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THE CAUSES AND CONSEQUENCES OF SOCIAL RANK IN THE SPOTTED HYENA, CROCUTA CROCUTA

By

Anne Linnea Engh

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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ABSTRACT

THE CAUSES AND CONSEQUENCES OF SOCIAL RANK IN THE SPOTTED HYENA, CROCUTA CROCUTA

By

Anne Linnea Engh

Social rank can have a profound impact on an individual's life. Here, I examined how spotted hyenas attain their ranks, and how the hyenas' rank system influences social cognition, male reproductive success, and parasite loads. I began by testing predictions of four mechanistic hypotheses proposed to explain maternal rank "inheritance", a phenomenon observed in both hyenas and monkeys. In hyenas, neither genetic superiority nor aggression from adult females plays a strong role in rank "inheritance". Maternal interventions and supportive coalitions appeared to reinforce aggression directed at appropriate conspecific targets, whereas coalitionary aggression directed at cubs apparently functioned to extinguish their aggressive behavior towards inappropriate targets. Young hyenas and primates thus appear to "inherit" their mothers' ranks by strikingly similar mechanisms.

Given the similarities between societies of hyenas and primates, I next tested a prediction of the social complexity hypothesis, that animals living in similar social environments should possess similar abilities in the realm of social cognition. Specifically, I used two tests to determine whether hyenas can recognize third-party rank relationships. I found that young hyenas in the presence of food were able to exploit the arrival of potential allies by increasing rates of aggression toward lower-ranking animals. In addition, hyenas joined in on-going fights in support of the dominant contestant, even when that animal was losing. These lines of evidence suggest that hyenas can recognize relative rank relationships and strongly support the idea that social complexity drives the evolution of intelligence in phylogenetically disparate taxa.

In many mammalian societies structured by rank hierarchies, male reproductive success (RS) is positively correlated with social rank. Hyenas are unusual in that adult females are dominant to males, and there is relatively little fighting among males. Using genetic markers, I tested whether RS was related to social rank or dispersal status among male hyenas. Dispersal status and length of residence were the strongest determinants of RS. Immigrant males sired most cubs, despite the fact that immigrants are socially subordinate to all adult natal males. High-ranking immigrants did not monopolize reproduction, and tenure accounted for more of the variance in male reproductive success than did rank. The lack of reproductive skew among male hyenas may be a result of female choice of mates, rather than male-male contest competition.

Finally, I examined whether several social or demographic variables were related to parasite burden in hyenas. For several species of parasite, burden was higher in higher-ranking hyenas, probably because high-ranking individuals were exposed to more parasite eggs at kills than were low-ranking individuals.

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Chapter 1

GENERAL INTRODUCTION

Although gregarious mammals may gain through protection against predators (Carl 1971), division of labor (Sherman et al. 1991), or numerous other benefits (see Feldhammer et al. 1999), they also face costs associated with group living. In particular, animals living in groups suffer from increased intraspecific competition over critical resources (e.g., Hoogland 1979). When disputes occur over who controls particular resources, animals typically settle disputes based on asymmetries in resource holding power (RHP). In stable social groups where animals interact repeatedly, they may form a dominance hierarchy (Pusey & Packer 1997). In societies structured by dominance hierarchies, an individual's rank within the hierarchy typically has a massive impact upon access to resources, and ultimately, upon reproductive success (e.g., Sherman et al. 1991: De Ruiter et al. 1994: Altmann et al. 1996: Holekamp et al. 1996; Creel et al. 1997 (but see Packer et al. 1995; Gross 1996)). Here, I investigate the causes and consequences of social rank in the spotted hyena (Crocuta crocuta). I examine how young hyenas attain their social ranks, whether they recognize relative rank relationships between conspecifics, the relationship between male rank and reproductive success, and how rank influences parasitic infection.

Hyena biologists often think of spotted hyenas as baboons (*Papio* spp.) with big teeth. Although they are separated by over 90 million years of

evolutionary change and fill very different ecological niches (Lillegraven et al. 1979; Kingdon 1997), spotted hyenas and cercopithecine primates share many characteristics of their social lives (Holekamp et al. 1999a). Cercopithecine primates are one of two subfamilies of Family Cercopithecidae, the Old World monkeys. Subfamily Cercopithecinae consists of 48 species of monkeys, including baboons, mangabeys (*Cercocebus* spp.), guenons (*Cercopithecus* spp.), macaques (*Macaca* spp.), and vervet monkeys (*Chlorocebus* aethiops), that are distributed throughout Africa and Asia (Feldhammer et al. 1999). With the possible exception of the guenons (Cords 1987), most cercopithecine primates live in groups containing multiple adult males and multiple matrilines of females and their offspring. These cercopithecine social groups are among the best-studied of all primate societies (Melnick and Pearl 1987).

Spotted hyenas, members of Family Hyaenidae, are the most abundant large carnivores in Africa (Feldhammer et al. 1999). Like most cercopithecine primates, spotted hyenas live in multimale groups, with multiple matrilines of female kin making up the stable core of the social group (Kruuk 1972; Frank 1986; Holekamp et al. 1999a). In addition to living in groups of similar composition and complexity, these two taxa also share many aspects of their social behavior. In the following chapters, I compare several aspects of the spotted hyena social system to the social systems of typical cercopithecine primates.

Cercopithecine primates

Cercopithecine primates live in a wide variety of habitats, from forests to

savannahs, and feed on a diverse array of vegetation, including grasses, leaves. fruits, tubers, flowers, and seeds. In addition to their plant-based diet, some species supplement their diets with insects or meat. Multimale cercopithecine groups tend to be very cohesive and rarely split into subgroups. On average, they include 30 to 50 members who cooperatively defend a group territory (Melnick and Pearl 1987). Male cercopithecine primates usually disperse from their natal troops, whereas females are philopatric (Pusey and Packer 1987). Within each troop, individuals can be ranked in a linear dominance hierarchy in which males are usually dominant to females, often as a result of pronounced sexual size dimorphism. Male-male interactions are typically more aggressive and less affiliative than female-female interactions, and male rank is usually determined by body size, fighting ability, or age (Drickhamer and Vessey 1973; Packer 1979; Smuts 1985). In baboons and vervet monkeys, the highest-ranking males are young to middle aged adults who are in prime condition (Walters and Seyfarth 1987). Among females, social rank is determined by maternal rank. In a process termed "maternal rank inheritance", young monkeys eventually attain social ranks just below those of their mothers (Kawai 1958; Melnick & Pearl 1987; Chapais 1992). Although maternal rank plays an important role in determining social ranks of both male and female juveniles, young males grow larger than their mothers and begin to outrank most or all adult females in the natal troop before dispersing (Lee and Oliver 1979; Periera and Altmann 1985; Walters and Seyfarth 1987). Among female cercopithecine primates, high rank is usually associated with higher reproductive success (e.g., Gouzoules et al.

1982), probably because high-ranking females have better access to food than do low-ranking females (Silk 1987). Like females, high-ranking males also tend to have higher reproductive success than do low-ranking males (e.g., Altmann et al. 1996).

Spotted hyenas

Spotted hyenas are gregarious carnivores found throughout sub-Saharan Africa (Kingdon 1997). A group of hyenas, called a clan, can range in size from five to over 100 individuals, depending on local resource abundance, and members of a clan cooperate to defend a territory (Mills 1990; Kingdon 1997; Boydston et al. 2001). In contrast to cercopithecine primates, hyenas live in a fission-fusion society, and sub-group composition can change quite dramatically from day-to-day or even hour-to-hour (Boydston et al. 2001). Although often considered scavengers, spotted hyenas are in fact quite capable hunters, and kill up to 96% of their prey themselves (Kruuk 1972). Within a clan, as within a monkey troop, individuals can be ranked in a linear dominance hierarchy in which social rank determines an individual's priority of access to food and other resources (Tilson and Hamilton 1984; Frank 1986).

Hyenas are very unusual compared to cercopithecine primates and most other gregarious mammals in that adult females are dominant to adult males (Kruuk 1972; Frank 1986). Like cercopithecine primates, young hyenas inherit their mothers' social ranks. By the time they are 18 months old, male and female hyenas rank immediately below their mothers (Holekamp & Smale 1991; Smale et al. 1993). Most male hyenas disperse from their natal clans between the ages

of 2 and 5 years (Frank 1986; Henschel & Skinner 1987; Smale et al. 1997; East & Hofer 2001). Although they retain their maternal ranks as long as they remain in their natal clans, immigrating males behave submissively to all new hyenas encountered outside of the natal clan. As a result, immigrant males assume the lowest rank positions in the hierarchy when they join a new clan (Smale et al. 1997). Aggression among male hyenas is less common than aggression among females, and immigrant male rank is based on tenure in the new clan after dispersal (Smale et al. 1997; East & Hofer 2001). Immigrant male rank only increases when higher-ranking animals either die or disappear, and the alpha male is simply the male who has lived in the clan for the longest time (Smale et al. 1997). Although the highest-ranking male is called the "alpha" male, he nonetheless ranks below all natal animals and can be displaced from resources even by small cubs (Holekamp et al. 1993).

High-ranking female hyenas, like high-ranking female monkeys, enjoy higher reproductive success than do lower-ranking females. Compared to lowranking females, high-ranking females begin to reproduce earlier, have shorter interbirth intervals, and have higher cub survivorship (Frank et al. 1995; Holekamp et al. 1996). Over the course of a lifetime, this difference can result in a 6-fold difference in reproductive success between the lowest- and highestranking females (Holekamp et al. 1996). Among male hyenas, the relationship between social rank and reproductive success was unknown at the start of this study, although anecdotal observations suggested that reproductive success was strongly skewed toward the highest-ranking immigrant males (Kruuk 1972; Frank

1986; Mills 1990).

Similarities between the social systems of hyenas and cercopithecine primates

Besides similarities in the basic structures of their societies, hyenas and cercopithecine primates exhibit many behaviors that are strikingly similar in both form and function. As described above, in both taxa, youngsters inherit their mothers' social ranks, and female dominance relations are extremely stable across a variety of contexts and over long periods of time (Holekamp & Smale 1991). Among hyenas, non-littermate siblings assume relative ranks that are inversely related to age in a pattern of 'youngest ascendency' like that seen in many cercopithecine primates (e.g., Horrocks & Hunte 1983). In both primates and hyenas, kin associate more closely than do non-kin, and individuals direct affiliative behavior towards kin more frequently than towards non-kin (Seyfarth 1980; Seyfarth & Cheney 1984; East et al. 1993; Holekamp et al. 1997). Both hyenas and cercopithecine primates have been shown to reconcile after fights (Aureli & De Waal 2000; Wahaj et al. 2001), and in both taxa, high-ranking animals are preferred over lower-ranking individuals as social companions (Seyfarth 1980, 1981; Holekamp et al. 1997). In addition, patterns of greeting behavior in Crocuta follow primate patterns of social grooming (East et al. 1993), in which individuals are more likely to direct affiliative behavior towards highranking than low-ranking non-kin (Seyfarth & Cheney 1984). Finally, triadic and more complex interactions (e.g., coalitions) appear to play important roles in the acquisition and maintenance of social rank in Crocuta (Mills 1990; Zabel et al. 1992; Holekamp & Smale 1991; 1993; Smale et al. 1993; Jenks et al. 1995), as

they do in many cercopithecine primates (Cheney 1977; Walters 1980; Datta 1983, 1986; Harcourt 1988, 1992; Pereira 1989; Chapais et al. 1991; Chapais 1992).

Here I sought to compare several aspects of hyena social life to primate social life, and to assess the influence of social rank on particular aspects of hyena biology. In Chapters 2 and 3, I asked whether hyenas and cercopithecine primates share similar mechanisms of maternal rank inheritance, and whether they exhibit similar abilities with respect to social cognition. In Chapters 4 and 5, respectively, I examined the impact of social rank on male reproductive success, and on the intestinal parasite loads of individuals. All of the data in this dissertation were collected from a single clan of hyenas, the Talek clan, which defends a 70 km² territory on the northeastern edge of the Masai Mara National Reserve in Kenya. The research presented here would not have been possible without the efforts of many other people. Much of the behavioral and physiological data presented throughout the dissertation were collected by Kay Holekamp, Laura Smale, and numerous field assistants and graduate students working on the Mara Hyena Project. Undergraduates Katrina Esch, Anna Baumgrass, Erin Siebert, and David Greenberg assisted me in extracting relevant data from archived notes for Chapters 2 and 3. The data presented in Chapter 4 are the result of several people's work. The labs of Mike Bruford and Kim Scribner were critical in identifying hyena microsatellites, and Russ Van Horn genotyped many Talek animals. In addition, Micaela Szykman provided data used in analyses of association patterns and copulatory behavior. I use the

term "we" in each data chapter to indicate that my dissertation research was, in fact, a collaborative effort.

Overview of the chapters

In Chapter 2. I investigated how young hyenas attain their social ranks. One of the most striking similarities between hyenas and cercopithecine primates is that both have a system of maternal rank inheritance (Holekamp and Smale 1991). When a hyena is born, it fights viciously with its littermates to establish dominance over its sibling or siblings (Frank et al. 1991). As the cubs mature, they begin to develop dominance relationships with cubs born to other mothers within the social group. At first, these dominance relationships are unrelated to maternal rank, body size, age, or sex, but by the age of 8 months, cubs have social ranks in relation to those of their peers that are isomorphic with those of their mothers. By the time they are 18 months old, young hyenas are treated by adult clan members as if they have social ranks identical to those of their mothers (Holekamp & Smale 1993; Smale et al. 1993). Here, I sought to assess whether young hyenas inherit their maternal ranks via the same processes as do young monkeys by testing predictions of four mechanistic hypotheses. In both taxa, coalitionary support, both from relatives and non-relatives was extremely important. The remarkable similarity between the rank inheritance of hyenas and primates raised the question of whether they operate using similar cognitive mechanisms, or whether they arrived at the same basic social patterns via different mechanisms.

Two different types of selection pressures have been hypothesized to favor the evolution of large brains and great intelligence in primates. The first hypothesis suggests that intelligence has been favored in primates by selection pressures associated with complexity in the physical environment, particularly that confronted when navigating through a three-dimensional arboreal world (e.g., Povinelli & Cant 1995; Povinelli & Preuss 1995) or when finding and obtaining food (e.g., Jerison 1973; Clutton-Brock & Harvey 1980; Milton 1981). The second hypothesis suggests instead that key selection pressures have been imposed by complexity associated with the labile behavior of conspecific group members (Jolly 1966; Humphrey 1976; Byrne & Whitten 1988). Because the societies of spotted hyenas and cercopithecine primates are so similar, I asked in Chapter 3 whether their abilities were also similar in the domain of social cognition. Specifically, I sought to test one prediction of the social complexity hypothesis, that animals living in similar social environments should possess similar intellectual skills. Although the social complexity hypothesis is supported by interspecific comparisons among primates (reviewed in Byrne and Whiten 1988), the generality of the hypothesis is limited by a lack of information about the cognitive abilities of non-primates. In fact, some primatologists hypothesize that primates differ qualitatively from other animals, and that certain mental abilities, such as recognition of third-party relationships, are unique to primates (Tomasello and Call 1997). The ability to recognize third-party relationships, that is, relationships in which the observer is not directly involved, has been demonstrated in several species of cercopithecine primates (Cheney and

Seyfarth 1980; Silk 1999). Here I used several tests to assess whether hyenas, too, could recognize third-party relationships based on the social ranks of conspecifics. I found that hyenas were indeed able to distinguish the relative ranks of other clan members, thus providing strong support for the social complexity hypothesis.

Social dexterity and morphological traits both appear to affect reproductive success in a number of primate species (De Ruiter et al. 1994; Altmann et al. 1996; Bercovitch & Nurnberg 1997). In chapter 4, I examined the role of social rank in determining the reproductive success of male hyenas. Numerous studies have assessed the effect of social rank on reproductive success in male mammals, and most have found that reproductive success among males is positively correlated with rank, which, in turn, is largely determined by fighting ability (e.g., Clutton-Brock 1988; Creel et al. 1997; Girman et al. 1997). In contrast to most other mammals, spotted hyenas exhibit some striking sex-role reversals. That is, among adult hyenas, females are larger and more aggressive than males, and females dominate males in all dyadic contexts (Kruuk 1972; Frank 1986). In addition, fighting among adult male hyenas is less frequent and less intense than is that observed among adult females (Frank 1986; Kruuk 1972; Mills 1990), suggesting that male-male contest competition over mates may not be as important in hyenas as it is in many other mammals. We found that, while rank was correlated with reproductive success, tenure was a much better predictor of a male's reproductive success than social rank per se. In contrast to what was observed in baboons (Altmann et al. 1996), among hyenas,

male reproductive success did not fit a priority of access model, in which both male rank and the number of females simultaneously in estrus were taken into account. Also, the highest ranking male observed with a fertile female was no more likely to be the father of her cubs than were other males. It appears that in this female-dominated species, high-ranking males are unable to monopolize access to reproductive females, possibly as a consequence of female choice.

Finally, I examined the effects of social rank on parasite burden in Chapter 5. Although parasites and pathogens appear to have substantial impacts on fitness of wild animals, only rarely do studies incorporate social variables into studies of parasitism. One of the few studies to examine parasite load in relation to social rank (Hausfater & Watson 1976) obtained the surprising result that high social rank was correlated with high parasite load among male baboons. Here, I tested whether several social and demographic variables influenced the load or prevalence of intestinal parasites in hyenas. For each parasite species, a different suite of social and/or demographic variables influenced parasitism. Similar to Hausfater and Watson (1976), I found that high-ranking hyenas had higher loads of some parasites than did low-ranking hyenas. That different factors were associated with high parasite prevalence or intensity of infection for each parasite species probably reflects differences in the transmission biology of that species.

Each of these chapters examines the causes and consequences of social rank in the loves of spotted hyenas. In Chapters 2 and 3, I found patterns of rank inheritance and social cognition that were nearly identical to those observed in

cercopithecine primates who lice in similar social groups. These data suggest that hyenas and cercopithecine primates have undergone convergent evolution and raise the question of whether the neural mechanisms regulating these behaviors are also similar in these taxa. The results of Chapter 4 suggest that, unlike what is observed in most mammalian societies organized by dominance hierarchies, reproductive skew among male hyenas is not very strong. Highranking male hyenas are unable to monopolize reproductive opportunities, probably because the pattern of female dominance characteristic of hyena societies diminishes the ability of males to control reproduction. Finally, in Chapter 5, I found that high-ranking individuals had higher loads of some parasites than did lower-ranking individuals.

Chapter 2

MECHANISMS OF MATERNAL RANK "INHERITANCE" IN THE SPOTTED HYENA

INTRODUCTION

A variety of factors affect dominance status in gregarious vertebrates These include genetic influences (e.g., Craig et al. 1965; Moss et al. 1982; Kikkawa et al. 1986), body size (e.g., Clutton-Brock et al. 1982), age (e.g., Goodall 1986; Pusey & Packer 1997), tenure in the social group (e.g., Sugiyama 1976; Smale et al. 1997), and political machinations (de Waal 1982). In many cercopithecine primates, maternal rank is an extremely important determinant of offspring social rank. That is, during early ontogeny, the ranks of young primates come to be highly correlated with those of their mothers (Macaca fuscata: Kawai 1958; M. mulatta: Missakian 1972; M. sylvanus: Paul & Kuester 1987; M. fascicularis: de Waal 1977; M. arctoides: Estrada 1978; M. nemestrina: Bernstein 1969; M. radiata: Silk et al. 1981a,b; Papio cynocephalus: Hausfater 1975; P. anubis: Johnson 1987; Cercopithecus aethiops: Horrocks & Hunte 1983; Theropithecus gelada: Dunbar 1980). As in these myriad primate species, the social ranks of young spotted hyenas (Crocuta crocuta) are also strongly influenced by the ranks of their mothers (Frank 1986; Holekamp & Smale 1991; 1993; Smale et al. 1993; Jenks et al. 1995). The process by which youngsters assume positions in the dominance hierarchy adjacent to those of their mothers is called maternal rank 'inheritance' by primatologists (e.g., Harcourt & Stewart

1987). Although social rank is relational and is not literally inherited, we adopt this same terminology here. Further, following Chapais (1992) we assume that maternal rank 'inheritance' includes processes of both rank acquisition and rank maintenance.

The social lives of spotted hyenas are comparable in many respects to those of cercopithecine primates (Frank 1986; Holekamp & Smale 1993; Smale et al. 1993; Holekamp et al. 1999a). Like most primates, Crocuta are long-lived mammals that bear small litters requiring a long period of nutritional dependence on the mother. Like cercopithecine primates, *Crocuta* live in permanent social groups, the members of which cooperatively defend communal territories. Social groups in both taxa contain multiple adult males and multiple matrilines of adult female kin with offspring, including individuals from several overlapping generations. Males in both taxa typically disperse from their natal groups whereas females are usually philopatric (Cheney & Seyfarth 1983; Henschel & Skinner 1987; Pusey & Packer 1987; Mills 1990; Smale et al. 1997). Adults of both taxa can be ranked in a linear dominance hierarchy based on outcomes of agonistic interactions, and priority of resource access varies with social rank (Tilson & Hamilton 1984; Andelman 1985; Frank 1986). In both Crocuta and various Old World primates, female reproductive success is strongly correlated with social rank (Altmann et al. 1988, 1996; Frank et al. 1995; Holekamp et al. 1996). In both taxa, members of the same matriline occupy adjacent rank positions in the group's hierarchy, and female dominance relations are extremely stable across a variety of contexts and over periods of many years. Juvenile

hyenas of both sexes acquire ranks immediately below those of their mothers (Holekamp & Smale 1991, 1993; Smale et al. 1993), and nonlittermate siblings assume relative ranks that are inversely related to age in a pattern of 'youngest ascendency' like that seen in many cercopithecine primates (e.g., Horrocks & Hunte 1983). In both primates and hyenas, kin associate more closely than do non-kin, and individuals direct affiliative behavior towards kin more frequently than towards non-kin (Seyfarth 1980; Seyfarth & Cheney 1984; East et al. 1993; Holekamp et al. 1997). In both taxa, high-ranking animals are preferred over lower-ranking individuals as social companions (Seyfarth 1980, 1981; Holekamp et al. 1997). Furthermore, patterns of greeting behavior in *Crocuta* follow primate patterns of social grooming (East et al. 1993), in which individuals prefer to direct affiliative behavior towards high-ranking non-kin (Seyfarth & Cheney 1984). Finally, triadic and more complex interactions (e.g., coalitions) appear to play important roles in the acquisition and maintenance of social rank in Crocuta (Mills 1990; Zabel et al. 1992; Holekamp & Smale 1991; 1993; Smale et al. 1993; Jenks et al. 1995), as they do in many cercopithecine primates (Cheney 1977; Walters 1980; Datta 1983, 1986; Harcourt 1988, 1992; Pereira 1989; Chapais et al. 1991; Chapais 1992).

A number of studies have attempted to determine how young primates 'inherit' their mothers' ranks, and several possible mechanisms have been proposed. The simplest hypothesis suggests that genetic inheritance of rankrelated behavioral tendencies or physical characteristics account for the 'inheritance' of maternal rank. Unprovoked aggression directed preferentially by

adult females toward offspring of lower-ranking females has also been proposed as a mechanism of maternal rank 'inheritance' (Berman 1980; Horrocks & Hunte 1983). Another mechanism known to function importantly in primates involves defensive interventions by mothers on behalf of their offspring when the latter are engaged in disputes with conspecifics (Cheney 1977; Berman 1980; Horrocks & Hunte 1983; Netto & Van Hooff 1986). Finally third-party support, or coalition formation, during aggressive interactions appears to play an important role in acquisition of maternal rank in primates (Cheney 1977; Walters 1980; Datta 1983; Bernstein & Ehardt 1985; Ehardt & Bernstein 1992).

'Inheritance' of maternal rank occurs in both wild and captive groups of spotted hyenas, including groups that vary widely in size and composition (Holekamp & Smale 1993; Smale et al. 1993; Jenks et al. 1995). Free-living *Crocuta* cubs attain their ranks within their peer cohorts within the first 8 months of life (Holekamp & Smale 1993), and they attain their ranks relative to older clan members somewhat later (Smale et al. 1993). In light of the striking similarities between the social lives of spotted hyenas and cercopithecine primates, we set out to determine here whether young hyenas 'inherit' maternal rank via the same processes as do young monkeys. Working with one large group of free-living hyenas in Kenya, we tested predictions of each of the four mechanistic hypotheses enumerated above.

METHODS

We monitored a single clan of spotted hyenas from June 1988 to June

1999 in their 65 km² core home range in the Talek area of the Masai Mara National Reserve, Kenya. We made daily behavioral observations of the 67 offspring of 22 adult female clan members present in the clan between June 1988 and April 1991. Throughout this period, observers were present in the study area 23 to 31 days per month. Individual hyenas were identified by their spot patterns and other unique characteristics, such as ear notches. Motheroffspring relationships were determined on the basis of nursing associations.

Behavioral observations took place near dawn (0600-0900) and dusk (1630-1930), when hyenas were most active. Data were recorded throughout the clan's home range and during all activities. Behavior was recorded during weekly 30-minute focal animal surveys of individual cubs, and continuous critical incident ('all-occurrence' Altmann 1974) sampling of agonistic behavior emitted by all Talek hyenas. Aggressive behaviors included threat, bite, chase, and approach in attack posture, whereas submissive behaviors included avoidance or withdrawal from interaction, submissive posture, head bob, and carpal crawl (see Kruuk 1972 for definitions). All aggressive behaviors by adult females toward cubs were classified as 'provoked' if they occurred during nursing or feeding, or if they immediately followed pesky or aggressive behavior by the targeted cub. Aggressive behaviors not meeting any of these criteria were classified as 'unprovoked.' Coalitions were defined as two or more hyenas concurrently behaving aggressively toward a third. When coalitions formed, the identities of all aggressors were recorded, as well as the order in which they joined the interaction. The first aggressor involved in a coalition was called the initiator, any

individuals joining the initiator were called supporters, and the recipient of the aggression was termed the victim.

Maternal interventions were identified when an adult female interrupted an interaction between her cub and another individual. Interventions were classified as either 'aggressive' or 'non-aggressive.' Aggressive interventions involved approach followed by threat, attack, or displacement behavior by the mother toward the individual interacting with her cub. Non-aggressive interventions involved approach followed by distraction (e.g., initiation of a greeting ceremony) or blocking (e.g., the mother positioning herself between her cub and its opponent). Additionally, the context of each intervention was classified as either food-related or non-food related. A food-related intervention took place during a dispute over access to or possession of a food item. A maternal intervention was considered effective when the hyena interacting with the cub in question desisted from interacting with that cub during or immediately after the intervention.

The social rank of each clan member was determined based on its position in a matrix of appeasement behaviors exhibited during dyadic agonistic interactions (Martin & Bateson 1988). The 'winner' was the animal being appeased, while the 'loser' was the animal exhibiting appeasement behavior. By convention, the most dominant animal in the hierarchy was assigned a rank of one. A juvenile's 'maternal rank' referred to its mother's position within the adult female hierarchy. Low-born individuals were those of lower maternal rank than the focal animal, while high-born animals had a higher maternal rank than the focal animal (e.g., Datta 1983). A cub was considered high-ranking if its mother's

rank was 10 or higher and low-ranking if her rank was below 10. There was no significant sex bias within the sample set (Table 2.1; $X_2^2 = 0.75$, NS) and rank was unrelated to cub sex in all of the sample subgroups examined (Table 1; *N*=67, *t*₆₅=0.78, *P*=0.44; *N*=38, *t*₃₆=0.57, *P*=0.58; *N*=20, *t*₁₈=-0.28, *P*=0.79)

Ages of all juvenile hyenas were known to within one week, as described by Holekamp et al. (1996). In all analyses below, hyenas were called cubs until 18 months of age, subadults from 18 to 24 months, and adults over 24 months (Matthews 1939; Smale et al. 1993). Spotted hyenas acquire their adult ranks by 18 months of age, and generally maintain these ranks as long as they remain in the natal clan (Smale et al. 1993). However, as in primates, rank acquisition occurs in stages in Crocuta: social rank relative to peers is acquired from 0-6 months of age, and this rank relative to peers becomes perfectly aligned with maternal rank by 6 to 8 months of age (Holekamp & Smale 1993). Cubs acquire their social ranks relative to adults between 8 and 18 months of age (Smale et al., 1993). Therefore, for analyses below of behavioral changes over time, separate rate values were calculated for each cub during each of the following age intervals: 0-6 months, 7-8 months, 9-18 months, and 19-24 months. Only individuals who survived at least 24 months (N=20) were included in these longitudinal analyses. Siblings, offspring, and parents were considered to be kin in the analyses below, and all other animals were considered to be non-kin.

Rate data were compared in most analyses. Hourly rates of maternal intervention, aggressions received, and coalition formation were calculated for each cub by dividing the total number of interventions, aggressions received, or

Sample Group	All cubs participating in coalitions	Cubs surviving to 18 months of age	Cubs surviving to 24 months of age
Figures using			
sample group	2.4, 2.5	2.1, 2.2, 2.3	2.6
N	67	38	20
Female	30	15	7
Male	37	23	13
Mean Female Rank (SD)	11.27 (5.85)	10.47 (5.38)	8.71 (5.47)
Mean Male Rank (SD)	10.11 (6.22)	9.39 (5.94)	9.54 (6.79)
# Subjects with ≥1 Sib	64	31	12
# Littermate Pairs	23	10	5

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Table 2.1. Relationships among the sample sets of hyena cubs.

coalitions involving that cub by the total number of hours during which the cub was observed. We calculated rates of female aggression by dividing the number of unprovoked aggressions directed by each adult female toward each cub by the number of hours during which each female-cub dyad was observed within 200m of each other. Mean rates of aggression directed against high-born and low-born cubs were then calculated for each adult female. Only cubs that survived for at least 18 months (*N*=38) were considered in analyses of female aggression and maternal intervention.

Directionality in coalitionary interactions was assessed for each cub by calculating the proportion of all coalitions that reinforced the adult hierarchy in which that cub participated. Thus, if a cub joined five coalitions, three of which were directed against low-born victims, then that cub was assigned a value of 0.60 for supporting coalitions. We then calculated 95% confidence intervals (CIs) for these proportions averaged over all cubs. If 95% CIs did not include the 0.50 predicted if cubs were equally likely to participate in coalitions directed at high and low-born animals, then results were considered to be significantly different from chance expectations. All cubs participating in at least one coalition were included in these analyses.

Spearman's correlation coefficients were calculated in all analyses using social rank as an independent variable, and the significance of each relationship was assessed via Kruskal-Wallis tests. In all cases in which data were not normally distributed, standard non-parametric tests, such as Wilcoxon and Freidman tests, were used for analysis.

RESULTS

Genetic heritability

Although rank relationships among adult females were generally extremely stable throughout the 11-year study period, changes in rank relationships associated with a single clan fission event early in the study indicated that genetic heritability cannot account for 'inheritance' of maternal rank in spotted hyenas. That is, when members of three low-ranking matrilines permanently emigrated from the Talek clan between November 1989 and June 1990, they were initially accompanied by two adult females (sisters) and their offspring from a middle-ranking matriline, as described previously (Holekamp et al. 1993). Although no members of the low-ranking matrilines ever returned to Talek, the two middle-ranking females returned after an absence of one year. As they attempted to rejoin the Talek clan, both of these females were the targets of severe attacks by all other adult females, including those which they had previously outranked (Holekamp et al. 1993). Both absentee females were ultimately able to rejoin the Talek clan in 1991, but their new ranks were at the bottom of the adult female hierarchy, where they have remained ever since. Offspring born to these females before clan fission fell in rank along with their mothers when they returned to Talek, and all of the subsequent offspring produced by these two females 'inherited' their mothers' new ranks, rather than their mothers' initial ranks in the clan's hierarchy. The fact that the ranks of these females and their offspring changed so dramatically during the study period
strongly suggested that genetic heritability is unlikely to function as an important mechanism mediating rank acquisition in this species.

Unprovoked aggression

If unprovoked female aggression contributes to maternal rank 'inheritance', then rates of unprovoked aggression directed by adult females toward offspring of lower-ranking females should be higher than rates at which they harass offspring of higher-ranking females. Furthermore, this hypothesis predicts that rates of unprovoked aggression received by cubs from adult females should be correlated with the cubs' maternal ranks. We observed no difference between the hourly rates of unprovoked aggression directed by adult females at low-born and high-born cubs (Wilcoxon Z_{21} =0.601, P=0.548). In addition, hourly rates at which cubs received unprovoked aggression from adult females were not correlated with cubs' maternal ranks (R_{s} =0.14, *K*- W_{18} =16.16 P=0.51; Figure 2.1). Thus unprovoked female aggression does not appear to function importantly in acquisition of maternal rank in *Crocuta*.

Maternal intervention

If maternal interventions function to promote maternal rank 'inheritance' in spotted hyenas, then intervention rates should be inversely correlated with maternal rank, and high-ranking females should intervene on behalf of their offspring more effectively than should low-ranking females. The rates at which female hyenas intervened on behalf of their cubs were indeed significantly correlated with maternal rank (R_s =-0.41, *K*- W_{18} =31.08, *P*=0.03; Figure 2.2). Only 27/818 (3.3%) of maternal interventions occurred in response to a direct



Figure 2.1. Hourly rates at which adult females directed unprovoked aggressive behaviors at cubs, ordered on the basis of the victim's maternal rank.

aggressive attack. Most interventions occurred before the "intruder" had a chance to behave aggressively toward the cub. For example, mothers frequently intervened against any individuals who approached their cubs while the cubs were feeding on small scraps. This supports Berman's (1980) suggestion that the mere presence of the mother may curb rates of aggression directed toward high-ranking cubs. Indeed, there was a tendency for high-ranking cubs to receive lower overall rates of aggression than did low-ranking cubs (R_S =0.64, *K*- W_{18} =24.27, *P*=0.15). Thus low-ranking mothers had more opportunities to intervene on behalf of their cubs, yet they intervened at far lower hourly rates than did high-ranking females.

Intervention strategies of adult females did not depend on either the relative ranks of the contestants (U_1 =133.5, P=0.375) or the context in which interventions occurred (U_1 =58.00, P=0.172). Aggressive interventions were common regardless of whether or not the situation involved food. In food-related contexts, mothers often stood next to cubs with food, and threatened any approaching animal. Overall, high-born females were found to be more effective when intervening on behalf of their offspring than were low-born females (U_1 =829.5, P=0.03). In particular, high-born females were more effective than low-born females in food-related contexts (U_1 =127.5, P=0.01; Figure 2.3), where there was an obvious benefit to winning. Thus, our data confirmed that high-ranking mothers intervened on behalf of their offspring both more frequently and more effectively than did low-ranking mothers.

Coalitionary support



Figure 2.2. Hourly rates of at which adult female hyenas intervened on behalf of their offspring, ordered on the basis of their social rank.



Figure 2.3. Mean proportion $(\pm SEM)$ of maternal interventions against high-born and low-born opponents that were effective in food and non-food contexts. Sample sizes represent numbers of mother-cub pairs observed.

Acquisition of maternal rank in *Crocuta* might be facilitated either by coalitionary support of young or coalitionary targeting of young. First, if a cub is supported by conspecifics when it attacks another animal, then this supportive behavior may function in both militaristic and operant conditioning senses to reinforce the cub's behavior toward that target animal. Second, if a cub engaged in a dispute with another animal is attacked by a coalition of conspecifics, then its aggressive behavior toward the original target may be rapidly extinguished. This hypothesis predicts that, when hyena A joins hyena B in an aggressive interaction against hyena C, hyena A will join the individual who should win according to the 'rules' of maternal rank inheritance. This hypothesis also predicts that hourly rates of coalition formation in support of cubs, or rates of coalition formation against cubs, should vary with maternal rank. Besides receiving higher rates of coalitionary support, the offspring of high-ranking females should have more allies, and higher-ranking allies, to support them than should the offspring of low-ranking females. Additionally, youngsters may facilitate acquisition or maintenance of maternal rank by providing support in coalitions against low-born individuals. Such joining behavior should permit cubs to reinforce their dominant status over that of target animals.

When adult hyenas supported cubs in coalitions against other cubs or adults, they were more likely to do so against low-born than high-born opponents. This was true both for conflicts between cubs and their peers (95% CI =0.73 - 1.00; Figure 2.4), and for conflicts between cubs and adults (95% CI =0.70 - 0.99; Figure 2.4). Cubs also supported other cubs more frequently

against low-born than high-born adults (95% CI =0.87 - 1.00) and cubs (95% CI=0.60 - 0.89). Adult aggression against cubs was rarely supported by others, and when this occurred, there was no tendency for the adult initiator of aggression to be higher-ranking than the cub's mother (cub supporter: 95% CI = 0.46 - 0.89; adult supporter: 95% CI = 0.15 - 0.95).

When supporters were divided into kin and non-kin categories, youngsters of high maternal rank were found to have significantly more kin providing support than were youngsters of low maternal rank (t = 3.48, P=0.004), but we found no significant difference in the number of non-kin providing support (t = 1.73, P=0.102). Additionally, the ranks of supporters were correlated with the maternal ranks of the youngsters receiving support ($R_s=0.600, K-W_{16}=26.86, P=0.04$). Despite having more and higher ranking allies, high-ranking cubs received coalitionary support at hourly rates that did not differ significantly from rates at which low-ranking youngsters received coalitionary support ($R_{\rm S}$ =-0.06, K- W_{18} =22.74, P=0.20). Thus, in comparison to cercopithecine primates, spotted hyenas receive relatively little coalitionary support from non-relatives during rank acquisition. Hourly rates of coalitionary attacks directed against cubs were not significantly related to maternal rank (R_s =0.49, K- W_{18} =21.70, P=0.25), but in most cases in which a cub was the victim of coalitionary attack, the initiator of aggression was of higher maternal rank than was the victim (Figure 2.4).

When cubs joined coalitions against other animals, they tended to do so against low-born individuals (Figure 2.5). Cubs joined coalitions with both adults (95% CI = 0.86 -1.00) and cubs (95% CI = 0.81 - 0.99) against low-born adults



Figure 2.4. Mean proportion (\pm SEM) of coalitions that reinforced the existing dominance hierarchy organized in terms of victim, initiator, and supporter of the attack. Numbers of cub are indicated above bars.

much more commonly than against high-born adults. They also joined coalitions initiated by cubs against low-born cubs more frequently than against high-born cubs (95% CI = 0.60 - 0.89). Although cubs also tended to join adults attacking low-born cubs more than high-born cubs, this tendency was not significant (95% CI = 0.46 - 0.89).

Age-related trends

Spotted hyena cubs attain their ranks within their peer cohorts within the first 8 months of life (Holekamp & Smale 1993), and they attain their ranks relative to older clan members when they are 8 to 18 months of age (Smale et al. 1993). If some mechanisms are important for attainment of rank in relation to juvenile peers, but not for attainment of rank in relation to adults, then the rates of the behaviors associated with those mechanisms should drop after the cub has attained its rank in relation to its peers. Thus, behaviors which facilitate attainment of rank in relation to adults should occur at high rates during the first 8 months of life, behaviors which facilitate attainment of rank in relation to adults should occur frequently between 8 and 18 months of age, and behaviors functioning to maintain rank should be common after 18 months of age.

Hourly rates of maternal intervention on behalf of cubs dropped significantly between 8 and 18 months (F_1 =5.92, P=0.015; open triangles in Figure 2.6) and again between 18 and 24 months (F_1 =5.0, P=0.025). Thus maternal intervention appears to play a strong role in attainment of rank within the peer cohort and possibly also within the entire clan, but probably plays a relatively small role in rank maintenance. Hourly rates of third-party support



Figure 2.5. Mean proportion (\pm SEM) of coalitions joined by cubs in which the joining cub was higher-ranking than the victim of attack. Coalitions are grouped according to the age of the victim and initiator of the attack. Numbers of supporting cubs are indicated above bars.



Figure 2.6. Age-related changes during the first two years of life in the hourly rates (+ SEM) at which a mother intervened on behalf of her own cub, a cub joined another hyena attacking a third animal, a cub was the victim of coalitionary aggression, and a cub initiated an attack in which one or more conspecifics joined. Means for 20 cubs are represented by each data point.

dropped significantly between 18 and 24 months of age (F_7 =5.56, P=0.018; filled circles in Figure 2.6). This indicates that coalitionary support may figure prominently in rank attainment both within the peer cohort and in relation to the rest of the clan, but also that coalitionary support may be less critical for rank maintenance than for its establishment. Nevertheless, the high rates of coalitionary support given to youngsters older than 18 months of age, suggest that coalition formation against cubs were relatively low, and did not vary significantly with age over the first 24 months of life (F_3 =6.17, P=0.104; open circles in Figure 2.6). Hourly rates at which cubs joined coalitions also did not vary significantly among age intervals (F_3 =2.85, P=0.415; filled triangles in Figure 2.6), but were relatively high throughout the first two years of life. Thus joining behavior may function importantly in both acquisition and maintenance of maternal rank.

DISCUSSION

During the process of socialization, rank relations of juvenile spotted hyenas rapidly come to conform to their clan's existing social structure as expressed in the adult female hierarchy (Holekamp & Smale 1993; Smale et al. 1993; Jenks et al. 1995). Although youngsters are initially equally likely to direct aggression towards high-born and low-born conspecifics, their behavior rapidly changes such that they direct aggression exclusively at targets of lower maternal rank, and youngsters soon assume rank positions immediately below those of

their mothers in the clan's dominance hierarchy (Holekamp & Smale 1993; Smale et al. 1993). In the current study we tested predictions of four hypotheses, each suggesting a different mechanism by which the process of maternal rank 'inheritance' might be mediated in this species. Additionally, a fifth hypothesis that we were not able to address in the present study suggests that young hyenas may 'inherit' their ranks by observing their mothers interact and thereby learning their relative ranks (Kawai 1965; Sade 1972; Gouzoules 1975; Altmann 1980; Walters 1980).

Various lines of indirect evidence from free-living hyenas in our study population, and in those of other workers, fail to support the genetic heritability hypothesis. For example, the social rank of a juvenile hyena changes when its mother rises or falls in the clan's dominance hierarchy (Holekamp & Smale 1993; Holekamp et al. 1993), suggesting that social rank is far too labile to be directly determined by behavioral or morphological traits that are strongly heritable. In addition to our own observations of rank reversals associated with Talek clan fission, observers watching hyena populations elsewhere in Africa have observed revolutionary coalitions formed by members of low-born matrilines overthrowing the alpha matrilines in their respective study clans (Mills 1990; H. Hofer & M. L. East personal communication). It thus seems no more likely that genetic heritability directly mediates acquisition of maternal rank in spotted hyenas than it does in cercopithecine primates. This should perhaps be expected since, if genetic differences led directly to differences in social rank, then the genes associated with high rank would become fixed within only a few generations, and

hence the genetic basis for differences in social rank would quickly be eliminated.

Although unprovoked female aggression ('harassment') may play a strong role in rank acquisition in some primates (Gouzoules 1975; Lee & Oliver 1979; Berman 1980; Silk et al. 1981a; Horrocks & Hunte 1983), it does not appear to influence rank 'inheritance' in hyenas. Low-ranking juveniles in some monkey species receive more unprovoked aggression than do high-ranking juveniles, and rates at which such aggressive acts are received by youngsters are inversely correlated with maternal rank (e.g., Horrocks & Hunte 1983). However, our data failed to reveal these trends during the process of rank acquisition in *Crocuta*. Adult female hyenas did not direct unprovoked aggression more frequently toward low-born than toward high-born cubs, and we found no relationship between the rates of unprovoked aggression received by cubs and their maternal ranks.

As occurs in many primates (e.g., Cheney 1977; Berman 1980; Walters, 1980; Horrocks & Hunte 1983), interventions by mothers on behalf of their offspring appear to play a critical role in hyena rank 'inheritance'. High-ranking female hyenas intervened on behalf of their offspring more frequently, and more effectively, than did low-ranking females. When low-ranking females intervened, they tended to use physical blocking or distraction tactics, whereas high-ranking females used high levels of aggression against their cubs' opponents. In a study of maternal rank acquisition among captive *Crocuta*, Jenks et al. (1995) reported that only high-born females intervened on behalf of their cubs, whereas we often saw both low-born and high-born females intervene. We suspect this discrepancy

can be explained by the fact that Jenks et al. (1995) scored only aggressive behaviors as interventions whereas we recorded both aggressive and nonaggressive interventions. In any case, Jenks et al. (1995) concluded as we did that maternal interventions were extremely important mechanisms of maternal rank acquisition. Most maternal interventions occurred in response to a potential threat, rather than in response to aggression directed toward cubs. This type of intervention is likely to be very important in a species such as the hyena where the potential is high for cubs to sustain injury when engaged in altercations with larger, stronger adults. Low-ranking individuals who behave aggressively to high-born youngsters when the latter are present with their mothers risk severe retaliation for their actions. Subsequently, even when mothers are not present with their offspring, the threat of maternal intervention may influence the behavior of other group members (Cheney 1977; Berman 1980), thereby promoting both acquisition and maintenance of maternal rank.

Finally, coalitionary support appears to play an important role in rank 'inheritance' in hyenas. Although the rate at which cubs receive coalitionary support is not related to their maternal ranks, the vast majority of all support for cubs is given when cubs behave aggressively toward low-born opponents (Figures 2.4 & 2.5). Conspecific support of cubs during their aggressive interactions with low-born individuals may positively reinforce both aggressive behavior by the attacking cubs and appeasement behavior by their victims. The bulk of coalitionary attacks on juveniles are formed against low-born individuals, and these attacks may serve to punish aggressive acts by cubs that are directed

toward inappropriate (i.e. higher-ranking) targets. High-born cubs have more allies, and more powerful allies, than do low-born cubs, and the threat of coalitionary aggression from these allies may represent a ubiquitous and powerful reminder of the status quo.

Our findings germane to coalition formation in wild hyenas were similar to those obtained for captive prepubertal hyenas by Zabel et al. (1992). Although hourly rates of coalition formation in the wild were roughly an order of magnitude lower than those observed in captivity, in both situations high-born hyenas were more likely than low-born hyenas to initiate and support attacks, and low-born animals were more likely to be targets of group attacks. Among both captive and wild hyenas, coalitionary attacks appeared to reinforce the existing dominance hierarchy. However, ontogenetic trends described in the current study (Figure 2.6) indicate that coalition formation may play a far more important role in challenging the existing hierarchy, and thus in rank acquisition, than was suggested by captive data.

Cubs may play an active role in the acquisition and maintenance of maternal rank by joining coalitions, particularly those directed against low-born individuals, since cubs preferentially join hyenas attacking lower-born animals. By joining in aggression against low-born individuals, cubs can reinforce their own dominant status relative to the victim. Although maternal interventions may be critical for cubs to gain their peer ranks and align these with maternal ranks, coalitions may play a larger role for older cubs who are attaining and later maintaining their ranks in relation to hyenas outside their peer group.

When Crocuta cubs are first brought to the communal den at approximately one month of age, they exhibit appeasement behavior to all other hyenas they meet there, and adults generally only direct mild aggression toward very young cubs when their play interrupts adults' naps by the den. During the course of rank acquisition, cub submissive behavior appears to be extinguished in interactions with some conspecifics, such that appeasement persists only toward a subset of conspecifics. Cubs begin initiating attacks on non-sibling conspecifics during their third month of life (Holekamp & Smale 1993), and enter a stage during which they direct both aggressive and appeasement behaviors simultaneously at larger-bodied hyenas. Aggressive behavior directed by cubs toward high-born conspecifics appears to be rapidly extinguished via punishing counterattack or coalitionary aggression, and perhaps also by relatively rare and ineffective maternal interventions. By contrast, cub attacks on low-born conspecifics are likely to be reinforced by effective protection from the mother, coalitionary support from other clan members, and perhaps also by immediate improved access to contested resources.

Our analysis of age-related trends observed during maternal rank inheritance suggests that the process of rank acquisition begins with defensive maternal interventions in which the cub does not participate. If play turns too rough or another hyena gets nasty, cubs may solicit maternal aid with vocalizations (East & Hofer 1991; Holekamp et al. 1999a), but mothers often intervene without any apparent cub solicitation of aid. Later in development, cubs start joining mothers when mothers intervene on their behalf. Later still, cubs

begin initiating attacks on conspecifics, and cubs often enjoy third party support from their mothers or other allies when these attacks are directed at low-born animals. This sequence of events appears to lead to rank reversals, first with peers and then with older juveniles and adults. Low-born opponents first cease behaving aggressively toward high-born cubs, and later begin appeasing them. Once these rank reversals have occurred, cubs appear to maintain their ranks, not only by winning in dyadic encounters with low-born conspecifics (Holekamp & Smale 1993; Smale et al. 1993), but also by obtaining third party support against low-born animals, and perhaps also by joining attacks on low-born animals.

It appears that the proximate mechanisms of maternal rank 'inheritance' in spotted hyenas are strikingly similar to those found in cercopithecine primates. In both groups, maternal intervention in disputes plays a key role in rank attainment, with the mother asserting her dependent offspring's status just below her own. Coalitions also seem to play a strong role in rank 'inheritance' in both primates and hyenas. In hyenas, coalitionary support by kin and non-kin appears to reinforce aggression against 'appropriate' targets, whereas aggressive coalitions serve to punish 'inappropriately' directed aggressive behavior by cubs. Additionally, cubs may join in coalitions against low-born individuals to reinforce their own status. Genetic heritability is not an adequate explanation for maternal rank 'inheritance' in either primates or hyenas. The key mechanistic difference in rank 'inheritance' between these taxa is that low-ranking cercopithecine juveniles may experience a high degree of unprovoked aggression from high-born adult females (eq., Horrocks & Hunte 1983), whereas low-ranking juvenile hyenas do

not receive such harassment. However, the frequency with which unprovoked aggression occurs among adult female hyenas suggests that harassment might function in the maintenance of rank relationships in animals older than those examined here. In any case, the fact that the mechanisms of maternal rank 'inheritance' are so strikingly similar in *Crocuta* and cercopithecine primates suggests that rank acquisition in both taxa might be mediated by common cognitive processes.

SOCIAL COMPLEXITY AND THE EVOLUTION OF INTELLIGENCE IN THE SPOTTED HYENA

Chapter 3

INTRODUCTION

Intelligence, defined broadly by Kamil (1987) as "those processes by which animals obtain and maintain information about their environments, and use that information to make behavioral decisions," has been of the subject of many recent primate studies (reviewed in Byrne & Whitten 1988; Tomasello & Call 1997; Matsuzawa 2001). Primates appear to be endowed with cognitive abilities that are superior to, and qualitatively different from, those of most other mammals. Two different types of selection pressures have been hypothesized to favor the evolution of large brains and great intelligence in primates. The first hypothesis suggests that intelligence has been favored in primates by selection pressures associated with complexity in the physical environment, particularly that confronted when navigating through a three-dimensional arboreal world (e.g., Povinelli & Cant 1995; Povinelli & Preuss 1995) or when finding and obtaining food (e.g., Jerison 1973; Clutton-Brock & Harvey 1980; Milton 1981). The second hypothesis suggests instead that key selection pressures have been imposed by complexity associated with the flexible behavior of conspecific group members (Jolly 1966; Humphrey 1976; Byrne & Whitten 1988). This social complexity hypothesis is supported by interspecific comparisons suggesting that the evolution of intelligence in primates has been more strongly influenced by

social pressures than by nonsocial aspects of the environment (reviewed in Byrne 1994; Tomasello & Call 1997). In particular, brain size, which is roughly correlated with tactical deception (Byrne 1993), is strongly correlated with group size, and other variables, such as territory size, explain any additional variance (Dunbar 1992; Barton 1993).

One key area in which primates are thought to differ qualitatively from other gregarious mammals is in their ability to form mental representations of tertiary, or third-party relationships among conspecific group members (Tomasello & Call 1997). These involve interactions and relationships in which the observer is not directly involved. For example, female vervet monkeys (Chlorocebus aethiops) respond to the distress call of an infant by orienting toward the infant's mother, indicating that they perceive an association between the mother and infant (Cheney & Seyfarth 1980). Several primate species have been shown to utilize information about the social relationships of conspecifics in activities such as recruiting useful allies, challenging competitors, and reconciling after fights (Bachmann & Kummer 1980; Cheney & Seyfarth 1989; Silk 1999). Tomasello and Call (1997) hypothesize that the ability to recognize third-party relationships is unique to primates, and furthermore, that this distinguishes their mental abilities from those of all other animals. The ability to recognize third-party relationships has not been demonstrated in non-primate mammals, even in species living in complex, stable societies, such as elephants (Loxodonta africana: Moss 1988), dolphins (Tursiops truncatus: Conner et al. 1992), or lions (Panthera leo: Packer 1994). However, few published studies of these other

gregarious mammals have focused on cognitive abilities, and none to date has inquired specifically whether these animals can recognize third-party relationships. Therefore, it remains unclear whether the absence of evidence that any of these mammals can recognize tertiary relationships means that this ability is truly absent.

The current dearth of information about social cognition in non-primates severely limits the generality of the social complexity hypothesis (Kamil 1987; Harcourt & de Waal 1992). The social complexity hypothesis predicts that non-primate animals that share with cercopithecine primates most salient features of their social life should possess many or all of the same features of social intelligence as do these primates, assuming that the same proximate mechanisms are operating. Here we test this prediction, using behavioral data from a group of free-living spotted hyenas (*Crocuta crocuta*), gregarious carnivores that live in remarkably primate-like societies. Evidence for the existence of shared cognitive abilities would suggest convergent evolution in these two distantly related taxa and would lend support to the social complexity hypothesis. In contrast, the failure to find such evidence would suggest that the social complexity hypothesis should either be rejected or restricted to primate species.

The social lives of spotted hyenas are very similar to those of vervet monkeys, baboons (*Papio* spp.), and other cercopithecine primates (Frank 1986; Holekamp et al. 1999a). Like these primates, hyenas live in large, permanent social groups, and group members cooperatively defend a communal territory

(Harcourt & DeWaal 1992; Boydston et al. 2001). The composition of hyena clans is much like that of most cercopithecine primate troops, in that both contain multiple adult males and multiple matrilines of adult female kin and their offspring. Within a group, or clan, of hyenas, as in many cercopithecine societies, adults can be ranked in a linear dominance hierarchy, and an individual's position within the hierarchy determines its priority of access to resources (Wrangham & Waterman 1981; Tilson & Hamilton 1984; Frank 1986; East & Hofer 2001). In both taxa, females are philopatric, whereas males disperse from their natal territories (Cheney & Seyfarth 1983; Henschel & Skinner 1987; Pusey & Packer 1987; Smale et al. 1997). Juvenile hyenas acquire ranks immediately below those of their mothers (Holekamp & Smale 1991), and they do so via the same associative learning mechanisms as those documented in cercopithecine primates (Horrocks & Hunte 1983; Engh et al. 2000). Both hyenas and numerous cercopithecine primates have been shown to reconcile after fights (Aureli & De Waal 2000; Wahaj et al. 2001), and hyenas direct greeting behavior toward higher-ranking individuals (East et al. 1993) just as vervet monkeys direct grooming behavior toward higher-ranking individuals (Seyfarth 1980). Like vervet monkeys, hyena kin associate more closely than non-kin, and individuals direct affiliative behavior towards kin more frequently than towards non-kin (Seyfarth 1980; East et al. 1993; Holekamp et al. 1997). In addition, members of both taxa prefer higher-ranking individuals over lower-ranking individuals as social companions (Seyfarth 1980; Holekamp et al. 1997). This suggests that hyenas, like monkeys, may recognize that some group members are more valuable social

partners than others. Finally, triadic and more complex interactions appear to play an important role in the acquisition and maintenance of social rank in hyenas (Zabel et al. 1992; Smale et al. 1993; Engh et al. 2000), as they do in many cercopithecine primates (Cheney 1977; Datta 1986; Chapais 1992).

If the social complexity hypothesis is correct, then the similarities between the social lives of hyenas and monkeys suggest that hyenas should demonstrate abilities in the domain of social cognition that are similar to those of cercopithecine primates. In particular, we wanted to determine here whether or not hyenas can recognize third-party relationships. A previous attempt to inquire whether hyenas understand tertiary relationships (Holekamp et al. 1999a) failed to produce any evidence that they could do so; however, it was unclear in that study whether the lack of evidence meant that the hyenas lacked the ability to recognize third party relationships, or rather that they lacked the motivation to demonstrate this ability in that particular test situation. In the experiments presented here, we attempted to test hyenas in situations in which actions based on their social knowledge could improve the fitness outcomes of the actors. Since coalitions play an important role in the acquisition and maintenance of social rank (Zabel et al. 1992; Engh et al. 2000), we reasoned that triadic interactions might reveal a great deal about the cognitive abilities of hyenas. We expected that, if indeed hyenas can recognize third-party relationships based on the social ranks of other hyenas, then they would be able to utilize this knowledge in two ways. First, we predicted that hyenas would be able to exploit changes in sub-group composition, such that they would increase rates of

aggression toward lower-ranking animals when potential allies arrived on the scene. Second, we predicted that hyenas would be able to discriminate between the ranks of two individuals engaged in a fight, and that they would aid the higher-ranking combatant, regardless of their own social ranks in relation to those of the fighters.

METHODS

We collected data from a single large clan of spotted hyenas in the Masai Mara National Reserve, in southwestern Kenya. The study area is an open, rolling grassland interrupted by seasonal creek beds, and grazed year-round by resident populations of several species of ungulates. All data used in this study were collected in over 39,000 observation sessions between June 1988 and October 1998. Each observation session involved recording the behavior of all hyenas visible within 200m of one another. Duration of individual observation sessions ranged from 5 minutes to several hours. On average during the study period, the clan contained 63.2 ± 2.4 resident animals, including 18.5 ± 1.1 adult females, 14.4 ± 1.4 adult immigrant males, and 31.3 ± 1.1 subadults. Each hyena was identified by its unique pattern of spots and other natural marks (e.g., ear notches) and sexed based on the morphology of the erect phallus (Frank et al. 1990). Ages of all hyenas born in the study clan since 1988 were known to ± 7 days, as described previously (Holekamp & Smale 1993), and mother-infant relationships were determined on the basis of nursing associations. For all analyses reported here, we used only interactions between animals over six

months old who were not close relatives. Hyenas less than 6 months old are unlikely to have attained a stable social rank, and their knowledge of other individuals' social ranks is likely incomplete (Smale et al. 1993). In addition, close relatives, defined here as mothers, offspring, and maternal siblings, often support each other in disputes, regardless of the relative social ranks of their opponents (Engh et al. 2000).

During each observation session, all aggressive and appeasement behaviors (Kruuk 1972) were recorded as critical incidents (the all-occurrence sampling of Altmann 1974). We determined the social rank of each clan member based on its position in a matrix of appeasement behaviors displayed during dyadic agonistic interactions (Martin & Bateson 1988). By convention, the most dominant animal in the hierarchy was assigned a rank of 1.

Hyenas live in a fission-fusion society, in which sub-group composition is constantly shifting (Kruuk 1972), and individual hyenas are frequently arriving to, and departing from, subgroups. Here, we tested whether hyenas are able to judge the relative ranks of pairs of conspecifics, as predicted by the social complexity hypothesis. We first used data collected before and after the arrival of a new individual at a behavioral observation session to analyze hyenas' strategic use of potential allies. In a second analysis, we examined hyenas' tendencies to assist individuals engaged in on-going fights by joining with one combatant against the other.

Initiation of fights after the arrival of potential allies

Our first method of assessing hyenas' knowledge of third-party rank relationships involved determining whether hyenas were able to take advantage of the arrival of potential allies. When aggression between two hyenas escalates, one or more additional attackers often join the dyadic skirmish by forming a coalition with one contestant against the other. Typically, animals joining coalitions are all dominant to the victim of an attack (Zabel et al. 1992). Thus when attempting to displace a larger subordinate animal from food, a hyena might benefit, for example, by delaying its attack until the arrival of a potential coalitionary ally who is higher ranking than the target. We reasoned that, if hyenas can recognize third-party rank relationships, then when a new individual arrives at a scene, rates of aggressive behavior among hyenas already present there should change according to the rank of the arriving individual relative to the target animal. Since hyenas frequently join coalitions against individuals lowerranking than themselves, any arriving hyena whose rank is higher than that of the target of the attack is a potential ally, regardless of whether the arriving hyena ranks above or below the animal who initiates the aggression. If hyenas can recognize third-party rank relationships, then either when an arriving hyena ranks higher than both the initiator and its target or when it ranks intermediate to them, the higher-ranking (initiator) of the original pair should increase its rate of aggression against the lower-ranking (target) animal in order to take advantage of the presence of a potential ally. Alternatively, if hyenas do not recognize the relative ranks of their peers and use a simple rule of thumb when assessing

potential allies, such as "utilize individuals higher-ranking than yourself as allies", then the attack rate should increase when a higher-ranking individual arrives, but not when an individual arrives whose rank position was intermediate between the initiator and its target. Because animals rarely join coalitions against individuals higher-ranking than themselves, we made no predictions about the behavior of pairs of hyenas when lower-ranking conspecifics arrives.

All aggressive behavior observed during 10-minute intervals prior to, and immediately after, the arrival of a new hyena was recorded during an observation session, as was the rank of the individual arriving relative to all pairs of animals already present in the session. For this analysis, we only used sessions in which a single animal arrived. If additional individuals arrived or left the scene during the 20 minutes surrounding the arrival of the focal animal, we excluded the session from analyses. We carried this analysis out first on a large dataset, which included all observation sessions, regardless of the location and context (e.g., whether food was present or not). Additionally, to focus on those animals whose motivation to make use of potential allies was greatest, we carried out the same analysis on a restricted dataset that included only aggressive behaviors preformed by individuals between 6 months and 2 years of age in the presence of a food source. In this situation, the presence of a desired resource should theoretically maximize the willingness of relatively small but high-ranking aggressors to take advantage of newly-arrived help against larger, lower-ranking hyenas.

We evaluated the initiation of fights in two contexts: 1) when the aggressor ranked intermediate between its target and a potential ally (potential ally > aggressor > target), and 2) when the aggressor was dominant to both its target and a potential ally (aggressor > potential ally > target). For each context, we compared the rates of aggression of individuals toward lower-ranking targets in 10-minute intervals before and after the arrival of a potential ally. Each individual scored a point for the 10-minute interval (before or after the potential ally arrived) during which it initiated higher rates of aggression associated with each observed arrival, and scored a zero for the interval with the lower rate of aggression. If there was no change in an individual's rate of aggression between the two 10minute intervals, that individual received a zero score for both intervals. We then compared before and after scores of individuals summed across all observation sessions using a Wilcoxon matched-pairs test. The Wilcoxon test allowed us to utilize repeated observations of individuals without the problems associated with pseudoreplication.

Joining on-going fights

Next, we tested whether individuals demonstrated knowledge of the relative ranks of conspecifics when they joined on-going dyadic fights. We expected that, if a hyena recognizes relative rank relationships, then it should join fights in support of the higher-ranking individual, even when both contestants are lower-ranking than itself. Alternatively, if hyenas don't recognize relative rank relationships, then high-ranking individuals should not necessarily support the dominant individual involved in a fight when both opponents are lower-ranking

than the joining hyena. Instead, they might simply join whichever member of the pair initiates the aggression. This would be expected, for example, if hyenas were merely being socially facilitated (sensu Zajonc 1965) to join a fight based on a rule of thumb such as "join whichever hyena is behaving aggressively" or "join whichever hyena is winning." Because hyenas rarely join coalitions against animals dominant to themselves, we did not expect to detect a pattern among joiners subordinate to both members of a fighting pair.

In interactions in which a third party joined in an on-going fight, we used binomial tests to determine whether higher-ranking contestants received more support than lower-ranking contestants. When a hyena joined in a fight between two others, we recorded whether it joined in support of the dominant or subordinate individual. We only collected data from the first individual to join a fight, even when other hyenas joined the fight subsequently. Because we had clear, directional predictions for each test, all statistics reported are 1-tailed.

RESULTS

Initiation of fights after the arrival of potential allies

We recorded data from 231 sessions in which a stable group of hyenas was present 10 minutes before and 10 minutes after the arrival of a new hyena. Eighty-eight individuals in 114 of these sessions behaved aggressively during the observation period. Forty-nine sessions involved an animal arriving at a scene where there was at least one animal between 6 months and 2 years of age and

food was present. Of these 49 sessions, 26 included aggressive behavior by 25 different subadult hyenas.

When data were analyzed together from all animals in contexts both where food was absent and where it was present, we observed a pattern that appeared to support the "rule of thumb" hypothesis rather than suggesting that hyenas can recognize third party relationships (Figure 3.1). That is, when the individual arriving was higher-ranking than both members of a pair of opponents, the dominant opponent increased its aggression rate against the subordinate significantly more often after than before the arrival (*N*=44, *Z*=1.627, *P*=0.050). However, we observed no difference when the arriving individual ranked between the two opponents (*N*=32, *Z*=0.219, *P*=0.414).

When we restricted our analysis to only those situations in which exploiting knowledge about third party rank relationships would unambiguously improve fitness of aggressors, we observed a pattern of behavior consistent with the hypothesis that spotted hyenas can recognize third-party rank relationships (Figure 3.2). In situations where food was present and aggressors had not yet reached adult size (<2 years old), we reasoned that hyenas would gain clear benefits by utilizing potential allies against larger, lower-ranking opponents. Although this greatly reduced sample sizes, since youngsters receive relatively little coalitionary support from non-relatives (Engh et al. 2000), the results of the restricted analysis suggest that hyenas can and do strategically exploit knowledge of third-party rank relationships. As in the initial analysis, the dominant contestant tended to increase its aggression rate more often after the



Rank of arriving hyena relative to contestants

Figure 3.1. Initiation of fights by hyenas in all contexts. Bars represent the mean number of instances per hyena in which an individual's rate of aggression was higher either before (black) or after (gray) the arrival of a hyena that ranked dominant to, or intermediate between, each pair of opponents. An asterisk indicates a significant difference (P<0.05).



Rank of arriving hyena relative to contestants

Figure 3.2. Initiation of fights by subadult hyenas in food-related contexts. Bars represent the mean number of instances per animal in which an individual's rate of aggression was higher either before (black) or after (gray) the arrival of a hyena that ranked dominant to, or intermediate between, each pair of opponents. An asterisk indicates a significant difference (P<0.05).

arrival of a higher-ranking individual than before (*N*=8, *Z*=1.414, *P*=0.078). In contrast to the initial analysis, however, in fitness-enhancing situations the dominant contestant also increased its aggression rate significantly more often after the arrival of an individual ranking below itself but above its opponent (*N*=9, *Z*=1.732, *P*=0.042). The increase in aggression rates was not due simply to the arrival of an additional animal, because there was not a significant increase in aggression after the arrival of an individual lower-ranking than both contestants (*N*=12, *Z*=-0.277, *P*=0.391).

Joining on-going fights

We used data from 114 coalitions to test whether individuals demonstrated knowledge of the relative ranks of conspecifics when they joined on-going dyadic fights. Hyenas supported the dominant individual in a fight, even when they outranked both contestants (Figure 3.3), suggesting that they recognize third-party rank relationships. When an individual joining a skirmish was intermediate in rank between the two contestants, it inevitably supported the dominant individual (N=28, Y=28, P<0.001). Similarly, when an individual lending support was dominant to both fighting animals, it almost always supported the dominant animal (N=81, Y=75, P<0.001). Animals lower-ranking than both members of a fighting pair rarely supported either party, and when they did lend support, they did not differentiate between the dominant and the subordinate contestants (N=5, Y=3, P=0.50).

To assess whether hyenas were simply joining fights in support of attacking animals regardless of their relative ranks, we restricted our next



Rank of joining hyena relative to fighting pair

Figure 3.3. Coalitionary support in on-going disputes. Bars represent the number of times that hyenas ranking dominant to both members of a fighting pair, or ranking intermediate between the members of the pair, joined in fights. Bar color indicates whether supporters joined on the side of the dominant (black) or subordinate (gray) contestant. An asterisk indicates a significant difference (P<0.05).

analysis to reversals, defined here as situations in which a subordinate initiates an aggressive attack against a dominant animal, and we found a pattern suggesting that hyenas base their decisions to join skirmishes on the relative ranks of the contestants (Figure 3.4). Reversals are quite rare; of 7,990 dyadic aggressive interactions recorded over more than 10 years, only 177 (2.2%) were reversals. Of these 177 reversals, 19 involved a third animal joining in support of one contestant. When the animal joining the fight was higher ranking than both contestants, it joined in support of the dominant contestant, even though that animal was losing the fight at that time (N=18, Y=3, P<0.01).

DISCUSSION

Results from earlier attempts to assess hyenas' cognitive abilities have been equivocal. When hyenas move N cubs from one den location to another, they make N + 1 trips, suggesting that they operate according to a rule of thumb that says "revisit your old den until you find no more of your cubs there" (Holekamp et al. 2000). In addition, the cooperative hunting behavior of hyenas and other carnivores, which often appears to involve intelligent coordination and division of labor among hunters (e.g., Guggisberg 1962; Stander 1992), can also be explained most parsimoniously by simple rules, such as "always keep the selected prey animal between you and another hunter" (Holekamp et al. 2000). A previous experiment in which hyenas' knowledge of third-party relationships was directly investigated failed to provide any support for the social complexity hypothesis. That is, in an experiment modeled after that performed by Cheney


Rank of joining hyena relative to fighting pair

Figure 3.4. Coalitionary support in attacks initiated by the subordinate member of a fighting dyad (reversals). Bars represent the number of times that hyenas ranking dominant to, or intermediate to, fighting pairs joined in disputes. Bar color indicates whether supporters joined on the side of the dominant (black) or subordinate (gray) contestant. An asterisk indicates a significant difference (P<0.05). and Seyfarth (1980), Holekamp et al. (1999) played recordings of cub whoops to groups of female hyenas and monitored reactions of the mother and other adult (control) females. Mothers and relatives of the whooping cub responded strongly, indicating that hyenas can recognize the whoops of individuals. However, control females were no more likely to look toward the mother of the whooping cub after the playback than before. One interpretation of these results is that hyenas do not recognize tertiary relationships. An alternative explanation, however, is that hyenas do recognize third party relationships, but that the orientation responses of control females measured in that study were poor indicators of this ability.

Several lines of indirect evidence suggest that hyenas might, in fact, possess some intellectual abilities similar to those of monkeys. First, neocortex sizes of hyenas and other carnivores are correlated with group size and lie on the same grade as do neocortex sizes of primates (Dunbar & Bever 1998). In other words, hyenas have neocortices comparable in size to those of group-living primates. Second, like many cercopithecine primates, the ranks of very young hyenas are dependent on the presence or absence of their mothers (Holekamp & Smale 1991). When the mother is absent, animals lower-ranking than the mother sometimes behave aggressively toward the cub, but when the mother is nearby, lower-ranking animals are rarely aggressive toward her cub. Because hyenas treat these youngsters differently in the presence of their mothers than in the presence of other higher-ranking adults, it may be that they are mentally categorizing the association between the mother-cub pair. On the other hand, it may be that the hyenas are simply responding to a discriminative stimulus. If they

distress the cub when its mother is present, they are likely to be counterattacked, whereas bothering the cub in the absence of the mother results in no punishment. Studies of long-tailed macaques (*Macaca fascicularis*: Dasser 1988) and vervet monkeys (Cheney & Seyfarth 1980) indicate that these primates understand something about the relationship between mothers and their offspring. At present, we cannot discriminate between the hypothesis that hyenas also understand mother-infant relationships and the hypothesis that dependent rank is a phenomenon based upon simple punishment.

Finally, male preferences for high-ranking females suggest that male hyenas are able to discern relative rank relationships among their prospective mates. Even when female reproductive state was controlled for, immigrant male hyenas, who always rank lower than adult females, associated more with highranking females than with low-ranking females (Szykman et al. 2001). Further evidence that males can distinguish female ranks comes from the fact that immigrant males who are relatively recent arrivals to the clan do not distinguish between high and low-ranking females, indicating that it may take them some time to learn the females' relative ranks. Although this evidence indicates that males can distinguish between high and low-ranking females, the males' preferences for high-ranking females may be a result of using simple direct cues, such as body condition or odors.

The results of the current study show that hyenas can and do recognize third party rank relationships. In the first test of the hypothesis, we found evidence that young hyenas altered their rates of aggressive behavior in food-

related contexts when potential allies arrived who ranked between themselves and the victims of their attacks. These young hyenas are usually smaller than most of their lower-ranking competitors and may be taking advantage of the arrival of larger conspecifics to maintain better access to food.

The behavior of hyenas who join on-going disputes also supports the assertion that hyenas recognize tertiary relationships. When hyenas joined fights between other hyenas, they almost always joined on the side of the dominant animal, even when that animal was lower-ranking then they were. Zabel et al. (1995) suggest that hyenas have a strong tendency to do what other hyenas are doing and therefore that hyenas often join coalitions as a result of social facilitation (Zajonc 1965) rather than based on an assessment of relative ranks. Since most aggression in hyena society is directed toward lower-ranking individuals, simply joining an aggressor is likely to result in the pattern observed here, in which the dominant animal is aided far more frequently than the subordinate animal. However, when we looked at rare instances of rank reversals, situations in which the initiator of aggression was lower-ranking than the victim, animals that intervened in the fight overwhelmingly came to the aid of the dominant animal. This demonstrates that hyenas do indeed use knowledge of rank relationships. They are not just following simple rules, such as "join in support of aggressors" or "join whichever animal is winning." Clearly, hyenas will aid the dominant animal even when that individual is losing the fight.

The evidence presented here shows that hyenas, like many primates, can recognize the relative ranks of the members of their social groups, but these

data do not tell us how they mentally represent information about dominance relationships. Tomasello and Call (1997) argue that non-primates may not understand transitive rank relationships and instead memorize relationships between all possible pairs of conspecifics. While we cannot rule out this hypothesis, it seems unlikely that each hyena in our study clan has memorized the outcomes of conflicts between 1891 potential pairwise combinations of clan members (number of clanmates!/[(number of clanmates - 2)!(2!)]), and that it accesses this large mental database when joining or recruiting allies. In over 30,000 hours of observation, we have not yet observed agonistic interactions between all possible pairs of adult hyenas. It therefore seems reasonable to expect that hyenas may not have observed all pairs interacting and may have to make inferences about rank based upon patterns of relatedness, association, or rank relationships with other individuals. Although there is no evidence that they can recognize 3rd party relationships, laboratory rats (*Rattus norvegicus*) appear to organize information about food sources hierarchically (Macuda & Roberts 1995), and it seems likely that hyenas may be utilizing similar mental capabilities to store relevant information about social relationships.

Carnivore and primate lineages diverged over 90 million years ago and are not sister taxa (Lillegraven et al. 1979, Waddell et al. 1999), yet in both taxa, similar social environments are associated with similar cognitive abilities. This convergent evolution provides support for the generality of the hypothesis that social complexity led to the evolution of intelligence in primates and other mammalian taxa. As with the data from primates, our hyena data are

correlational. Instead of social complexity promoting the evolution of intelligence, it may be that intelligence is a prerequisite of social complexity, or that both social complexity and social intelligence are correlated with some third variable of major importance. Nonetheless, the results of this study raise the question of whether the neural mechanisms underlying the abilities of hyenas and cercopithecine primates to recognize 3rd party relationships are also convergent. Additionally, these results suggest that we might expect to find similar cognitive abilities among elephants, cetaceans, and other mammals living in large, complex societies in which individual fitness is strongly influenced by social dexterity.

Chapter 4

REPRODUCTIVE SKEW AMONG MALES IN A FEMALE-DOMINATED MAMMALIAN SOCIETY

INTRODUCTION

Mammalian societies vary in the extent to which reproduction is skewed toward one or a few socially dominant individuals. In societies organized by hierarchical rank relationships, reproductive success (RS) among males is often positively correlated with social rank, which in turn is largely determined by fighting ability. Rank-related reproductive skew among males has now been documented with behavioral and molecular data in many group-living mammals (ungulates: Clutton-Brock 1988; Pemberton et al. 1992; rodents: Sherman et al. 1991; primates: Altmann et al. 1996; Bercovitch & Numberg 1997; De Ruiter et al. 1994; Smith et al. 1993; carnivores: Creel et al. 1997; Girman et al. 1997; Griffin 1999; Keane et al. 1994). In all of these species, and in most other mammals as well, sexual selection has favored males that are larger, stronger, and more pugnacious than females (Darwin 1871). Like societies of many other gregarious mammals, social groups of spotted hyenas (Crocuta crocuta) are structured by linear dominance hierarchies (Frank 1986; Holekamp & Smale 1990, 1993; Kruuk 1972; Mills 1990). However, in contrast to most other mammals, spotted hyenas exhibit some striking sex-role reversals. That is, among adult hyenas, females are larger and more aggressive than males, and females dominate males in all dyadic contexts (Kruuk 1972; Frank 1986).

Furthermore, fighting among adult male hyenas is less frequent and less intense than is that observed among adult females (Frank 1986; Kruuk 1972; Mills 1990), suggesting that male-male contest competition over mates may not function as importantly in sexual selection in hyenas as it does in many other mammals.

Reproductive success among female *Crocuta* is strongly correlated with social rank (Frank et al. 1995; Holekamp et al. 1996), but little is known about RS in males. Limited observations of wild spotted hyenas have suggested that only the highest-ranking immigrant male fathers offspring in this species (Frank 1986; Mills 1990). However, copulations are rarely observed, so the extent of reproductive skew among male hyenas remains unknown. Here we combine field observations with the use of genetic markers as indicators of paternity to examine patterns of reproductive skew among male hyenas, as well as to test predictions of competing models suggesting alternative relationships between male rank and RS in this species. The first, null, hypothesis suggests that males of all social ranks should be equally likely to father cubs. Second, a dominancebased priority of access model predicts that the number of offspring sired by a given male should depend on both his social rank and the number of females simultaneously in estrus. In a less restrictive test of the priority of access model, we inquire whether the highest-ranking male observed with a fertile female is the male most likely to sire her cubs.

Spotted hyenas are gregarious carnivores that live in social groups, called clans, composed of multiple matrilines of adult females and their offspring, as well as one or more adult immigrant males. An individual's social rank determines

its priority of access to food (Frank 1986; Kruuk 1972; Tilson and Hamilton 1984). Both male and female cubs "inherit" their mothers' ranks; that is, they attain ranks in the dominance hierarchy immediately below those of their mothers (Engh et al. 2000; Holekamp & Smale 1993; Smale et al. 1993). Females are usually philopatric, whereas males invariably emigrate from their natal clans at 25 to 62 months of age (Frank 1986; Henschel & Skinner 1987; Holekamp & Smale 1998; Smale et al. 1997). Adult natal males dominate adult females ranked lower than their own mothers in the clan's dominance hierarchy for as long as they remain in their natal clans. However, when males disperse, they behave submissively to all new hyenas encountered outside the natal area (Holekamp & Smale 1998; Smale et al. 1993, 1997). Thus, by joining a new clan, each immigrant assumes the lowest rank in that clan's dominance hierarchy, and his status only improves through attrition by death or secondary dispersal of the immigrant males that arrived before him (Smale et al. 1997).

Because males typically remain in their natal clans for several months or years after puberty, there are two classes of reproductively mature males in every *Crocuta* clan: adult natal males born in the clan and adult immigrant males born elsewhere. Since all natal animals outrank all immigrants, a male's rankdetermined priority of access to food is inevitably worse after he emigrates from his natal clan than before dispersal (Holekamp & Smale 1998; Smale et al. 1993, 1997). Nevertheless, virtually all males eventually disperse. If dispersal is adaptive, then the fitness benefits of dispersing must exceed costs associated with reduced access to food. The ultimate cause of male dispersal in this species

remains unknown. The most plausible hypothesis to account for a behavior pattern with such dire nutritional consequences is that males may only be able to mate outside of their natal clans. Therefore, in addition to using our genetic data to examine patterns of reproductive skew among males, we also use them to test this hypothesis.

METHODS

Study population

We conducted this study in the Talek area (1° 40'S, 35° 50'E) of the Masai Mara National Reserve. This is an area of open grasslands grazed year round by large concentrations of several ungulate species. The subject population was one large *Crocuta* clan inhabiting a home range of approximately 65 km². We monitored Talek hyenas from June 1988 to January 1999.

We identified all hyenas in the Talek clan by their unique spot patterns, and we determined their sex from the dimorphic glans morphology of the erect phallus (Frank et al. 1990). All hyenas initially appearing in the Talek home range as adults were photographed when first sighted, and the day an individual was first seen in Talek was considered its date of arrival. Immigrant males remaining in Talek for at least six months were called 'resident immigrant males,' whereas males remaining for shorter periods were called 'transients.' The duration of residence of any given immigrant male in the Talek clan was called his 'tenure' in the clan. Between 1988 and 1999, the Talek study clan varied in size from 50 to 78 individuals, and usually contained 20 to 22 adult females (range: 16-28) and their juvenile offspring. On average during the study period, 13.8 ± 2.1 resident

immigrant males and 4.4 ± 0.6 adult natal males were present in the clan. In addition, 2 or 3 transient immigrant males appeared in the clan's territory each month and remained for shorter periods, usually only a few days (Smale et al. 1997).

Mother-offspring relationships were established on the basis of regular nursing associations, which last up to 21 months in this species (Hofer & East 1995; Holekamp et al. 1996). We assigned birth dates to litters by estimating cub ages when they were first observed above ground at natal or communal dens. Cub ages could be estimated to \pm 7 days based on pelage, size, and other aspects of cub appearance and behavior (Holekamp et al. 1996). Male *Crocuta* have viable sperm in their testes by 24 months of age (Matthews 1939), and we therefore considered natal males older than 24 months to be adults. We estimated the ages of immigrant males based upon the degree of tooth wear (Van Horn et al. in review).

We conducted behavioral observations from vehicles between 0530 and 0900 h and between 1700 and 2000 h. During the study period, we observed hyenas for over 30,000 person hours during 35,040 observation sessions. We defined an observation session to include all of the time spent watching hyenas located within 200 m of one another. We identified all individual hyenas present in these sessions, and we excluded from analyses any sessions in which one or more unidentified hyenas were present. Throughout the study period, all mounting behavior and complete copulatory sequences (those involving intromission and ejaculation) were recorded during critical incident sampling (the

'all occurrence sampling' of Altmann 1974).

We determined social ranks of individuals based on outcomes of several thousand dyadic agonistic interactions during which one individual exhibited appeasement behavior to the other, as described previously (Holekamp & Smale 1990; Smale et al. 1993). All resident immigrants present in the clan concurrently were organized into a matrix based on direction, not number, of interactions (Martin & Bateson 1988). The resident immigrant matrix was composed of 997 dvadic agonistic interactions in which 38 interactions (3.8%) were inconsistent with assigned ranks. By convention, the highest-ranking immigrant, who was able to win against all other immigrants in agonistic interactions, was called the 'alpha male,' and was assigned a rank of 1. The period during which any male held alpha status was referred to as his 'reign.' Due to male attrition and the arrival of new immigrants, not all resident males present in Talek during a given reign were necessarily there concurrently. For tenure-based analyses, only resident immigrant males whose tenure began after the start of the study period were used.

Sample collection and paternity analysis

Most DNA samples originated from venous blood collected while hyenas were anaesthetized with Telazol (2.5 mg/kg) delivered from a CO₂-powered darting rifle (Telinject Inc, Saugus, CA). Most cubs were darted between 8 and 12 months of age, and immigrant males were darted as early in their tenure as possible. We collected body and tooth measurements from all immobilized hyenas. We used a Puregene (Gentra Systems, Minneapolis, MN) kit to extract DNA from blood shortly after collection, and then stored the DNA in liquid

nitrogen. We also collected tissue samples from dead hyenas whenever we found them. DNA was isolated from tissues using either standard phenolchloroform extraction techniques or Qiagen kits (Qiagen, Inc, Bothel, WA). We genotyped sampled individuals using eleven autosomal microsatellite loci and one X-linked microsatellite locus (Funk & Engh in review; Libants et al. 2000; Tables A.1, A.2 & A.3 in Appendix A of this dissertation). Across the 12 loci, on average, there were 5.1 alleles/locus (range: 2-8), and the expected heterozygosity was 0.62. We estimated typing error (1.0%) from the frequency of mother-cub mismatches. Overall exclusion probability was 0.998.

All resident immigrant, transient, and unrelated adult natal males present in the clan at conception of a particular litter were considered as potential fathers. Males were considered unrelated to particular females when their maternal coefficients of relatedness, calculated from genealogies, were less than 0.125. We employed a maximum likelihood-based approach (Thompson 1975; Meagher 1986) to assign paternity to cubs with known, genotyped mothers using the program CERVUS (Marshall et al. 1998). We used the following parameters in CERVUS: 85 candidate males (total number of resident immigrant males + adult natal males + sampled transient males), 92% of candidate males sampled, 91% of loci typed, and a 1% error rate. A male was considered the father of a cub when CERVUS assigned him at 95% confidence. Confidence levels were derived based upon population allele frequencies at each locus and represent levels of tolerance of false paternity that would be assigned to males whose genotypes are consistent with those of cubs by chance alone (see Marshall et al. 1998 for

details).

Modeling the relationship between male rank and male RS

We used results of our paternity analysis to examine predictions of two mutually exclusive models, each suggesting a different relationship between male rank and RS in *Crocuta*. The first hypothesis suggests that males of all social ranks should be equally likely to father cubs. A second, dominance-based priority of access model predicts that the number of offspring fathered by a given male should depend on both his dominance status and the number of females simultaneously in estrus (Altmann et al. 1996). Since a male can monopolize only one fertile female at a time, the priority of access model predicts that the alpha immigrant male will father all offspring conceived when only one female in the group is in estrus, the alpha and beta males will equally share paternity of cubs sired when two females are simultaneously in estrus, and so on (Altmann et al. 1996). Conception dates of hyena litters were calculated by subtracting the gestation period of 110 days (Schneider 1926) from birth dates. The 2-week interval surrounding each conception date was considered the fertile period during each breeding cycle of each female hyena. In addition, we determined whether the highest-ranking male present with a particular female during her fertile period was the male most likely to father her cubs. To do so, we recorded the identities and social ranks of all males found with that female during her fertile period. Finally, to evaluate whether access to females was affected by male rank, we calculated the percent of all adult Talek females that were encountered by each immigrant male per observation session during 26 twoweek intervals in 1994 as [(number of females encountered/number of females

present in the clan)/number of sessions each male observed]*100.

Statistical analysis

Correlations between behavioral variables or measures of male RS and male social rank were evaluated with Spearman's correlation coefficients using SYSTAT software. Other correlations were assessed using Pearson's R. Probabilities of fathering cubs were compared for adult natal and adult immigrant males using Chi-square tests, as were observed and predicted values obtained in testing the priority of access model. We compared reproductive rates of agematched immigrant and adult natal males with a Mann-Whitney U test, and we used Analysis of Variance to evaluate differences in measures of RS among males based upon total tenure and highest rank achieved. For analyses in which the dependent variable was a proportion (percent of assigned cubs sired), we used an arcsine-square root transformation to normalize the distribution of the data. Differences between groups were considered significant when P<0.05.

Please note that the data presented in figures 4.1 and 4.6 represent the same male at more than one rank or in more than one year. Almost all resident immigrant males were present for several years (range=0.67-8.08) and occupied several ranks (range=1-12) during their tenure in the clan, and we believe that using data from these same individuals over multiple years and ranks presents a more complete view of long term male reproductive success than simply presenting a "snapshot" of RS at only one point in a male's life. However, to avoid pseudoreplication, we include additional analyses in which individual males are represented only once or repeated measures where each male is represented over the same time/rank span.

RESULTS

Paternity assignment and multiple paternity

DNA samples from 199 hyenas were collected between December, 1990 and August, 2000, including 85 natal females, 74 natal males, 5 transient males, and 35 resident immigrant males. Between December, 1990 and January, 1999, each of eight different resident immigrant males held alpha status in Talek for 1 to 34 months. DNA was sampled from at least 92% of all resident immigrant and adult natal males during this period, and paternity was verified in 75 (68.2%) out of 110 cubs sampled (Table 4.1). Twelve of the 75 cubs assigned fathers had mismatches with their putative fathers at one locus. The rate of cub-father mismatches is 0.97%, which is similar to the 1.0% mismatch rate for known mother-cub pairs. No male assigned paternity by CERVUS at 95% confidence had more than a single mismatch with his putative offspring.

Seventeen cubs for which paternity could be assigned were from singleton litters, and 58 were from 31 twin litters. Of 14 twin litters in which sires could be assigned for both littermates, three (21.4%) were fathered by two different males, and 11 (78.6%) were fathered by single males. In 5 (38.5%) of an additional 13 twin litters in which only one cub could be assigned a father, the assigned father could be excluded from siring the other cub at 2 or more loci. Because litter size varied from 1 to 2 cubs and the proportion of cubs in a litter sired by a single male differed in this population, all analyses below use individual cubs rather than litters as the units of analysis unless otherwise indicated.

Alpha male	Dates of reign as alpha	% Resident immigrants sampled (N)	% Adult natal males sampled (N)	# Of known conceptio	# Cubs sampled ins	# Cubs assigned fathers	# Sired by alpha male	# Sired by adult natal males	# Sired by non-alpha resident immigrant males
1019	12/7/90-11/9/91	100% (15)	92% (12)	15	13	6	1 (11%)	0	8 (89%)
MRB	11/10/91-6/1/92	100% (13)	86% (7)	80	5	2	0	0	2 (100%)
N E	6/2/92-2/20/93	100% (10)	86% (7)	9	5	4	2 (50%)	0	2 (50%)
HOL	2/21/93-3/29/93	100% (7)	100% (5)	5	4	e	0	0	3 (100%)
QUA	3/30/93-6/21/93	100% (6)	100% (5)	9	4	5	0	0	2 (100%)
ZIP	6/22/93-4/21/94	100% (9)	86% (7)	29	12	7	0	2 (29%)	5 (71%)
SΥ	4/22/94-2/13/97	95% (21)	100% (10)	69	37	23	0	0	23 (100%)
FN	2/14/97-1/1/99	95% (22)	100% (8)	. 61	36	25	1 (4%)	0	24 (96%)
ALL	12/7/90-1/1/99	95% (37)	92% (38)	189	110	75	4 (5%)	2 (3%)	69 (92%)

Table 4.1. Patterns of paternity during eight alpha male "reigns".

Male dispersal status

Of the 75 cubs for which paternity could be assigned, 73 (97.3%) were fathered by immigrant males, and two (2.7%) by adult natal males (Table 1). No cubs were found to be sired by transient immigrant males; however, only five transients were sampled. Of 31 sampled cubs conceived during the 24 months when all 5 natal and 22 resident immigrant males were sampled (August, 1995 – September, 1997), 22 (71.0%) were fathered by immigrants and none were sired by natal males. Twenty-nine of these 31 cubs (93.5%) could be assigned to Talek males using CERVUS at 80% or greater confidence, and the remaining two cubs (6.5%) could not be assigned with confidence to any Talek males. Uncertain paternity of these two cubs could be due to their having been sired either by unsampled transient males in the Talek area or by males encountered during female excursions into surrounding territories. We observed several transient males in the Talek home range each month (Smale et al. 1997), and females occasionally made forays into surrounding territories. On average, 94.4 \pm 1.9% of all locations at which adult Talek females are found fall within the clan's territorial boundaries (Boydston et al. 2001).

Mean annual RS among immigrant males was 0.66 ± 0.12 cubs/year (range: 0 - 2.33; *N*=35), and was thus over ten times higher than mean annual RS among adult natal males (mean= 0.06 ± 0.06 cub/year; range: 0-2.15; *N*=35). Natal males were less likely to father any cubs at all than were immigrants (1 of 35 sampled adult natal males vs. 22 of 35 immigrants; χ^2_1 =28.6, *P* < 0.001). When we restricted our analysis of RS to immigrant males estimated to be less than 3 years old, the mean annual RS of immigrant males (mean= 0.33 ± 0.19

cubs/year; N=12) was still higher than that of adult natal males (Mann-Whitney $U_1=255.0$; P=0.02). It is therefore unlikely that adult natal males are simply too young to reproduce. These data indicate that adult natal males generally experience very low RS compared to that of males managing to join a new clan after emigration from their natal groups.

Male rank and the priority of access model

Most immigrant males that eventually attained alpha status sired at least one cub (range: 0-13 cubs; *N*=8 males), but these males sired an average of $87.5 \pm 11.0\%$ of their sampled offspring before they attained alpha status. Clearly, alpha males were not monopolizing reproductive opportunities (Table 4.1, Figure 4.1).

Social rank of resident immigrant males was positively correlated with their annual reproductive rate (Figure 4.1; R_s =-0.31; P=0.041; N=35 males). In a conservative analysis in which each male's rate of yearly cub production was calculated for a single, randomly assigned rank, we still found a positive correlation between male rank and RS (R_s =-0.30; P<0.042; N=35). These data allowed us to rule out the null hypothesis, which suggested that males of all ranks were equally likely to sire cubs. However, although the correlation we found between male rank and RS was significant, rank failed to account for even half of the variance in male RS, and the pattern of RS observed among Talek males failed to match that predicted by the priority of access model (Figure 4.2; χ^2_1 =170.2, P<0.001).

One potential problem with the application of the priority of access model to the fission-fusion society of the spotted hyena is that it assumes that males



Figure 4.1. Mean (\pm SEM) reproductive rate of immigrant males at each rank position. Numbers above bars represent the number of males at each rank position.



Figure 4.2. Observed paternity of 75 cubs in relation to male social rank compared with the pattern of paternity predicted by a dominance-based priority of access model (Altmann et al. 1996).

obtain perfect information about the whereabouts and reproductive status of breeding females. In fact, however, higher-ranking immigrants typically encountered a larger proportion of clan females per time interval than did lower-ranking immigrants (Figure 4.3; $R_s = -0.66$; *P* <0.005; *N*=20 males). Thus high-ranking immigrant males may be more efficient than their lower-ranking peers with respect to moving around the Talek territory or meeting up with multiple females. On average, males are only observed with 22.7% of females during each two week period, suggesting that even high-ranking males may not have accurate information about the reproductive status of most clan females.

We next assessed the possibility that the sire of a female's litter is likely to be the highest-ranking male meeting up with her during her fertile period. We recorded the behavior of 29 females during 53 fertile periods in which we assigned paternity to the litter conceived. On average, each fertile female was observed for 260 ± 32 minutes in 11.4 ± 1.4 sessions. In 10 (18.9%) of the 53 fertile periods, the highest-ranking male observed with the mother fathered at least half of the litter she produced 110 days later. However, in 43 (81.1%) of these fertile periods, the highest-ranking male observed with the female failed to sire any of her cubs. In fact, the highest-ranking male observed with a fertile female was no more likely to sire her cubs than any other immigrant male observed with her (X^2_1 =1.37, *P*<0.25, *N*=64 cubs). On average during these fertile periods, females were found with 2.51 ± 0.33 immigrants that were higher-ranking, and with 1.17 ± 0.19 unrelated adult natal males that were higher-ranking, than the sires of the cubs conceived.



Figure 4.3. Mean proportion of all 21 adult females present in the Talek clan in 1994 that were encountered per observation session during each of 209 2-wk long intervals by the immigrant males present in the clan during this period, ordered on the basis of male rank in the immigrant hierarchy.

Copulatory behavior

We watched Talek hyenas for over 30,000 person hours during the study period, but we observed only 39 mounting bouts and 20 bouts of complete copulation (Figure 4.4). Each bout typically included several mounts or complete copulations over a period of hours. Five of 39 mounting bouts (12.8%) were performed by five different adult natal males, and the remainder (87.2%) by 16 different immigrant males. Adult natal males were never observed to achieve intromission, so all complete copulations involved immigrants. Neither the number of mounting bouts performed ($R_s = -0.38$; NS) nor the number of copulations achieved (R_s =-.14; NS) was significantly correlated with immigrant male social rank (N=25 ranks), although this may have been due to the small sample size of observed copulations. Alpha males achieved only 1 (5.0%) of 20 complete copulations observed, and over 50% of all observed copulations were achieved by animals ranked fourth through sixth in the immigrant male hierarchy. No observed mounts or copulations involved transient males. The overall trends of the behavioral data are similar to those observed in the molecular paternity data. During a single estrus period, Talek females were mounted by one to three different males (mean =1.18 \pm 0.08 males/estrus; *N*=33 estrus periods). On average, each resident immigrant male seen copulating mated with 1.42 ± 0.29 different females. Thus mating appears to be highly promiscuous in both sexes. Male rank and tenure

Immigrant male social rank in this species is highly correlated with arrival order in the new clan (Pusey and Packer 1997; Smale et al. 1997), so we next attempted to evaluate effects of immigrant male tenure on RS. Among immigrant



Figure 4.4. Distribution of mounting and copulatory behavior across immigrant male social rank.

males who fathered any cubs, the mean period between arriving in Talek and fathering a first cub was 20.8 ± 4.0 months (range: 0 - 55.2; *N*=24 males), and long term male RS was positively correlated with total time in the clan (Figure 4.5; $R_p = 0.82$; *P*<0.001; *N*=24 males). One possible explanation for this pattern is that males failing to reproduce soon after immigrating to Talek engaged in secondary dispersal whereas successful males remained there longer. However, this interpretation seems unlikely since immigrant males that remained in Talek for several years were no more likely to have fathered cubs during their first two years in Talek than were immigrants that disappeared during their third year (2 of 6 vs. 3 of 8 males: X_1^2 with Yates' correction for small samples = 0.18; NS).

To disentangle the effects of rank and tenure in Talek on immigrant male RS, we simultaneously regressed the transformed dependent variable of percent of assigned cubs sired against total male tenure in the clan and highest social rank achieved during that tenure. Whereas both of these independent variables were significantly related to percent cubs sired by immigrant males, total tenure (P=0.02) explained 60% of the total variance in this model whereas highest rank achieved (P=0.45) explained only 18% of the variance (N=24 males). The rate at which males produce cubs is low early in their tenure, then it increases after they have resided in the clan for several years (Figure 4.6; $F_{7,128}$ =2.457; P=0.021). Repeated measures analysis of the 3 males who were present in the clan for a minimum of 5 years and 8 social ranks detected a similar relationship between tenure and reproductive rate despite the small sample size and low power ($F_{4,8}$ =4.25; P=0.04), but found no relationship between rank and reproductive



Figure 4.5. Total number of cubs sired by 24 immigrant males shown in relation to their tenure in the Talek clan.





rate (F_{7,14}=0.58; NS).

Tenure was not significantly correlated with any measure of male body size, including body length ($R_p = 0.277$, NS; *N*=35), skull length ($R_p = 0.289$, NS; *N*=35) and shoulder height ($R_p = 0.201$; NS; *N*=35). Thus immigrant males who had been present in the Talek clan for an extended period were not any larger than those males that had arrived more recently, and the observed relationship between male tenure and RS did not appear to be due to an effect of increasing body size.

DISCUSSION

The spotted hyenas in our Kenyan study clan exhibit a promiscuous mating system. Approximately one fifth of all twin litters are sired by multiple males. Genetic paternity tests have revealed that multiple paternity similarly occurs in other carnivore species (Eurasian badgers: Da Silva et al. 1994; Ethiopian wolves: Gottelli et al. 1994; dwarf mongooses: Keane et al. 1994; lions: Packer et al. 1991). The most important determinants of RS in male hyenas appear to be an individual's dispersal status and the duration of his residence in his new clan after dispersal. Adult natal male hyenas win all fights against immigrants and show sexual interest in clan females (Holekamp & Smale 1998), yet they seldom father any cubs. It seems unlikely that natal males are too young to father cubs, since reproductive rates of natal males were significantly lower than reproductive rates of age-matched immigrant males. This suggests a compelling ultimate explanation for natal (primary) dispersal behavior in *Crocuta*,

a behavior that inevitably leads to a substantial drop in social rank and hence in priority of access to food. The current data suggest that dispersing males may be trading superior access to food in their natal areas for superior access to mates elsewhere. Male-biased dispersal is common in mammals (Chepko-Sade & Halpin 1987; Dobson 1982; Greenwood 1980; Pusey and Packer 1987; Stenseth & Lidicker 1992), and this behavior may have evolved in many species as a mechanism to promote outbreeding, either directly via selection on males or indirectly via female preferences for immigrant males as mates.

Among resident immigrant males, social rank is correlated with male RS, but tenure is a far better predictor of RS than is rank. Our data do not conform to predictions of a dominance-based priority of access model (Altmann et al. 1996). and the data documenting associations between males and fertile females are inconsistent with the hypothesis that the highest-ranking male present with a female during her fertile period is most likely to sire some or all of her offspring. Our results thus stand in striking contrast to those obtained from other mammalian carnivores in which male RS increases with social dominance and ability to win fights with other males (eg., sea lions: Campagna & LeBoeuf 1988; Cape hunting dogs: Creel et al. 1997; raccoons: Gehrt & Fritzell 1999; meerkats: Griffin 1999; kinkajous: Kays et al. 2000; wolves: Packard et al. 1985; polar bears: Ramsay & Stirling 1986). The social lives of spotted hyenas are similar in many respects to those of most cercopithecine primates (Frank 1986; Holekamp et al. 1999a). However, most studies of paternity in wild cercopithecine primates generally find that, as in most other mammals (Ellis 1995), male social rank is

highly correlated with reproductive success (Altmann et al. 1996; de Ruiter et al. 1994; Melnick 1987).

Several different hypotheses might explain why high-ranking male hyenas are not monopolizing reproduction. Social rank of male hyenas is not correlated with body size, so unlike high-ranking males in other polygynous mammals, highranking male hyenas cannot necessarily physically exclude lower-ranking males from mating. In fact, fighting among male hyenas is rare, and when it does occur, it is usually restricted to low-level threats (Frank 1986; Kruuk 1972). The only stage in the life history of this species in which males confront intense aggression from other males is during the process of immigrating into a new clan, and malemale fighting is rare even under these circumstances. Whereas all males disperse, few successfully immigrate. From 1988 to 1997, although 49% of 291 prospective immigrants remained in Talek for more than 1 month, only 15% remained there for longer than 2 years (Smale et al. 1997). Aggression directed toward potential immigrants might permit only the best fighters to gain entry into the clan, and successful immigrants might then be too well matched to risk escalated fights. This scenario, however, seems unlikely, since most new immigrants behave extremely submissively to both male and female residents when trying to enter a new clan (Smale et al. 1997), and because substantial variation in body size, and thus presumably in fighting ability, exists within the immigrant male hierarchy.

High-ranking male hyenas may not be able to monopolize reproduction because they cannot adequately keep track of female location and reproductive

state. Hyenas live in fission-fusion societies in which subgroup composition changes from day to day, or even hour to hour (East et al. 1993; Holekamp et al. 1997), so tracking multiple reproductive females might be difficult. Our analysis of male rank in relation to the proportion of clan females encountered shows that high-ranking males have a slight advantage over low-ranking males with respect to encountering females, so high-ranking males may fare better in scramble competition over mates. However, unlike lions, hyenas do not appear to respect "ownership" of estrous females by the first male to mate (Packer & Pusey 1983). Indeed, we have observed two males alternately mounting a single estrous female (Szykman 2001). Furthermore, our behavioral data show that even when high-ranking males are observed with fertile females, they are unlikely to father cubs. This is unlikely to be the result of sperm depletion (Preston et al. 2001), since estrus is asynchronous in female hyenas, and 60% of fertile periods do not overlap at all with those of any other females (Szykman et al. 2001). Thus, neither difficulty in finding receptive females nor inability to fertilize them can satisfactorily explain the patterns of reproductive skew observed among male hyenas.

Prohibitive energetic costs might keep high-ranking males from monopolizing reproduction. We frequently observed males following particular females for days or even weeks (Szykman 2001). These 'consorting' males may undergo serious energetic stress unless they periodically leave the females to feed. Female hyenas always have higher priority of access to food than immigrant males, so it may be difficult for a male to guard a female continuously

for extended periods of time without starving. Male hyenas with the highest priority of access to food at ungulate kills may be best able to fortify themselves for extended attendance of females, and thereby obtain an advantage during male-male scramble competition (see also Bercovitch & Nurnberg 1996, 1997; Bercovitch 1997). If this were true, however, we would expect to see a stronger relationship between male rank and RS than between tenure and RS.

Finally, high-ranking males may not be able to monopolize reproduction if females choose not to mate with them. Female hyenas are dominant to immigrant males, and their unusual genital morphology makes forced copulation impossible. Several lines of evidence suggest that female choice has important effects on patterns of paternity in *Crocuta*. First, despite the fact that adult natal males can always win in fights with immigrants, and although they express sexual interest in Talek females, natal males rarely father any cubs. These patterns suggest that females strongly prefer immigrants over natal males, perhaps to avoid the deleterious consequences of inbreeding. Second, patterns of association between Talek females and immigrant males show that the highest-ranking male present with a female during her fertile period fathers her cubs in only 19% of cases, and mid-ranking males do better than expected based on their ability to win in either agonistic interactions or scramble competition with other males. Third, RS varies substantially within most male rank positions, and also within any given year of immigrant tenure in the Talek clan, suggesting that some males present during each alpha reign are more attractive to females than others. These data suggest that female choice of

mates may limit control of reproduction by high-ranking male hyenas.

Optimal skew models (e.g., Vehrencamp 1983; Reeve et al. 1998) suggest that dominant individuals have full control of subordinate reproduction and allow subordinates to breed only when necessary to entice them to remain in the group and cooperate. Although optimal skew models may be applicable to some animal societies, they fail to account for observed partitioning of reproduction within many vertebrate social groups, including those of other mammalian carnivores (e.g., Clutton-Brock et al. 2001). Instead, these recent empirical data are more consistent with predictions of limited control models of reproductive skew, which predict that subordinates will breed when dominants' capacity for control of reproduction is reduced. Similarly, the data presented here for male spotted hyenas are more compatible with limited control than optimal skew models, but control in this species is clearly limited by variables other than those associated with male-male fighting. Indeed, as suggested recently by Koenig and Haydock (2001), interactions between males and females, including incest avoidance and mate choice, may limit dominants' control of reproduction.

In contrast to what occurs in most polygynous mammals, male-male contest competition appears to have little influence over male reproductive success in the spotted hyena. The highest-ranking (natal) males have very low reproductive success, and high-ranking immigrant males cannot prevent lowerranking males from copulating with females. Rather than favoring big, fierce males, sexual selection in hyenas has apparently favored males who compete by successfully immigrating, persisting in their new clans for several years, and

overcoming the energetic handicaps imposed by low social rank.

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CHAPTER 5

SOCIAL AND DEMOGRAPHIC VARIABLES INFLUENCE PARASITISM IN A WILD CARNIVORE

INTRODUCTION

Various factors are known to influence the susceptibility of hosts to parasitic infections, including age, sex, genotype, behavior, and habitat features (Rau 1983: Wakelin 1985: Alexander & Stimson 1988: Wakelin & Blackwell 1988: Keymer & Read 1991; Poulin 1996; Müller-Graf et al. 1999; MacDonald et al. 1999). Little is known, however, about how these variables interact to influence the distribution of parasites in populations of wild vertebrates. For example, although high-ranking captive house mice (*Mus domesticus*) are known to be more susceptible to Babesia infections than are low-ranking mice (Barnard et al. 1993), social status and other behavioral variables are seldom considered in relation to parasite prevalence among animals living in their natural habitats (but see Hausfater & Watson 1976; Müller-Graf et al. 1996). Because detailed information about host populations is rarely available, few studies have investigated the combined impact of social and demographic variables on parasitism. Because both social and demographic variables may influence an individual's exposure and resistance to parasites, studies incorporating both types of variables should yield a more complete understanding of parasite epidemiology in wild populations than is currently available.
Studies conducted to date with free-living animals have revealed that even seemingly benign levels of infection can lead to dramatic decreases in reproductive success and survivorship (Edwards & Barnard 1987; Moller 1990; Hudson et al. 1992). For example, in a study of snowshoe hare (*Lepus americanus*) predation, Murray et al. (1997) found that hares treated with an antihelminthic drug experienced a 17% reduction in annual mortality due to predation compared to control animals. Because natural levels of parasitism may have substantial impacts upon host survival, understanding patterns and processes of parasitic infections in wild animals is critical to our understanding of their population dynamics. Here we use data collected during a 12-year study of the behavioral ecology of free-living spotted hyenas (*Crocuta crocuta*) to examine the effects of age, sex, season, social rank, and dispersal status on the prevalence and intensity of three common species of hyena endoparasites.

METHODS

Study Animals

Spotted hyenas are gregarious carnivores that live in large groups, called clans, structured by rigid dominance hierarchies. Although often thought of as scavengers, hyenas are in fact capable hunters, and kill up to 96% of their prey themselves (Kruuk 1972). Their diets include a wide variety of prey species, ranging from invertebrates and passerine birds to wildebeest and zebras (Holekamp et al. 1997; Cooper et al. 1999) (Table 5.1.). Hyenas frequently compete with lions (*Panthera leo*), jackals (*Canis mesomelas*), and other

Table 5.1. Foods consumed by spotted hyenas in the Masai Mara National Reserve, Kenya (data from Cooper et al. 1999).

Common Name	Scientific Name	
Ungulates		
Wildebeest	Connochaetes taurinus	
Thompson's gazelle	Gazella thompsoni	
Торі	Damaliscus lunatus	
Zebra	Eauus burchelli	
Impala	Aepyceros melampus	
Grant's gazelle	Gazella granti	
Hartebeest	Alcelaphus buselaphus	
Giraffe	Giraffa camelopardalis	
Buffalo	Syncerus caffer	
Warthog	Phacochoerus africanus	
Hippopotamus	Hippopotamus amphibius	
Dik dik	Madoqua kirkii	
Other		
Elephant	Loxodonta Africana	
Springhare	Pedetes capensis	
Hare	Lepus capensis	
Hyena	Crocuta crocuta	
Jackal	Canis mesomelas	
Bat-eared fox	Otocyon megalotis	
Mongoose	Helogale parvula	
Amphibian	Various	
Bird	Various	
Invertebrate	Various	

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carnivores at kill sites (Kruuk 1972). As a result, they may be exposed to a variety of parasites and pathogens from both their prey species and their carnivore competitors.

Between 1998 and 1999, there were 26 adult females, 20 adult immigrant males, 11 adult natal males, and 29 subadults in the clan. Individual hyenas were identified based upon unique patterns of spots and natural markings (e.g., ear notches). Although hyena females have a peniform clitoris, we could distinguish males from females by differences in the morphology of the erect glans (Frank Glickman & Powch 1990). Ages of all hyenas born in the clan were known to within \pm 7 days, based upon characteristic developmental changes in juvenile pelage and other features.

Social ranks were assigned to all clan members by organizing the outcomes of dyadic agonistic interactions into a matrix based upon the direction of interactions (as described in Smale et al. 1993). Individuals who exhibited appeasement behavior during dyadic interactions were considered lower-ranking than their partners. By convention, the highest-ranking animal was assigned a rank of 1.

Male hyenas reach sexual maturity at 2 years of age (Matthews 1939), and we considered all animals over 2 years old to be adults. Females generally spend their entire lives in their natal clans, whereas all males emigrate from their natal clans between the ages of 2 and 5 years (Smale et al. 1997). When males immigrate into new clans, they join at the bottom of the rank hierarchy. Thus, all natal animals (adult females and their offspring) are socially dominant to all

immigrant males (Smale et al. 1993).

Study Site & Sampling

Fecal samples were collected from a single, large clan of hyenas in the Talek area of the Masai Mara National Reserve, Kenya. The Mara is an area characterized by open, rolling grasslands grazed year-round by large concentrations of ungulates. Between June 1999 and July 2000, we collected 205 fecal samples from 70 individuals (19 adult females, 19 adult immigrant males, 9 adult natal males, and 23 subadults). All samples were collected from known individuals observed defecating. In order to avoid pseudo-replication, we used only one randomly selected sample from each individual for our analyses. Parasite prevalence and intensity of infection were calculated using a modified McMaster technique (Engh et al. in review; Appendix B of this dissertation). Throughout the study, we recorded daily precipitation (in mm) and conducted censuses of local ungulate populations twice each month, as described previously (Holekamp et al. 1999b).

Statistical analyses

Patterns of prevalence and intensity of infection were analyzed for three common parasites within the population: *Ancylostoma* sp., *Spirometra* sp., and *Isospora* sp. (Engh et al. in review; Table B.1 in Appendix B). Prevalence, the proportion of animals infected with a parasite, was analyzed using logistic regression (SAS Proc Logistic, SAS Institute, 1988). Independent variables were age, sex, social rank, month, and dispersal status (natal or immigrant). An initial logistic regression was run using forward stepwise selection (p < 0.05) to

determine which individual variables should be included in the model. If more than one variable was included, we entered appropriate 2nd order interactions and tested for significance (Hosmer and Lemeshow, 2000).

We used general linear models (SAS Proc GLM, SAS Institute, 1988) to analyze intensity, the number of eggs of a particular parasite species present in infected hosts, as well as total eggs counted and the total number of species present in each sample (range=1-5). All egg counts were log (x + 1) transformed to correct for overdispersion. We included all independent variables used in the logistic regression, plus appropriate second order interaction terms. Interaction terms that were not biologically feasible were not included in the model. For example, we did not include dispersal status by sex or dispersal status by age interactions, because all immigrants were adult males.

We calculated Pearson correlation coefficients (r_P) between parasite prevalence and intensity and monthly rainfall total and mean ungulate counts. To evaluate the relationship between social rank and intensity of parasite infections, we used Spearman correlations (r_S). Analyses of dichotomous variables were carried out using Student's t-tests.

RESULTS

Egg counts and species richness

The number of parasite species with which hyenas were infected was significantly related to the month of the year in which the sample was collected (Table 5.2). Sample sizes were small in some months and may have resulted in

Table 5.2. Results of general linear modeling analysis on parasite intensity data. An asterisk indicates a significant relationship.

					Spec	ies			
All E	ggs	# Sp	р	Ancy	lostoma	Spire	ometra	Isosp	ora
F	p	F	p	F	p	Fμ)	Fρ)
4.88	0.03*	2.37	0.12	1.58	0.21	5.26	0.02*	2.52	0.15
0.01	0.92	4.67	0.03*	0.46	0.49	2.83	0.10	0.38	0.55
0.28	0.59	0.71	0.40	0.95	0.33	1.49	0.22	1.47	0.25
0.00	0.97	0.23	0.63	0.02	0.89	0.22	0.63	5.34	0.04*
0.06	0.81	1.61	0.20	1.74	0.19	0.67	0.41	0.04	0.85
0.02	0.89	0.14	0.71	0.09	0.76	0.26	0.61	1.32	0.28
0.00	0.99	0.00	0.94	0.01	0.91	0.52	0.47	1.85	0.21
3.93	0.05*	1.31	0.25	0.10	0.75	1.74	0.19	0.74	0.41
0.12	0.73	0.09	0.75	1.09	0.30	0.20	0.65	0.99	0.34
0.00	0.95	0.02	0.89	0.19	0.66	3.27	0.07	0.01	0.99
	All E F 4.88 0.01 0.28 0.00 0.06 0.02 0.00 3.93 0.12 0.00	All Eggs F p 4.88 0.03* 0.01 0.92 0.28 0.59 0.00 0.97 0.06 0.81 0.02 0.89 0.00 0.99 3.93 0.05* 0.12 0.73 0.00 0.95	All Eggs # Sp F p F 4.88 0.03* 2.37 0.01 0.92 4.67 0.28 0.59 0.71 0.00 0.97 0.23 0.06 0.81 1.61 0.02 0.89 0.14 0.00 0.99 0.00 3.93 0.05* 1.31 0.12 0.73 0.09 0.00 0.95 0.02	All Eggs# SppFpF4.880.03*2.370.120.010.924.670.03*0.280.590.710.400.000.970.230.630.060.811.610.200.020.890.140.710.000.990.000.943.930.05*1.310.250.120.730.090.750.000.950.020.89	All Eggs# SppAncyFpFp4.880.03*2.370.121.580.010.924.670.03*0.460.280.590.710.400.950.000.970.230.630.020.060.811.610.201.740.020.890.140.710.090.000.990.000.940.013.930.05*1.310.250.100.120.730.090.751.090.000.950.020.890.19	Spect All Eggs # Spp Ancylostoma F p F p F p 4.88 0.03* 2.37 0.12 1.58 0.21 0.01 0.92 4.67 0.03* 0.46 0.49 0.28 0.59 0.71 0.40 0.95 0.33 0.00 0.97 0.23 0.63 0.02 0.89 0.06 0.81 1.61 0.20 1.74 0.19 0.02 0.89 0.14 0.71 0.09 0.76 0.00 0.99 0.00 0.94 0.01 0.91 3.93 0.05* 1.31 0.25 0.10 0.75 0.12 0.73 0.09 0.75 1.09 0.30 0.00 0.95 0.02 0.89 0.19 0.66	All Eggs# SppAncylostoma SpiratFpFpFp4.88 0.03^* 2.37 0.12 1.58 0.21 5.26 0.01 0.92 4.67 0.03^* 0.46 0.49 2.83 0.28 0.59 0.71 0.40 0.95 0.33 1.49 0.00 0.97 0.23 0.63 0.02 0.89 0.22 0.06 0.81 1.61 0.20 1.74 0.19 0.67 0.02 0.89 0.14 0.71 0.09 0.76 0.26 0.00 0.99 0.00 0.94 0.01 0.91 0.52 3.93 0.05^* 1.31 0.25 0.10 0.75 1.74 0.12 0.73 0.09 0.75 1.09 0.30 0.20 0.00 0.95 0.02 0.89 0.19 0.66 3.27	All Eggs# SppAncylostoma SpirometraFpFpFp4.88 0.03^* 2.37 0.12 1.58 0.21 5.26 0.02^* 0.01 0.92 4.67 0.03^* 0.46 0.49 2.83 0.10 0.28 0.59 0.71 0.40 0.95 0.33 1.49 0.22 0.00 0.97 0.23 0.63 0.02 0.89 0.22 0.63 0.06 0.81 1.61 0.20 1.74 0.19 0.67 0.41 0.02 0.89 0.14 0.71 0.09 0.76 0.26 0.61 0.00 0.99 0.00 0.94 0.01 0.91 0.52 0.47 3.93 0.05^* 1.31 0.25 0.10 0.75 1.74 0.19 0.12 0.73 0.09 0.75 1.09 0.30 0.20 0.65 0.00 0.95 0.02 0.89 0.19 0.66 3.27 0.07	SpeciesAll Eggs# SppAncylostoma SpirometraIsospFpFpFpFp4.88 0.03^* 2.37 0.12 1.58 0.21 5.26 0.02^* 2.52 0.01 0.92 4.67 0.03^* 0.46 0.49 2.83 0.10 0.38 0.28 0.59 0.71 0.40 0.95 0.33 1.49 0.22 1.47 0.00 0.97 0.23 0.63 0.02 0.89 0.22 0.63 5.34 0.06 0.81 1.61 0.20 1.74 0.19 0.67 0.41 0.04 0.02 0.89 0.14 0.71 0.09 0.76 0.26 0.61 1.32 0.00 0.99 0.00 0.94 0.01 0.91 0.52 0.47 1.85 3.93 0.05^* 1.31 0.25 0.10 0.75 1.74 0.19 0.74 0.12 0.73 0.09 0.75 1.09 0.30 0.20 0.65 0.99 0.00 0.95 0.02 0.89 0.19 0.66 3.27 0.07 0.01

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a spurious relationship between month and species richness. There was no correlation between mean monthly parasite richness and monthly rainfall (R_P = -0.023, d.f. = 11, p = 0.95) or mean monthly prey counts (R_P = -0.161, d.f. = 11, p = 0.62).

Total egg counts were higher in higher-ranking individuals (Table 5.2), but this result was apparently strongly influenced by high *Spirometra* counts. On average, the total egg count was 9601 ± 1892 eggs per gram of feces, with 7037 \pm 1770 of those eggs identified as *Spirometra*. In addition to the effect of social rank on egg burden, there was a marginally significant effect of month and sex on egg burden.

Ancylostoma

None of the variables tested appeared to affect the intensity of *Ancylostoma* infections (Table 5.2). However, we found a significant relationship between hyena age and prevalence of infection with *Ancylostoma* (Table 5.3). Ninety percent of all individuals and 100% of juveniles were infected.

<u>Spirometra</u>

The prevalence of *Spirometra* infection was strongly affected by dispersal status (Table 5.3), with natal animals being over 4 times more likely to be infected than immigrants (Odds Ratio = 4.20). Social rank was an important determinant of the intensity of *Spirometra* infection (Table 5.2). Higher-ranking individuals had higher intensities than did lower-ranking animals (R_S = -0.36, N = 52, p = 0.01) (Figure 5.1). In addition, there was a nearly significant (p = 0.07) age by sex interaction affecting intensity. The interaction was mainly a result of

Table 5.3. Results of logistic regression on parasite prevalence data. An asterisk indicates a significant relationship.

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Variable	Spec Ancy	cies /lostoma	Spirc	ometra	lsosp	ora
	χ^2	p	x ²	p	χ^2	p
Social Rank	1.04	0.30	2.12	0.14	0.75	0.38
Month	1.35	0.24	0.00	0.96	1.81	0.17
Age	3.80	0.05*	0.28	0.59	0.28	0.59
Sex	0.00	0.93	1.17	0.27	4.91	0.02*
Dispersal Status	0.97	0.32	6.40	0.01*	0.29	0.58



Figure 5.1. Log(x + 1) transformed *Spirometra* intensity in relation to hyena social rank.

the high intensity of infections in sub-adult females (mean \pm s.e. = 3.99 ± 0.29) compared to all other age/sex classes (sub-adult males: mean = 3.33 ± 0.24 ; adult females: mean = 3.17 ± 0.22 ; adult males: mean = 3.29 ± 0.16); however, post-hoc pairwise comparisons revealed no significant differences between age/sex groups.

Isospora

Both the intensity and prevalence of *Isospora* infection were higher in females than in males (Tables 5.2 & 5.3). Female hyenas were almost 3.5 times (Odds Ratio = 3.47) more likely than males to be infected, and the mean intensity of infection was significantly higher in females than in males (female mean = 2.60 \pm 0.14; male mean = 2.05 \pm 0.05; t_{16} = 2.67, p = 0.02) (Figure 5.2).

DISCUSSION

No single independent variable was able to predict differences in susceptibility of hosts to three common parasite species. In fact, for each parasite species, different variables had high predictive value. Certainly, no single factor can be expected to account for the distribution of all parasites in the field (Price 1980). Instead, complicated interactions between host physiology and behavior, in combination with the transmission biology of the parasite, are likely to shape patterns of parasite prevalence and intensity.

Egg Counts and Species Richness

Although month of the year was related to the number of species present in samples, there was no apparent relationship between monthly egg counts and



Figure 5.2. Log(x + 1) transformed *Isospora* intensity in male and female hyenas.

either rainfall or ungulate abundance. While both of these variables should theoretically be expected to strongly affect exposure and resistance to parasites, there may be a time delay between changes in environmental variables and changes in gut fauna. In addition, the relationship between environmental variables and parasite richness may be extremely complex, and thus may not be evident in simple statistical tests.

The number of parasite eggs present in a sample was related to social rank. This result, however, was strongly influenced by the *Spirometra* data. *Spirometra* had the highest mean intensity of infection. Almost 75% of all eggs recovered from fecal samples were *Spirometra*, so the fact that social rank predicts egg intensity is largely due to the underlying relationship between *Spirometra* and social rank. Although there was a statistically significant relationship between the month by sex interaction and total egg count, there was no clear-cut pattern to the relationship.

Ancylostoma

Ancylostoma is a hookworm parasite that is extremely prevalent (90%) among Talek hyenas (Engh et al. in review). Eggs are passed in feces, and larvae usually infect their hosts by penetrating the skin and migrating to the digestive tract. Young animals are frequently infected with *Ancylostoma* when they ingest eggs passed in their mothers' milk (Bowman 1995). Severe hookworm infections can cause blood loss anemia, dermatitis, and pneumonia (Roberts & Janovy 1996). We found no good predictors of intensity of *Ancylostoma* infection. Most animals were infected, but the vast majority of

individuals maintained a low level of infection. However, prevalence of *Ancylostoma* was higher in subadults than in adults. In fact, all subadults sampled were infected. Hyena cubs spend the first 6-10 months of life living in an underground communal den and thus may be exposed to more larvae than adults; however, all hyenas frequently sleep on bare soil, and hyenas rarely defecate near the den site (pers. obs.). It therefore seems unlikely that young hyenas are exposed to the parasite more frequently than adults. Instead, sub-adult hyenas are probably more likely to be infected because they have not developed acquired immunity to the parasite. Numerous studies have attributed higher parasite prevalence in young animals to their naïve immune systems (e.g., MacDonald et al. 1999; Müller-Graf et al. 1999).

Spirometra

Spirometra, a pseudophyllidean tapeworm, was responsible for the bulk of the total egg burden carried by hyenas. Spirometra eggs are passed in the feces and hatch in water. The coracidium is eaten by copepod intermediates, which are later eaten by additional intermediate hosts (Bowman 1995). In the Serengeti ecosystem, Spirometra plerocercoids (spargana) are found in the muscles and tendons of a variety of ungulates that serve as intermediate hosts (Sachs & Sachs 1968). Hyenas presumably become infected when they ingest the muscles and viscera of infected prey animals. Although Spirometra is not particularly pathogenic, severe infections can cause vitamin B12 deficiency anemia (Bowman 1995).

To our surprise, we found that natal animals were far more likely than immigrants to be infected with *Spirometra*. Immigrant males necessarily move through multiple hyena territories during dispersal, whereas females spend the vast majority of their time within their natal territory (Boydston et al. 2001); therefore we expected that immigrant males would be more likely to be exposed each parasite species. Additionally, immigrant males invariably have low social status and thus experience poor priority of access to food (Tilson & Hamilton 1984). Presumably, poor access to food should inhibit immune function and result in a higher likelihood of becoming infected when exposed to parasites. Due to this presumed combination of greater exposure and lower resistance. we expected that if any relationship between dispersal status and prevalence of a parasite were to exist, infection would be more prevalent in immigrants. Instead, infection was less likely in immigrants. The explanation here may be derived from concurrent consideration of both hyena behavioral ecology and the transmission biology of Spirometra. Social rank determines a hyena's priority of access to food (Tilson & Hamilton 1984). Since immigrant males hold low ranks, they tend to spend less time feeding on meat, and more time feeding on skin and bones than do females (Heschel & Skinner 1987, 1990). As a result, immigrant males may be exposed to fewer Spirometra spargana than are higher-ranking natal animals.

Alternatively, it may be that *Spirometra* is locally adapted to particular clans of hyenas (e.g., Lively & Dybdahl 2000). If this were true, then immigrant males who do not share the most common genotypes in their new clans might be less susceptible to parasitic infection. This, however, seems unlikely, because

natal hyenas within a single clan have low average relatedness values, and there appears to be little genetic distinction between clans (RC Van Horn, unpublished data). Another possible explanation for this pattern is that the males that successfully immigrate have superior abilities to fend off parasitic infection. Since female hyenas rarely mate with natal males (Engh et al. 2002), if this second hypothesis were correct, then sexual selection could be acting to favor immunologically-superior males. It is possible that vitamin B12 deficiency anemia from *Spirometra* combined with a lack of fresh meat in the diet of dispersing males forces infected males to abandon attempts at dispersal.

The idea that natal animals have a higher *Spirometra* prevalence as a result of greater exposure at ungulate kills fits nicely with the intensity data. We observed a correlation between intensity of *Spirometra* infection and social rank, with higher-ranking individuals tending to have worse infections. This makes intuitive sense because higher-ranking animals eat larger quantities of fresh meat than lower-ranking conspecifics, and they also tend to have better access to viscera and muscle tissue. Hausfater and Watson (1976) found a similar relationship between high rank and high parasite load in male baboons (but see Müller-Graf et al. 1996). Although Hausfater and Watson (1976) could not identify the source of variation among baboons, they speculated that it was due to rank-based differences in feeding behavior.

Sub-adult female hyenas tended to have more intense *Spirometra* infections than any other age/sex class. Sub-adults, in general, may be less resistant to *Spirometra* than are adults. Müller-Graf et al. (1999) examined

Spirometra infections in lions and found the highest intensity of infection in unweaned cubs, suggesting that sub-adults may be more susceptible to infection by this parasite than are adults. A key physiological difference between sub-adult male and female hyenas is that young females have higher levels of circulating androstenedione, a weak androgen, than do sub-adult males (Lindeque et al. 1986; Glickman et al. 1992). This contrasts sharply with the pattern observed in most mammals, in which males have higher androgen levels than do females. Androgens have been implicated as immunosuppressants, and in numerous studies, the higher parasite burdens observed in male animals have been linked to higher androgen levels (Alexander & Stimson 1988; Poulin 1996). Thus, a combination of poor resistance and androgen-mediated immunosuppression may lead to exceptionally intense *Spirometra* infections in young female hyenas. Isospora

Isospora is a coccidian protozoan that can denude gut mucosa, cause bloody diarrhea, and be life-threatening, particularly when exacerbated by stress (Roberts & Janovy 1996). The parasite is usually directly transmitted from fecal contamination, but some forms of *Isospora* have paratenic hosts (Bowman 1995).

Female hyenas were both more likely to have *lsospora*, and have higher loads of *lsospora*, than were males. Again, differences in feeding ecology may explain this pattern. Hyenas rarely feed on fecal matter, but while they are feeding on viscera, particularly the nutrient-rich liver and spleen, they are likely to ingest some intestinal contents of their prey. As a result, they may be infected

from direct exposure to oocysts in their prey's feces or by ingesting sporozoites encysted in paratenic hosts. Because female hyenas are higher-ranking than males, they tend to have access to the muscles and viscera of their prey more often than do males (Henschel & Skinner 1987). Alternatively, physiological differences between males and females may result in differential resistance to *Isospora.* The energetic stress of maintaining pregnancy and lactation, and the relatively high androstenedione levels of female hyenas compared to males (Glickman et al. 1992) may make female hyenas particularly susceptible to parasite infections. Certainly, high androgen levels among males have been linked to higher levels of parasitic infection in males than in females of numerous species (Klein 2000), and future studies combining the hormone levels and parasite loads of individual hyenas may provide further evidence of androgeninduced immunosuppression.

Implications

There is some debate about how well fecal egg counts represent actual levels of parasitic infection (Keymer & Hiorns 1986; Uhlinger 1993). The number of eggs shed by parasites can be influenced by hormonal cycles (Hausfater & Watson 1976), parasite density (Anderson & Schad 1985), or rates of feeding (Keymer & Hiorns 1986). We were unable to verify whether the egg counts we recorded here were accurate indicators of actual parasite loads in hyenas, but evidence from other species suggests that fecal egg counts are correlated with intestinal parasite load (Roberts & Swan 1981; Sithithaworn et al. 1991).

The results of this study suggest a strong role for social behavior in understanding the epidemiology of parasitic infections. The prevalence and intensity of *Spirometra* infections were overwhelmingly influenced by dispersal status and social rank, two social variables that have a huge impact on the diet of an individual hyena. In addition, sex- and rank-related differences in feeding behavior may also account for differences in *Isospora* infections between males and females. While many studies examine parasitism in the wild, they rarely take into account the impact of social behavior on individual susceptibility. This study suggests that there is a strong link between social behavior and parasite epidemiology.

APPENDICES

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APPENDIX A

Table A.1. Characteristics of microsatellite repeats used to assess paternity in spotted hyenas.

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Locus	No. Alleles	Allele Range	Repeat Size	Heterozygosity
CCR01	4	191-199	2	0.365
CCR04	7	123-149	2	0.660
CCR05	5	145-153	2	0.675
CCR07	8	179-195	2	0.480
CCR11	2	142-146	4	0.505
CCR12	4	143-149	2	0.727
CCR13	4	95-101	2	0.702
CCR14	6	179-189	2	0.796
CCR16	2	176-178	2	0.429
CCR17	7	140-156	2	0.789
CCRA3*	6	151-166	3	0.919

*CCRA3 is sex-linked

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tellite	CCR0	1 CCR0	4 CCR0	5 CCR01	7 CCR1	1 CCR1	2 CCR13	3 CCR14	CCR1	5 CCR16	6 CCR1	CCRA3
	94	94	94	94	94	94	94	94	94	94	94	94
	120	120	120	120	120	120	120	120	120	120	120	120
	-	-	-	-	.	-	-	←	-	-	-	-
	94	94	94	94	94	94	94	94	94	94	94	94
	60	60	45	60	60	45	45	45	45	60	45	45
	50	56	62	56	50	2	58	50	50	58	50	58
	60	60	45	09	60	45	45	45	45	09	45	45
	68	68		68	68					68		
	60	60		60	60					60		
	30	30	7	30	30	2	2	7	2	30	7	7
			94			94	94	94	94		94	94
			45			45	45	45	45		45	45
			62			54	58	50	50		50	58
			45			45	45	45	45		45	45
			68			68	68	68	68		68	68
			5 2			S	Ŋ	5	5		Ŋ	5
			35			35	35	35	35		35	35
	12	12	12	12	12	12	12	12	12	12	12	12

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Microsatellite	CCR01	CCR04	CCR05	CCR07	CCR11	CCR12	CCR13	CCR14	CCR15	5 CCR16	CCR17	CCRA 3
Buffer	2.5	0	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Low Mg buffer	0	2.5	0	0	0	0	0	0	0	0	0	0
Mg	0	-	0	0	0	0	0	0	0	0	0	0
dNTP	2.5	1.25	1.25	2.5	2.5	1.25	1.875	2.5	2.5	1.25	1.25	2.5
Primer	2.5	2.5	2.5	2.5	2.0	0.75	1.0	2.0	2.0	0.75	0.75	0.5
Taq polymerase	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
H ₂ O	12.1	12.35	13.35	12.1	12.6	15.1	14.225	12.6	12.6	15.1	15.1	12.1
20 ng/µl DNA	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0

APPENDIX B

Analysis of fecal samples

From June, 1999 to July, 2000, we collected 207 fresh fecal samples from 70 hyenas residing in a single social group in the Masai Mara National Reserve, Kenya. Individual hyenas were recognized from their unique patterns of spots and other physical characteristics, such as ear notches. All samples were collected from individuals observed defecating. We used liquid displacement to measure ½ ml of fecal matter into 7 ml of Sheather's sugar water solution (Zajac 1994). The mixture was homogenized and centrifuged for 5 minutes at 7200 rpm, then supernatant was transferred to a McMaster slide. All eggs and oocytes observed within the gridlines were identified and the number of eggs per gram was recorded. Because we analyzed eggs and oocytes rather than whole worms, we were able to identify most parasites only to genus. In order to avoid pseudoreplication in analyses of prevalence and intensity of infection, only a single, randomly chosen sample from each individual was used.

Nine parasite taxa were identified in the 70 fecal samples (Table B.1), including 1 spurious species (*Nematodirus* sp.). In 135 additional samples from the same individuals, 2 more species, *Trichuris* sp. and *Moniezia* sp. were identified. Like *Nematodirus* sp., *Moniezia* sp. was probably spurious; that is, it was a parasite of the hyenas' prey rather than of the hyenas. Neither spurious species was included in measures of parasite richness. All 70 individuals were positive for at least one species of parasite. On average, each individual was

infected with 2.60 \pm 0.13 species (range: 1-5). Intensity of infection was overdispersed (variance > mean) for most parasite taxa, so median levels of infection are displayed in Table B.1.

Hookworms (*Ancylostoma* sp.) were the most common parasite, with 90% of individuals infected. Graber and Blanc (1979) reported infections of *Ancylostoma duodenale* in Ethiopian hyenas, and the eggs found in the current study were consistent with their description. The spirurid eggs measured approximately $36 \times 12 \mu m$ and were very likely *Spirocerca lupi*. *S. lupi* is frequently found in Kenyan dogs, but it was not observed in any of 3 hyenas dissected by Brodey et al. (1977). We also found eggs of *Toxocara* sp. Although *Toxocara canis* has been identified in hyenas by previous researchers (Baylis 1937), the dimensions of the eggs observed in the current study ($62 \times 60 \mu m$) more closely resembled those of *Toxocara cati*.

Spirometra sp. eggs were extremely common (74.3% of individuals infected) and had the highest median intensity of infection. These eggs were probably *Spirometra pretoriensis*, which Nelson et al. (1965) and Graber and Blanc (1979) found in hyenas. Pleurocercoids (spargana) of *Spirometra* are relatively common in the hock joints and flesh of several ungulate species that hyenas feed upon (Sachs & Sachs 1968), and *Spirometra* sp. was the most prevalent parasite in a survey of lion feces in the Tanzania (Müller-Graf 1995). Several other types of cestode eggs were also identified. We found numerous taeniid eggs, which could be *Taenia crocutae*, *T. hyaenae*, or *Echinococcus granulosus*, all of which have been reported in hyenas (Mettrick & Beverley-

Burton 1961; Nelson et al. 1965). In addition, we found eggs of *Mesocestoides* sp., which have not previously been recorded in hyenas but are known to infect other African carnivores, including lions (*Panthera leo*), servals (*Felis serval*), and carcals (*Felis caracal*) (Round 1968). In some samples, we found eggs of *Dipylidium* sp., a common parasite of Kenyan dogs (*Canis familiaris*) and jackals (*Canis mesomelas*) (Nelson et al. 1965), which was previously reported in hyenas (Round 1968).

A single protozoan, *Isospora* sp. was observed. The size of the oocysts $(35 \times 26 \ \mu\text{m})$ was intermediate between that of *Isospora felis* and *I. leonina*, two species that have been recorded in African lions but not in hyenas (Patnaik & Acharjyo 1970; Bjork et al. 2000). The paucity of protozoan species recovered in this study may have been a result of the concentration method used. Protozoans tend to become distorted and desiccated in saturated sugar and salt solutions (Zajac 1994). Finally, 2.9% of samples contained unidentified parasites.

Parasite	Prevalence (%)	Median Intensity (e.p.g.)	Maximum Intensity (e.p.g.)	Variance/Mean Ratio of Abundance
Ancylostoma sp.	90.0	1000	17600	0.44
Spirometra sp.	74.3	3000	67200	1.07
<i>lsospor</i> a sp.	25.7	200	4000	1.91
<i>Dipylidium</i> sp.	21.4	300	1200	2.00
Spirurida	15.7	200	300	1.90
Taeniidae	12.9	200	3400	2.36
Mesocestoides sp.	11.4	200	500	2.11
<i>Toxocara</i> sp.	5.7	200	1600	2.44
Nematodirus sp.	4.3	200	300	2.30
Unknown	2.9	150	200	-
<i>Trichuri</i> s sp.*	0	0	0	-
<i>Moneizia</i> sp.*	0	0	0	-

Table B.1. Prevalence and intensity (eggs per gram of feces) of parasite eggs and oocytes in the feces of 70 wild spotted hyenas.

**Trichuris* sp. and *Moniezia* sp. were observed in additional samples from the same individuals.

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