

American Society of Mammalogists

Patterns of Association among Female Spotted Hyenas (*Crocuta crocuta*)

Author(s): Kay E. Holekamp, Susan M. Cooper, Catherine I. Katona, Nancy A. Berry, Laurence G. Frank and Laura Smale

Source: *Journal of Mammalogy*, Vol. 78, No. 1 (Feb., 1997), pp. 55-64

Published by: [American Society of Mammalogists](#)

Stable URL: <http://www.jstor.org/stable/1382638>

Accessed: 12/06/2013 14:00

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



American Society of Mammalogists is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Mammalogy*.

<http://www.jstor.org>

PATTERNS OF ASSOCIATION AMONG FEMALE SPOTTED HYENAS (*CROCUTA CROCUTA*)

KAY E. HOLEKAMP, SUSAN M. COOPER, CATHERINE I. KATONA
NANCY A. BERRY, LAURENCE G. FRANK, AND LAURA SMALE

Department of Zoology, Michigan State University, East Lansing, MI 48824 (KEH, SMC)

Department of Psychology, Michigan State University, East Lansing, MI 48824 (CIK, LS)

School of Veterinary Medicine, Michigan State University, East Lansing, MI 48824 (NAB)

Department of Psychology, University of California, Berkeley, CA 94720 (LGF)

We examined subgroup association patterns among adult female members of a clan of free-living spotted hyenas (*Crocota crocuta*) and between adult females and their juvenile offspring during three consecutive stages of development of offspring. These stages represented the approximate periods of residence of offspring at the communal den, from 1 to 8 months of age, between leaving the communal den and weaning, from 8 to 14 months, and between weaning and reproductive maturity or dispersal, from 14 to 36 months of age. Mean association indices among adult female dyads varied with social rank, with the highest mean association index observed for the alpha female. Adult females associated more closely with their adult female kin than with unrelated adult females. Female kin from high-ranking matriline associated more closely than did kin from lower-ranking matriline. Within mother-offspring pairs, association patterns were strongly influenced by the mother's social rank during all three stages of development of offspring, with high-ranking mother-offspring dyads associating more tightly than low-ranking dyads at each stage. Mean mother-offspring association indices declined as offspring grew older, but we found no significant differences based on sex of offspring during any of the developmental stages examined.

Key words: *Crocota*, hyena, association patterns, kinship, dominance

Patterns of spatial proximity influence the frequency of occurrence and outcomes of competitive and cooperative interactions among group-living mammals. In so far as these interactions affect the reproductive success of individual group members, subgroup association patterns exert important effects on fitness. Among female primates, kinship and social status affect patterns of association and frequencies of agonistic and affiliative interactions within troops. Related female primates often are found near one another, and may travel, feed, and sleep together (Altmann, 1980; Gouzoules and Gouzoules, 1987). Many cercopithecine primates associate with, and direct affiliative behaviors toward, high-ranking conspecifics and close kin more frequently than toward low-ranking or unrelated individuals

(Altmann, 1980; Cheney and Seyfarth, 1990; Dunbar, 1980; Seyfarth, 1977; Silk et al., 1981). Furthermore, maternal rank may influence the frequency of occurrence of various types of social interactions experienced by juvenile primates, and thereby profoundly affect their behavioral development (Berman, 1980; Cheney, 1977, 1983; Gouzoules, 1975; Horrocks and Hunte, 1983; Silk et al., 1981).

Like troops of cercopithecine primates, clans of spotted hyena (*Crocota crocuta*) are permanent multi-male, multi-female social groups containing one (Mills, 1990) to several (Frank, 1986a) matriline of adult females and their offspring. Like groups of *Ateles* and *Pan* (Symington, 1990), clans of *Crocota* are fission-fusion societies. That is, individuals travel, rest, and forage in sub-

groups that can change in membership from day to day, or even hour to hour. All clan members seldom, if ever, aggregate simultaneously. Size and composition of subgroups are not rigidly structured, but subgroups of hyenas always are composed of hyenas from the same clan. Like troops of cercopithecine primates, but unlike groups of most social carnivores, clans of *Crocota* are structured by linear, rigid, rank relationships among their individual members (Frank, 1986b; Kruuk, 1972; Smale et al., 1993). An individual hyena's social rank determines its priority of access to food during competition at kills with other clan members (Frank, 1986b; Tilson and Hamilton, 1984). Here we examine social rank and kinship as possible determinants of subgroup association patterns among adult female spotted hyenas. We also evaluate effects of social rank, sex of offspring, and age of offspring on association patterns between adult females and their young.

MATERIALS AND METHODS

The study was conducted in the Masai Mara National Reserve, Kenya, an area of open rolling grassland grazed year-round by several species of ungulates. Our subject population was one large clan of *Crocota* occupying a home range of ca. 65 km². All hyenas in the study clan were known individually by their spot patterns, and sex was determined from the dimorphic morphology of the glans of the erect phallus (Frank et al., 1990). Mother-offspring relations were established on the basis of regular nursing associations. Social ranks of adult females were assessed based on outcomes of dyadic agonistic interactions, as described previously (Holekamp and Smale, 1990; Smale et al., 1993).

Female hyenas bear litters of one or two offspring in isolated natal dens (East et al., 1989), and maintain litters there during the first few weeks post-partum. Mothers then transfer their young to the clan's communal den, where up to 20 offspring may reside concurrently (Kruuk, 1972). The communal den is a social focal point for clan members, and frequently is visited by adults of both sexes, and by immature individuals who no longer use the den for shelter. Juveniles remain at the communal den until they

are ca. 8 months old, and their mothers visit the den regularly during this period to nurse them (Holekamp and Smale, 1993). When young leave the den and begin travelling around the home range of the clan they start feeding regularly at killed ungulates, although they may also continue nursing for several more months. Mean age at weaning in our study population was 13.4 ± 0.6 months. Male *Crocota* reach reproductive maturity at 24 months of age, and females typically bear their first litters at ca. 36 months. All male *Crocota* disperse from their natal clans (Henschel and Skinner, 1987), usually between 24 and 40 months of age (Smale et al., in press). For analyses presented here, we assigned juvenile hyenas to one of three age groups; 1–8 months, 8–14 months, and 14–36 months. These age intervals corresponded approximately to three consecutive stages of development. The period of residence at the clan's communal den; the period between leaving the communal den and weaning; weaning to reproductive maturity (females) or dispersal (males). Natal animals older than 36 months, and all immigrant animals were considered to be adults.

Subjects of the analyses presented here were 28 adult females and their 97 offspring who survived ≥ 8 months. Data were drawn from 10,256 observation sessions conducted 1 June 1988 to 15 February 1994. All hyenas present were identified in these sessions, and we excluded from analyses other sessions in which one or more unidentified hyenas were present. Observations were made from vehicles between 0600 and 0900 h or between 1700 and 1900 h. Each observation session was initiated when we found one or more hyenas separated from others by ≥ 200 m, and terminated when we left that individual or group. Subgroups of hyenas were located while observers drove daily circuits in which all highpoints within the study clan's home range were visited. By making 360° visual scans with binoculars from each highpoint, we were able to sample all parts of the home range every day for presence of subgroups of hyenas. Each subgroup sighted was then visited to determine its composition.

We calculated association indices for pairs of hyenas using the twice-weight index of association (Cairns and Schwager, 1987). Thus, to calculate an association index for each pair of animals A and B, we divided the number of observation sessions in which both A and B were

present by the sum of that number plus the number of sessions in which either A or B was observed without the other being present. We thereby generated association indices for each adult female with every other adult female throughout the period during which both were present as adults in the study clan's home range. High-ranking adult female *Crocota* wean their offspring faster, and enjoy shorter interbirth intervals, than do low-ranking females (Frank et al., 1995; Holekamp and Smale, 1995). Thus, high-ranking females have offspring at the clan's communal den more frequently than do low-ranking females. To avoid this factor as a confounding variable, observation sessions at the communal den ($n = 2,967$) were excluded from calculations of association indices among adult females. We compared association patterns of adult females between individuals of different social rank, and between kin and non-kin. In the latter analysis, kin included only mothers, adult daughters, and adult maternal sisters. Detailed data describing pedigrees for the study animals are available in Frank (1986a) and Holekamp et al. (1993).

We also calculated association indices between adult females and their juvenile offspring in the 1–8-, 8–14-, and 14–36-month age groups. We compared mean association indices of mother-offspring pairs between age groups. We also examined relationships within age groups between maternal rank and mother-offspring association indices. Finally, using only the 19 juveniles of each sex for which mother-offspring association indices could be calculated during all three stages of development, we examined effects of stage and sex on mother-offspring association patterns. Differences between groups were evaluated with analysis of variance (ANOVA) and independent t -tests. Differences were considered significant when $P < 0.05$.

RESULTS

Each of the 28 adult female subjects was observed, on average, during 232 ± 39 sessions. Mean association indices between each adult female and every other unrelated adult female in the clan varied significantly with social rank (Fig. 1; $n = 300$ non-kin dyads; Spearman's $R = -0.827$; $F = 52.25$; $d.f. = 1,26$; $P < 0.001$), with the highest mean association index observed for the

clan's alpha female. Furthermore, adult females associated significantly more closely with their adult female kin than with unrelated adult females (Fig. 2; $t = -4.15$; $d.f. = 314$; $P < 0.001$). However, female kin belonging to high-ranking matriline associated more closely than did female kin from lower-ranking matriline (Fig. 3; $n = 13$ kin dyads; $F = 4.95$; $d.f. = 1,11$; $P = 0.048$). We found no significant relationship between association index and distance in rank between members of non-kin adult female dyads (distance in rank was calculated by subtracting the rank of one female from that of the other; Pearson's $R = -0.084$; $F = 2.15$, $d.f. = 1,298$, $P = 0.144$; $n = 300$ adult female pairs). Thus, unrelated animals of adjacent ranks were no more likely to be found together than were those of widely differing ranks.

Association patterns between mothers and their juvenile offspring were strongly influenced by maternal rank. In all three age groups of juveniles, high-ranking mothers and cubs associated more tightly than did low-ranking mother-offspring pairs (Fig. 4a: 1–8 months; $F = 5.78$; $d.f. = 1,95$; $P = 0.018$; Fig. 4b: 8–14 months, $F = 13.46$; $d.f. = 1,70$; $P < 0.001$; Fig. 4c: 14–36 months; $F = 6.41$; $d.f. = 1,49$; $P = 0.015$). Spearman's correlation coefficients between maternal rank and mother-offspring association index increased with age of young (1–8 months; $R_s = -0.219$, $n = 97$; 8–14 months; $R_s = -0.390$, $n = 72$; 14–36 months; $R_s = -0.441$, $n = 51$). Thus, effects of maternal rank on mother-offspring association indices became more pronounced as juveniles grew older.

Nineteen juveniles of each sex were present throughout all three developmental stages. Association indices between these juveniles and their mothers were influenced by age of offspring but not by sex of offspring (Fig. 5). Specifically, mean association indices between mothers and their offspring declined with age of offspring (two-way ANOVA; $F = 40.29$; $d.f. = 2$; $P < 0.001$), but no significant differences be-

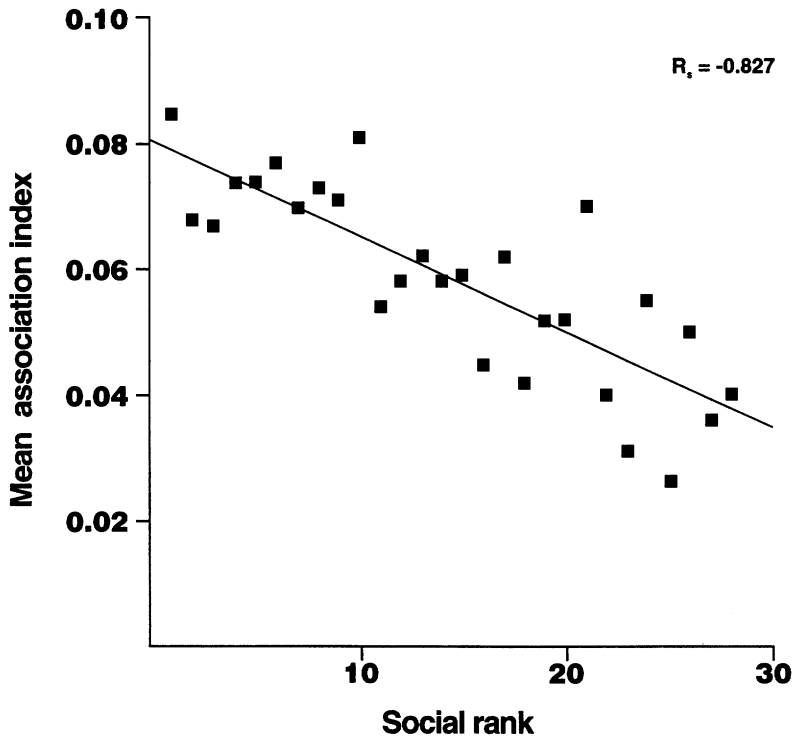


FIG. 1.—Mean association indices calculated for each of 28 adult female hyenas with all other unrelated adult female clan-members, plotted as a function of social rank. By convention, the highest rank possible is one.

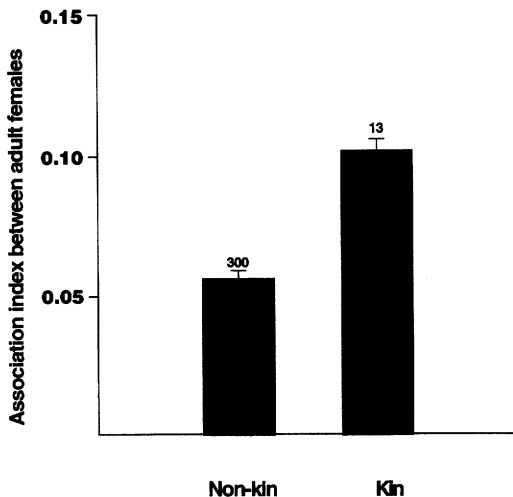


FIG. 2.—Mean association indices between adult females compared for kin and non-kin. Only adult females whose maternal kin relations were known precisely were used in this analysis. Sample sizes represent numbers of female dyads.

tween sexes were observed in any age group of juveniles, nor were stage-by-sex-interaction effects significant.

DISCUSSION

Our data revealed that association patterns among adult female *Crocuta* were strongly influenced by kinship, with closely related females associating more tightly than unrelated females. Kinship influences association patterns and social relationships of females in a wide range of mammalian societies including those of sciurid rodents (Michener, 1973, 1983; Sherman, 1981), proboscideans (Moss and Poole, 1983), odontocete cetaceans (Connor and Peterson, 1994), primates (Dunbar, 1980; Gouzoules and Gouzoules, 1987), and felids (Packer et al., 1991). In fact, spatial proximity appears to be influenced by genetic relatedness even among solitary mammals (e.g., *Sciurus car-*

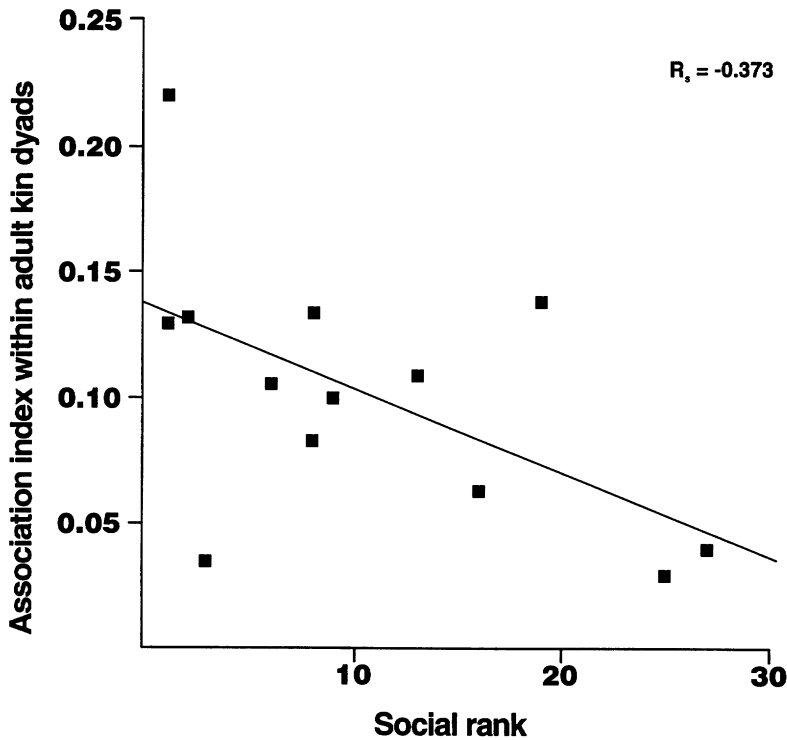


FIG. 3.—Association indices calculated for each of 13 adult female hyenas with their adult female kin, plotted as a function of social rank.

olinensis—Koprowski, 1993). In most mammalian species in which kinship is known to affect association patterns, fitness of individual animals is enhanced through close association with kin via increased rates of beneficial social interaction.

How might female *Crocota* benefit from associating more closely with their kin than with unrelated females? We suggest that no such benefits are likely to accrue in this species by increased cooperative interaction among females during the rearing of young. Adult female *Crocota* do not nurse, provision, or collectively care for juveniles other than their own offspring (Holekamp and Smale, 1990; Mills, 1985), as occurs in other social carnivores (felids—Pusey and Packer, 1994; canids—Malcolm and Marten, 1982; Moehlman, 1979, 1989; viverrids—Creel and Creel, 1991; Rood, 1983). By contrast, higher rates of cooperative interaction while obtaining and defending

food resources might yield substantial fitness benefits to female hyenas associating closely with their kin. Related adult female hyenas forage together, kin are better tolerated at carcasses than are unrelated females, and kin engage in coalitionary attacks against unrelated animals during feeding competition (Mills, 1985, 1990). In fact, close kin are usually the most common partners in coalitionary attacks on unrelated hyenas (Smale et al., 1995). In addition to generating these immediate benefits, close associations among kin may also play a central role in maintaining long periods of stability in the adult-female dominance hierarchy, and perhaps also in causing occasional disruptions in that hierarchy. During periods of stability, coalitionary attacks by related females against lower-ranking females may help reinforce existing rank relationships. However, these relationships may occasionally undergo radical change.

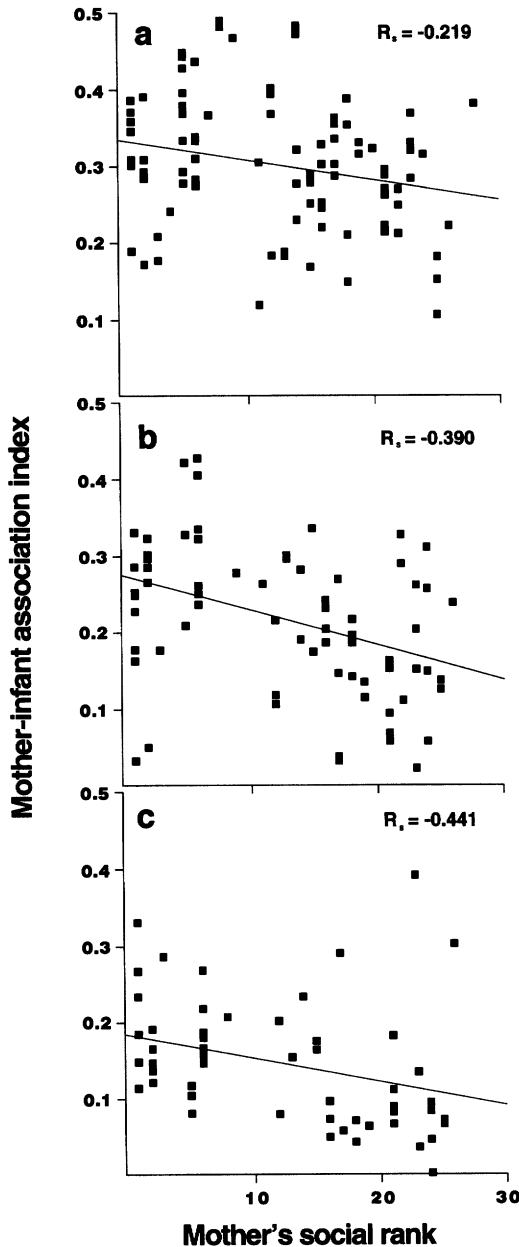


FIG. 4.—Mother-infant association indices plotted as a function of maternal rank, for juvenile hyenas that were: a) 1–8 months old; b) 8–14 months old; c) 14–36 months old.

For example, rank reversals between entire matriline have been observed in spotted hyenas (Mills, 1990). Similarly, in cercopithecine primates, close bonds among maternal kin can help high-ranking matriline

maintain their status or allow low-ranking matriline to rise over others (Gouzoules, 1980; Koyama, 1979; Samuels et al., 1987). Reproductive success among female *Crocota* varies with social rank (Frank et al., 1995; Holekamp and Smale, 1995) as it does in many cercopithecine primates (e.g., Altmann et al., 1988). Our data suggest that one important variable in the mediation of rank-related variance in reproductive success among females might be how closely kin associate.

If attraction among kin is the sole determinant of association patterns in the spotted hyena, then association indices between close female kin should be similar in all matriline, regardless of social rank. However, our results suggest that social rank also strongly influences association patterns between members of matriline of hyenas. Our findings are thus consistent with those of East et al. (1993) who found that both rank and relatedness influence distributions of social interactions within clans of spotted hyenas. Among primates in which maternal rank determines rank of offspring, distributions of affiliative behavior among troop members often are shaped by interaction effects of rank and kinship (*Cercopithecus aethiops*—Cheney, 1977; Seyfarth, 1976; *Macaca radiata*—Silk et al., 1981). As in these species of primates, high-ranking matriline of *Crocota* appear to be more cohesive than lower-ranking matriline.

Like high-ranking female primates, high-ranking female hyenas appear to be more popular companions than do lower-ranking females. This is surprising in view of the fact that high-ranking hyenas often usurp food from their lower-ranking companions (Frank, 1986b; Mills, 1990; Tilson and Hamilton, 1984). What benefits might accrue to adult female hyenas who associate with higher-ranking unrelated females? In addition to collective care of young, cooperative acts commonly observed among social carnivores other than *Crocota* include assistance in hunting and food-sharing. However, *Crocota* actively shares defensi-

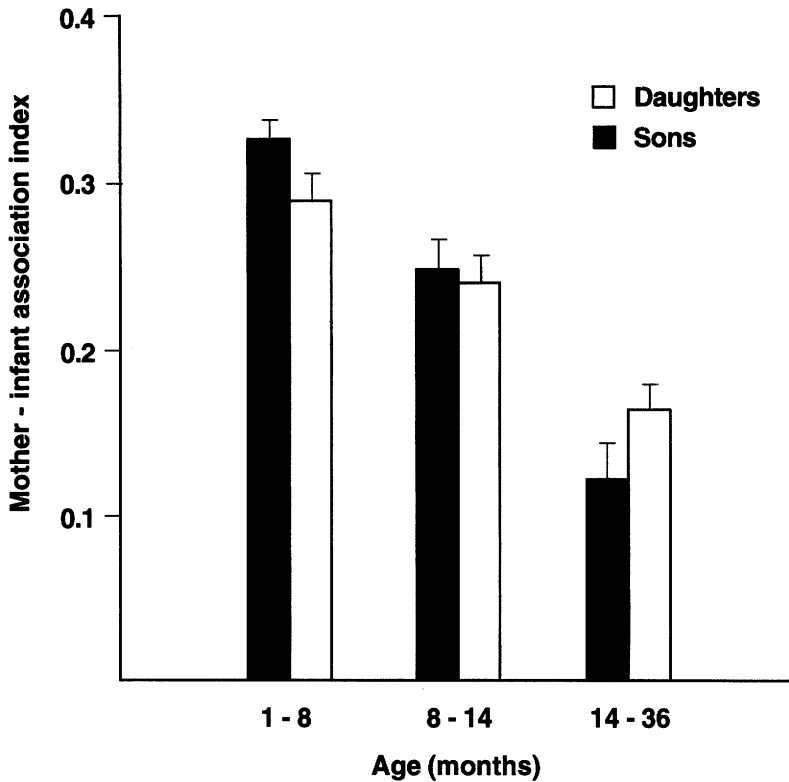


FIG. 5.—Mean mother-infant association indices for 19 juveniles of each sex who were observed throughout all three stages of development of juveniles.

ble food resources only with kin (Holekamp and Smale, 1990, 1993; Mills, 1990). Although it is conceivable that some benefit accrues to female hyenas from associating with higher-ranking non-kin during capture of large prey, this seems unlikely because individuals requiring such assistance should prefer to hunt with lower-ranking, not higher-ranking, companions. More likely explanations for the apparent attractiveness of high-ranking hyenas can be drawn from the literature on primates. Evidence from grooming and alliance formation among cercopithecine primates indicates that females attempt to establish bonds with higher-ranking individuals (Cheney and Seyfarth, 1990). Low-ranking females may benefit from such bonds because cooperative behavior is reciprocally exchanged between unrelated individuals (Seyfarth, 1977). Among spotted hyenas, a compara-

ble process might result in three possible benefits for females who associate with high-ranking non-kin: reduced social harassment from dominant individuals; increased probability of receiving coalitionary support from dominant animals in fights; improved tolerance by dominant females while feeding together at large carcasses. Tests of these hypotheses in *Crocota* are currently underway.

Unlike troops of cercopithecine primates, clans of spotted hyenas are fission-fusion societies. Except under rare and unusual circumstances, members of monkey or baboon troops are always together. By contrast, large groups of hyenas gather only at dens, kills, lion-hyena interactions, and clan wars (Kruuk, 1972). From these large gatherings, hyenas then drift away alone or in small groups, and spend much of their time in smaller social units. Nevertheless, our

data suggest that effects of social rank and kinship on subgroup association patterns in spotted hyenas may be comparable in nature and importance to the rank and kinship effects found in groups of cercopithecine primates.

Association indices between adult female hyenas and their offspring decline with age of young. As offspring mature, their dependence on the mother for obtaining food decreases. Then, during the 14–36-month age interval, mothers generally become involved with production and care of subsequent litters. Nevertheless, during this period, as during earlier developmental stages, high-ranking mother-infant pairs associate more closely than do lower-ranking pairs. Similarly, infants in high-ranking lineages of macaques spend more time with their kin than do infants in lower-ranking matriline (Berman, 1982). Furthermore, bonds between adult-female primates and their offspring have been found to be stronger in high- than low-ranking matriline (Cheney and Seyfarth, 1990; Ehert-Seward and Bramblett, 1980).

High-ranking female hyenas can do more to help their offspring than can lower-ranking females. High-ranking females can displace lower-ranking animals from food, so high-ranking mothers might consequently travel less widely in search of food, enabling their young to stay with them without becoming exhausted. In addition, when mother-offspring pairs are present together at carcasses with other clan members, high-ranking mothers intervene on behalf of their offspring to ensure that they can feed more easily at kills than can offspring of lower-ranking mothers (Frank, 1986*b*). Co-feeding relationships within mother-offspring pairs of *Macaca fascicularis* decline with age of offspring, but this decline is less apparent in high-ranking matriline (Imakawa, 1988; Yamada, 1963). In *Macaca radiata*, high-ranking youngsters are less likely to sustain physical injury during foraging or fighting than are their lower-ranking peers (Silk et al., 1981), and this might also

be true among spotted hyenas. Likely consequences of rank-related differences in mother-offspring association patterns among hyenas include lower mortality among offspring of high-ranking females, faster growth of young and more rapid acquisition of rank.

Our results suggest that maternal rank and age of offspring influence mother-offspring association patterns, but that sex of offspring does not. This is consistent with our earlier finding that major differences between sexes in the social experiences of young hyenas do not emerge until males disperse from their natal clans. It also is consistent with reports from the literature on primates (e.g., Glick et al., 1986). Among cercopithecine primates, maternal rank has been found to influence not only spatial proximity between juveniles and their mothers, but also vigilant behavior (Alberts, 1994) and rates of affiliative and aggressive interactions experienced by juveniles (Berman, 1983; Bernstein and Ehardt, 1986; Glick et al., 1986; Gouzoules, 1975). Our data suggest that behavioral development of young hyenas might be influenced by maternal rank in at least as many diverse and important ways as is that of young primates.

ACKNOWLEDGMENTS

We thank personnel in the Office of the President of Kenya for granting us permission to conduct this research. We also thank the Senior Warden of the Masai Mara National Reserve, the Narok County Council, and the Kenya Wildlife Service for their cooperation. This work was supported by National Science Foundation grants BNS87-06939, BNS90-21461, and IBN93-09805, by a fellowship to L. Smale from the American Association of University Women, and by fellowships to K. E. Holekamp from the David and Lucille Packard Foundation and the Searle Scholars Program/The Chicago Community Trust.

LITERATURE CITED

- ALBERTS, S. 1994. Vigilance in baboons: effects of habitat, age, sex and maternal rank on glance rate. *Animal Behaviour*, 47:749–755.

- ALTMANN, J. 1980. Baboon mothers and infants. Harvard University Press, Cambridge, Massachusetts, 242 pp.
- ALTMANN, J., G. HAUSFATER, AND S. A. ALTMANN. 1988. Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. Pp. 403–418, in *Reproductive success* (T. H. Clutton-Brock, ed.). The University of Chicago Press, Chicago, 538 pp.
- BERMAN, C. 1980. Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *International Journal of Primatology*, 1: 153–170.
- . 1982. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys: I. Social networks and differentiation. *Animal Behaviour*, 30:149–162.
- . 1983. Matriline differences and infant development. Pp. 132–134, in *Primate social relationships: an integrated approach* (R. A. Hinde, ed.). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, 385 pp.
- BERNSTEIN, I. S., AND C. EHARDT. 1986. The influence of kinship and socialization on aggressive behavior in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour*, 34:739–747.
- CAIRNS, S. J., AND S. J. A. SCHWAGER. 1987. A comparison of association indices. *Animal Behaviour*, 35:1454–1469.
- CHENEY, D. L. 1977. The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behavioral Ecology and Sociobiology*, 2:303–318.
- . 1983. Extra-familial alliances among vervet monkeys. Pp. 278–286, in *Primate social relationships: an integrated approach* (R. A. Hinde, ed.). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, 385 pp.
- CHENEY, D. L., AND R. M. SEYFARTH. 1990. How monkeys see the world. The University of Chicago Press, Chicago, 377 pp.
- CONNOR, R. C., AND D. M. PETERSON. 1994. The lives of whales and dolphins. Henry Holt and Co., New York, 233 pp.
- CREEL, S. R., AND N. M. CREEL. 1991. Energetics, reproductive suppression, and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology*, 28:263–270.
- DUNBAR, R. I. M. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. *Behavioral Ecology and Sociobiology*, 7:253–265.
- EAST, M. L., H. HOFER, AND A. TURK. 1989. Functions of birth dens in spotted hyenas (*Crocota crocuta*). *Journal of the Zoological Society of London*, 219: 690–697.
- EAST, M. L., H. HOFER, AND W. WICKLER. 1993. The erect “penis” is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology*, 33: 355–370.
- EHERT-SEWARD, C., AND C. A. BRAMBLETT. 1980. The structure of social space among a captive group of vervet monkeys. *Folia Primatologica*, 34:214–238.
- FRANK, L. G. 1986a. Social organization of the spotted hyaena (*Crocota crocuta*) I. Demography. *Animal Behaviour*, 35:1500–1509.
- . 1986b. Social organization of the spotted hyaena (*Crocota crocuta*) II. Dominance and reproduction. *Animal Behaviour*, 35:1510–1527.
- FRANK, L. G., S. E. GLICKMAN, AND I. POWCH. 1990. Sexual dimorphism in the spotted hyaena. *Journal of Zoology* (London), 221:308–313.
- FRANK, L. G., K. E. HOLEKAMP, AND L. SMALE. 1995. Dominance, demography, and reproductive success of female spotted hyenas. Pp.364–384, in *Serengeti II: Research, conservation, and management* (A. R. E. Sinclair and P. Arcese, eds.). The University of Chicago Press, Chicago, 665 pp.
- GLICK, B. B., G. G. EATON, D. F. JOHNSON, AND J. WORLEIN. 1986. Social behavior of infant and mother Japanese macaques (*Macaca fuscata*): effects of kinship, partner sex, and infant sex. *International Journal of Primatology*, 7:139–155.
- GOUZOULES, H. 1975. Maternal rank and early social interactions of infant stump-tail macaques, *Macaca arctoides*. *Primates*, 16:405–418.
- . 1980. A description of genealogical rank change in a troop of Japanese monkeys, *Macaca fuscata*. *Primates*, 21:262–267.
- GOUZOULES, S., AND H. GOUZOULES. 1987. Kinship. Pp. 299–305, in *Primate societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. T. Wrangham, and T. T. Struhsaker, eds.). University of Chicago Press, Chicago, 578 pp.
- HENSCHEL, J. R., AND J. D. SKINNER. 1987. Social relationships and dispersal patterns in a clan of spotted hyenas *Crocota crocuta* in the Kruger National Park. *South African Journal of Zoology*, 22:18–24.
- HOLEKAMP, K. E., AND L. SMALE. 1990. Provisioning and food sharing by lactating spotted hyenas (*Crocota crocuta*). *Ethology*, 86:191–202.
- . 1993. Ontogeny of dominance in free-living spotted hyenas: juvenile rank relations with other immature individuals. *Animal Behaviour*, 46:451–466.
- . 1995. Rapid change in offspring sex ratios after clan fission in the spotted hyaena. *The American Naturalist*, 145:261–277.
- HOLEKAMP, K. E., J. O. OGUTU, H. T. DUBLIN, L. G. FRANK, AND L. SMALE. 1993. Fission of a spotted hyena clan: consequences of prolonged female absenteeism and causes of female emigration. *Ethology*, 93:285–299.
- HORROCKS, J., AND W. HUNTE. 1983. Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Animal Behaviour*, 31:772–782.
- IMAKAWA, S. 1988. Development of co-feeding relationships in immature free-ranging Japanese monkeys. *Primates*, 29:493–504.
- KOPROWSKI, J. L. 1993. The role of kinship in field interactions among juvenile gray squirrels (*Sciurus carolinensis*). *Canadian Journal of Zoology*, 71:224–226.
- KOYAMA, N. 1979. Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. *Primates*, 11:335–390.
- KRUUK, H. 1972. The spotted hyena: a study of pre-

- dation and social behavior. University of Chicago Press, Chicago, 335 pp.
- MALCOLM, J. R., AND K. MARTEN. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, 10:1–13.
- MICHENER, G. R. 1973. Field observations on the social relationships between adult female and juvenile Richardson's ground squirrels. *Canadian Journal of Zoology*, 51:33–38.
- . 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pp. 528–572, in *Advances in the study of mammalian behavior* (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication, The American Society of Mammalogists, 7:1–753.
- MILLS, M. G. L. 1985. Related spotted hyaenas forage together but do not cooperate in rearing young. *Nature*, 316:61–62.
- . 1990. *Kalahari hyaenas*. Unwin Hyman Academic, London, United Kingdom, 304 pp.
- MOEHLMAN, P. D. 1979. Jackal helpers and pup survival. *Nature*, 277:382–383.
- . 1989. Intraspecific variation in canid social systems. Pp. 143–163, in *Carnivore behavior, ecology and evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 620 pp.
- MOSS, C. J. AND J. H. POOLE. 1983. Relationships and social structure of African elephants. Pp. 314–325, in *Primate social relationships: an integrated approach* (R. A. Hinde, ed.). Sinauer Associates Inc., Publishers, Sunderland, Massachusetts, 385 pp.
- PACKER, C., D. A. GILBERT, A. E. PUSEY, AND S. J. O'BRIEN. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, 351:562–565.
- PUSEY, A. E., AND C. PACKER. 1994. Non-offspring nursing in social carnivores. *Behavioral Ecology*, 4: 362–374.
- ROOD, J. P. 1983. The social system of the dwarf mongoose. Pp. 454–488, in *Advances in the study of mammalian behavior* (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication, The American Society of Mammalogists, 7:1–753.
- SAMUELS, A., J. B. SILK, AND J. ALTMANN. 1987. Continuity and change in dominance relations among female baboons. *Animal Behaviour*, 35:785–793.
- SEYFARTH, R. M. 1976. Social relationships among adult female baboons. *Animal Behaviour*, 24:917–938.
- . 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65:671–698.
- SHERMAN, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. *Behavioral Ecology and Sociobiology*, 8:251–259.
- SILK, J. B., A. SAMUELS, AND P. RODMAN. 1981. The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour*, 78:111–137.
- SMALE, L., L. G. FRANK, AND K. E. HOLEKAMP. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adults. *Animal Behaviour*, 46:467–477.
- SMALE, L., S. NUNES, AND K. E. HOLEKAMP. In press. Sexually dimorphic dispersal in mammals: patterns, proximal causes, and consequences. In *Advances in the study of behavior* (P. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and M. Milinski, eds.). Academic Press, HBJ Publishers, Inc., San Diego, California, 26.
- SMALE, L., K. E. HOLEKAMP, M. WELDELE, L. G. FRANK, AND S. E. GLICKMAN. 1995. Competition and cooperation between litter-mates in the spotted hyaena, *Crocuta crocuta*. *Animal Behaviour*, 50: 671–682.
- SYMINGTON, M. M. 1990. Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, 11:47–61.
- TILSON, R. T., AND W. J. HAMILTON. 1984. Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour*, 32:715–724.
- YAMADA, M. 1963. A study of blood-relationship in the natural society of the Japanese macaque: an analysis of co-feeding, grooming, and playmate relationships in Minoo-B troop. *Primates*, 4:43–65.

Submitted 4 April 1995. Accepted 7 June 1996.

Associate Editor was Karen McBee.