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Rank-related partner choice in the fission–fusion society of the spotted hyena (*Crocuta crocuta*)

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Abstract When social partners vary in their relative value, individuals should theoretically initiate partnerships with conspecifics of the highest value. Here, we tested this prediction in a wild population of spotted hyenas (*Crocuta crocuta*). *Crocuta* live in complex, fission–fusion societies structured by dominance hierarchies in which individuals vary greatly in their value as social companions. Because patterns of association among *Crocuta* reflect social preferences, we calculated association indices (AIs) to examine how social rank influences intrasexual partner choice among unrelated adults of both sexes. The highest-ranking individuals were generally most gregarious in both sexes. Females associated most often with dominant and adjacent-ranking females. Females joined subgroups based on the presence of particular conspecifics such that subordinates joined focal females at higher rates than did dominants. Dominants benefit from associations with subordinates by enjoying priority of access to resources obtained and defended by multiple group members, but the benefits of these associations to subordinates are unknown. To investigate this, we tested three hypotheses suggesting how subordinates might benefit from rank-related partner choice among unrelated females. We found that subordinates who initiated group formation benefited by gaining social and feeding tolerance from dominants. However, rates at which dominants provided coalitionary support to subordinates did not vary with AIs. Overall, our data resemble those documenting patterns of association among cercopithecine primates. We consider our results in light of optimal reproductive skew

theory, Seyfarth's rank attractiveness model, and biological market theory. Our data are more consistent with the predictions of Seyfarth's model and of biological market theory than with those of skew theory.

Keywords Association · Biological markets ·
Decision-making · Group living · Optimal reproductive
skew · Partner choice · Seyfarth's rank attractiveness

Introduction

Recognizing the adaptive significance of choices made by gregarious animals with regard to their social partners, behavioral ecologists have recently begun evaluating the potential fitness consequences of partner choice outside the context of sexually selected mate choice (Dugatkin and Sih 1995, 1998). Primatologists have long known that many species of cercopithecine monkeys associate most closely with unrelated individuals of similar or higher rank than their own in the social hierarchy (Cheney et al. 1986; Schino 2001). Other researchers, however, have paid little attention to partner choice involving non-kin (Gouzoules and Gouzoules 1987). Spotted hyenas (*Crocuta crocuta*) are highly gregarious carnivores that reside in social groups called clans (Kruuk 1972), which are strikingly similar in their size and hierarchical structure to troops of cercopithecine primates (Drea and Frank 2003). This offers a unique opportunity to compare rank-related partner choice between primates and carnivores, taxonomic groups that last shared a common ancestor 90–100 Mya (Springer et al. 2003, 2005). It also offers an important opportunity to evaluate the power and generality of alternative models of social partner preference based on dominance rank and related factors.

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Like many species of monkeys, *Crocuta* frequently compete over limited resources and cooperate by joining forces to direct coalitionary aggression towards conspecifics (Engh et al. 2005). As in most primates, nepotism is common among *Crocuta*, and kin associate with one another more often than do non-kin (Holekamp et al. 1997a; Wahaj et al. 2004). Among non-kin, high-ranking adult female *Crocuta* are more gregarious than low-ranking females (Holekamp et al. 1997a), but we know very little about which individuals make decisions about partner choice to generate this pattern, or why such decisions are made. Furthermore, although adult male *Crocuta* associate closely with their mates (Szykman et al. 2001), it is not understood to what extent immigrant males associate with each other or how patterns of intrasexual association differ between the sexes. Understanding these decision-making processes should help elucidate the evolutionary costs and benefits of social partner choice in *Crocuta*.

Crocuta clans are fission–fusion societies in which individuals travel, rest, and forage in subgroups that frequently change in size and composition (Kruuk 1972; Mills 1990), so preferences for social partners among *Crocuta* are revealed by how often they occur in subgroups with particular conspecifics (Holekamp et al. 1997a; Szykman et al. 2001; Wahaj et al. 2004). Preferences for certain social partners are likely to emerge in societies where asymmetries in partner value exist (Dugatkin and Sih 1998). High-ranking *Crocuta* can potentially confer greater fitness benefits to the individuals selecting them as social partners than can low-ranking animals because dominants can permit access to monopolized resources such as food and space merely by withholding aggression (Frank 1986; Boydston et al. 2003). Feeding competition is extremely intense among *Crocuta* and access to ungulate carcasses profoundly affects their lifetime reproductive success (Frank et al. 1995; Holekamp et al. 1996). Dominants can also provide more effective coalitionary support than subordinates during within-group contests (Smale et al. 1995; Engh et al. 2005). Thus, *Crocuta* should be selective when making decisions to join subgroups containing particular social partners.

Here, we inquired whether social rank or rank distance influences intrasexual partner choice among unrelated adult *Crocuta* of both sexes. We also investigated the potential benefits of rank-related partner choice among females. In particular, we asked whether dominant or subordinate females initiate associations by promoting group formation. Dominant *Crocuta* benefit from the presence of other clan members in that they enjoy priority of access to resources cooperatively obtained and defended by multiple group members (Cooper 1991; Holekamp et al. 1997b; Boydston et al. 2001, 2003), but the benefits of such partnerships to subordinates are unknown. We tested three hypotheses,

each suggesting a potential benefit to be gained by subordinates from rank-related partner choice. Specifically, we asked whether subordinate females benefit from: (1) reduced harassment (or increased social tolerance) by conspecifics, (2) increased tolerance during feeding, or (3) increased coalitionary support during aggressive interactions. The reduced harassment hypothesis predicts that subordinate females should receive less frequent dyadic aggression and better access to monopolized space from unrelated dominant females with which they associate more often. We examined this in situations in which no food was involved. The feeding tolerance hypothesis predicts that, during feeding competition, females should receive less frequent dyadic aggression from unrelated dominant females with which they associate more often; they should be permitted better access to monopolized food, or both. Finally, the coalitionary support hypothesis predicts that subordinate females should receive more frequent coalitionary support during aggressive interactions from unrelated dominant females with which they associate more often.

Materials and methods

Study site and subject animals

From 1988 to 1999, we studied members of one large clan of *Crocuta* inhabiting a territory of 62 km^2 in the Talek region of the Masai Mara National Reserve, Kenya (Boydston et al. 2001). Excluding transient males (immigrants remaining in the clan for less than 6 months), clan size during the study period ranged from 45 to 78 residents. Each resident was known individually by its unique spots and sexed based on the dimorphic morphology of its erect phallus (Frank et al. 1990). We estimated birth dates (to ±7 days) using methods described previously (Holekamp et al. 1996). We classified natal females as adults at 36 months of age or at their first known date of conception, whichever occurred first. Whereas female *Crocuta* are philopatric, males disperse 1–76 months after puberty (Smale et al. 1997; Van Horn et al. 2003), which occurs at approximately 24 months of age in this species (Glickman et al. 1992; Dloniak et al. 2006). On average, genetic relatedness among natal members of a clan is extremely low (Queller–Goodnight $R=-0.05\pm0.007$), as is mean relatedness among adult immigrant males (Queller–Goodnight $R=0.009\pm0.007$; Van Horn et al. 2004). Because we were interested here in partner choices involving unrelated adult females, we excluded all dyads containing grandmothers and adult granddaughters, mothers, and adult daughters, and adult maternal sisters, based on known maternal relationships and genotyping. We considered all males immigrating into the Talek clan to be unrelated adults.

Behavioral data collection

Crocuta clans are structured by linear dominance hierarchies (Kruuk 1972; Frank 1986) like those in cercopithecine societies (Smale et al. 1995; Engh et al. 2000). Here, we determined the social rank of each individual hyena based on the outcomes of dyadic agonistic interactions; all adult females were dominant to all immigrant males (Holekamp and Smale 1993; Smale et al. 1993). We ranked adult males and females in separate hierarchies, with the highest possible rank in each being one. Based on these ranks, we calculated rank distance as the absolute value of the difference in ranks between the members of a same-sex dyad. We used the terms "dominant" and "subordinate" to refer to the relative ranks of members of each dyad. We assessed association patterns based on the co-occurrence of dyad members in observation sessions recorded during each year of our study. We initiated a session each time we encountered one or more *Crocuta* separated from conspecifics by at least 200 m within the Talek home range. Sessions lasted from 5 min to several hours and ended when we left an individual or group. At each session, researchers recorded the location, the identity of each individual present, and whether or not food was present. We defined sessions as having food when a fresh ungulate carcass was present and considered food to be absent only in sessions where no food whatsoever was present. Sessions not meeting either of these criteria were excluded from the aggression calculations. At sessions with food, we performed scans every 15 to 20 min to record which individuals were present and whether or not those individuals fed concurrently.

All aggressive and appeasement behaviors were recorded as critical incidents using the all-occurrence sampling technique of Altmann (1974). Dyadic aggression only involved a single aggressor, whereas coalitionary aggression involved at least two *Crocuta* directing aggression towards the same target animal. Aggressive behaviors included head wave, lunge, aggressive posture (e.g., ears cocked forward with the tail bristled and raised), chase, displace, stand over, bite, and push. We required at least 1 min to elapse between aggressive interactions within a pair of individuals for a second interaction to be included here; renewed attack within a single minute was considered a continuation of the original interaction.

Measures of intrasexual association

We estimated the degree of affiliation between members of each dyad using the twice-weight association index (AI) of Cairns and Schwager (1987), as done previously (Holekamp et al. 1997a; Szykman et al. 2001). We employed this method because it was appropriate for *Crocuta* and because it enabled us to compare our current data to earlier

association data for *Crocuta*. We elected not to use the fission–fusion decision index (Cross et al. 2005) because *Crocuta* do not satisfy its key assumption that travel costs are high when individuals move among subgroups within the territory (Kruuk 1972; Holekamp et al. 2000). We calculated intrasexual AIs for immigrant males for the first time here and extended earlier analyses of female–female association by including data collected from 15 February 1994 through 31 December 1999, not available in our earlier study (Holekamp et al. 1997a). An AI was calculated for each same-sex dyad of unrelated adults, hyenas A and B, for each year during which they were concurrently present in the clan as adults for at least 6 months. We calculated $AI_{A,B}$ as: $(A+B_{together})/[(A_{without\ B})+(B_{without\ A})+(A+B_{together})]$ where $(A+B_{together})$ represents the number of observation sessions in which A and B were both present, $(A_{without\ B})$ represents the number of sessions in which A was observed but B was not present, and $(B_{without\ A})$ represents the number of sessions in which B was observed but A was not present.

During the 11-year study, multiple individuals occupied most of the available rank positions in both male and female hierarchies. Immigrant males queue for rank, with their social status increasing within the male hierarchy as they gain tenure in the clan (Smale et al. 1997; East and Hofer 2001). Females assume social ranks immediately below those of their mothers, but ranks can change due to births and deaths of clan members (Frank 1986; Engh et al. 2000). Therefore, we calculated an overall mean AI for each rank position within each sex by summing AIs across all individuals holding that rank during the study and dividing by the total number of AIs for that rank position. We also calculated a mean AI for each rank distance by summing the AIs across all individuals with the same rank distance within each sex and dividing by the total number of AIs for each rank distance. In another analysis, we controlled for rank distance by comparing how often a focal adult, hyena B, associated with a same-sexed adult ranking directly above it in the dominance hierarchy, hyena A, to how often that focal individual associated with the adult ranking directly below it, hyena C. That is, we compared $AI_{A,B}$ and $AI_{B,C}$ to inquire whether hyena B associated more often with the dominant or subordinate adjacent-ranking individual.

High-ranking females have offspring at the communal den more frequently than do low-ranking females because high-ranking adult females wean their young faster and enjoy shorter interbirth intervals than do low-ranking females (Frank et al. 1995; Holekamp et al. 1996). To avoid this factor as a confounding variable, sessions at the communal den were excluded from all calculations of AIs. Because immigrant males search for mating opportunities by actively joining subgroups containing sexually receptive females (Szykman

et al. 2001), we conservatively used only sessions in which potentially fertile females, those more than 24 months of age, were absent to evaluate patterns of male-male partner choice while controlling for the effects of mate choice.

Decisions to join subgroups containing other adult females

To determine whether subgroups containing each focal female were more likely to be joined by subordinate or dominant females during subgroup fusion events within the clan, we conducted focal animal surveys, totaling at least 2 h per animal, on eight adult females from our study clan holding ranks of 7, 8, 9, 11, 12, 13, 18, and 21. Adult females ranking above 7 were from the alpha matriline and those ranking below 21 were from the lowest-ranking matriline. Individuals within these two matrilines were excluded from this analysis because no unrelated dominant females were available to join the former and no unrelated subordinate females were available to join the latter. We ended surveys when the focal female went out of view for more than five consecutive minutes. We recorded all unrelated females that actively joined each focal female during fusion events throughout the focal animal survey. To control for kinship, a prospective joining animal was only counted if none of her kin were present in the subgroup containing the focal female. We conducted surveys in the absence of food and away from the den to exclude other factors that might promote group formation, and possibly confound joining rates.

From these data, we calculated (1) the proportion of subordinate females that joined each focal female out of the number of subordinate females alive in the population at the time of the survey and (2) the proportion of dominant females that joined each focal female out of the number of dominant females alive in the population at that time. Both proportions were divided by the total number of focal hours during which each female was observed to correct for variation in sampling effort among females. We also compared the number of subordinate and dominant females available to join each focal female to ensure that our joining rates did not simply result from biases in the number of individuals available from each category.

Tests of hypotheses suggesting benefits of rank-related partner choice

Within each dyad where female A outranked female B, we calculated an hourly rate of aggression observed in each of two contexts, when food was absent and when it was present. We calculated rates of aggression within each dyad by dividing the total number of aggressive acts female A directed towards female B in a particular context by the total number of hours A and B spent together in that

context. We required that both members of each dyad be observed together in each context for at least 6 h during their adult lives. We measured feeding tolerance by dividing the number of scans in which female B fed when female A was present by the number of scans in which both A and B were recorded together during their adult lives in sessions where food was present, and then multiplied by 100. The only dyads included in this analysis were those in which both members were present concurrently as adults at sessions with food during at least 15 scans.

To evaluate rates at which females provided coalitionary support to other females, we analyzed fights in which individuals transformed dyadic fights into coalitionary aggression by intervening to support particular aggressors. For example, we analyzed fights in which female A directed dyadic aggression towards female B, and female C intervened in the ongoing fight to support female A. In this case, A was the 'aggressor' (recipient of coalitionary support), B was the 'target' of coalitionary aggression, and C was the 'supporter' (donor of coalitionary support). First, we determined how relative rank influenced rates at which females supported aggressors in coalitionary aggression by comparing the percent of available subordinate and dominant supporters joining each focal aggressor per hour. For each focal aggressor, we counted the number of fights in which a subordinate or dominant supporter intervened on behalf of the focal aggressor in sessions in which at least one female was present ranking above the focal aggressor and one ranking below. We calculated the percent of available supporters joining each focal aggressor per hour in each session by dividing the number of subordinate supporters by the number of subordinates present, and the number of dominant supporters by the number of dominants present during that fight, then dividing these values by the number of hours each session lasted. For each focal aggressor supported by more than one subordinate or more than one dominant in multiple sessions meeting our criteria, we calculated an average rate at which subordinate and dominant females supported the focal aggressor. We then asked whether AIs within dyads were correlated with hourly rates of coalitionary support provided by the dominant member. To calculate a rate of coalitionary support for each dyad, we counted all occurrences of coalition formation in which the dominant supporter intervened to provide coalitionary support to the subordinate aggressor, and divided by the number of hours we observed that pair together as adults. Dyads observed together for less than 20 h were excluded.

Statistical analyses

We employed nonparametric statistical techniques because the distributions of our data were statistically different from

normal ($P<0.001$ in all cases). We calculated correlation coefficients, Spearman's R, to ascertain whether AIs varied with social rank or rank distance and to test the direction and strength of relationships between AIs or rank distance and (1) hourly rates of dyadic aggression, (2) feeding tolerance by dominant females, and (3) hourly rates of coalitionary support provided to subordinates by dominant females. A Mann–Whitney U-test was used to inquire whether mean AIs differed between the sexes. Wilcoxon signed rank tests for matched samples were used to determine whether *Crocuta* associated to a different extent with subordinate and dominant partners of the same-sex that were adjacently ranked. We also used this test to compare the percentages of available subordinate and dominant females joining focal females per hour, and to test whether the numbers of subordinate and dominant individuals that were available to join focal females differed. We used Wilcoxon signed rank tests to determine whether aggression within dyads differed between sessions in which food was present and those in which it was absent, and whether subordinate and dominant females differed with respect to the rates at which they provided coalitionary support to focal females. We reported the sum of ranks for the Wilcoxon signed rank tests as exact values (T) and asymptotic values (Z) for tests with sample sizes of less than 16 and at least 16, respectively, as suggested by Mundry and Fischer (1998). We used SYSTAT Version 8.0 (Systat Software, Richmond, CA, U.S.A) to perform Mann–Whitney U-tests and Wilcoxon signed rank tests, and STATISTICA 6.1 (StatSoft, Tulsa, OK, U.S.A.) to fit distributions and perform Spearman rank correlations. We conducted all tests based on two-tailed probabilities, considered differences to be statistically significant when alpha was less than 0.05, and where appropriate, report mean values±S.E.

Results

Effects of sex, social rank, and rank distance on association patterns

Unrelated adult females associated significantly more closely with each other (AI=0.037 ± 0.002, $n=50$ females) than did unrelated adult males (AI=0.018 ± 0.002; Mann–Whitney $U=2467.00$, $n=57$ males; $P<0.001$). For both sexes, mean intrasexual AIs increased with social rank (Fig. 1a). This relationship was statistically significant among females but not among males (Spearman rank correlation for females: $R_s=-0.88$, $n=24$ rank positions, $P<0.001$; for males: $R_s=-0.39$, $n=18$ rank positions, $P=0.098$). Both sexes of *Crocuta* associated most often with non-kin holding social ranks similar to their own, as indicated by significant

negative relationships between intrasexual AIs and rank distance (Spearman rank correlation for females: $R_s=-0.97$, $n=24$ rank distances, $P<0.001$; males: $R_s=-0.86$, $n=18$ rank distances, $P<0.001$; Fig. 1b).

When we controlled for rank distance, females associated significantly more often with females occupying rank positions immediately above them than they did with females occupying rank positions immediately below them (Wilcoxon signed ranks test; $Z=-1.99$, $n=33$ females, $P=0.046$; Fig. 2). However, the relationship between rank and AIs among immigrant males was not statistically significant after we controlled for rank distance (Wilcoxon signed ranks test; $Z=0.16$, $n=49$ males, $P=0.87$; Fig. 2). That is, the AIs of focal immigrant males with adjacent-ranking, subordinate males did not differ from the AIs of focal immigrant males with adjacent-ranking, dominant males. We, therefore, focused our subsequent analyses exclusively on AIs among unrelated adult females, the more selective sex in the context of rank-related, intrasexual partner choice.

Decisions to join subgroups containing other adult females

The total time of focal animal surveys for each of the eight focal females ranged from 2.13 to 6.30 h, averaging 4.39 ± 0.46 h per female. During these surveys, unrelated adult females joined subgroups containing one of the eight focal females a total of 18 times such that unrelated adult females joined each focal female at an average rate of 0.54 ± 0.11 times/h. Subordinate females joined focal females 15 times (83.3% of fusion events), whereas dominant females joined focal females only three times (16.7% of fusion events). After correcting for the number of potential subordinate and dominant joiners available in the population for each focal female, we found that the percentage of available subordinate females joining focal females per hour was significantly greater than the percentage of available dominant females joining focal females per hour (Wilcoxon signed ranks test, $T=36$, $n=8$ females, $P<0.008$; Fig. 3). This result was not simply an artifact of the number of unrelated subordinates ($n=9\pm2$) and dominants ($n=11\pm2$) available to join focal females because numbers of individuals from each category did not differ significantly (Wilcoxon signed ranks test; $T=19$, $n=8$ females, $P=0.95$). Overall, subordinate females selectively joined subgroups containing dominant females significantly more often than vice versa.

Tests of hypotheses suggesting benefits of rank-related partner choice

Among dyads of unrelated adult females, the majority (95.2%) of all aggressive acts ($n=2374$) were directed by dominants towards subordinates. Therefore, all rates of aggression reported here refer to aggressions directed by

Fig. 1 Mean (±SE) intrasexual association indices plotted as a function of **a** intrasexual social rank and **b** intrasexual rank distance for unrelated adult *Crocuta*. *Squares* represent adult females and *circles* represent adult males that held a particular rank while observed with an unrelated adult of the same sex. By convention, the highest rank possible is 1
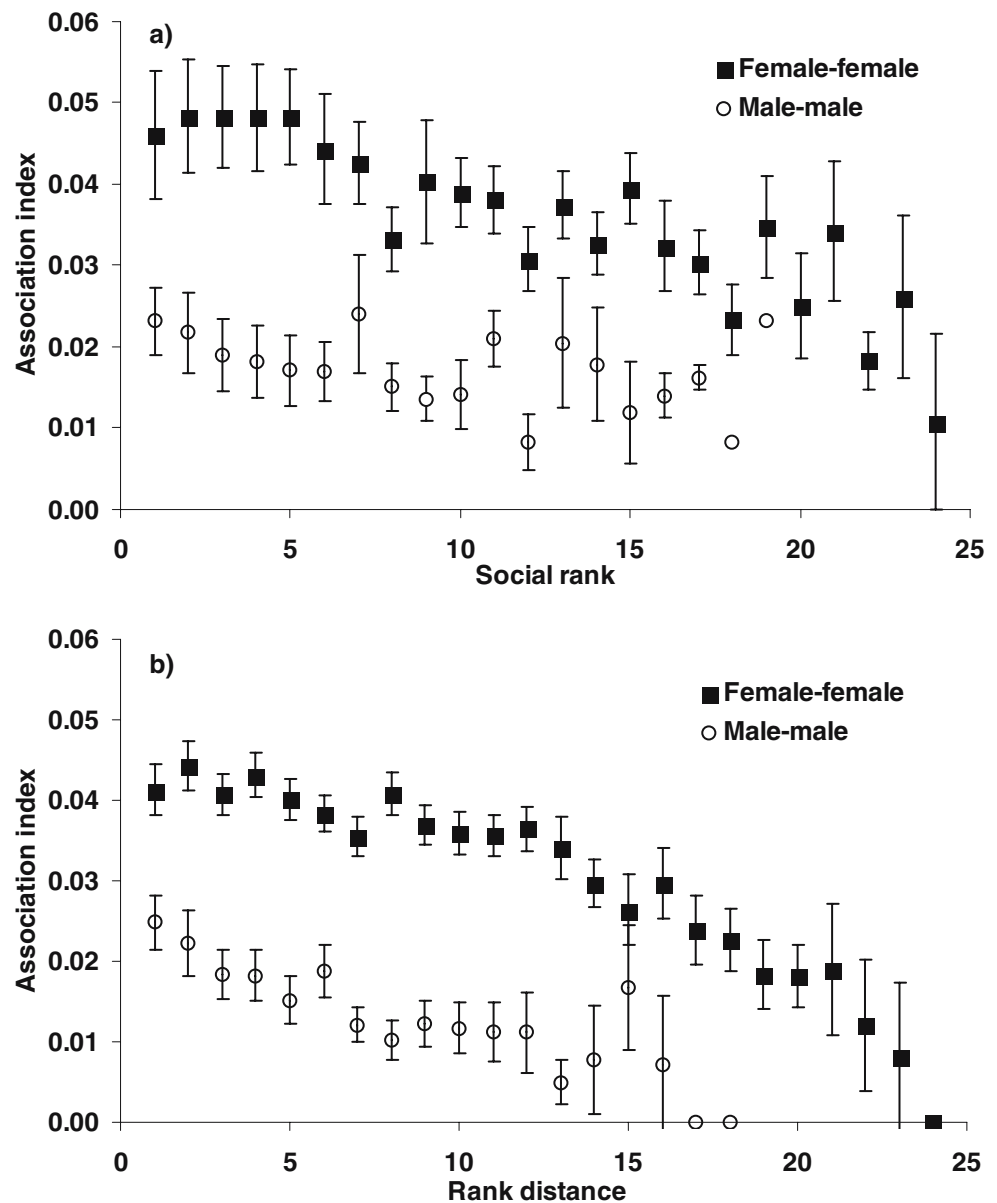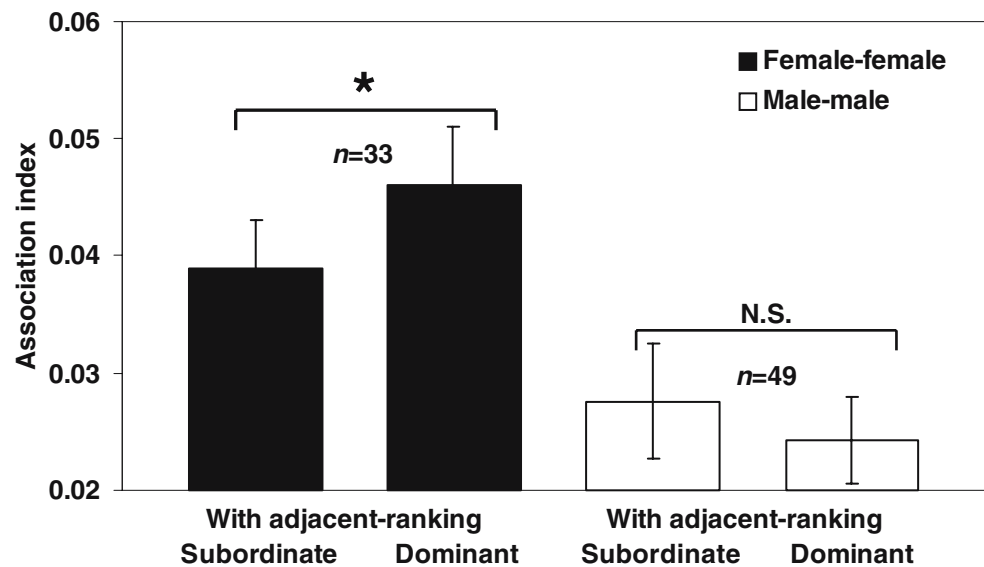

dominants towards subordinates within dyads. The mean rate of dyadic aggression was slightly higher at sessions in the presence of food (0.06±0.005 aggressions/h) than in its absence (0.05±0.003 aggressions/h), but this difference was not statistically significant (Wilcoxon signed ranks test, $Z=1.51$, $n=367$ dyads, $P=0.13$). The benefits received by subordinates from dominants were more strongly related to AIs than to rank distance for all measures of aggression when we considered AIs and rank distance as explanatory variables (Table 1). In every case, the effect of rank distance was substantially weaker than that of AIs. As predicted by the reduced harassment hypothesis, rates of dyadic aggression were significantly negatively related to AIs within dyads when food was absent (Spearman rank correlation, $R_s=-0.33$, $n=367$ dyads, $P<0.001$; Fig. 4a). The same relationship emerged when food was present,

supporting the first prediction of the feeding tolerance hypothesis (Spearman rank correlation, $R_s=-0.12$, $n=367$ dyads, $P<0.001$; Fig. 4b). Tolerance by dominants of subordinates during feeding was significantly higher within dyads that associated more often than within dyads that associated less often, supporting the second prediction of the feeding tolerance hypothesis (Spearman rank correlation, $R_s=0.33$, $n=37$ dyads, $P=0.045$; Fig. 4c).

Unrelated adult females provided coalitionary support to focal female aggressors during a total of 28 ongoing dyadic fights involving 12 adult female aggressors that started fights in sessions where both subordinate and dominant unrelated females were present. As expected, dominant females supported aggressors at a significantly higher mean hourly rate than did subordinates (Wilcoxon signed ranks test, $T=66$, $P=0.034$; Fig. 5a). However, our data did not support the

Fig. 2 Mean (±SE) association indices of *Crocuta* of each sex with animals of the same sex occupying rank positions either immediately above, or immediately below, them in the hierarchy of the clan. The *asterisk over the bracket* indicates *P*< 0.05 and *N.S.* indicates *P*=0.87

main prediction of the coalitionary support hypothesis; we detected no significant relationship between AIs and hourly rates at which dominant females provided coalitionary support to subordinate females within dyads (Spearman rank correlation, R_s=0.093, *P*=0.078, *n*=367 dyads; Fig. 5b).

Discussion

Sex differences in rank-related partner choice

Overall, high-ranking animals of both sexes were more gregarious than low-ranking individuals. Our data suggest that *Crocuta* assess the ranks of same-sexed conspecifics and associate most often with the adjacent-ranking individuals based on those assessments. Females associated more often with same-sexed adults occupying rank positions

directly above them than they did with individuals ranking immediately below them in the clan's dominance hierarchy. Unrelated adult female hyenas also generally associated with one another more closely than did immigrant males, reflecting the same patterns as those found during greeting ceremonies of *Crocuta* (East et al. 1993). Greeting is an affiliative behavior exhibited during subgroup reunions (Kruuk 1972); females initiate more greetings with same-sexed partners than do males, and subordinates initiate greetings more often than do dominants (East et al. 1993). Similarly here, adult females associated more often with same-sexed partners than did adult males, and subordinates initiated associations more often than did dominants. Adult males in our study also associated less often with one another (AI=0.018±0.002) than with adult females (AI=0.062±0.002: reported by Szykman et al. 2001). The association patterns we observed among hyenas were

Fig. 3 Proportion of unrelated subordinate and dominant adult females available to join that actively joined subgroups containing focal females, divided by the number of hours during which we monitored each focal female. The *asterisk over the bracket* indicates *P*<0.05
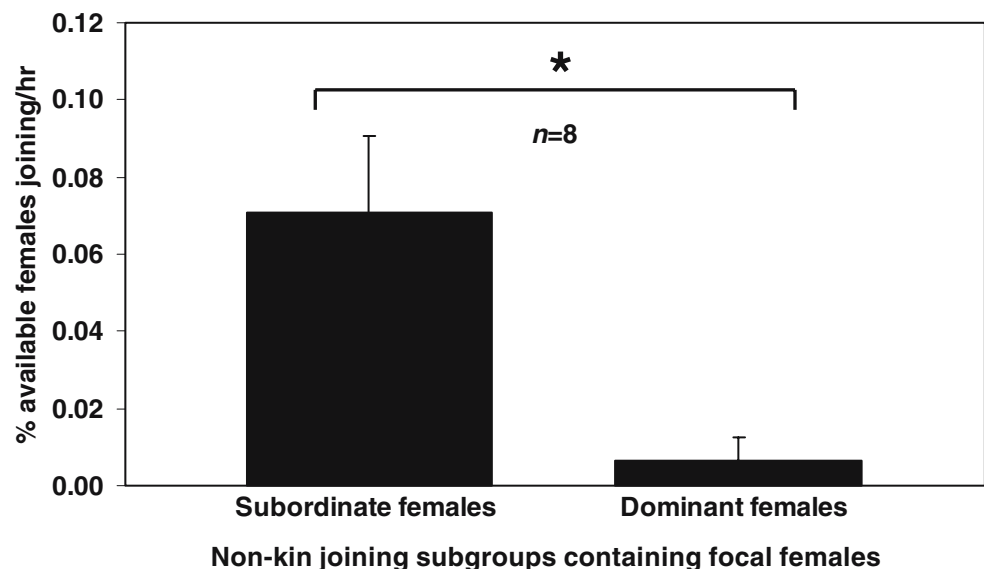
Table 1 Spearman rank correlations between association indices or rank distances and hourly rates of (A) nonfood and (B) food-related dyadic aggression directed by dominants towards subordinates, (C) feeding tolerance of subordinates by dominates, and (D) hourly rates at which dominants provided coalitionary support to subordinates within dyads of unrelated adult females (n=367 dyads for all relationships except for feeding tolerance where n=37 dyads)

Dependent variable	Independent variable			
	Association index (AI)		Rank distance	
	R_s	P-value	R_s	P-value
Nonfood aggressions/h	−0.33	<0.001**	0.14	<0.006**
Food-related aggressions/h	−0.12	<0.001**	−0.003	0.96
Feeding tolerance (% scans)	−0.33	0.045*	−0.13	0.44
Fights supported/h	0.93	0.078	−0.033	0.53

Asterisks indicate significant relationships at **$P<0.001$ and *$P<0.05$.

Fig. 4 Hourly rates of dyadic aggression directed by dominant females towards subordinate females when food was **a** absent and **b** present (n=367 dyads for both). **c** Feeding tolerance, measured as the percent of scans in which a dominant female tolerated a subordinate female feeding at a kill when both were concurrently present, plotted against association indices within 37 dyads
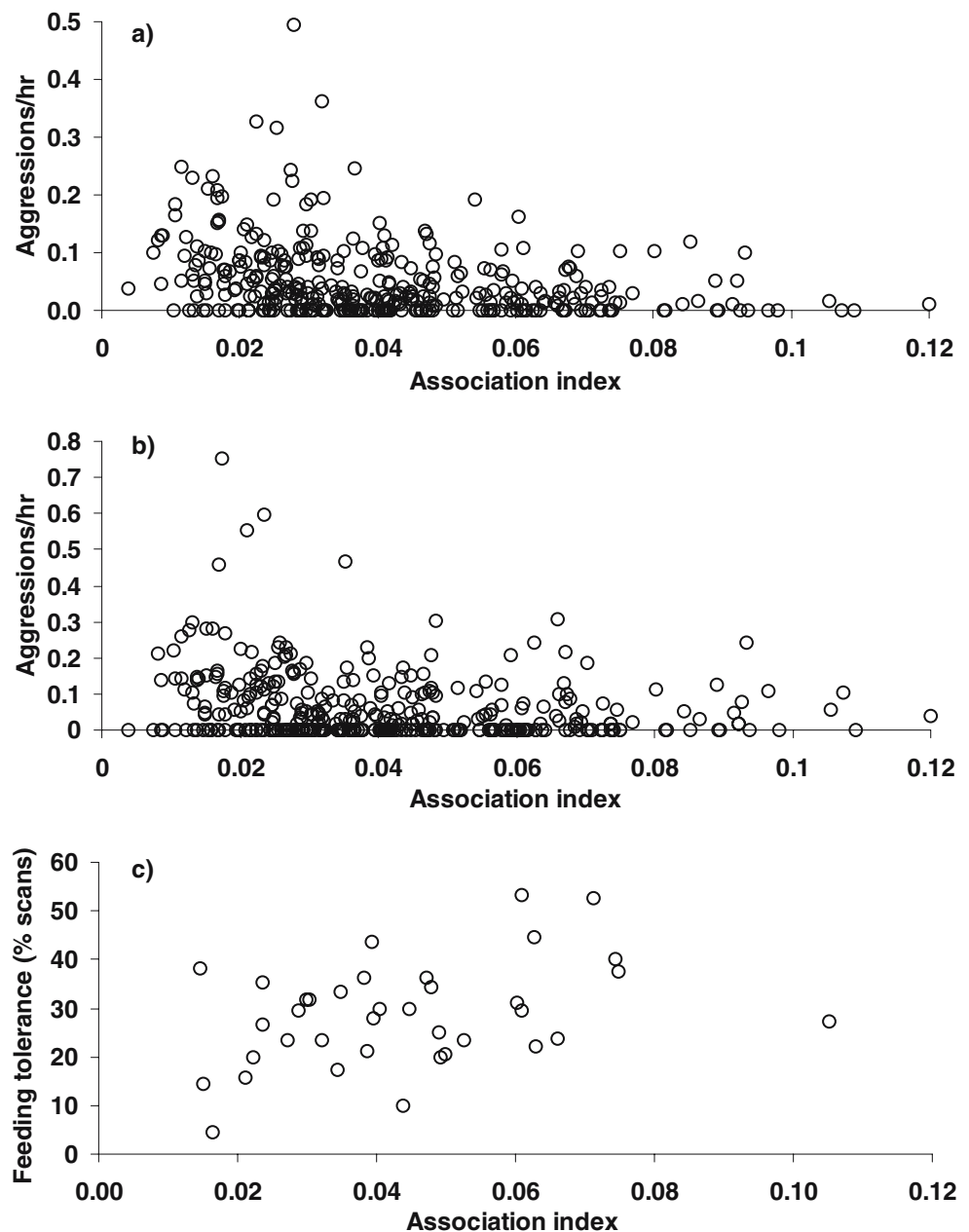
Fig. 5 a Proportion of subordinate and dominant females present during ongoing fights that intervened to provide coalitionary support to focal female aggressors per hour. The *asterisk over the bracket* indicates *P*<0.05. **b** The relationship between association indices and rates at which dominant females provided coalitionary support to subordinate females within 375 dyads
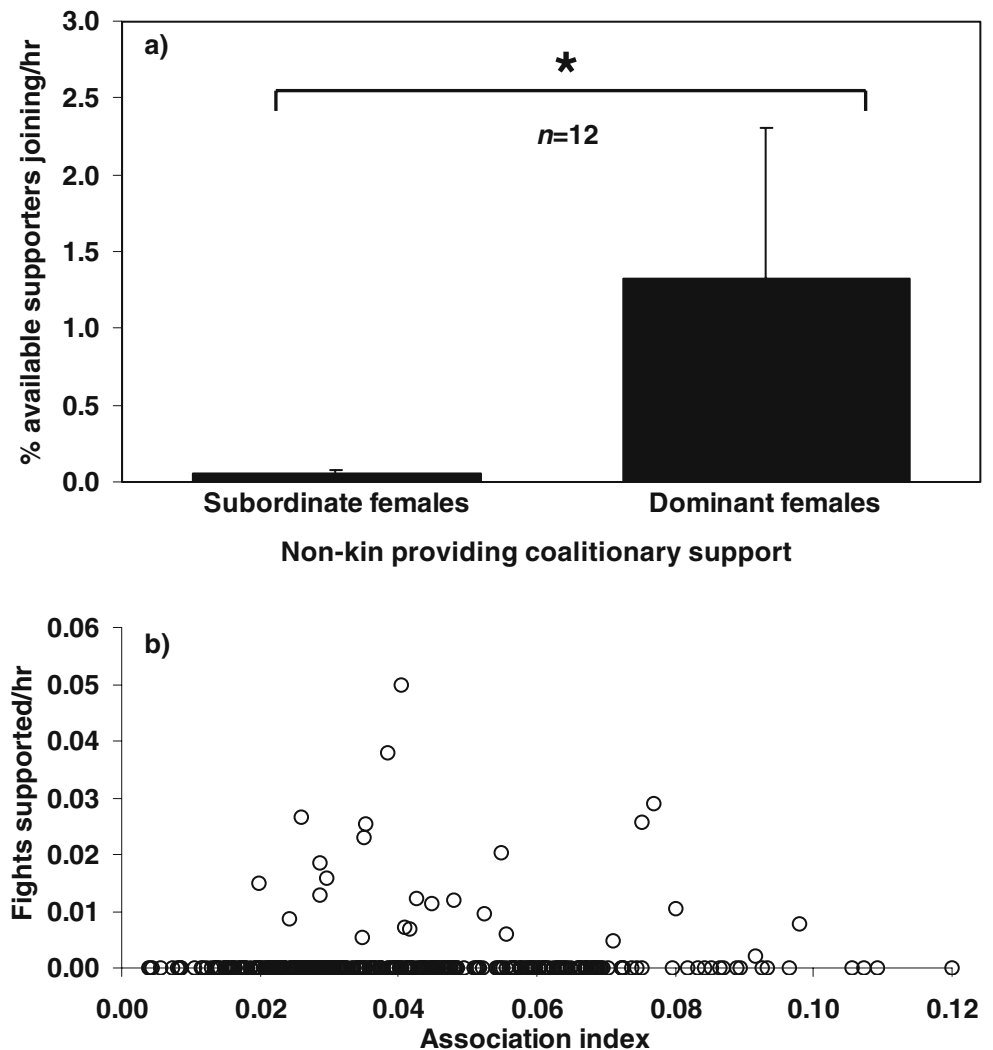
generally consistent with those in female-bonded groups of cercopithecines (Wrangham 1980; Sterck et al. 1997; Isbell and Young 2002), suggesting that sexually dimorphic patterns of reproduction and dispersal generate sex differences in association in hyenas as they do in primates.

Adaptive partner choice in fission–fusion societies

Dominant hyenas benefit from cooperative partnerships with subordinates (Kruuk 1972; Cooper 1991; Boydston et al. 2001), but our current analysis suggests that low-ranking females actively join subgroups containing dominants. At first, this surprised us, given that dominants often usurp food from subordinates and that animals are more likely to be targets of dyadic aggression in the presence than in the absence of dominants (Frank 1986; Mills 1990). However, the benefits gained by subordinates from joining subgroups containing dominant females may outweigh these potential costs. Subordinate females who associated more often with dominant females were the recipients of relatively low hourly rates of aggression both away from food and at kills,

and they also gained relatively good access to food. These data suggest that females minimize the costs of group living by initiating social interactions with conspecifics that outrank them, and by forming relationships likely to offer them return benefits in a variety of ways. By refraining from driving close subordinate associates away from food, dominants allow subordinates to access a highly valued resource, which should enhance subordinates' fitness.

Life in a fission–fusion society appears to permit *Crocuta* to be more flexible in their decisions about partner choice than animals living in more cohesive social groups, including most cercopithecines (Conradt and Roper 2000; Couzin 2006). The salient features of fission–fusion societies likely to affect decisions about partner choice are that subgroups are highly labile and that opportunities exist for dispersive conflict resolution (Wahaj et al. 2001). Patterns of social tolerance in *Crocuta* resemble those documented for other mammals living in fission–fusion societies. For example, African elephants (*Loxodonta africana*) avoid one another to minimize conflict (de Villiers and Kok 1997). Moreover, red deer (*Cervus elaphus*) stags living in

fission–fusion societies structured by stable linear dominance hierarchies (Clutton-Brock et al. 1982) direct the lowest rates of dyadic aggression towards close associates (Appleby 1983). Low rates of aggression result when subordinate stags actively avoid dominants, but low rates of aggression within *Crocuta* dyads appeared to be the product of partner solicitation, not avoidance, by subordinates.

Alternative theoretical frameworks in which to view partner choice in hyenas

Three types of models have been developed to explain patterns of partner choice among gregarious animals outside the context of mating. These models include those derived from optimal reproductive skew theory, Seyfarth's (1977) rank attractiveness model, and models derived from biological market theory. Here, we consider the extent to which predictions from each of these classes of models are consistent with our data documenting partner choice in *Crocuta*.

Early skew models (e.g., Vehrencamp 1983) were developed to predict patterns of reproductive partitioning, but more recent skew models also predict patterns of group size and resource partitioning within groups of social foragers. Patterns of partner choices among *Crocuta* are partially consistent with predictions of a transactional skew model (Clutton-Brock 1998; Reeve et al. 1998). Specifically, the model of Hamilton (2000) predicts when subordinates should choose to join a foraging group in which a dominant animal controls resource access. This model predicts how high-ranking individuals who control resource division should adjust their monopolization of resources according to the costs and benefits of grouping, and the extent of their ability to control resource partitioning within the group. It also predicts that dominants should permit subordinates to feed as an incentive to stay when the presence of additional group members at a feeding site increases the fitness of dominants (Hamilton 2000).

The skew model of Hamilton (2000) assumes that the presence of subordinates enhances the fitness of dominants, and this is true among *Crocuta*; dominants need subordinate allies during cooperative defense of the clan's territory and carcasses against lions or other hyenas (e.g., Boydston et al. 2001), and when hunting certain types of ungulates (Kruuk 1972; Holekamp et al. 1997b). Furthermore, Hamilton's model correctly assumes that subordinate *Crocuta* will be less likely to leave a group if offered a proportion of the resources obtained by the group and that dominants can control the division of at least some of the resources obtained by the group. However, this model further assumes that the subordinate's only alternative to joining the group is to forage alone and that subordinates cannot choose among additional groups; neither of these

assumptions hold in *Crocuta*. Most importantly, the skew model assumes that all subordinates will receive an equal share of the dominant's leftovers, an assumption not met in hyenas because subordinates themselves vary in rank. This highlights the more general inability of skew theory to predict patterns of association and partner choice in *Crocuta*. That is, skew models ignore individual variation within dominant or subordinate classes and assume that all members of each class are identical. Whereas the model of Hamilton (2000) successfully predicts that subordinates will join groups containing dominants and that dominants will offer subordinates incentives to stay by permitting them to feed, it fails to predict that subordinates will choose to associate with dominants ranking just above them in the clan's social hierarchy. One type of model derived from skew theory that takes intra-class variation into account is referred to as a "bidding game (Reeve 1998, 2000)." However, this is in effect a "biological market" model (Noë and Hammerstein 1994, 1995; Hammerstein 2001). We suggest biological market and rank attractiveness (Seyfarth 1977) models are more consistent with our observations than are skew models.

Originally proposed to explain rank-related association and grooming patterns in primates, Seyfarth's (1977) rank attractiveness model predicts that rates at which dominant animals offer protective coalitionary support to subordinates during fights should be proportional to the rates at which subordinates initiate affiliative interactions with dominants. This model thus assumes that multiple types of cooperative behaviors are involved in the formation and maintenance of long-term social bonds and that any particular helpful behavior might be exchanged, even after a substantial lapse of time, for cooperative behavior of a different sort. Similarly, biological market theory assumes individuals can exchange various types of goods and services, such that cooperative interactions may involve use of multiple "currencies" traded over extended periods of time (Noë and Hammerstein 1994; Hammerstein 2001; Noë 2006). Through these exchanges, market theory predicts that individuals should make decisions to gain immediate benefits from social interactions in the short term, net benefits at the end of a series of social interactions in the long term, or both (Noë and Hammerstein 1994; Noë 2001, 2006). For example, baboons gain immediate hygienic and hedonic benefits from grooming (Barrett et al. 1999; Barrett and Henzi 2001) and the net benefits associated with long-term social bonds (Silk et al. 2003).

Rank attractiveness and biological market models assume that asymmetries exist between the goods or services offered by dominants and subordinates within hyena dyads because dominants control access to resources. A key prediction made by these theories is that subordinates living in despotic societies should trade services in exchange for

tolerance by dominants (Noë 2006). These theories, however, relax the assumption of most transactional skew models that dominants have complete control over resources shared by the entire clan and assume instead that dominants only control commodities within their immediate subgroup or current marketplace. Dominant hyenas can facilitate subordinates' access to commodities such as food and space (Frank 1986; Boydston et al. 2003), and they can also provide effective coalitionary support to subordinates during within-group contests (Frank 1986; Smale et al. 1995; Engh et al. 2005). In exchange for these commodities, subordinates can offer services to dominants with which they associate, including help with prey capture and defense of resources from conspecifics and lions. Association provides a proxy measure of the potential aid of these sorts that subordinates can offer to the dominants with which they associate. Here dominant hyenas differentially permitted access to monopolized food and space by the subordinates with which they associated most often.

Both rank attractiveness and market models predict that the rates at which dominant animals offer social tolerance, feeding tolerance, and protective coalitionary support to subordinates during fights should be proportional to the rates at which subordinates initiate social interactions. Among *Crocuta*, dominant females participated more frequently in coalitionary aggression than did subordinates, but our data were inconsistent with the coalitionary support prediction because rates of support provided by dominants to subordinates were not correlated with AIs. However, our data were consistent with the other two predictions: rates of both social and feeding tolerance were correlated with AIs among unrelated adult females.

In contrast to skew theory, models of rank attractiveness and biological markets emphasize the importance of individual variation within dominant and subordinate trading classes. That is, when conspecifics within trading classes vary in their relative ability to provide commodities, individuals should be able to assess the value of each potential social partner and compete for partners of the highest relative value based on those assessments. The rank attractiveness model suggests that priority of access to social partners is largely determined by an individual's social rank. By virtue of their status, high-ranking animals can provide greater benefits to other individuals than can middle- or low-ranking animals. This ability to provide more benefits makes high-ranking animals the most attractive social partners, but only other high-ranking individuals have sufficient free choice to interact frequently with them. Similarly, market theory predicts that this outcome results from market forces favoring those individuals in weak bargaining positions to become less selective by lowering their demands, but allowing individuals in strong bargaining positions to become more selective and demanding.

Unlike traditional skew theory, these other models predict that low-ranking individuals cannot compete effectively for access to the highest-ranking conspecifics. Specifically, market forces associated with competition are expected to generate patterns of assortative, mutual partner choice involving evolutionary trade-offs between the demands that an individual would prefer to ask of a particular partner in the biological marketplace and the demands imposed by other animals competing for access to that same partner. This occurs in human markets (Pawlowski and Dunbar 1999) and in the societies of various nonhuman primates (Barrett et al. 1999; Barrett and Henzi 2001; Henzi and Barrett 2002; Henzi et al. 2003; Manson et al. 2004). Our joining data are consistent with these expectations because female *Crocuta* prefer partners that outranked them. Although the highest-ranking animals in the clan could potentially offer more goods and services, we found that subordinates associated most closely with the animals holding ranks immediately above them rather than with the highest-ranking females in the clan. Skew models cannot account for this result. However, if the highest-ranking females pair off first with other high-ranking individuals, then our result could be the outcome of competition in which females must settle for social partners ranking just above them in the overall hierarchy.

Dominant *Crocuta* tolerated subordinates based on social relationships lasting from 1 to 11 years. Our findings suggest that dyads of female *Crocuta* make repeated "cooperative investments" (Noë 2006) in long-term partnerships, as predicted by both rank attractiveness and biological market models. Biological market theory, in particular, is consistent with the large amount of unexplained variation we observed in rates of aggression and feeding tolerance during our study, which suggests that the values of services offered by social partners vary dynamically within the life span of these relationships and that a *Crocuta* clan might indeed be a biological marketplace. If this is the case, then decisions made by *Crocuta* about partner choice should also be influenced by immediate circumstances encountered within shorter portions of our study based on the socio-ecological conditions prevailing during those periods, as predicted by market theory. Thus, future work should inquire how variation in these larger-scale market forces shapes patterns of social interaction and partner choice among spotted hyenas. To more fully understand the rules governing decision making with respect to partner choice, it will be necessary to identify the cues used in assessment of partner value and to determine how the dynamics of social behavior at the individual level vary with larger scale socio-ecological conditions.

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