immediate opportunities to feed (Mesterton-Gibbons and Sherratt 2007). This hypothesis predicts that females should intervene most often during fights over food and during times of year when feeding competition is most intense, as indicated by low prey abundance (Holekamp et al. 1996). Although recently attacked hyenas rarely depart altogether from kills in response to conspecific aggression (Smith et al. 2008), coalition partners might be more likely to gain access to food if coalitionary aggression more effectively displaces competitors from kills (e.g., the victim of aggression retreats from the carcass) than does dyadic aggression.

Status quo hypothesis

Because high-ranking female hyenas enjoy greater reproductive success than low-ranking females (Frank et al. 1995; Holekamp et al. 1996; Hofer and East 2003), females might directly benefit by providing support if doing so either reinforces or improves their rank positions in the dominance hierarchy. If support reinforces the status quo, then high-ranking females should intervene most often and direct most coalitionary attacks toward subordinate targets. Conversely, if females generally intervene to improve their own social status, then low-ranking females should intervene most often, and direct most attacks toward dominant targets.

MATERIALS AND METHODS

Study site and subjects

The study area, in the Masai Mara National Reserve, Kenya, is characterized by open, rolling grasslands. Prey availability varies seasonally and feeding competition is reduced annually when migratory ungulates join resident herds (Holekamp et al. 1996, 1999; Holekamp, Smale, et al. 1997; Smith et al. 2008). Our subjects belonged to a single large clan of spotted hyenas that defended a common territory in the study area (Boydston et al. 2001). Although this clan has been continuously monitored since May 1988, limited paternity data were available prior to 1996 (Engh et al. 2002) and the clan permanently split into 2 clans by 2001 (Smith JE and Holekamp KE, unpublished data). Thus, all coalition data reported here were collected from January 1996 to December 2000 to ensure that subjects belonged to the same social group, and that they were of known maternal and paternal relatedness.

We identified individual hyenas by their unique spots, and we sexed them based on the morphology of the erect phallus (Frank et al. 1990); we estimated the ages of cubs to ± 7 days (Holekamp et al. 1996). We classified females as adults at 36 months of age or at their first known date of conception, whichever occurred first. Males disperse 1–76 months after puberty (Smale et al. 1997; Van Horn et al. 2003), which occurs around 24 months of age. We considered natal males older than 24 months and all immigrant males to be adults, and all natal animals that had not yet reached adulthood to be juveniles.

All adult female hyenas are socially dominant to all adult immigrant males (Frank 1986). We ranked adult females in a linear dominance hierarchy for each month of the study (Holekamp and Smale 1993; Smale et al. 1993). Adult females generally maintained stable dominance relations, and most

ranks changed gradually over time due to maturation and deaths (Frank 1986; Holekamp and Smale 1993). However, 2 brief periods of social instability occurred during this study (Van Meter et al. 2009).

Terminology

We defined a “dyadic fight” as any agonistic interaction involving only 2 contestants. The act of a third individual (here called the “donor of support”) joining an ongoing dyadic fight transformed it into a triadic interaction, called a “coalitionary intervention” (de Waal and Harcourt 1992). The donor intervened on behalf of one of the original contestants (here called the “beneficiary of support”), but behaved aggressively toward the other original opponent (here called the “target of coalitionary aggression”). The donor and beneficiary of support were “coalition partners.” “Coalitionary aggression,” or “coalition formation,” referred more broadly to all agonistic acts involving at least 2 aggressors simultaneously joining forces to direct aggression toward the same target. “Coalition size” was the total number of coalition partners (e.g., donors of support plus the beneficiary of support) that joined forces to direct coalitionary aggression toward the same target.

We characterized the intensity of each aggressive act based on the highest level of threat involved, and thus the potential risk of injury, as low or high intensity (Van Horn, Wahaj, and Holekamp 2004). Based on the events immediately before the conflict, we assigned each agonistic interaction to 1 of 5 contexts. “Scapegoating” occurred when a target redirected aggression toward an individual not previously involved in the fight. Aggressive encounters directly related to fresh meat occurred in the context of “food.” Mothers directed “maternal interventions” toward targets in defense of their offspring. Aggressive acts were considered “pesky” when the aggressor attacked the target in response to the target disrupting ongoing behavior, as for example, when a target involved in play inadvertently bumped into the aggressor, who was sleeping. “Unprovoked” aggressions occurred in the absence of any stimuli obvious to observers, and in situations in which the aggressor and target had little or no contact during the minutes preceding the attack.

Behavioral data collection

We observed hyenas daily using our field vehicles as mobile blinds. We initiated an observation session each time we encountered one or more hyenas in a subgroup separated from other subgroups by at least 200 m, as detailed elsewhere (Smith et al. 2008). On arrival at each session, and during subsequent scans performed every 15–20 min, we recorded the identity and activity of every hyena present. We also recorded all occurrences of hunts, greetings, aggressive acts and appeasement gestures as critical incidents (Altmann 1974). We recorded the identity of lone hunters, and when multiple hunters cooperated during a hunting attempt, we recorded the order in which other hunters joined the original hunter in pursuit of prey. Because a hyena solicits a greeting by lifting its leg, we recorded which member of each dyad lifted her leg first during greetings.

When multiple females joined the same fight, we recorded the sequence in which individuals intervened and considered this to be a single coalitionary attack. We tabulated the hourly rate of coalition formation for each hyena belonging to a particular age-sex class category. To correct for variation in the amount of time we observed each hyena in situations during which it had opportunities to form coalitions, we based rates on sessions in which each focal animal was concurrently observed with at least one potential coalition partner and at least

one potential target. Specifically, we calculated the rate at which hyena A engaged in coalitions as ([number of coalitions hyena A formed to attack any clan member]/[number of hours hyena A was observed with at least 2 clan members]). We also calculated a rate of attack directed toward adult females as ([number of coalitions hyena A formed to attack any adult female]/[number of hours hyena A was observed with at least one adult female and at least one other clan member]).

Because the intended beneficiary of support is unclear in cases involving multiple aggressors (Silk 1992), we limited our model selection analyses to interventions by individual adult females in fights between 2 other adult females. Following Widdig et al. (2002, 2006), only when more than one supporter simultaneously intervened in the same dyadic conflict did we divide the event into multiple triads that included the same target and beneficiary but different donors. When multiple acts of support involving the same donor, beneficiary, and target of coalitionary aggression occurred within the same minute, we considered these interactions to be part of the original fight (Engh et al. 2005). We, therefore, considered potential donors to have only one opportunity per minute to join an ongoing fight between the same contestants.

Testing the kin selection hypothesis

To assess the effects of kinship on agonistic aiding, we assigned coefficients of relatedness to pairs of adult females based on demographic records combined with genetic data indicating paternity (see Engh et al. 2002; Van Horn, Engh, et al. 2004). Information on maternal and paternal lineages included up to 5 generations for each adult female whose presence as an adult in the clan overlapped with that of at least one of her surviving adult female relatives for some part of the 5-year study period ($N = 31$ adult females). Here, we assigned a coefficient of relatedness of zero only to those dyads for which 1) no genetic data indicated shared paternal descent, 2) females belonged to different matrilines, and 3) the pairwise Queller–Goodnight R -values for the dyad was less than -0.118 , a value that was less than that of 95% of the known half siblings ($N = 244$ pairs of half siblings) in our study clan.

We entered coefficients of relatedness directly into our statistical models as continuous predictor variables, but we also assigned pairs of adult females to one of the 3 following kinship categories to graphically represent our results and to perform social network analyses: Close kin (coefficient of relatedness (r) = 0.5; mother–daughter or full sisters), Distant kin (r = 0.125 to 0.25; grandmother–granddaughter, maternal or paternal half sisters, aunt–niece), and “Nonkin” ($r \sim 0.00$). On average, R -values within female dyads examined here were 0.462 ± 0.028 for close kin ($N = 25$), 0.279 ± 0.040 for distant kin ($N = 36$), and -0.228 ± 0.006 for nonkin ($N = 161$).

To simultaneously investigate patterns of support among multiple females, we constructed a representative, weighted network in NetDraw Version 2.064 for each kin group of adult females concurrently alive from January 1997 to December 1998. First, we constructed a directed graph to represent supportive interventions. Here arrows connecting females were called ‘arcs’. Arcs originated from each donor of support, and terminated at each beneficiary of support. Members of each dyad were connected by: 1) 2 arcs (reciprocal support), 2) 1 arc (unilateral support), or 3) zero arcs (no support). For each kinship group, we calculated the “density” of its support network as ([number of realized arcs]/[number of potential arcs]). Density is a measure of network cohesion that describes how well connected group members are to one another (Wasserman and Faust 1994; Wey et al. 2008). Second, we applied similar methods to construct an agonistic network for this same subset of adult females. In the coalitionary attack

network, arcs originated from intervening females and terminated at victims of coalitionary attacks.

Testing the reciprocal altruism hypothesis

We used partial matrix correlations to test the null hypothesis of no correspondence between support given and future commodities received among unrelated adult females (Hemelrijk 1990a, 1990b; de Vries 1993). This method accounts for non-independence among dyads. Following Hemelrijk (1990a), we limited this analysis to those cases in which each female was observed providing support or receiving a monitored commodity at least once, and both members of each dyad had the opportunity to intervene on behalf of the other. On average, members of nonkin dyads had 13 ± 1 opportunities to support one another (Range: 2–24 opportunities, $N = 49$ dyads).

We corrected for the number of opportunities available to females within each dyad to donate support as ([number of times female A joined to support female B in dyadic fights]/[number of dyadic fights in which A observed B fight with another adult female]) or to help during hunting as ([number of hunts in which A aided B]/[number of hunts in which A observed B hunting]). We calculated hourly rates of greeting initiation by A toward B as ([number of greetings A solicited from B]/[number of hours A and B spent together]). To measure social tolerance, we calculated hourly rates of dyadic aggression received as ([number of dyadic aggressive acts A directed toward B]/[number of hours A and B spent together]). We initially calculated separate rates for tolerance at food and away from food, but because both analyses produced equivalent results, we simply report a combined measure of tolerance.

Testing the direct benefits hypotheses

First, we tested the food access hypothesis by inquiring whether females were most likely to intervene in fights occurring over food, and during months of prey scarcity. We also asked if coalitionary aggression was more effective at displacing competitors from kills than was dyadic aggression by comparing the proportion of fights in which each female retreated from carcasses after receiving dyadic or coalitionary aggression from a particular female aggressor. Second, we tested the status quo hypothesis by comparing the relative ranks of intervening females and targets of coalitionary attacks. We also compared the proportion of interventions in which one adult female intervened on behalf of the dominant or subordinate contestant in dyadic fights.

Statistical analyses

We tested the effects of kinship, and variables indicating direct benefits, on intervention decisions using the generalized estimating equation (GEE) approach to logistic regression for fitting marginal generalized linear models (Liang and Zeger 1986; Hardin and Hilbe 2003; Faraway 2006). This procedure is particularly good at handling binary data, while including both fixed and random effects, when model residuals are non-independent and nonnormally distributed (Liang and Zeger 1986; Hardin and Hilbe 2003). GEE models for binomial data are similar to, but extend, traditional logistic regression by controlling for pseudoreplication resulting from repeated measures (Williams 2000; Carlin et al. 2001). We implemented these models using geepack (Halekoh et al. 2006) in R Version 2.6.2 (The R Foundation for Statistical Computing 2008).

Sample sizes, limited by knowledge of paternal kinship, did not permit us to build a single model. Instead, as done in similar studies (e.g., Schino, Tiddi, and Polizzi di Sorrentino

2007), we built 2 separate models to evaluate the effects of the explanatory variables on decisions made by females to 1) support beneficiaries and 2) direct coalitionary attacks toward targets when given the opportunity to do so. We used an information-theoretic approach to identify the most parsimonious models (Burnham and Anderson 1998). We sequentially entered and dropped all potential explanatory terms, including all 2-way interactions, and deemed the candidate model with the smallest quasilikelihood information criterion value to be the best model (Pan 2001).

We used STATISTICA 6.1 (StatSoft, Inc., Tulsa, OK, United States) to conduct post hoc comparisons. Whenever possible, we used GPOWER (Faul et al. 2007) to perform post hoc power calculations for nonsignificant, univariate analyses that were based on small sample sizes. We compared means for 2, or among more than 2, independent groups using the Mann-Whitney *U* and Kruskal-Wallis tests, respectively. We used matched pairs for post hoc comparisons whenever this was permitted by our sample sizes. We used Wilcoxon signed rank tests and Friedman's analysis of variance (ANOVA) for repeated measures when comparing the means of 2, or more than, dependent groups, respectively. We compared frequencies using the Chi-square test and tested correlations using Spearman's *R*. We applied the sequential Bonferroni adjustment to correct for multiple testing, and report *P* values in their corrected form (Rice 1989). Where appropriate, we report mean values \pm 1 standard error (SE) and sample proportions \pm 1 standard deviation (SD) for binomial trials (Agresti and Coull 1998). We based Kendall's (*Kr*) matrix partial correlations on 2000 random permutations and one-tailed probabilities because the reciprocal altruism hypothesis makes clear, directional predictions (Hemelrijk 1990a; de Vries 1993). All other tests were based on 2-tailed probabilities and considered significant at alpha less than 0.05.

RESULTS

Coalitions formed by primates and nonprimates share similar characteristics

Overall, the results from our literature review suggest that primates and nonprimates fail to differ significantly with respect to the proportion of agonistic interactions that involve coalitions, rates at which individuals form coalitions, mean coalition size, or the proportion of coalitions involving only 2 allies (Table 1). The available data suggest that primates of both sexes are significantly more likely to form intragroup coalitions (87.5% of 32 species studied) than are nonprimates of both sexes (58.8% of 17 species, Chi-square test: $\chi^2 = 5.24$, degrees of freedom = 1, *P* = 0.022). However, this pattern may be attributed to the literature bias, favoring studies on intragroup coalitions in primates (72 references available). Only 26 references on nonprimates were found. Nonetheless, adult animals joined forces during intragroup conflicts in virtually all species reviewed, except for some species of pair-bonded birds for which limited data are currently available. Finally, we failed to detect any differences in the evolutionary forces favoring coalition formation between primates and nonprimates. In fact, although evidence of reciprocal trading of coalitionary support among nonkin was generally rare, most species reviewed here gained both direct and indirect benefits from participating in coalitionary interventions.

Size, composition, and context of intragroup coalitions among spotted hyenas

Coalition formation among hyenas of all age-sex classes

On average, from 1996 to 2000, our study clan contained 75 \pm 1 hyenas (Range: 58 to 95), including 23 \pm 1 adult females, for

each month of the study (Range: 21 to 25, Table 2). We observed 11194 aggressive interactions and 6944 greetings among all clan members. Coalitions formed during 14% of aggressive interactions ($N = 1589$ coalitions). Whereas affiliative greetings occurred at a rate of 1.7 greetings per hour, intragroup coalitions formed only once every 2.7 h of observation (0.38 coalitions/h). Based on these 1589 coalitions, we calculated the frequency, percentage, hourly rate and mean size of coalitions for each clan member ($N = 185$ subjects, including 37 adult females). Unless stated otherwise, sample sizes were the same as the number of subjects belonging to each age-sex category represented in Table 2.

Overall, the rates at which hyenas formed coalitions varied among age-sex classes (Kruskal-Wallis test: $H_{4,208} = 36.50$, *P* = 0.023, Table 2B). Adult females ($N = 37$) directed coalitionary attacks toward clan members of any age-sex class at higher hourly rates than did immigrant males ($N = 38$, Mann-Whitney *U* tests: $Z = -2.84$, *P* = 0.022), but at rates similar to those of juvenile males ($N = 52$) or females ($N = 57$), and adult natal males ($N = 24$, $Z = 0.07$, 0.62, and -1.30 , respectively; $P \geq 0.582$ for all cases). Modal coalition size (71% of coalitions) was 2 hyenas, and coalition size did not vary significantly among age-sex classes (Kruskal-Wallis test: $H_{4,179} = 7.65$, *P* = 0.11, Table 2).

Coalition formation among adult female hyenas

Adult females ($N = 37$) were the victims of 51% of all coalitionary attacks; this was disproportionately high based on their representation in the clan (31% of clan). In fact, adult females received a greater proportion of attacks (27 \pm 2%, $N = 37$ victims) in the form of coalitionary aggression than did other members of the clan (10 \pm 1% of attacks, $N = 148$ victims, Mann-Whitney *U*-test: $Z = 6.941$, *P* < 0.00001). Moreover, the hourly rates at which hyenas directed coalitionary attacks toward adult female victims varied among age-sex classes of aggressors (Kruskal-Wallis test: $H_{4,208} = 36.5$, *P* < 0.0001, Table 2). Natal animals were significantly more likely to direct coalitionary attacks toward adult females than were immigrant males (Mann-Whitney *U*-tests: $U \leq -2.769$ and $P < 0.0006$ for all comparisons, see Table 2 for sample sizes). On average, adult females directed coalitionary attacks toward other females more often than did individuals belonging to any other age-sex category, but we detected no sex differences in the rates at which juveniles or natal adults directed coalitionary attacks toward adult females (Mann-Whitney *U*-tests: $U = 1468.5$ and 352.0 , *P* = 0.934 and 0.528, respectively).

Overall, adult females participated in 480 coalitions attacking other adult females (Table 2). Of these attacks, 57% involved juveniles joining forces with adult females and 29% involved 2 or more adult females joining forces to attack a third adult female. Adult females never joined forces with immigrant males to attack adult females. Most (86%) all-female coalitions contained 2 partners, 12% contained 3 partners, and only 2% contained more than 3 partners. Fifty four percent of third-party interventions in disputes between 2 adult females were by lone adult females. Thus, adult females intervened more often than expected based on their representation in the clan (31% of clan). Adult females intervened in fights between adult females about 3 times more often than did juveniles of both sexes and almost 6 times more often than did adult natal males (Table 2).

Social and ecological contexts of interventions by adult female hyenas

Lone adult females intervened in 81 of 1171 (7%) ongoing dyadic fights between other adult females, and a context could be assigned to 63 of these interventions. Overall, these interventions were more frequent during unprovoked fights (56%)

Table 1
Patterns of coalition formation during intragroup conflicts

Species	Subject # (group size) ^{Type}	Donor and beneficiary		% Of aggressive acts	Coalitions per hour		Coalition size: mean (range)	% Of coalitions w/2 allies	Kinship	Evidence for kin selection, reciprocity, or direct benefits			Sources
		Age	Sex		Per group	Per subject				—	—	Y*	
A) Primates													
<i>Homo sapiens</i> (humans)	20 ^W —	JJ BB	BB BB	15% —	5.2 —	0.3 —	— —	— —	— —	— —	Y*	Y ^R	Grammer (1992) Flinn et al. (2005)
	Mean across studies:			15%	5.2	0.3	—	—	—	—	—	—	—
<i>Pan troglodytes</i> (chimpanzees)	20–23 ^C	BB	BB	40%	1.7	0.09	3.6 (2–13)	42%	M	Y	Y	Y ^{CH,R}	de Waal and van Hooff (1981), de Waal (1984), de Waal and Luttrell (1988)
	9 (20–30) ^C	AA	MM	—	0.4	0.04	—	—	M	—	Y*	—	Hemelrijk and Ek (1991)
	16 (20–30) ^C	AA	FF	—	0.3	0.02	—	—	M	—	Y*	—	Hemelrijk and Ek (1991)
	9 (82) ^W	AA	MM	19%	0.1	0.01	? (2–3)	—	—	—	—	—	Nishida and Hosaka (1996) ^a , Uehara et al. (1994) ^a
	8 (?) ^W	AA	MM	25%	0.1	0.01	2.7 (2–3)	84%	—	—	—	Y ^R	Boesch and Boesch-Achermann (2000) ^a
	22–24 (~150) ^W	AA	MM	—	0.5	0.06	—	—	M	N	Y*	Y ^R	Mitani et al. (2000, 2002), Watts (2002) ^a
	Mean across studies:			25%	—	0.08	3.2 (2–13)	63%	—	—	Y*	Y ^R	—
<i>Pan paniscus</i> (bonobo)	6 (8) ^W	AA	BB	14%	0.6	0.1	2.4 (2–5)	58%	—	—	Y*	Y ^R	Stevens et al. (2005), Vervaecke et al. (2000)
<i>Gorilla g. beringei</i> (mountain gorilla)	11–18 (13–24) ^W	AA	BF	4%	—	—	—	77%	M,P	Y	Y*	—	Watts (1997)
<i>Papio anubis</i> (olive baboon)	3–1 (?) ^W	AA	MM	69%	—	—	—	—	—	—	Y*	—	Packer (1977) ^b
<i>Papio papio</i> (Guinea baboon)	30 (34) ^C	BB	BB	15%	0.4	0.01	—	—	M	—	—	—	Petit et al. (1997)
<i>Papio cynocephalus</i> (yellow baboon)	8 (24) ^W	AA	FF	7%	—	—	—	—	—	—	Y*	—	Seyfarth (1976)
	6 (41–46) ^W	BB	FF	32%	0.1	0.02	—	—	M	Y	—	Y ^R	Walters (1980)
	6–7 (51–57) ^W	AA	MM	8%	0.3	0.05	—	—	—	—	N*	Y ^{CH}	Noë (1984, 1990) ^c
	12 (78–90) ^W	AA	MM	17%	0.03	0.003	2.1 (2–3)	89%	—	—	N*	Y ^{CH}	Bercovitch (1988) ^c
	7–17 (20–57) ^W	AA	FF	8% (6–9)	—	—	2.7 (2–?)	—	M	Y	N	Y ^R	Silk et al. (2004) ^d
	Mean across studies:			14%	—	0.02	2.4 (2–?)	89%	—	—	—	Y ^R	—
<i>Papio hamadryas</i> (hamadryas baboon)	6 (12) ^C	AA	FF	38%	0.2	0.05	—	—	—	—	—	—	Stammbach (1978) ^e
<i>Theropithecus gelada</i> (gelada baboon)	14 ^C 3–6 ^W	BB	BB	21%	4.4	0.3	—	—	—	—	—	—	Bramblett (1970) Dunbar (1980)
	Mean across studies:			21%	—	0.3	—	—	—	—	—	—	—
<i>Mandrillus sphinx</i> (mandrill)	12 ^C	BB	BB	17%	1.5	0.1	2.3 (2–3)	72%	—	—	—	—	Schnino, G. (unpublished data)
<i>Macaca arctioides</i> (stump-tail macaque)	9 (68) ^{SC}	AA	BB	4%	—	0.01	—	—	—	—	N	Y ^R	Richter et al. (2009)
<i>Macaca assamensis</i> (Assamese macaque)	14 (25) ^C	AA	BB	—	—	—	—	—	M	—	Y	Y ^R	de Waal and Luttrell (1988)
<i>Macaca radiata</i> (bonnet macaque)	25 (64) ^{SC}	AA	BB	28%	0.3	0.01	—	—	—	—	—	Y ^R	Cooper et al. (2005), Cooper and Bernstein (2008)
	10 (72–80) ^C	AA	FF	—	0.3	0.03	—	—	M	Y	N	Y ^R	Silk (1982)
	16 (54) ^C	AA	MM	25%	1.5	0.09	3.0 (2–9)	78%	M	Y	Y	Y ^R	Silk (1992, 1993)

Table 1
continued

Species	Subject # (group size) ^{Type}	Donor and beneficiary		Coalitions per hour		Coalition size: mean (range)	% Of coalitions w/2 allies	Kinship	Evidence for kin selection, reciprocity, or direct benefits	Sources		
		Age	Sex	% Of aggressive acts	Per group							
	Mean across studies:			25%	—	0.06	3.0 (2–9)	78%				
<i>Macaca fuscata</i> (Japanese macaque)	17–24 ^C	BB	BB	—	0.1	0.01	—	M	Y	N	Y ^{R,CH}	
	14 (37) ^C	AA	FF	6%	1.4	0.1	—	M	—	—	Y ^{R,CH}	
	22 (24) ^C	BB	BB	14%	0.06	0.003	—	M	—	—	Petit et al. (1997)	
	8–20 (25–55) ^W	AA	FF	—	0.1	0.01	—	M	Y	N	Ventura et al. (2006) ^d	
	57 (57) ^C	BB	BB	16%	3.7	0.07	—	M	Y	Y	Schino, di Sorrentino, and Tiddi (2007), Schino, Tiddi, and Polizzi di Sorrentino (2007)	
	Mean across studies:			12%	—	0.04	—	86%				
<i>Macaca mulatta</i> (rhesus macaque)	20–24 (50–62) ^C	AA	BB	—	—	—	—	M	Y	Y	de Waal and Luttrell (1986, 1988)	
	18 (~62) ^{SC}	BB	FF	—	0.1	0.007	—	M	—	—	Datta (1988) ^g	
	12 (?) ^W	AA	FF	—	—	—	—	M	Y	N	Kapsalis and Berman (1996)	
	39 (67–94) ^C	AA	BB	—	0.6	0.1	—	M	Y	N	Matheson and Bernstein (2000)	
	34 (172) ^W	AA	FF	—	1.1	0.03	—	M,P	Y	—	Widdig et al. (2006)	
	Mean across studies:			—	—	0.05	—	—				
<i>Macaca fascicularis</i> (long-tailed macaque)	14–17 ^C	BB	BB	28%	3.4	0.2	2.7 (2–7)	—	—	—	de Waal (1977)	
	21 (30–40) ^C	AA	FF	—	—	—	—	M	Y	Y	Hemelrijk (1994)	
	Mean across studies:			28%	—	0.2	2.7	—				
<i>Macaca nemestrina</i> (pig-tailed macaque)	49 ^C	BB	BB	46%	4.2	0.09	—	—	M	Y	N	Massey (1977)
<i>Macaca tonkeana</i> (tonkean macaque)	19–21 ^{SC}	BB	BB	10%	0.4	0.02	—	—	M	Y	—	Petit and Thierry (1994)
<i>Macaca nigra</i> (crested macaque)	20 (23) ^C	BB	BB	16%	0.2	0.01	—	—	M	—	—	Petit et al. (1997)
<i>Macaca sylvanus</i> (barbary macaque)	51 (~250) ^{SC}	AA	FF	—	0.1	0.002	—	—	M	Y	—	Prudhomme and Chapais (1993) ^e
	31 (81) ^{SC}	AA	MM	—	0.5	0.02	3.0 (2–8)	51%	M	Y	Y	Widdig et al. (2000)
	Mean across studies:			—	—	0.01	3.0 (2–8)	51%				
<i>Presbytis entellus</i> (Hanuman langurs)	5 (16–28) ^W	AA	MM	15%	0.04	0.008	—	—	—	—	Sommer (1988) ^c	
	13 (39) ^W	AA	FF	—	0.02	0.002	—	—	M	Y	—	Borries (1993)
	Mean across studies:			15%	—	0.005	—	—				
<i>Cercopithecus aethiops</i> (vervet monkey)	17 (18) ^W	BB	BB	21%	1.7	0.1	—	—	M,P	Y	Y	Hunte and Horrocks (1987) ^f
	23 (10–29) ^W	AA	FF	—	—	—	—	—	—	Y*	—	Seyfarth (1980) ^d
	Mean across studies:			21%	—	0.1	—	—				
<i>Cercocebus torquatus atys</i> (sooty mangabey)	24 (78–100) ^W	AA	FF	3%	0.09	0.004	—	—	—	—	Y ^R	Range and Noë (2002)
	12 (27–28) ^W	BJ	BB	—	0.3	0.02	—	—	M	Y	—	Range (2006)
	Mean across studies:			3%	—	0.01	—	—			Y ^R	
<i>Lemur catta</i> (ring-tailed lemur)	10 (20) ^{SC}	AA	BB	1%	0.2	0.02	—	—	M	Y	—	Pereira and Kappeler (1997) ^d
<i>Eulemur fulvus rufus</i> (red-fronted lemur)	8 (10) ^{SC}	AA	BB	4%	0.8	0.1	—	—	M	Y	N*	—
<i>Saimiri oerstedi</i> (squirrel monkeys)	23 ^W	BB	BB	—	—	—	? (2–12)	—	M	Y	—	Pereira and Kappeler (1997) ^d , Pereira and McGlynn (1997) ^d , Baldwin and Baldwin (1972)

Table 1
continued

Species	Subject # (group size) ^{Type}	Donor and beneficiary		% Of aggressive acts	Coalitions per hour		Coalition size: mean (range)	% Of coalitions w/2 allies	Kinship	Evidence for kin selection, reciprocity, or direct benefits			Sources
		Age	Sex		Per group	Per subject				—	—	—	
<i>Saimiri boliviensis</i> (squirrel monkeys)	45–75 ^W	BB	BB	—	—	—	—	—	M	Y	—	—	Boinski et al. (2005)
<i>Cebus apella</i> (brown/tufted capuchin)	13 ^C	BB	BB	24%	0.3	0.02	2.6 (2–7)	71%	M	Y	N	—	Schino et al. (2009)
<i>Cebus capucinus</i> (white-faced capuchin)	6 (21) ^W 4 (21) ^W 30–35 ^W	AA AA BB	FF MM BB	— — 16%	0.1 0.09 —	0.02 0.02 —	2.0 (2–3) — —	96% — —	— — —	— N [*] —	Y ^R Y ^R Y	Perry (1996) Perry (1998) Vogel et al. (2007) ^{c,d}	
	Mean across studies:			16%	—	0.02	2.0 (2–3)	96%					
<i>Cebus olivaceus</i> (wedge-capped capuchin)	3–9 (7–26) ^W	AA	FF	—	—	—	—	—	M	—	Y*	—	O'Brien (1993)
<i>Alouatta palliata</i> (mantled howler monkey)	18 (?) ^W	AA	BB	—	0.06	0.003	2.0 (2–3)	96%	M	Y	—	Y ^R	Jones (1980)
<i>Ateles geoffroyi</i> (spider monkey)	4–11 (20–35) ^W 5 (20) ^W	BB AA	MM MM	— —	— —	— —	4.3 (4–5) 3.4 (2–5)	0% 25%	— —	— —	— —	Y ^{CH} Y ^{CH}	Campbell (2006) ^h Valero et al. (2006) ^h
	Mean across studies:			—	—	—	3.9 (2–5)	13%					
B) Nonprimates													
<i>Crocuta crocuta</i> (spotted hyena)	10 ^C 58–95 ^W	JJ BB	BB BB	— 14%	2.6 0.4	0.3 0.1	3.2 (2–9) 2.4 (2–7)	47% 71%	— M,P	— Y	— N	Y ^R Y ^{R,CH}	Zabel et al. (1992) ^d Current study, ^a Engh et al. (2000), Wahaj et al. (2004)
	Mean across studies:			14%	—	0.2	2.8 (2–9)	59%					
<i>Panthera leo</i> (African lion)	3 (?) ^W	AA	FF	—	—	—	3	0%	M	Y	—	—	Schaller (1972)
<i>Nasua nasua</i> (ring-tailed coati)	8–30 ^W 13 ^C	BB AA	BB FF	6% 38%	— 0.9	— 0.07	2.5 (2–6) 2.5	69% 64%	— —	— —	— Y*	— —	Hirsch (2007) ^d Romero and Aureli (2008) ⁱ
	Mean across studies:			22%	—	0.07	2.5 (2–6)	67%					
<i>Nasua narica</i> (white-nosed coati)	6–22 ^W	BB	BB	68%	—	—	—	—	M,P	Y	—	—	Gompper et al. (1997) ^d
<i>Canis lupus</i> (grey wolf)	4–23 ^C 10–12 ^C 15 ^C	BB BB AA	BB BB BB	— 2% 4%	— 0.06 9.3	— 0.005 0.6	— 5.6 (2–11) —	— 4% —	— — M,P	— — —	— — —	Y ^R Y ^R Y ^R	Zimen (1976) Fentress et al. (1987) Derix et al. (1993)
	Mean across studies:			3%	—	0.3	5.6 (2–11)	4%					
<i>Lycaon pictus</i> (African wild dog)	38 ^W	BB	BB	—	0.2	0.006	—	50%	M,P	—	—	Y ^R	de Villiers et al. (2003)
<i>Tursiops aduncus</i> (bottlenose dolphin)	21 (~300) ^W	AA	MM	—	0.5	0.1	2.9 (2–5)	68%	M,P	Y	—	Y	Connor et al. (1992) ^{a,c} Parsons et al. (2003) ^b Krützen et al. (2003)
<i>Loxodonta africana</i> (African elephant)	2–25 ^W 6–12 (18–39) ^W	AJ AA	FB FF	— 4%	— —	— —	— 2.2 (2–4)	— 84%	M M,P	Y Y	— —	— —	Lee (1987) ^d Archie, Moss, and Alberts (unpublished data)
<i>Equus quagga</i> (plains zebra)	23–29 ^{SC}	BB	BB	11%	—	—	—	—	M	Y	—	Y	Schilder (1990) ^c
<i>Equus caballus</i> (wild horse)	13 (94) ^{SC}	AA	MM	3%	0.01	0.0008	2 (2)	100%	M,P	N	Y	Y ^R	Feh (1999) ^c
<i>Dama dama</i> (fallow deer)	34–42 (~570) ^W	AA	MM	9%	0.04	0.001	—	—	—	—	—	Y ^R	Jennings et al. (2009), Jennings JE and Gammell DJ (unpublished data)
<i>Ovis aries</i> (feral sheep)	8 (81) ^{SC}	AA	MM	—	0.4	0.05	—	—	—	—	—	—	Rowell and Rowell (1993) ^a

Table 1
continued

Species	Subject # (group size) ^a	Donor and beneficiary		Coalitions per hour		Coalition size: mean (range)	% Of coalitions w/2 allies	Kinship	Evidence for kin selection, reciprocity, or direct benefits	Sources	
		Age	Sex	% Of aggressive acts	Per group						
<i>Ovis canadensis</i> (bighorn sheep)	24–28 (66–68) ^w	BB	MM	10%	—	—	2.2 (2–3)	80%	M,P	Y — Y ^R	Pelchat (2008)
<i>Anser anser</i> (greylag geese)	53 (170) ^{SC}	BB	BB	10%	18	0.3	2.2 (2–6)	86%	M,P	Y — Y ^R	Scheiber et al. (2005, 2009) ^j
<i>Cygnus bewickii</i> (Bewick's swan)	~250 (583) ^w	AJ	BB	34%	—	—	? (2–3)	—	M,P	Y — Y ^R	Scott (1980)
<i>Corvus frugilegus</i> (rook)	12 ^c	JJ	BB	—	—	—	—	—	M,P	N Y* YCH	Emery et al. (2007)
<i>Corvus monedula</i> (jackdaw)	26 (36) ^c	AA	BB	—	—	—	—	—	—	— Y ^{CH}	Wechsler (1988)

Summary										
% Of studies per species with evidence for:										
Mean ± SE (range, N = species w/data ^k)	% Of aggressive acts (that were coalitions)	Coalitions per hour per subject	Coalition size	% Of coalitions w/ only 2 allies	Kin selection	Reciprocal altruism (kinship controlled)	Direct benefits			
A) Primates	19 ± 3% (2–69%, N = 25)	0.07 ± 0.02 (0.002–0.3, N = 26)	2.9 ± 0.2 (2–13, N = 11)	71 ± 7% (0–100, N = 12)	98 ± 2% (N = 20)	52 ± 13% (N = 11)	100 ± 0%			
B) Nonprimates	17 ± 8% (3–68%, N = 11)	0.11 ± 0.04 (0.0008–0.6, N = 9)	2.7 ± 0.3 (2–11, N = 10)	63 ± 11% (0–100, N = 11)	83 ± 10% (N = 14)	50 ± 50% (N = 2)	100 ± 0%			
Mann-Whitney U-tests (Primates vs. Nonprimates)	Z = 1.31, P = 0.19 Effect size: 0.134 Power = 0.072	Z = 0.44, P = 0.66 Effect size: 0.447 Power = 0.285	Z = -1.20, P = 0.23 Effect size: 0.166 Power = 0.074	Z = -0.34, P = 0.73 Effect size: 0.250 Power = 0.110	Z = 1.25, P = 0.21 Effect size: 0.528 Power = 0.438	Z = 0.10, P = 0.92 Effect size: 0.028 Power = 0.050	(N/A)			
Overall	19 ± 3%	0.08 ± 0.02	2.8 ± 0.2	67 ± 6%	92 ± 5%	51 ± 12%	100 ± 0%			

Subject number = number of animals that could potentially provide coalitionary support. Group size = total number of all animals in study group, if different from subject number. Type: C = captive, SC = semicaptive (including provisioned, free-ranging groups), or W = wild study group. Donor and beneficiary ages and sexes: J = juveniles (any immature animal), A = adults (any reproductively mature animal), or B = both juveniles and adults; M = males, F = females, or B = both sexes; % of aggressive acts (that were coalitions) = $(100 * [\text{number of coalitions}] / [\text{number of all aggressive interactions}])$; Coalitions per hour per group = (number of coalitions recorded as critical incidents)/(number of hours in which at least one potential donor, at least one potential beneficiary, and at least one potential target were concurrently observed); Coalitions per hour per subject = (number of coalitions)/(number of hours in which at least 3 subjects were concurrently observed)/(mean number of subjects in group or subgroup). Hourly rates were based on critical incident or ad libitum sampling; the latter technique typically represented a complete record of coalitions because coalitions are noisy and conspicuous events (Altmann 1974). Mean coalition size (range) = average number of coalition partners that join forces to direct coalitionary aggression toward the same target(s). % of coalitions with only 2 allies = $100 * [(\text{number of coalitions with only 2 partners joining forces}) / (\text{total number of coalitions})]$. Kinship: M = maternal kinship and P = paternal kinship reported. Evolutionary forces of kin selection, reciprocal altruism, or direct benefits?: Y = yes (evidence supporting the hypothesis), N = no (evidence against the hypothesis), and — = hypothesis was not evaluated. Evidence for the reciprocal altruism hypothesis included data reporting exchanges of support for itself (reciprocity) or for other currencies (interchange). An * indicates that studies of reciprocal altruism failed to control for maternal kinship; only those studies that controlled for maternal kinship were included in the summary analysis. A superscript of R or CH indicates that direct benefits accrued in the form of animals attacking subordinates or dominants to either reinforce or challenge, respectively, the status quo.

^a Hourly rates were divided by mean subgroup size to estimate rates on a per subject basis because not all members of the fission-fusion society were simultaneously available as potential coalition partners or targets.

^b Data based only on interventions in disputes in response to adult males soliciting help from donors.

^c Data suggest that donors gain direct benefits in the form of increased access to immediate feeding or mating opportunities rather than, or in addition to, influencing rank relationships per se.

^d Data generated from multiple study groups.

^e Data based on all occurrences of peaceful and aggressive interventions during ongoing interactions of any type between 2 other group members.

^f Data limited to interventions during conflicts among individuals belonging to different matrilines.

^g Data based only on interventions during ongoing disputes between 2 siblings.

^h Data based on coalitionary attacks by males during ultimately lethal, intragroup conflicts.

ⁱ One female was immature during the study whereas all other data were collected on adult females.

^j Aggressions only recorded during feeding time.

^k Pair-bonded rock pigeons (*Columba livia*, Lefebvre and Henderson 1986) also join forces to direct coalitionary aggression toward conspecifics in their flocks, but comparable data were unavailable.

Table 2

Patterns of coalition formation among spotted hyenas belonging to different age-sex classes within a single, large clan in the Masai Mara National Reserve, Kenya

Demography of study clan ^a		Coalitionary attacks directed toward any member of the clan ^b			Coalitionary attacks directed toward any adult female victim ^c			Interventions in female–female fights ^d
Age–sex class	̄x hyenas/month (% of clan) (N = total subjects)	Coalition # (% of all aggressive acts) ^e	Mean ± SE hourly rate per subject	Mean ± SE coalition size per subject	Coalition # (% of all aggressive acts) ^e	Mean ± SE hourly rate per subject	Mean ± SE coalition size per subject	Intervention # (% of all third party interventions) ^f
Adult females	̄x = 23 (30.7) (N = 37)	824 (52)	0.16 ± 0.02	2.5 ± 0.03	480 (59)	0.09 ± 0.01	2.7 ± 0.08	81 (54)
Juvenile females	̄x = 14 (18.7) (N = 57)	711 (45)	0.16 ± 0.02	2.5 ± 0.03	388 (48)	0.04 ± 0.005	2.8 ± 0.07	28 (18.5)
Juvenile males	̄x = 14 (18.7) (N = 52)	691 (43)	0.19 ± 0.02	2.5 ± 0.03	321 (40)	0.04 ± 0.006	2.8 ± 0.08	28 (18.5)
Natal adult males	̄x = 7 (9.3) (N = 24)	302 (19)	0.13 ± 0.02	2.6 ± 0.05	128 (16)	0.08 ± 0.02	2.7 ± 0.10	14 (9)
Immigrant adult males	̄x = 17 (22.6) (N = 38)	230 (15)	0.09 ± 0.01	2.5 ± 0.01	67 (8)	0.02 ± 0.004	3.1 ± 0.10	0 (0)
Entire clan	̄x = 75 hyenas (N = 185) ^g		0.14 ± 0.12 (range: 0–0.79) ^h	2.6 ± 0.03 (range: 2–7)		0.04 ± 0.003 (range: 0–0.38) ⁱ	2.8 ± 0.04 (range: 2–6)	151

^a Mean ± SE hourly rates and coalition sizes were calculated for individuals belonging to each age–sex class based on the same sample sizes presented here.^b Characteristics of coalitions that included at least one partner belonging to the specified age–sex class that were directed towards any member of the clan.^c Characteristics of coalitions that included at least one partner belonging to the specified age–sex class that were directed towards an adult female victim.^d Frequency and percentage of third-party interventions in which a lone individual intervened during disputes between two adult females.^e Because most coalitions involved multiple individuals from different age–sex classes joining forces to target the same victim (see text for details), the sum of all category percentages exceeds 100.^f Percentages sum to 100 because third-party interventions were limited to those interactions in which only a single hyena belonging to the relevant age–sex class intervened.^g Because several individuals belonged to multiple age classes during this study, the total hyenas observed was less than the sum of hyenas belonging to the different age–sex classes.^h On average, we observed 0.38 coalitions form per hour to attack any member of the clan (1,591 coalitions ÷ 4,216 hours).ⁱ 0.40 coalitions form per hour to attack female victims (811 coalitions ÷ 2,040 hours) within subgroups in which it was possible for such coalitions to form.

than during fights in the contexts of food (22%), maternal intervention (16%), pesky (6%), or scapegoating (0%). After correcting for opportunities to join, we found that the tendency for adult females ($N = 24$) to intervene in ongoing fights varied significantly with the context of the original fight (Friedman's ANOVA: $F_{4,24} = 32.7, P < 0.00001$, Figure 1). Specifically, females were more likely to intervene in unprovoked dyadic fights than in fights involving scapegoating or food (Wilcoxon signed-ranks tests: $Z \geq 3.24$ and $P \leq 0.005$ in both cases). Females also intervened to a greater extent over food than during scapegoating ($Z = 3.059$ and $P = 0.016$).

In those fights ($N = 744$) for which detailed information was available on all behaviors displayed by the original attacker, we investigated the possibility that attackers bristled their tails to solicit support from bystanders. Surprisingly, females were significantly less likely to donate support in fights during which original attackers bristled their tails ($2.3 \pm 1.2\%$ of opportunities) than when attacking females failed to do so ($2.6 \pm 0.3\%$ of opportunities; Wilcoxon Signed Ranks Test: $N = 25$ donors, $Z = 2.224, P = 0.026$). It remains possible that females solicit help using subtle forms of solicitation not obvious to human observers.

Modeling factors to explain interventions by adult female hyenas

We used model selection to assess the effects of kinship, and variables indicating direct benefits, on the tendency for females to intervene in disputes between adult females. We only included those pairs of adult females for which we could unambiguously assign a coefficient of relatedness in our statistical models. Multiple females were often simultaneously available to intervene at each fight; each focal female ($N = 31$) represented in the statistical models, on average, provided support or directed coalitionary attacks, respectively, in $2.7 \pm 0.7\%$ and $1.9 \pm 0.5\%$ of the cases in which she was available to do so. The same adult females ($N = 31$) were included in both models, and the extent to which females intervened in fights

was statistically equivalent for both data sets (Wilcoxon Signed-Ranks Test: $N = 31$ females, $Z = 1.153, P = 0.249$, Effect size: 0.257, Power = 0.403). Final models identified the subset of candidate predictor variables that most strongly structure patterns of coalitionary support and attacks (Tables 3 and 4). Neither model retained strongly intercorrelated variables ($r^2 \leq 0.10$).

Kin selection hypothesis

Nepotistic coalitionary support among adult females

As predicted by the kin selection hypothesis, interventions by adult females were highly nepotistic (Table 3, Figure 2). Females biased support toward kin, and did so regardless of the intensity of the original fight (Kinship * Intensity interaction: -0.019 ± 0.150 , Wald Statistic = 0.015, $P = 0.902$). This pattern is best illustrated by placing a subset of female dyads, all of known kinship and all present together as adults in the clan, into a weighted cooperation network (Figure 3). Network density increased with the level of relatedness among kinship groups. The density of the close kin network (realized arcs/total possible arcs = 0.38) was more than 3 times that of distant kin (0.12) and more than 7 times that of nonkin (0.05, Figure 3). In addition to providing a concrete example of interindividual dynamics and coalition formation within a single "cohort" of adult females, these diagrams show how female dyads are embedded in the larger network of female social relationships. They also highlight our particularly striking finding that, despite the relative paucity of close kin as potential allies, close kin were clearly the likeliest allies.

Overall, the extent to which adult females intervened on behalf of their sisters varied with their genetic relationship to those sisters (Kruskall-Wallis ANOVA: $H_{2,34} = 7.025, P = 0.030$). First, adult females supported their full sisters ($10.1 \pm 3.6\%, N = 8$ donors) 3 or 4 times more often than they supported their maternal half sisters ($2.9 \pm 1.3\%, N = 9$ donors) or paternal half sisters ($1.5 \pm 1.0\%, N = 17$ donors),

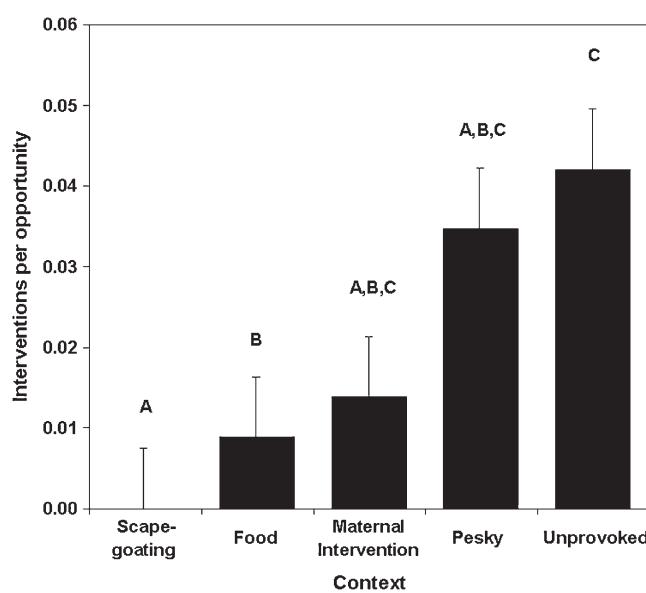


Figure 1

Mean \pm SE interventions per opportunity in which the same adult females ($N = 24$) intervened in fights between 2 other adult females based on the context of the original fight. Different letters above bars indicate statistically significant differences after correcting for multiple testing.

Table 3

Independent variables predicting patterns of coalitionary support donated by adult females on behalf of adult female beneficiaries during interventions in dyadic fights

Coefficients	Estimate \pm SE	Wald Statistic	P value
(Intercept)	-3.317 ± 0.446	55.370	0.00001
Higher-ranking (HR) bystander number	-0.248 ± 0.043	32.769	0.00001
Kinship	3.472 ± 1.043	11.081	0.00087
Beneficiary subordinate to potential donor	0.538 ± 0.389	1.917	0.16620
Food	-0.069 ± 0.081	0.738	0.39018
HR bystander number *	0.435 ± 0.126	12.009	0.00053
Kinship			
Beneficiary subordinate	0.392 ± 0.099	15.559	0.00008
* Food			

Comparison of the candidate models ruled out the following additional factors as predictors of whether or not females provided coalitionary support: absolute social rank of the potential donor (Estimate \pm SE: 0.024 ± 0.041 , Wald Statistic = 0.337, $P = 0.562$), intensity of the original fight (-0.053 ± 0.057 , Wald Statistic = 0.844, $P = 0.358$) and prey abundance (-0.042 ± 0.071 , Wald Statistic = 0.346, $P = 0.556$). The overall fit of the model yielded a Wald-type statistic of 375.8, whose distribution is approximately Chi-squared. Model results are based on adult females intervening in 45 out of 1477 ongoing fights ($N = 241$ dyads). On average, each adult female ($N = 31$) intervened to donate support in $2.7 \pm 0.7\%$ of opportunities that she was available to do so.

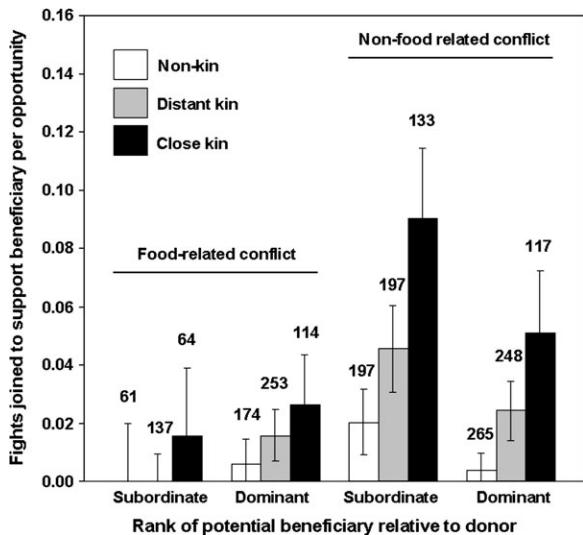
Table 4

Independent variables predicting patterns of coalitionary attacks directed by adult females toward adult female victims during interventions in dyadic fights

Coefficients	Estimate \pm SE	Wald Statistic	P value
(Intercept)	-5.274 ± 1.040	25.734	0.00001
Food	-2.219 ± 0.975	5.180	0.02284
Victim subordinate to potential attacker	2.263 ± 1.048	4.665	0.03077
Intensity of original fight	-1.203 ± 0.557	4.664	0.03080

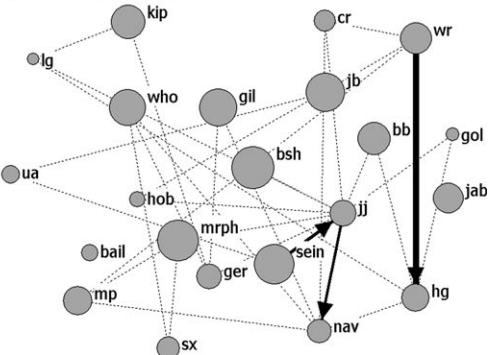
Model selection excluded the following variables as useful predictors of whether or not females initiated coalitionary attacks: absolute social rank of the potential attacker (-0.108 ± 0.068 , Wald Statistic = 2.545, $P = 0.111$), prey abundance (-0.229 ± 0.479 , Wald Statistic = 0.229, $P = 0.632$), the number of higher-ranking bystanders present (-0.100 ± 0.223 , Wald Statistic = 0.202, $P = 0.653$), the absolute rank distance between the potential attackers and victims (-0.020 ± 0.053 , Wald Statistic = 0.142, $P = 0.706$), and the kinship between potential attackers and victims (0.074 ± 1.155 , Wald Statistic = 0.004, $P = 0.949$). The overall fit of the model yielded a Wald-type statistic of 257.4, whose distribution is approximately Chi-squared. Model results are based on adult females intervening in 22 out of 1477 ongoing fights ($N = 31$ females). On average, each adult female ($N = 31$) intervened to direct coalitionary attacks toward other adult females in $1.9 \pm 0.5\%$ of opportunities that she was available to do so.

respectively. This bias in support toward full sisters remained statistically significant for paternal half sisters after correcting for multiple testing (Mann–Whitney U -test: $Z = 2.462$, $P = 0.014$, Effect size: 1.093, Power: 0.859). However, the difference between full siblings and maternal half sisters did not remain statistically significant after the correction (Mann–Whitney U -test: $Z = -1.000$, $P = 0.317$, Effect size: 0.925, Power: 0.608). Although females were twice as likely to donate support to maternal than paternal half sisters, this difference

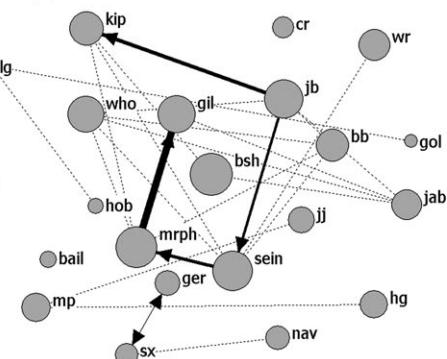
**Figure 2**

Proportion of fights in which adult females supported beneficiaries subordinate or dominant to themselves, out of all opportunities to intervene in the presence or absence of food. Bar color indicates kinship of each dyad as nonkin (white), distant kin (gray), and close kin (black). Sample sizes over each bar indicate the number of opportunities potential donors had to support potential beneficiaries. Error bars represent \pm 1SD for binomial trials.

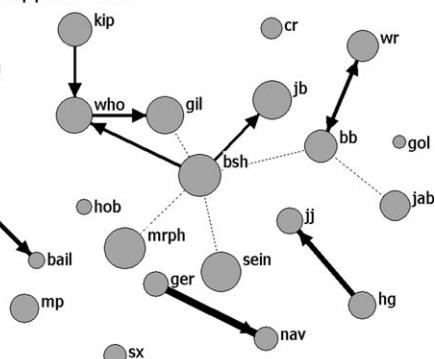
A) Non-kin:
Density of support = 0.05



B) Distant kin:
Density of support = 0.12



C) Close kin:
Density of support = 0.38

**Figure 3**

Cooperation networks among females present concurrently as adults from 1997 to 1998 that were (A) nonkin, (B) distant kin, and (C) close kin. Each circle (node) represents an adult female. Node size is proportional to the social rank held by that female (e.g., alpha female is largest). Connected dyads within each network represent dyads belonging to a particular kinship group based on maternal and paternal kinship. Whereas dyads connected by solid black arcs formed coalitions, dyads connected by dashed gray lines failed to support one another in fights despite the fact that both dyad members had opportunities to do so. Solid, black arrows (arcs) originate at donors of support, and arrowheads point toward beneficiaries of support. Double-headed arcs represent reciprocal support within dyads, whereas single-headed arcs represent unilateral support. Densities reflect the number of realized arcs (number of solid black lines) divided by the total number of possible connections (number of dashed gray lines and solid black lines for each kin group). Line thickness (weighted edges) indicates the proportion of times adult females intervened out of all opportunities to do so.

failed to reach statistical significance (Mann–Whitney *U*-test: $Z = 1.812, P = 0.070$), perhaps because of our low statistical power (Effect Size: 0.080, Power: 0.056). On average, mothers supported their adult daughters roughly twice as often as those same adult daughters supported their mothers in fights, but this difference was not statistically significant ($9.6 \pm 4.2\%$ and $4.7 \pm 2.6\%$ of opportunities, respectively; Wilcoxon signed-ranks test: $T = 19, P = 0.678, N = 13$ matched pairs, Effect size: 0.291, Power: 0.231). Interestingly, however, females supported their full sisters ($N = 8$ donors, $10.1 \pm 3.6\%$ of opportunities) more often than they supported their mothers or daughters ($N = 18$ donors; $6.3 \pm 2.4\%$ of opportunities; Mann–Whitney *U*-test: $Z = 2.060, P = 0.039$).

Audience effects modulated by kinship

Donating support was costly in the presence of higher-ranking bystanders. Donors of support were attacked by an adult female bystander immediately after $14 \pm 6\%$ of their interventions occurring in the presence of at least one higher-ranking adult female bystander ($N = 30$ donors), whereas none of the 18 donors were subsequently attacked when higher-ranking bystanders were absent (Mann–Whitney *U*-test: $Z = 2.186, P = 0.029$). The effects of higher-ranking bystanders were modulated by kinship, as predicted by Hamilton's rule (Table 3). That is, adult females were significantly less likely to intervene on behalf of distant kin or nonkin victims of aggression as the number of higher-ranking bystanders increased (Spearman rank correlations: $R_s = -0.719$ and $-0.840, P < 0.004$ and $0.005, N = 14$ and 9 audience sizes, respectively). Interestingly, however, females intervened on behalf of close kin regardless of the increased risk of doing so near large numbers of dominant bystanders ($R_s = -0.431, P = 0.213, N = 9$ audience sizes). Because the number of higher-ranking bystanders was correlated with the absolute number of adult females present ($r^2 = 0.25$), we investigated the prospect that the latter variable explained the apparent bystander effects. However, our data allowed us to rule out this possibility because the fit of our best statistical model of coalitionary support was not improved by either the addition of the absolute number of adult females present (-0.019 ± 0.031 , Wald Statistic = 0.374, $P = 0.540$) or the interaction between this number and kinship (-0.044 ± 0.074 , Wald Statistic = 0.352, $P = 0.553$).

Kinship fails to protect females from coalitionary attacks

Although adult females strongly biased their supportive interventions toward kin, kinship failed to protect potential victims from becoming targets of coalitionary attacks (Estimate: 0.074 ± 1.155 , Wald Statistic = 0.004, $P < 0.949$). Our best model revealed that coalitionary attacks were significantly more likely when the intensity of the fight was low than when it was high (Table 4), independent of kinship (Intensity * Kinship interaction: 1.693 ± 1.970 , Wald Statistic = 0.738, $P = 0.390$). For the subset of dyadic fights in which triadic genetic relationships were known, adult females ($N = 25$) were slightly more likely to intervene in fights when their kinship to each of the contestants differed ($3 \pm 1\%$) than when females were equally related to both contestants ($1 \pm 1\%$), but this difference was not statistically significant (Wilcoxon signed-ranks test: $T = 5, P = 0.500$, Effect size: 0.143, Power: 0.136). When intervening in fights in which they were more closely related to one of the 2 contestants, female aggressors ($N = 8$) were significantly more likely to attack the more distantly related ($94 \pm 6\%$) than the more closely related of the contestants ($6 \pm 6\%$, Wilcoxon signed-ranks test: $T = 0, P = 0.018$). Although kinship generally failed to protect females from attacks, this final result is consistent with predictions of kin selection theory because females biased attacks away from the more closely related contestant.

Reciprocal altruism hypothesis

No evidence of reciprocity or interchange trading among nonkin
To test for reciprocal trading, we examined the correlation between support given and services received within dyads of nonkin. After controlling for effects of kinship, no significant relationship emerged between support donated and received by adult females (Partial rowwise matrix correlations: $TauKr = -0.155, P = 0.860$). We also found no evidence of interchange trading. Nonkin failed to trade support in exchange for help during hunting ($TauKr = 0.012, P = 0.420$), opportunities to greet ($TauKr = -0.079, P = 0.861$), or social tolerance ($TauKr = 0.327, P = 1.000$). Our data also fail to indicate that natural selection favors agonistic aiding on the basis of indirect reciprocity; females provided the least support when the number of dominant bystanders in the audience was high (Table 3).

No evidence of stable alliances among nonkin

Unrelated adult females failed to form stable coalitionary alliances. This could be most clearly seen in the support networks, where double-headed arcs, representing reciprocal support, were limited to kin (Figure 3B and C). Moreover, the support network among nonkin was extremely sparse, and nonkin capitalized on only 5% of the possible network connections (Figure 3A). When we focused on all 106 dyads in which kinship category could be assigned and in which both members had opportunities to provide support, dyads engaging in reciprocal support (6%) were far less common than dyads providing unilateral support (25%) or no support (69%) on behalf of either member of the dyad (Figure 4). Reciprocal support was only observed between genetically related adult females (Figure 3B and C) such that dyads of kin participated in reciprocal support more often than did nonkin dyads. Repeated interventions by the same donor on behalf of the same beneficiary were rare. No adult female was ever observed supporting the same unrelated adult female in more than one fight ($N = 31$ females involved in 115 dyads). Even among kin, multiple instances of interventions by the same donor on behalf of the same beneficiary only occurred in 2.2% of 90 distant kin dyads and 11.1% of 36 close kin dyads.

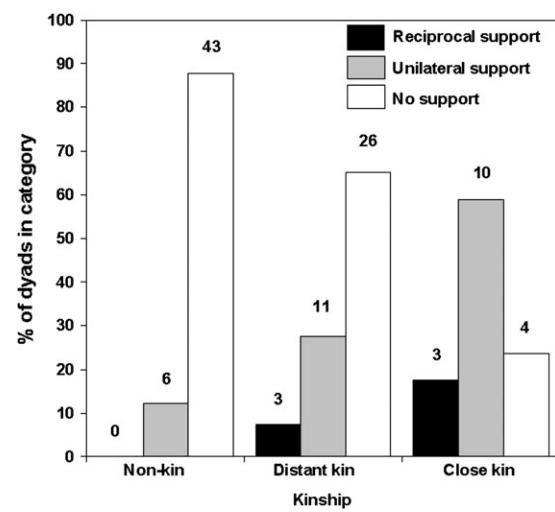
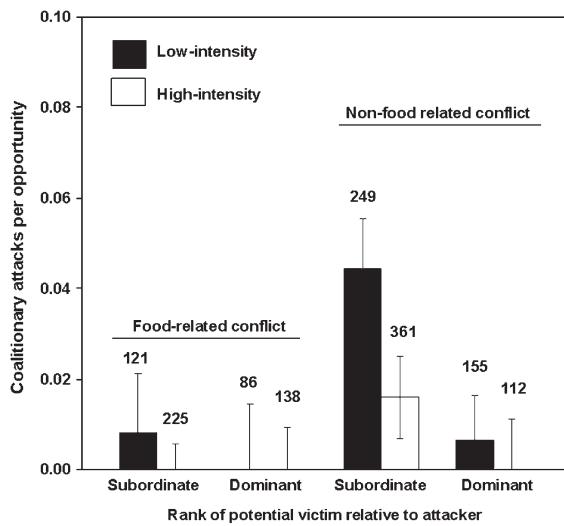


Figure 4

Variation among kinship categories regarding the proportion of dyads in which both members supported one another (reciprocal support: black), only one member supported the other member (unilateral support: gray), or neither member provided support to the other (no support: white). Sample sizes over bars indicate the number of dyads in which both members had opportunities to provide reciprocal support ($N = 106$ dyads).

**Figure 5**

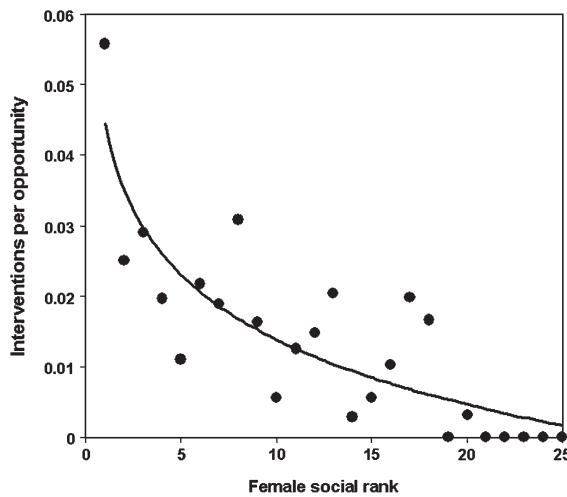
Proportion of fights in which adult females attacked victims subordinate or dominant to themselves, given the opportunity to intervene in the presence or absence of food. Bar colors indicate whether females intervened in ongoing dyadic fights of low (black) or high (white) intensity. Dyads belonging to all kinship categories are pooled because kinship failed to protect victims from attacks. Sample sizes over bars indicate the number of opportunities females had to attack targets already under attack by another adult female. Error bars represent $\pm 1\text{SD}$ for binomial trials.

Direct benefits hypothesis

Coalitionary interventions fail to increase immediate access to food
 Three lines of evidence indicate that intervening females do not accrue direct benefits in the form of immediate, enhanced intake of food. First, females were significantly less likely to intervene during fights involving food than in fights unrelated to food (Tables 3 and 4, Figures 2 and 5). Whereas females were significantly more likely to support subordinates ($6.2 \pm 1.7\%$) than dominants ($1.7 \pm 0.5\%$) in the nonfood context (Wilcoxon signed-ranks test: $Z = 2.20$, $P = 0.028$, $N = 22$ females), females were unlikely to provide support during fights over food, regardless of their rank relative to that of potential beneficiaries ($Z = 1.05$, $P = 0.294$, $N = 21$ females, Effect size: 0.169, Power: 0.151). Second, coalitionary aggression was no more effective in displacing competitors from kills ($52.6 \pm 11.8\%$) than was dyadic aggression ($51.6 \pm 9.2\%$) by the same aggressor (Z = 44.50, $P = 0.944$, $N = 19$ females, Effect size: 0.059, Power: 0.606). Finally, local prey abundance failed to predict female interventions in fights (Tables 3 and 4).

Coalitionary interventions reinforce the status quo

Our data are generally consistent with the idea that females benefit directly from reinforcing the status quo. A univariate approach revealed that high-ranking females, with comparable opportunities to intervene, on average, did so significantly more often than did low-ranking females (Spearman rank correlations: $R_s = -0.733$, $P < 0.0001$, $N = 25$ rank positions, Figure 6). Nonetheless, relative ranks within dyads (e.g., beneficiary subordinate to potential donor in Table 3 and victim subordinate to potential attacker in Table 4) were better predictors of whether adult females intervened than were the absolute ranks of potential donors (Table 3) or attackers (Table 4). Females directed the majority of coalitionary attacks toward subordinate victims (Table 4, Figures 5 and 7), and in most fights ($93.9 \pm 2.5\%$) supported the higher-ranking of the 2 contestants (Wilcoxon signed-ranks test: $Z = 5.012$, $P <$

**Figure 6**

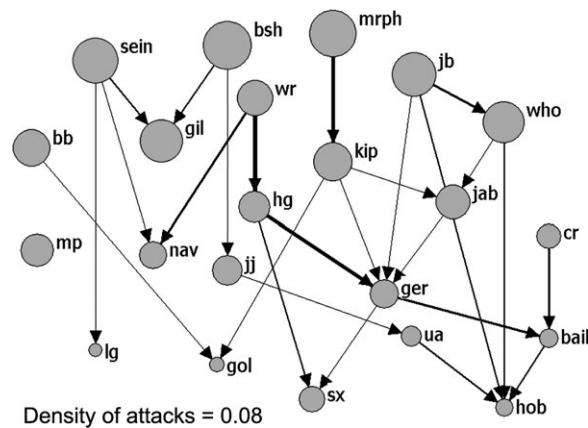
The effect of absolute social rank on the proportion of fights in which females intervened on behalf of other adult females out of all opportunities in which females holding a particular social rank might have supported potential beneficiaries. By convention, the highest possible rank is one (e.g., the alpha female).

0.00001, $N = 36$ donors). Cooperation and agonistic networks reflect these rank effects. High-ranking females, indicated by large node sizes (Figure 3), provided the most support in cooperation networks. Because females directed most attacks down the hierarchy toward victims subordinate to themselves, arrows originated at nodes larger than those at which they terminated in the agonistic network (Figure 7). The density of the agonistic network (0.08 realized arcs/potential arcs) was low in part because these females only attacked subordinates (Figure 7).

DISCUSSION

Intragroup coalitions in spotted hyenas compared with those in other taxa

Overall, we failed to detect any differences in the salient characteristics of intragroup coalitions formed by primates and

**Figure 7**

Agonistic network: A directed, weighted attack network structured by the same adult females as in Figure 3. Solid, black arrows (arcs) originate at intervening aggressors, and arrowheads terminate at victims of coalitionary attack. Line thickness (weighted edges) indicates the proportion of times adult females targeted the other member of the dyad out of all opportunities to do so. All dyads are shown on a single network because kinship failed to protect females from coalitionary attacks.

nonprimates. Moreover, the evolutionary forces favoring intra-group coalitions in spotted hyenas were strikingly similar to those found for many cercopithecines. Indeed, many monkeys simultaneously direct coalitionary support toward kin while limiting their individual costs by directing attacks toward subordinates to reinforce the status quo. For example, this pattern occurs among female baboons (*Papio cynocephalus*) as well as male stump-tail (*Macaca arctoides*), bonnet (*Macaca radiata*), and barbary (*Macaca sylvanus*) macaques (see Table 1 for references). In fact, our findings that nepotism and direct benefits shape intervention decisions among adult female hyenas parallels findings from most vertebrate species for which comparable data are available.

Despite growing interest in the topic, our review revealed that the number of studies on intragroup coalitions in primates and nonprimates remains unbalanced. This suggests the need for additional comparative data. Indeed, future work might yet expose other aspects of coalition formation, such as the extent to which adults solicit agonistic aid from bystanders (e.g., Packer 1977; de Waal and van Hooff 1981; Perry 1998; Slocombe and Zuberbühler 2007) or trade support with non-kin in exchange for other currencies (reviewed by Schino 2007), that distinguish primate coalitions from those formed by nonprimates. We found no evidence here that adult female hyenas or other nonprimates solicit aid or trade support for other commodities.

As in most of the species reviewed here, coalitions were generally rare among spotted hyenas and most often involved only 2 aggressors. Interestingly, adult female spotted hyenas directed coalitionary aggression toward other females at higher rates than did any other age-sex classes, and did so at rates 4 times higher than those of immigrant males. Furthermore, adult females and immigrant males never joined forces to attack adult females. In this respect, coalitions formed by spotted hyenas differ from those of many other mammals. Unlike most mammals, spotted hyenas live in female-dominated societies (Frank 1986) in which adult females compete most intensely with one another (Van Meter 2009). Our current results demonstrate that adult females are also each other's most important allies, and that females with the most allies, such as those in the alpha matriline, are the most powerful.

Nepotism among adult female spotted hyenas

As in most adult mammals reviewed here (Table 1) and earlier (e.g., Silk 2002; Widdig 2007), intragroup coalitions among adult female spotted hyenas were generally nepotistic. Consistent with the predictions of kin selection theory (Lehmann et al. 2007), the density of cooperation networks clearly increased with the degree of genetic relatedness among adult female hyenas. Moreover, mothers received support from their adult daughters as often as adult daughters received support from their mothers. These data support the hypothesis proposed by Holekamp and Smale (1995) suggesting that, in addition to gaining indirect benefits by helping their young daughters acquire their dominance status, mothers directly benefit by gaining new adult allies when their daughters mature.

Females preferentially supported full sisters over half sisters, biasing more support toward maternal than paternal half sisters. Although the latter result was not statistically significant, we suspect that our low statistical power may have kept us from detecting a biologically meaningful difference. This proved to be the case, for example, when Silk et al. (2006) discovered that the inability of Smith et al. (2003) to distinguish between nepotism directed toward maternal and paternal kin in ba-

boons was an artifact of small sample sizes. More broadly, our results indicate that nepotism directed by adult females toward both maternal and paternal kin resemble patterns observed among adult female mountain gorillas (*Gorilla g. beringei*, Watts 1997), adult female rhesus macaques (Widdig et al. 2006), and juvenile spotted hyenas (Wahaj et al. 2004). Despite its seemingly important influence on coalition formation, paternal kinship was rarely considered in the vast majority of studies reviewed here, underscoring the need for future studies that evaluate the role of paternal kinship in structuring cooperative decisions in animals.

As predicted by kin selection theory, adult female hyenas supported relatives most often when the cost of providing support was low. In particular, the mere presence of dominants influenced the tendency for focal females to donate support, suggesting an audience effect (Zuberbühler 2008). Interestingly, whereas adult female hyenas reduced their tendency to donate support to distant kin and nonkin as the number of higher-ranking bystanders increased, donors continued to support close kin independent of the increased risk of doing so. Our results are consistent with the idea that, unless they are helping close relatives, females generally avoid counter-attacks by refraining from involving themselves in disputes when dominants are present. In particular, female hyenas monitored the composition of their current subgroup, assessed their relatedness to potential beneficiaries, tracked the number of dominant bystanders in the audience, and modified their level of cooperation based on this knowledge. These findings extend recent experimental evidence from captive spotted hyenas in which pairs of hyenas were most likely to solve a cooperation task when additional conspecifics were present in the audience (Drea and Carter 2009). Moreover, our work provides another key example of how the mere proximity of dominants influences decision-making in animals. Proximity to dominants also influences food calls by brown capuchins (*Cebus apella*; Pollick et al. 2005), caching by Western scrub-jays (*Aphelocoma californica*; Dally et al. 2006), recruitment screams by chimpanzees (*Pan troglodytes*; Slocombe and Zuberbühler 2007), and maternal care by rhesus macaques (*Macaca mulatta*; Semple et al. 2009).

In contrast to the predictions of kin selection theory, however, kinship failed to protect adult female hyenas from coalitionary attacks here, as is also true for immature hyenas (Wahaj et al. 2004) and for many primates (reviewed by Widdig 2007). This finding might be explained by the direct benefits gained by intervening females. That is, insofar as coalitions help to maintain the status quo, it is just as important to an adult female's reproductive success for her to keep a lower-ranking sister or daughter in her place as it is for her to maintain her dominance over unrelated adult females.

More broadly, coalitions forming during intragroup conflicts among spotted hyenas were more nepotistic than those forming during intergroup conflicts with alien hyenas during "clan wars" or with lions (*Panthera leo*, Kruuk 1972; Cooper 1991; Boydston et al. 2001; Höner et al. 2005). In fact, intergroup interactions promote clan-level cooperation such that hyenas from multiple matrilines with low mean relatedness join forces (Van Horn et al. 2004). On average, coalitions forming during intragroup interactions here contained only 2.4 ± 0.01 hyenas, whereas those forming during conflicts with alien hyenas or lions contain 14 ± 1 and 16 ± 2 hyenas, respectively (Smith et al. 2008). We suggest that unrelated hyenas form large coalitions during intergroup conflicts because coalition size determines outcomes in these conflicts, and thus affects access to resources shared by all group members.

No evidence of reciprocity among unrelated adult female hyenas

We found no evidence of direct reciprocity or interchange trading among adult females. Specifically, we failed to detect a correlation between support given and services received among unrelated dyads of adult females. Further, females were generally least likely to donate support when many higher-ranking bystanders were present. This finding is inconsistent with reputation-based models of indirect reciprocity (Nowak and Sigmund 1998; Nowak and Sigmund 2005) and models based on coercive tactics such as harassment or punishment in which dominants force subordinates to cooperate (Clutton-Brock and Parker 1995). Finally, we found no evidence that female spotted hyenas establish stable, enduring alliances with nonkin based on repeated acts of unilateral or reciprocal support. Unlike stable male alliances among lions (Packer and Pusey 1982), baboons (Noë 1984), cheetahs (*Acinonyx jubatus*, Caro and Collins 1987), dolphins (*Tursiops aduncus*, Connor et al. 1992, 2001), or wild horses (*Equus caballus*, Feh 1999), coalitions were temporary among adult female spotted hyenas.

Feeding competition limits coalition formation among adult female hyenas

In contrast to the predictions of the food access hypothesis, females intervened least often in disputes over food, and coalitionary aggression was no more effective than dyadic aggression in displacing competitors from carcasses. Intragroup coalitions often provide improved access to food in species that are primarily herbivorous such as rock pigeons (*Columba livia*, Lefebvre and Henderson 1986) and (*Cebus capucinus*, white-faced capuchin, Vogel et al. 2007). However, extremely high opportunity costs appear to prevent such immediate benefits from accruing for spotted hyenas. Interventions may be particularly costly in these contexts because intervening females must allocate time to cooperating that could otherwise be spent consuming fresh meat at a rate of up to 1.3 kg/min (Kruuk 1972). Moreover, escalated aggression reduces per capita energy gain by attracting additional competitors (Mills 1989; Smith et al. 2008). Overall, these lines of evidence suggest that adult females likely gain more energy from directly allocating time to feeding than from forming coalitions when food is present.

Adult female hyenas gain direct benefits from reinforcing the status quo

Although females forming coalitions at a carcass apparently do not improve their immediate access to food, females that direct coalitionary attacks toward subordinates away from food should nevertheless benefit directly in feeding situations. That is, because dominance relationships are stable across contexts in this species (Frank 1986), by using coalitions to reinforce the status quo away from food, females guarantee their priority of access to resources during subsequent competitive interactions at carcasses. Indeed, coalitions appear central to the maintenance of rank relations long after adult female spotted hyenas establish their ranks as juveniles (Holekamp and Smale 1993; Smale et al. 1993; Engh et al. 2000). Consistent with our findings here, a number of other mammals living in despotic groups similarly use coalitionary attacks to reinforce the status quo (see Table 1 for details and references).

Females occasionally directed coalitionary attacks toward dominant hyenas in this study. Infrequent challenges of the

status quo in the form of revolutionary coalitions can have profound fitness consequences for spotted hyenas when they result in permanent rank reversals (Mills 1990; Holekamp et al. 1993; Hofer and East 2003). Coalitions from low-ranking matrilines are known to have overthrown higher-ranking matrilines in 3 different study populations of spotted hyenas (Serengeti: Hofer and East 2003; Mara: Holekamp et al. 1993; and Kalahari: Mills 1990). Thus, as in many primates (reviewed in Kummer 1967; Silk 2002, 2007a, 2007b), even rare challenges of the status quo can have important effects on individual fitness among hyenas.

Do members of highly cooperative groups enjoy enhanced fitness?

The group selection hypothesis has recently resurfaced as a potential explanation for the evolution of altruistic acts, including agonistic aiding (Wilson and Wilson 2007). Our current data are only consistent with the group selection hypothesis if we consider family groups to be the relevant targets of selection. Whereas fully addressing the group selection hypothesis at the level of the clan is beyond the scope of this study, members of hyena clans with more stable cooperation networks might enjoy higher fitness than those belonging to clans with less stable networks (Nowak 2006; Kun and Scheuring 2009). Flack et al. (2006) demonstrated the stabilizing function of third-party interventions among pigtailed macaques (*Macaca nemestrina*); their experimental removal of intervening animals destabilized the social network within a single generation. Our data suggest that third-party interventions by high-ranking female spotted hyenas might similarly stabilize social relationships among clan members. Future work should therefore inquire whether clans with the most stable coalition networks enjoy the greatest fitness.

To cooperate or not: a complex decision

Because of the polyadic nature of intragroup coalitions, many argue that agonistic aiding represents a decision-making process that is particularly cognitively demanding (e.g., Kummer 1967; Harcourt 1992; Connor 2007). Indeed, our data suggest that adult female spotted hyenas base such decisions on multiple factors. Our results extend earlier work demonstrating that spotted hyenas recognize third-party rank relationships; hyenas support the higher-ranking of 2 contestants when intervening in fights, even when the dominant individual is losing (Engh et al. 2005). Although social facilitation appears to promote coalition formation among captive juveniles (Zabel et al. 1992; Glickman et al. 1997), wild adult spotted hyenas in this study were selective when donating support to social partners, and generally adopted a strategy that reduced their personal costs of intervening. Here, adult female hyenas made flexible decisions about whether or not to cooperate not only based on multiple forms of information including dyadic rank and kin relationships but also based on their immediate ecological and extradyadic social circumstances. More broadly, the results from both our literature review and our current study of spotted hyenas are consistent with the emerging view that, although evolutionary explanations for cooperation are often proposed as mutually exclusive options, multiple factors typically shape complex patterns of cooperation found in nature (West et al. 2007a; Clutton-Brock 2009). Therefore, although progress is being made in solving the evolutionary puzzle of cooperation, our work emphasizes the need for novel, integrative theoretical frameworks in which to view complex forms of cooperation.

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REFERENCES

- Agresti A, Coull BA. 1998. Approximate is better than "exact" for the interval estimation of binomial proportions. *Am Stat Assoc.* 52: 119–126.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour.* 49:227–267.
- Baldwin JD, Baldwin J. 1972. Ecology and behavior of squirrel monkeys (*Saimiri oerstedii*) in a natural forest in western Panama. *Folia Primatol.* 18:161–184.
- Bercovitch FB. 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. *Anim Behav.* 36:1198–1209.
- Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai forest: behavioural ecology and evolution. Oxford: Oxford University Press.
- Boinski S, Kauffman L, Ehmke E, Schet S, Vreedzaam A. 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): i. Divergent costs and benefits. *Behaviour.* 142:525–632.
- Borries C. 1993. Ecology of female social relationships: hanuman langurs (*Presbytis entellus*) and the Van Schaik Model. *Folia Primatol.* 61:21–30.
- Boydston EE, Morelli TL, Holekamp KE. 2001. Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). *Ethology.* 107:369–385.
- Bramblett CA. 1970. Coalitions among gelada baboons. *Primates.* 11:327–333.
- Brown JL. 1983. Cooperation: a biologist's dilemma. *Adv Study Behav.* 13:1–37.
- Burnham KP, Anderson DR. 1998. Model selection and inference: a practical information-theoretic approach. New York: Springer-Verlag.
- Campbell CJ. 2006. Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). *Am J Primatol.* 68:1197–1201.
- Carlin JB, Wolfe R, Brown CH, Gelman A. 2001. A case study on the choice, interpretation and checking of multilevel models for longitudinal binary outcomes. *Biostatistics.* 2:397–416.
- Caro TM, Collins DA. 1987. Male cheetah social organization and territoriality. *Ethology.* 74:52–64.
- Chapais B. 1988. Rank maintenance in female Japanese macaques: experimental evidence for social dependency. *Behaviour.* 104: 41–59.
- Chapais B. 1992. The role of alliances in the social inheritance of rank among female primates. In: Harcourt AH, de Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford Science Publications. p. 29–60.
- Chapais B, Girard M, Primi G. 1991. Non-kin alliances and the stability of matrilineal dominance relations in Japanese macaques. *Anim Behav.* 41:481–492.
- Clutton-Brock TH. 2009. Cooperation between non-kin in animal societies. *Nature.* 462:51–57.
- Clutton-Brock TH, Parker GA. 1995. Punishment in animal societies. *Nature.* 373:209–216.
- Connor RC. 1995. Altruism among non-relatives: alternatives to the "Prisoner's Dilemma". *Trends Ecol Evol.* 10:84–86.
- Connor RC. 2007. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Phil Trans Roy Soc B Biol Sci.* 362:587–602.
- Connor RC, Heithaus MR, Barre LM. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proc Roy Soc Lond Ser B Biol Sci.* 268: 263–267.
- Connor RC, Smolker RA, Richards AF. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). *Proc Natl Acad Sci USA.* 89:987–990.
- Cooper MA, Bernstein IS. 2008. Evaluating dominance styles in Assamese and rhesus macaques. *Int J Primatol.* 29:225–243.
- Cooper MA, Bernstein IS, Hemelrijk CK. 2005. Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). *Am J Primatol.* 65:269–282.
- Cooper SM. 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyenas. *African J Ecol.* 29:130–136.
- Creel S, Macdonald D. 1995. Sociality, group size, and reproductive suppression among carnivores. *Adv Study Behav.* 24:203–257.
- Dally JM, Emery NJ, Clayton NS. 2006. Food-caching western scrub-jays keep track of who was watching when. *Science.* 312:1662–1665.
- Darwin C. 1859. On the origin of species by means of natural selection. London: John Murray.
- Datta S. 1988. The acquisition of dominance among free-fanging rhesus monkey siblings. *Anim Behav.* 36:754–772.
- de Villiers MS, Richardson PRK, van Jaarsveld AS. 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). *J Zool Lond.* 260:377–389.
- de Vries H. 1993. The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika.* 58:53–69.
- de Waal FBM. 1977. The organization of agonistic relations within two captive groups of java monkeys (*Macaca fascicularis*). *Zeitschr Tierpsychol.* 44:225–282.
- de Waal FBM. 1984. Sex differences in the formation of coalitions among chimpanzees. *Ethol Sociobiol.* 5:239–255.
- de Waal FBM. 1997. The chimpanzee's service economy: food for grooming. *Evol Hum Behav.* 18:375–386.
- de Waal FBM, Harcourt AH. 1992. Coalitions and alliances: a history of ethological research. In: Harcourt AH, de Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press. p. 1–19.
- de Waal FBM, Luttrell LM. 1986. The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatol.* 46: 215–234.
- de Waal FBM, Luttrell LM. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition. *Ethol Sociobiol.* 9:101–118.
- de Waal FBM, van Hooff JARAM. 1981. Side-directed communication and agonistic interactions in chimpanzees. *Behaviour.* 77:164–195.
- Derix R, van Hooff JARAM, Devries H, Wensing J. 1993. Male and female mating competition in wolves: female suppression versus male intervention. *Behaviour.* 127:141–174.
- Drea CM, Carter AN. 2009. Cooperative problem solving in a social carnivore. *Anim Behav.* 78:967–977.
- Drea CM, Frank LG. 2003. The social complexity of spotted hyenas. In: de Waal FBM, Tyack PL, editors. Animal social complexity: intelligence, culture, and individualized societies. Cambridge (MA): Harvard University Press. p. 121–148.
- Dugatkin LA. 2002. Animal cooperation among unrelated individuals. *Naturwissenschaften.* 89:533–541.

- Dunbar RIM. 1980. Determinants and evolutionary consequences of dominance among female Gelada baboons. *Behav Ecol Sociobiol.* 7:253–265.
- East ML, Hofer H, Wickler W. 1993. The erect ‘penis’ as a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behav Ecol Sociobiol.* 33:355–370.
- East ML, Honer OP, Wachter B, Wilhelm K, Burke T, Hofer H. 2009. Maternal effects on offspring social status in spotted hyenas. *Behav Ecol.* 20:478–483.
- Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007. Cognitive adaptations of social bonding in birds. *Phil Trans Roy Soc B Biol Sci.* 362:489–505.
- Engh AL, Esch K, Smale L, Holekamp KE. 2000. Mechanisms of maternal rank ‘inheritance’ in the spotted hyaena, *Crocuta crocuta*. *Anim Behav.* 60:323–332.
- Engh AL, Funk SM, Van Horn RC, Scribner KT, Bruford MW, Libants S, Szykman M, Smale L, Holekamp KE. 2002. Reproductive skew among males in a female-dominated mammalian society. *Behav Ecol.* 13:193–200.
- Engh AL, Siebert ER, Greenberg DA, Holekamp KE. 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third-party relationships. *Anim Behav.* 69:209–217.
- Faraway JJ. 2006. Extending the linear model with R: generalized linear, mixed effects, and nonparametric regression models. New York: Chapman and Hall.
- Fashing PJ. 2001. Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. *Behav Ecol Sociobiol.* 50:219–230.
- Faul F, Erdfelder E, Lang AG, Buchner A. 2007. G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods.* 39:175–191.
- Feh C. 1999. Alliances and reproductive success in Camargue stallions. *Anim Behav.* 57:705–713.
- Fentress JC, Ryon J, McLeod PJ, Hawkin GZ. 1987. A multidimensional approach to agonistic behavior in wolves. In: Frank H, editor. *Man and wolf: advances, issues and problems in captive wolf research*. Boston (MA): Dr. W. Junk Publishers. p. 253–274.
- Flack JC, Girvan M, de Waal FBM, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. *Nature.* 439:426–429.
- Flinn MV, Geary DC, Ward CV. 2005. Ecological dominance, social competition, and coalitionary arms races: why humans evolved extraordinary intelligence. *Evol Hum Behav.* 26:10–46.
- Frank LG. 1986. Social organization of the spotted hyaena (*Crocuta crocuta*). II. Dominance and reproduction. *Anim Behav.* 34: 1510–1527.
- Frank LG, Glickman SE, Powch I. 1990. Sexual dimorphism in the spotted hyaena (*Crocuta crocuta*). *J Zool Lond.* 221:308–313.
- Frank LG, Holekamp KE, Smale L. 1995. Dominance, demography, and reproductive success of female spotted hyenas. In: Sinclair ARE, Arcese P, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. Chicago (IL): University of Chicago Press. p. 364–384.
- Glickman SE, Zabel CJ, Yoerg SI, Weldele ML, Drea CM, Frank LG. 1997. Social facilitation, affiliation, and dominance in the social life of spotted hyenas. *Ann NY Acad Sci.* 807:175–184.
- Gompper ME, Gittleman JL, Wayne RK. 1997. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Anim Behav.* 53:781–797.
- Grammer K. 1992. Intervention in conflicts among children: contexts and consequences. In: Harcourt AH, De Waal FBM, editors. *Coalitions and alliances in humans and other animals*. New York: Oxford University Press. p. 259–283.
- Halekoh U, Højsgaard S, Yan J. 2006. The R Package geepack for generalized estimating equations. *J Stat Software.* 15:1–11.
- Hamilton WD. 1964. The genetical evolution of social behavior, I and II. *J Theor Biol.* 7:1–52.
- Harcourt AH. 1992. Coalitions and alliances: are primates more complex than non-primates? In: Harcourt AH, de Waal FBM, editors. *Coalitions and alliances in humans and other animals*. Oxford: Oxford Science Publications. p. 445–471.
- Hardin JW, Hilbe JM. 2003. Generalized estimating equations. New York: Chapman & Hall/CRC.
- Hemelrijk CK. 1990a. A matrix partial correlation test used in investigations of reciprocity and other social-interaction patterns at group level. *J Theor Biol.* 143:405–420.
- Hemelrijk CK. 1990b. Models of, tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Anim Behav.* 39:1013–1029.
- Hemelrijk CK. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Anim Behav.* 48:479–481.
- Hemelrijk CK, Ek A. 1991. Reciprocity and interchange of grooming and support in captive chimpanzees. *Anim Behav.* 41:923–935.
- Hirsch BT. 2007. Spoiled brats: is extreme juvenile agonism in ring-tailed coatis (*Nasua nasua*) dominance or tolerated aggression? *Ethology.* 113:446–456.
- Hofer H, East ML. 2003. Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evol Ecol.* 17:315–331.
- Holekamp KE, Cooper SM, Katona CI, Berry NA, Frank LG, Smale L. 1997. Patterns of association among female spotted hyenas (*Crocuta crocuta*). *J Mammal.* 78:55–74.
- Holekamp KE, Ogutu JO, Frank LG, Dublin HT, Smale L. 1993. Fission of a spotted hyena clan: consequences of female absenteeism and causes of female emigration. *Ethology.* 93:285–299.
- Holekamp KE, Sakai ST, Lundrigan BL. 2007. Social intelligence in the spotted hyena (*Crocuta crocuta*). *Phil Trans Roy Soc B Biol Sci.* 362:523–538.
- Holekamp KE, Smale L. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Anim Behav.* 46:451–466.
- Holekamp KE, Smale L. 1995. Rapid change in offspring sex ratios after clan fission in the spotted hyena. *Am Nat.* 145:261–278.
- Holekamp KE, Smale L, Berg R, Cooper SM. 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *J Zool Lond.* 242:1–15.
- Holekamp KE, Smale L, Szykman M. 1996. Rank and reproduction in the female spotted hyaena. *J Reprod Fertil.* 108:229–237.
- Holekamp KE, Szykman M, Boydston EE, Smale L. 1999. Association of seasonal reproductive patterns with changing food availability in an equatorial carnivore, the spotted hyaena (*Crocuta crocuta*). *J Reprod Fertil.* 116:87–93.
- Höner OP, Wachter B, East ML, Runyoro VA, Hofer H. 2005. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos.* 108:544–554.
- Hunte W, Horrocks JA. 1987. Kin and non-kin interventions in the aggressive disputes of vervet monkeys. *Behav Ecol Sociobiol.* 20: 257–263.
- Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour.* 139:177–202.
- Jennings DJ, Carlin CM, Gammell MP. 2009. A winner effect supports third-party intervention behaviour during fallow deer, *Dama dama*, fights. *Anim Behav.* 77:343–348.
- Jones CB. 1980. The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous Neotropical primate. *Primates.* 21: 389–405.
- Kapsalis E, Berman CM. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). 2. Testing predictions for three hypothesized organizing principles. *Behaviour.* 133:1235–1263.
- Kruuk H. 1972. The spotted hyena: a study of predation and social behavior. Chicago (IL): University of Chicago Press.
- Krätschmer M, Sherwin WB, Connor RC, Barré LM, Van de Casteele T, Mann J, Brooks R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proc Roy Soc Lond Ser B.* 270:497–502.
- Kummer H. 1967. Tripartite relations in hamadryas baboons. In: Altman SA, editor. *Social communication among primates*. Chicago (IL): University of Chicago Press. p. 63–71.
- Kun A, Scheuring I. 2009. Evolution of cooperation on dynamical graphs. *Biosystems.* 96:65–68.
- Lee PC. 1987. Allomothering among African elephants. *Anim Behav.* 35:278–291.
- Lefebvre L, Henderson D. 1986. Resource defense and priority of access to food by the mate in pigeons. *Can J Zool.* 64:1889–1892.

- Lehmann L, Keller L, Sumpter DJT. 2007. The evolution of helping and harming on graphs: the return of the inclusive fitness effect. *J Evol Biol.* 20:2284–2295.
- Liang KY, Zeger SL. 1986. Longitudinal data analysis using generalized linear models. *Biometrika.* 73:13–22.
- Massey A. 1977. Agonistic aids and kinship in a group of pigtail macaques. *Behav Ecol Sociobiol.* 2:31–40.
- Matheson MD, Bernstein IS. 2000. Grooming, social bonding, and agonistic aiding in rhesus monkeys. *Am J Primatol.* 51:177–186.
- Maynard Smith J, Price GR. 1973. The logic of animal conflict. *Nature.* 246:15–18.
- Mesterton-Gibbons M, Sherratt TN. 2007. Coalition formation: a game-theoretic analysis. *Behav Ecol.* 18:277–286.
- Mills MGL. 1989. The comparative behavioral ecology of hyenas: the importance of diet and food dispersion. In: Gittleman JL, editor. *Carnivore behavior, ecology, and evolution.* Ithaca (NY): Cornell University Press. p. 125–142.
- Mills MGL. 1990. Kalahari hyenas: comparative behavioral ecology of two species. London: Unwin Hyman.
- Mitani JC, Merriwether DA, Zhang C. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Anim Behav.* 59: 885–893.
- Mitani JC, Watts DP, Pepper JW, Merriwether DA. 2002. Demographic and social constraints on male chimpanzee behaviour. *Anim Behav.* 64:727–737.
- Nishida T, Hosaka K. 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew W, Nishida T, Marchant L, editors. *The Great Ape Societies.* Cambridge (MA): Cambridge University Press. p. 114–134.
- Noë R. 1984. Lasting alliances among adult male savannah baboons. In: Else JG, Lee PC, editors. *Primate ontogeny, cognition and social behavior.* Cambridge (MA): Cambridge University Press. p. 381–392.
- Noë R. 1990. A veto game played by baboons: a challenge to the use of the prisoners dilemma as a paradigm for reciprocity and cooperation. *Anim Behav.* 39:78–90.
- Noë R. 1992. Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, de Waal FBM, editors. *Coalitions and alliances in humans and other animals.* Oxford: Oxford University Press. p. 284–321.
- Noë R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Anim Behav.* 71:1–18.
- Noë R, Hammerstein P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol.* 35:1–11.
- Nowak MA. 2006. Five rules for the evolution of cooperation. *Science.* 314:1560–1563.
- Nowak MA, Sigmund K. 1998. Evolution of indirect reciprocity by image scoring. *Nature.* 393:573–577.
- Nowak MA, Sigmund K. 2005. Evolution of indirect reciprocity. *Nature.* 437:1291–1298.
- O'Brien TG. 1993. Allogrooming behavior among adult female wedge-capped capuchin monkeys. *Anim Behav.* 46:499–510.
- Olson LE, Blumstein DT. 2009. A trait-based approach to the evolution of complex coalitions in male mammals. *Behav Ecol.* 20: 624–632.
- Packer C. 1977. Reciprocal altruism in *Papio anubis*. *Nature.* 265: 441–443.
- Packer C, Pusey AE. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature.* 296: 740–742.
- Pan W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics.* 57:120–125.
- Parsons KM, Durban JW, Claridge DE, Balcomb KC, Noble LR, Thompson PM. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Anim Behav.* 66:185–194.
- Pelchat GO. 2008. Buddies for life: male associations and coalitions in bighorn sheep. *Ovis canadensis.* (Master's of Science): University of Calgary.
- Pereira ME, Kappeler PM. 1997. Divergent systems of agonistic behaviour in lemurid primates. *Behaviour.* 134:225–274.
- Pereira ME, McGlynn CA. 1997. Special relationships instead of female dominance for redfronted lemurs, *Eulemur fulvus rufus*. *Am J Primatol.* 43:239–258.
- Perry S. 1996. Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *Am J Primatol.* 40:167–182.
- Perry S. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour.* 135:139–172.
- Petit O, Abegg C, Thierry B. 1997. A comparative study of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). *Behaviour.* 134:415–432.
- Petit O, Thierry B. 1994. Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Anim Behav.* 48:1427–1436.
- Pollick AS, Gouzoules H, De Waal FBM. 2005. Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Anim Behav.* 70:1273–1281.
- Prudhomme J, Chapais B. 1993. Aggressive interventions and matri-lineal dominance relations in semifree-ranging barbary macaques (*Macaca sylvanus*). *Primates.* 34:271–283.
- Queller DC. 1985. Kinship, reciprocity and synergism in the evolution of social behavior. *Nature.* 318:366–367.
- Range F. 2006. Social behavior of free-ranging juvenile sooty mangabees (*Cercocebus torquatus atys*). *Behav Ecol Sociobiol.* 59: 511–520.
- Range F, Noë R. 2002. Familiarity and dominance relations among female sooty mangabeys in the Tai National Park. *Am J Primatol.* 56:137–153.
- Rice WR. 1989. Analyzing tables of statistical tests. *Evolution.* 43: 223–225.
- Richter C, Mevis L, Malaivijitnond S, Schulke O, Ostner J. 2009. Social relationships in free-ranging male *Macaca arctoides*. *Int J Primatol.* 30:625–642.
- Ridley J, Yu DW, Sutherland WJ. 2005. Why long-lived species are more likely to be social: the role of local dominance. *Behav Ecol.* 16:358–363.
- Romero T, Aureli F. 2008. Reciprocity of support in coatis (*Nasua nasua*). *J Compar Psychol.* 122:19–25.
- Rowell TE, Rowell CA. 1993. The social organization of feral *Ovis aries* ram groups in the pre-rut period. *Ethology.* 95:213–232.
- Sachs JL, Mueller UG, Wilcox TP, Bull JJ. 2004. The evolution of cooperation. *Quart Rev Biol.* 79:135–160.
- Schaller GB. 1972. *The Serengeti lion.* Chicago (IL): University of Chicago Press.
- Scheiber IBR, Kotrschal K, Weiss BM. 2009. Serial agonistic attacks by greylag goose families (*Anser anser*) against the same opponent. *Anim Behav.* 77:1211–1216.
- Scheiber IBR, Weiss BM, Frigerio D, Kotrschal K. 2005. Active and passive social support in families of greylag geese (*Anser anser*). *Behaviour.* 142:1535–1557.
- Schilder MBH. 1990. Interventions in a herd of semi-captive plains zebras. *Behaviour.* 112:53–83.
- Schinò G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav Ecol.* 18:115–120.
- Schinò G, Aureli F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior.* Vol. 39. San Diego (CA): Elsevier Academic Press Inc. p. 45–69.
- Schinò G, Di Giuseppe F, Visalberghi E. 2009. Grooming, rank, and agonistic support in tufted capuchin monkeys. *Am J Primatol.* 70: 101–105.
- Schinò G, di Sorrentino EP, Tiddi B. 2007. Grooming and coalitions in Japanese Macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *J Compar Psychol.* 121:181–188.
- Schinò G, Tiddi B, Polizzi di Sorrentino E. 2007. Agonistic support in juvenile Japanese macaques: cognitive and functional implications. *Ethology.* 113:1151–1157.
- Scott DK. 1980. Functional aspects of prolonged parental care in Bewick's swans. *Anim Behav.* 28:938–952.
- Semple S, Gerald MS, Suggs DN. 2009. Bystanders affect the outcome of mother–infant interactions in rhesus macaques. *Proc Roy Soc B.* 276:2257–2262.
- Seyfarth RM. 1976. Social relationships among adult female baboons. *Anim Behav.* 24:917–938.
- Seyfarth RM. 1977. Model of social grooming among adult female monkeys. *J Theor Biol.* 65:671–698.
- Seyfarth RM. 1980. The distribution of grooming and related behaviors among adult female vervet monkeys. *Anim Behav.* 28:798–813.
- Silk JB. 1982. Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour.* 79:162–188.

- Silk JB. 1992. Patterns of intervention in agonistic contests among male bonnet macaques. In: Harcourt AH, De Waal FBM, editors. *Coalitions and alliances in humans and other animals*. New York: Oxford University Press. p. 215–231.
- Silk JB. 1993. Does participation in coalitions influence dominance relationships among male bonnet macaques. *Behaviour*. 126: 171–189.
- Silk JB. 2002. Kin selection in primate groups. *Int J Primatol*. 23: 849–875.
- Silk JB. 2007a. The adaptive value of sociality in mammalian groups. *Phil Trans Roy Soc B Biol Sci*. 362:539–559.
- Silk JB. 2007b. Social components of fitness in primate groups. *Science*. 317:1347–1351.
- Silk JB, Alberts SC, Altmann J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Anim Behav*. 67: 573–582.
- Silk JB, Altmann J, Alberts SC. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol Sociobiol*. 61:183–195.
- Slocombe KE, Zuberbühler K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proc Natl Acad Sci USA*. 104:17228–17233.
- Smale L, Frank LG, Holekamp KE. 1993. Ontogeny of dominance in free-living spotted hyenas: juvenile rank relations with adult females and immigrant males. *Anim Behav*. 46:467–477.
- Smale L, Nunes S, Holekamp KE. 1997. Sexually dimorphic dispersal in mammals: patterns, causes, and consequences. *Adv Study Behav*. 26:181–250.
- Smith JE, Kolowski JM, Graham KE, Dawes SE, Holekamp KE. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Anim Behav*. 76:619–636.
- Smith JE, Memenis SK, Holekamp KE. 2007. Rank-related partner choice in the fission-fusion society of spotted hyenas (*Crocuta crocuta*). *Behav Ecol Sociobiol*. 61:753–765.
- Smith K, Alberts SC, Altmann J. 2003. Wild female baboons bias their social behaviour towards paternal half-sisters. *Proc Roy Soc Lond Ser B*. 270:503–510.
- Sommer V. 1988. Male competition and coalitions in langurs (*Presbytis entellus*) at Jodhpur, Rajasthan, India. *Hum Evol*. 3:261–278.
- Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. 2003. Placental mammal diversification and the Cretaceous–Tertiary boundary. *Proc Natl Acad Sci USA*. 100:1056–1061.
- Stammbach E. 1978. Social differentiation in groups of captive female hamadryas baboons. *Behaviour*. 67:322–338.
- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol*. 41:291–309.
- Stevens JMG, Vervaecke H, de Vries H, Van Elsacker L. 2005. The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (*Pan paniscus*). *Behaviour*. 142:941–960.
- Trivers RL. 1971. The evolution of reciprocal altruism. *Quart Rev Biol*. 46:35–57.
- Uehara S, Hiraiwahasegawa M, Hosaka K, Hamai M. 1994. The fate of defeated alpha male chimpanzees in relation to their social networks. *Primates*. 35:49–55.
- Valero A, Schaffner CM, Vick LG, Aureli F, Ramos-Fernandez G. 2006. Intragroup lethal aggression in wild spider monkeys. *Am J Primatol*. 68:732–737.
- Van Horn RC, Engh AL, Scribner KT, Funk SM, Holekamp KE. 2004. Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. *Mol Ecol*. 13:449–458.
- Van Horn RC, McElhinny TL, Holekamp KE. 2003. Age estimation and dispersal in the spotted hyena (*Crocuta crocuta*). *J Mammal*. 84:1019–1030.
- Van Horn RC, Wahaj SA, Holekamp KE. 2004. Role-reversed nepotism among cubs and sires in the spotted hyena (*Crocuta crocuta*). *Ethology*. 110:413–426.
- Van Meter PE. 2009. Hormones, stress and aggression in the spotted hyena. *Crocuta crocuta*. (Ph.D. Dissertation). East Lansing (MI): Michigan State University.
- Van Meter PE, French JA, Dloniak SM, Watts HE, Kolowski JM, Holekamp KE. 2009. Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Hormones Behav*. 55:329–337.
- Vasey PL. 1996. Interventions and alliance formation between female Japanese macaques, *Macaca fuscata*, during homosexual consorships. *Anim Behav*. 52:539–551.
- Ventura R, Majolo B, Koyama NF, Hardie S, Schino G. 2006. Reciprocity and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *Am J Primatol*. 68: 1138–1149.
- Vervaecke H, de Vries H, Van Elsacker L. 2000. Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates*. 41:249–265.
- Vogel ER, Munch SB, Janson CH. 2007. Understanding escalated aggression over food resources in white-faced capuchin monkeys. *Anim Behav*. 74:71–80.
- Wahaj SA, Guse KR, Holekamp KE. 2001. Reconciliation in the spotted hyena (*Crocuta crocuta*). *Ethology*. 107:1057–1074.
- Wahaj SA, Van Horn RC, Van Horn TL, Dreyer R, Hilgris R, Schwarz J, Holekamp KE. 2004. Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. *Behav Ecol Sociobiol*. 56:237–247.
- Walters J. 1980. Interventions and the development of dominance relationships in female baboons. *Folia Primatol*. 34:61–89.
- Wasserman S, Faust K. 1994. Social network analysis. Cambridge (MA): Cambridge University Press.
- Watts DP. 1997. Agonistic interventions in wild mountain gorilla groups. *Behaviour*. 134:23–57.
- Watts DP. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*. 139:343–370.
- Wechsler B. 1988. Dominance relationships in jackdaws (*Corvus monedula*). *Behaviour*. 106:252–264.
- West SA, Griffin AS, Gardner A. 2007a. Evolutionary explanations for cooperation. *Curr Biol*. 17:R661–R672.
- West SA, Griffin AS, Gardner A. 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol*. 20:415–432.
- West-Eberhard MJ. 1975. The evolution of social behavior by kin selection. *Quart Rev Biol*. 50:1–33.
- Wey T, Blumstein DT, Weiwei S, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav*. 75:333–344.
- Widdig A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biol Rev*. 82:319–334.
- Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch F. 2002. Affiliation and aggression among adult female rhesus macaques: a genetic analysis of paternal cohorts. *Behaviour*. 139:371–391.
- Widdig A, Streich WJ, Nuernberg P, Croucher PJP, Bercovitch FB, Krawczak M. 2006. Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). *Behav Ecol Sociobiol*. 61:205–214.
- Widdig A, Streich WJ, Tembrock G. 2000. Coalition formation among male Barbary macaques (*Macaca sylvanus*). *Am J Primatol*. 50:37–51.
- Williams RL. 2000. A note on robust variance estimation for cluster-correlated data. *Biometrics*. 56:645–646.
- Wilson DS. 1975a. Theory of group selection. *Proc Natl Acad Sci USA*. 72:143–146.
- Wilson DS, Wilson EO. 2007. Rethinking the theoretical foundation of sociobiology. *Quart Rev Biol*. 82:327–348.
- Wilson EO. 1975b. *Sociobiology: the new synthesis*. Cambridge (MA): Belknap Press of Harvard University Press.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour*. 75:262–300.
- Zabel CJ, Glickman SE, Frank LG, Woodmansee KB, Keppel G. 1992. Coalition formation in a colony of prepubertal spotted hyenas. In: Harcourt AH, de Waal FBM, editors. *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press. p. 112–135.
- Zimen E. 1976. On the regulation of pack size in wolves. *Zeitschr Tierpsychol*. 40:300–341.
- Zuberbühler K. 2008. Audience effects. *Curr Biol*. 18:R189–R190.