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SHAPING PATTERNS OF COOPERATION
AMONG SPOTTED HYENAS

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JENNIFER ELAINE SMITH

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# EVOLUTIONARY AND ECOLOGICAL FORCES SHAPING PATTERNS OF COOPERATION AMONG SPOTTED HYENAS

By

Jennifer Elaine Smith

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# ABSTRACT

## EVOLUTIONARY AND ECOLOGICAL FORCES SHAPING PATTERNS OF COOPERATION AMONG SPOTTED HYENAS

By

Jennifer Elaine Smith

The evolution of cooperation is a central problem in biology, but the current body of theory often fails to explain complex patterns found in nature. Biological market theory extends traditional paradigms by predicting that the relative values of social partners depend upon the current state of the marketplace. My dissertation tested this prediction using data from a long-term study (1988-present) of spotted hyenas (*Crocuta crocuta*) in Kenya. These carnivores live in fission–fusion societies, called clans, which contain up to 80 members. Dominance hierarchies structure clans, and all adult females are dominant to all immigrant males. Although all clan members defend a common territory, individuals make active decisions to leave (fission) and to join (fusion) subgroups of individuals within the clan. This flexible social structure, together with rank-related variation in partner value, offers an excellent system in which to test biological market theory. First, I tested the theoretical prediction that social and ecological circumstances influence fission-fusion dynamics in the spotted hyena. Whereas cooperative defense of shared resources during inter-clan competition and conflicts with lions promoted social cohesion, feeding competition was a strongly disruptive force that enhanced the tendency for hyenas to separate temporarily from group members. Second, market theory predicts that, when social partners vary in their relative value, individuals should favor partners of the highest value. As predicted, high-ranking adult females were most gregarious, and choosy subordinate females gained the most social and feeding tolerance, but not coalitionary support, from dominants. Third, I evaluated the evolutionary forces favoring intragroup coalitions among adult female spotted hyenas. I found evidence that adult females benefited indirectly via kin selection and directly by reinforcing the status quo, but not from reciprocal altruism. Fourth, I found that greeting ceremonies occurring outside of agonistic contexts represent honest signals of long-term social bond strength and that the act of greeting immediately promotes coalition formation among adult females. Overall, these results elucidate the market forces shaping the dynamics of cooperation and competition among spotted hyenas, and broaden our understanding of the rules governing social decision-making among gregarious animals.

# ACKNOWLEDGEMENTS

My doctoral research is the product of a long journey, full of twists and turns, much of which started before I ever set foot on the Michigan State University (MSU) campus. Growing-up in the small town of Cushing, Maine, my interest in biology stemmed from my early introduction to coastal marine life by my high school biology teacher, Phil Marcoux. Phil has since passed away, but his fascinating introduction to the thrill of making scientific discoveries has provided me with the strong foundation from which I still draw from today. In my early years, my parents and my sister, Christian, encouraged my passion for animals, always inspiring me to do my best while accepting me for who I am. To this day, my family continues to offer me a strong support network from which to grow and to challenge myself. For this, I cannot thank them enough.

As an undergraduate at Colby College in Maine, I left North America for the first time in my life. Under the amazing instruction of Russ Cole, I went to the British West Indies to study the behavior of land hermit crabs. I was shocked to learn that these animals were nocturnal and spent most of their time residing in the local chicken-coop, but was even more amazed to learn that people actually made a career out of studying the behavioral ecology of wild animals in remote locations. Thanks to Russ, I have been hooked on this type of research experience ever since. Upon completing his course, I immediately secured scholarship support to spend my entire junior year abroad in Australia and in Kenya. After pursuing a variety of internships, I then went on to pursue my

Master's at the University of Illinois at Urbana-Champaign (UIUC) with George Batzli. George took me under his wing and graciously introduced me to the art of scientific design and writing. I continue to implement George's sound guidance when I challenge myself to improve my writing. It was also at UIUC where I first met, Chris Strelioff. Chris has offered me his steady support and encouragement throughout my doctoral degree; albeit from across the ocean and across state lines during different stages of our relationship. I appreciate all of the sacrifices he has made for me. For his patience, insights, and kindness, I will forever be thankful to have him at my side.

After having spent a semester in Kenya as an undergraduate, I had always hoped to return, but I had never dreamed that I would one day have the unique experience of living in the bush for a year to pursue doctoral research on spotted hyenas, one of the most bizarre and fascinating species in existence. For this amazing opportunity and for all of her support at the many stages of my doctoral research, I thank Kay Holekamp. Kay is truly an outstanding advisor, passionate scientist and phenomenal female role model. She brings unparalleled aptitude and scholarly enthusiasm for learning to her research program and generously shares her insights with her students. For these reasons, and many more for which I lack the space to adequately enumerate, Kay has been truly an outstanding mentor. Although her life is surely a juggling act, Kay handles all of these responsibilities and competing demands marvelously, and always makes time to help me achieve my professional goals. I thank her for our countless meetings, her careful answers to my billions and the billions of emails, and her thoughtful guidance throughout every stage of this degree process. Kay's firm, yet encouraging, mentoring style continuously challenges me to strive for excellence in all of my pursuits. Kay is unquestionably one of the most intellectually curious and generous people that I have ever met. I thank her for giving me the opportunity to be her student, and to learn from her incredible example. As I develop into an independent scientist, I look forward to becoming her colleague and will always strive to similarly impact the lives of my own students in the future in the way she has impacted mine.

My other committee members, Laura Smale, Tom Getty and Andrew McAdam, have also generously offered me their support and insights at every critical stage of my doctoral program. Without their encouragement and wisdom, this dissertation would surely be a different product. Laura Smale, along with Kay, was responsible for devising the general observational protocols employed here and for collecting much of the long-term data examined here. Due to her first-hand knowledge of hyena biology, Laura has been an excellent resource, providing me with interesting insights with respect to patterns of coalition formation and sex differences in these animals. Tom Getty has also been an outstanding mentor. As his student, and then later as his teaching assistant, in his Behavioral Ecology course, Tom opened-up a new world for me and continuously challenged me to effectively communicate difficult concepts to my students and colleagues. Tom's rich understanding of the theoretical underpinnings of behavioral ecology has provided me with a fruitful foundation. I can only hope to emulate these qualities in my own mentoring of student research in the future. Andrew's support and insights have also been extraordinary. During the tenure of this dissertation, the distances between our offices have ranged from being separated by a single wall to being separated by an international border. Despite that fact that he currently resides at the University of Guelph in Canada, Andrew's enthusiasm for science remains clear and his insights continue to be instrumental in shaping my view of evolutionary ecology. Finally, although Richard Hill is not a member of my dissertation committee, I thank him for training me to educate the next generation of undergraduates. It has been an honor to assist him in his courses, and I thank him for taking the time to make personal connections with his students at this large university. His lessons on Thomas Kuhn's scientific revolutions and Charles Darwin's pluralism have deeply shaped my research and teaching philosophies.

The Holekamp lab is a large, constantly changing body of motivated individuals who have collectively offered me many insights along the way. During my six years at MSU, I have had the opportunity to share a lab with Sarah Benson-Amram, Pat Bills, Andy Booms, Katy Califf, Leslie Curren, Ben Dantzer, Andy Flies, Suzanne La Croix, Joe Kolowski, Eva-Maria Muecke, Wiline Pangle, Kate Shaw, Greg Stricker, Eli Swanson, Jaime Tanner, Kevin Theis, Ryan Taylor, Russ Van Horn, Page Van Meter, Aaron Wagner, Sofi Wahaj, and Heather Watts. I have learned a lot from these folks and thank them for their guidance along the way. In particular, the research of Anne Engh and Sofi Wahaj inspired much of my doctoral work. Although Anne and I never overlapped here on campus, I thank both of these women for their tremendous intellectual contributions and for bringing so many fascinating questions to the forefront.

In Kenya, Jaime Tanner was an excellent resource. She introduced me to the Mara Hyena Project, trained me on all of relevant hyena protocols, and was amazingly helpful in identifying all of the hyenas. I also thank Joe Kolowski and Sofi Wahaj for inviting me to join them at Mara Intrepids Lodge to enjoy some of life's creature comforts amidst the African savannah. I thank John Keshe and Moses Nairori for making me feel at home while living in the African bush. In particular, I thank Moses for chasing baboons away from my tent and always greeting me with a smile regardless of how flooded our driveway became during the rainy season. I thank John for sharing my love of cooking and for encouraging me to pursue my research on cooperation, even though I thought for sure at the time that we already knew everything there was to know about coalition formation among spotted hyenas. Boy was I wrong!

In addition to the Holekamp lab members mentioned above, many additional people participated in the collection and analysis of the data presented in this dissertation. Pat Bills has been outstanding in helping me to extract and organize data from the field notes. Importantly, two of my dissertation chapters were in collaboration with Joe Kolowski and Russ Van Horn. For Chapter 2, Joe tirelessly spent many continuous hours during the day and night collecting the 24-hour follow data. For Chapter 4, Russ diligently conducted many genetic analyses used to assign the paternal relationships among adult females. Importantly, Dr. Kim T. Scribner was critical in assisting Russ to identify these microsatellite markers. Also for Chapter 4, Pat Bills, Page Van Meter, and Michelle Fisher were instrumental in helping me to update and maintain the aggression table. Laura Sams and Wiline Pangle were extremely helpful in timing the duration of many of the greetings presented in Chapter 5. Due to their outstanding contributions, the following undergraduates have co-authored the research presented here: Alison Cole, Steph Dawes, Jill Estrada, Katie Graham, Adrienne Hopper, Sandra Memenis, Katie Powning, and Stacey Piotrowski. Heather Richards and Kari Mitsos continue to be immensely helpful in two ongoing projects that are not included in this dissertation.

I am also very grateful to Han de Vries, Vincent Carey, Julian Faraway, Charlotte Hemelrijk, Andrew McAdam, Brian McGill, Wei Pan, Chris Strelioff, and Jun Yan for helping me to implement statistical models. Along with my committee members, Peter Henzi, Wiline Pangle, Robert Seyfarth, Gabrielle Ramos-Fernandez, and multiple anonymous reviewers provided comments that greatly improved the overall quality of the published portions of this dissertation.

Many people have offered me friendship during my time at MSU. Although I will refrain from listing them all, I would like to thank Katie Wharton Boes, Carrie DeJaco, Shana Dumont, Carrie Kissman, Wiline Pangle, Amelia Kantrovitz, and Anita Stone for their continued support despite my strange obsessions with scholarly pursuits and my constant inability to answer the phone. I also thank all of my office mates for their encouragement over the years and for respecting my silence "when the headphones go on" (my version of the thinking cap). In particular, Wiline warmly welcomed me when I first arrived to MSU and continues

to offer me advice and friendship when I have needed it most. Without the collective humor, support and words of wisdom from these friends and others, surely none of this research would have been possible.

Finally, I thank the Office of the President of Kenya, the Kenya Wildlife Service, the Kenyan Ministry for Science Education and Technology, the Narok County Council, and the Senior Warden of the Masai Mara National Reserve for giving me permission to live and conduct research in Kenya. Because my research relied upon the long-term data set, this work was made possible by National Science Foundation grants awarded to Kay Holekamp (BNS8706939, BNS9021461, IBN9309805, IBN9606939, IBN9630667, IBN9906445, IBN0113170, IBN0343381, IOB0618022, and IOS-0819437). My research was also supported by grants from the P.E.O. International Sisterhood and the American Society of Mammalogists. I also thank MSU for their generous support during all phases of my dissertation work. The College of Natural Science awarded me Recruiting, Graduate Summer Research, Dissertation Completion, and Barnett Rosenberg Fellowships. I received the University Enrichment, Research Enhancement, and Travel Fellowships from the Graduate School. The Department of Zoology provided me with a John R. Shaver Award and Research Grants. I also received fellowships from the Quantitative Biology Initiative and the Program in Ecology, Evolutionary Biology, and Behavior. Without this financial support, none of this research would have been possible.

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# Chapter 1

# GENERAL INTRODUCTION

Understanding the evolution of sociality in general, and cooperation in particular, is a central problem in biology, with a rich history tracing back to Charles Darwin (reviewed by Clutton-Brock, 2009; Dugatkin, 2002; Noë, 2006; Nowak, 2006; Pennisi, 2005; Queller, 1985; Sachs et al., 2004; West et al., 2007a; West et al., 2007b). The traditional approach to studying the evolution of social behavior is to recognize that, although gregarious animals often gain fitness benefits from living in groups, sociality can be costly when group members compete for access to the resources necessary for survival and reproduction (Alexander, 1974; Ridley et al., 2005; Silk, 2007a; Sterck et al., 1997b; Vehrencamp, 1983). Thus, most empirical workers employ a cost-benefit approach, testing optimization theory, to evaluate the extent to which individuals make decisions that minimize the costs of group life and maximize its benefits.

Biological market theory, like traditional optimization theory, predicts that the benefits of cooperative partnerships should outweigh the costs (Noë and Hammerstein, 1994; Noë and Hammerstein, 1995; Noë et al., 1991). However, it further predicts that the relative values of partnerships depend upon the current state of the biological marketplace. Within this framework, the cooperative decisions that individuals make are expected to vary dynamically in response to local variation in social and ecological conditions. Specifically, market theory accounts for partner switching by extending two-player games to include multiple players. Within this paradigm, natural selection is expected to favor those individuals best able to track changes in their environments, and to make adaptive decisions based on their immediate circumstances.

Market forces should be of particular importance in those societies in which the immediate number and quality of available social partners is constantly in flux (Noë and Hammerstein, 1994). Such circumstances are prevalent in societies structured by fission-fusion dynamics (Aureli et al., 2008); members of these societies are continuously faced with decisions regarding whether to separate from (fission) or join (fusion) conspecifics who are members of their permanent social group, but who are usually present in small subgroups (Kummer, 1971; Wittemyer et al., 2005). As a result, although all group members recognize each other and belong to a single overarching social unit, all group members are rarely, if ever, concurrently together. Instead, individuals are distributed across the landscape within temporary subgroups that may change size and composition on an hour-to-hour basis.

This flexible lifestyle theoretically permits individuals to separate temporarily from one another when the costs of grouping are high and to aggregate when the costs of grouping are low or the benefits of sociality are high (Aureli et al., 2008; Chapman et al., 1995; Schino, 2000; Wrangham et al., 1993). Although this societal structure permits individuals to reduce conflicts of interest by temporarily separating from group members, it simultaneously imposes a unique set of challenges on group members who are regularly subject to prolonged separation (Aureli et al., 2008). As a result, individuals living in these continuously changing social environments must cope with uncertain social relationships at reunions (Barrett et al., 2003).

### *Why study biological market theory in spotted hyenas?*

My dissertation tests several predictions derived from market theory, primarily using data from a long-term study initiated in 1988 on a single, large social group of spotted hyenas (*Crocuta crocuta*) that defend a common territory in the Masai Mara Reserve in Kenya, East Africa. Spotted hyenas live in fission-fusion societies structured by dominance hierarchies in which group members vary dramatically in their value as social partners, and they are subject to extreme seasonal variation in local resource availability. Therefore, these animals offer an excellent system in which to test predictions of biological market theory. The longitudinal data available here provide a unique opportunity to investigate the dynamical nature of social relationships among a natural population of known individuals.

### *Why focus on adult female spotted hyenas?*

My dissertation research focuses mainly on explaining how evolutionary and ecological forces favor patterns of cooperation among adult female spotted hyenas. I focused on adult females in particular because these animals are philopatric (Smale et al., 1997), highly gregarious (Holekamp et al., 1997a; Smith et al., 2007), long-lived (up to 19 years in the wild, Drea and Frank, 2003), and demonstrate many of the same cognitive abilities as monkeys (Holekamp et al., 2007), permitting them to remember earlier interactions. Further, adult females are the most powerful animals in these female-dominated societies (Frank, 1986), and they use an extraordinarily bizarre, fully erectile penile clitoris to update relationship status at subgroup reunions (East et al., 1993; Kruuk, 1972).

### *Social lives of spotted hyenas resemble those of monkeys*

Interestingly, the hierarchical structure and size of spotted hyena societies, called clans, are more similar to those characteristics of troops of cercopithecine monkeys than to those characterizing groups of other social carnivores (reviewed by Drea and Frank, 2003; Holekamp et al., 2007). Although most social carnivores live in kin groups, hyena clans are multigenerational groups that usually contain up to 80 members, many of whom are unrelated to one another. Spotted hyena clans contain multiple matrilines of adult females and their offspring, as well as multiple adult immigrant males born elsewhere (Kruuk, 1972). Like most troops of monkeys (reviewed by Gouzoules and Gouzoules, 1987; Silk, 1987), each hyena clan is structured by a linear dominance hierarchy (Frank, 1986; Kruuk, 1972). As are many monkey societies (e.g. Bercovitch, 1988; Seyfarth and Cheney, 1984; Silk et al., 2004; Widdig et al., 2000), coalition formation plays an important role in the acquisition and maintenance of rank positions within this hierarchy (Engh et al., 2000; Holekamp and Smale, 1991; Smale et al., 1995). Further, the social rank of each hyena in the clan determines its priority of access to food and other resources (Frank, 1986; Tilson and Hamilton, 1984).

As is true in many cercopithecine primates (e.g. Bergman et al., 2003; Cheney and Seyfarth, 1982; Dasser, 1988), spotted hyenas recognize their group mates as unique individuals (Holekamp et al., 1999a), and they also recognize third-party kin and rank relationships among their clan mates (Engh et al., 2005). Moreover, like monkeys (reviewed by Silk, 2002; Widdig, 2007), spotted hyenas discriminate among potential social partners on the basis of maternal and paternal kinship, and associate most often with their close kin (Holekamp et al., 1997a; Van Horn et al., 2004b; Wahaj et al., 2004). Finally, as do many species of monkeys, spotted hyenas engage in intimate and risky behavioral interactions, called greetings, in which individuals inspect the genitalia of their social partners (East et al., 1993; Kruuk, 1972).

These similarities present a unique opportunity to compare the evolutionary forces shaping the societies of primates and carnivores, taxonomic groups that last shared a common ancestor 90-100 MYA (Springer et al., 2003; Springer et al., 2005). The convergent evolution in the social behavior of these animals will allow me to test the generalizability of current socioecological models. Although most of these models were originally proposed to explain social behavior in primates, they should theoretically also explain the social behavior of non-primates. Therefore, by testing their predictions in this model social carnivore, the broad goal of my dissertation research is to evaluate the widespread utility of current theoretical explanations for the evolution of sociality in general, and cooperation in particular.

### *Important differences between spotted hyenas and monkeys*

Despite all of the similarities outlined above, several key differences exist between the social lives of spotted hyenas and those of cercopithecine primates. First, unlike monkeys, which often live in highly cohesive groups, spotted hyena clans are fission fusion societies in which individuals make active decisions to leave (fission) and to join (fusion) subgroups of clan mates forming within the larger social unit. Individual members travel, rest, and forage in subgroups that change membership roughly every hour (Kruuk, 1972; Mills, 1990). Second, although monkeys feed mainly on fruits and vegetable matter (e.g. Chapman and Pavelka, 2005; Wrangham et al., 1998), spotted hyenas prey upon ungulates that they mainly hunt themselves (Cooper, 1990; Holekamp et al., 1997b; Höner et al., 2002; Kruuk, 1972; Mills, 1990). Because ungulate carcasses are both energetically rich and highly ephemeral, feeding competition is extremely intense among hyenas (Frank, 1986; Kruuk, 1972). Third, in contrast to the status of relationships in most mammals, all adult female hyenas are socially dominant to all adult immigrant males (Kruuk 1972; Frank 1986). Moreover, the reproductive anatomy of hyenas is unique in that adult females possess a fully erectile clitoris (Frank, 1983; Matthews, 1939; Neaves et al., 1980). Females urinate, copulate, and give birth through this “pseudo-penis” and the erect phallus plays a prominent role during reunion displays, called greeting ceremonies (East et al., 1993; Kruuk, 1972).

### *Overview of the chapters*

Here I outline the rationale and major findings of the four data chapters in this dissertation. In Chapter 2, I tested hypotheses to identify the social and ecological determinants shaping fission-fusion dynamics in spotted hyenas. In particular, I tested the theoretical prediction that individuals living in fission-fusion societies, in which group members frequently change subgroups, should modify grouping patterns in response to varying social and environmental conditions. I provide the first detailed description of fission-fusion dynamics available for this species. Then, because social and ecological circumstances can influence the cohesiveness of animal societies, I evaluated the extent to which specific circumstances promote the formation of hyena subgroups of various sizes. I found that cooperative defense of shared resources during interclan competition and protection from lions were cohesive forces that promoted formation of large subgroups. Finally, I tested multiple hypotheses, each of which suggests factors that might limit subgroup size. I found evidence for all three hypotheses, which are not mutually exclusive. First, as predicted by the infant safety hypothesis (Otali and Gilchrist, 2006), mothers with small cubs avoided conspecifics, thereby reducing risk of infanticide. Second, as predicted by the dispersive conflict resolution hypothesis (Schino, 2000), victims of aggression either reconciled fights or separated from former opponents to reduce the immediate costs of escalated aggression in the absence of food. Most importantly, however, as predicted by the ecological constraints hypothesis (Chapman et al., 1995), hyenas adjusted their grouping patterns over both short and long time scales in response to feeding competition. Spotted hyenas were most gregarious during periods of abundant prey, joined clanmates at ephemeral kills in numbers that correlated with the energetic value of the prey and gained the most energy when foraging alone because kills made during cooperative hunts attracted numerous competitors. Overall, these findings indicate that whereas intergroup competition promotes group augmentation, intense intragroup competition over limited resources constrains grouping in this species. These findings were published in

*Animal Behavior* (Smith et al., 2008).

In Chapter 3, I investigated how social rank influences individual differences with respect to the fission-fusion dynamics documented in Chapter 2. In particular, I studied rank-related partner choice by testing hypotheses suggesting the benefits of mutual partner choice among unrelated adult females. This study revealed that adult females actively join subgroups containing preferred social partners, and that market forces shape the decision-making process regarding whether or not to join a particular subgroup. Because patterns of association among spotted hyenas reflect social preferences, I calculated association indices (AIs, Cairns and Schwager, 1987) to assess the effects of social rank on intrasexual partner choice among unrelated adults. Among adult females, the highest-ranking individuals were generally most gregarious; females associated most often with dominant and adjacent-ranking females. Females joined subgroups based on the presence of particular conspecifics such that subordinates joined focal females at higher rates than did dominants. Dominants benefit from associations with subordinates by enjoying priority of access to resources obtained and defended by multiple group members, but the benefits of these associations to subordinates were previously unknown. To investigate this, I tested three hypotheses suggesting how subordinates might benefit from rank-related partner choice among unrelated females. Subordinates who initiated group formation benefited by gaining social and feeding tolerance from dominants. However, the extent to which females associated failed to predict the hourly rates at which the dominant member of the dyad intervened during ongoing fights to provide coalitionary support to the subordinate member of each dyad. Overall, my data resemble those documenting patterns of association among cercopithecine primates. I consider our results in light of optimal reproductive skew theory (Clutton-Brock, 1998; Hamilton, 2000; Reeve et al., 1998), Seyfarth's rank attractiveness model (1977), and biological market theory (Noë, 2001; Noë and Hammerstein, 1995). These data are more consistent with the predictions of Seyfarth's model and of biological market theory than with those of skew theory. This research was published in *Behavioral Ecology and Sociobiology* (Smith et al., 2007).

Because market forces failed to explain patterns of coalitionary support among unrelated adult females in Chapter 3, I then initiated Chapter 4 to elucidate the evolutionary forces that are acting to favor coalitionary interventions among adult female spotted hyenas. First, I performed a comprehensive literature review of 49 vertebrate species to test Harcourt's (1992) hypothesis that intragroup coalitions formed by primates differ systematically from those formed by non-primates. However, I found that patterns of intragroup coalition formation are in fact remarkably similar between primates and non-primates. Then, I tested hypotheses suggesting kin selection (Hamilton, 1964), reciprocal altruism (Trivers 1971), and direct benefits (also called by-product mutualisms, Brown, 1983; Connor, 1995; West-Eberhard, 1975) as adaptive explanations for coalitionary interventions among adult female spotted hyenas. As predicted by kin selection theory, female hyenas supported close kin most often, and the density (connectedness) of cooperation networks increased with genetic relatedness. Nevertheless, kinship failed to protect females from coalitionary attacks. I found no evidence of enduring alliances based on reciprocal support among unrelated adult females. Instead, donors generally minimized costs to themselves, intervening most often during low-intensity fights and when feeding opportunities were unavailable. Females also gained direct benefits by directing coalitionary attacks toward subordinates. Finally, females monitored the number of dominant bystanders present in the "audience" at fights, and modified their level of cooperation based on this knowledge. Overall, hyenas made flexible decisions regarding whether or not to intervene in fights, modifying their tendency to cooperate based on multiple types of information about their immediate social and ecological environments. Taken together, these findings indicate that the combined evolutionary forces of kin selection and direct benefits derived from reinforcing the status quo drive coalitionary interventions among adult female spotted hyenas. The results of this chapter were recently published in *Behavioral Ecology* (Smith et al., 2010).

Finally, in Chapter 5, I investigated the function of non-conciliatory greetings among adult female spotted hyenas during subgroups reunions. These interactions among spotted hyenas are of particular interest because, although their flexible lifestyle permits females to reduce conflicts of interest, fission-fusion sociality simultaneously imposes a unique set of challenges on group members that are regularly subject to prolonged separation (Aureli et al., 2008; Barrett et al., 2003). Theory predicts that animals whom separate frequently from one another should evolve ritualized displays to quickly update uncertain relationships at reunions (Endler, 1993; Maynard Smith and Price, 1973). I tested predictions derived from the submission (de Waal, 1986; de Waal and Luttrell, 1985; Preuschoft and van Schaik, 2000), tension reduction (Aureli and Schaffner, 2007; Dias et al., 2008; Kutsukake et al., 2006; Schaffner and Aureli, 2005), and social bonding hypotheses (Smuts, 2002; Smuts and Watanabe, 1990; Zahavi, 1977b). Because the directional consistency of hyena greetings was low, and because females greeted most per opportunity when food was absent, our data fail to support the submission or tension reduction hypotheses. Whereas rank effects were relatively weak, the best statistical model was consistent with predictions of the social bonding hypothesis; females greeted coalition partners and close associates, including kin, most often per opportunity at fusion events. Further, the act of greeting coordinated cooperation by promoting coalition formation among allies. Overall, the results of Chapter 5 indicate that risky greeting gestures permit hyenas to effectively communicate their immediate commitment to alliance affiliations within a continuously shifting social milieu.

### *Collaborative nature of this research project*

The results of my dissertation research elucidate the evolutionary and ecological forces shaping the dynamics of cooperation. More broadly, these findings deepen our understanding of the rules governing social decision-making in free-living vertebrates, and they inform theoretical approaches to the evolution of sociality by testing the generalizability of socioecological models across taxonomic groups. Importantly, these results and their potential influences on the fields of ecology, evolutionary biology and behavior would not have been possible without the efforts of multiple collaborators.

Drs. Kay E. Holekamp, Laura Smale, numerous field assistants and graduate students working on the Mara Hyena Project helped me to collect the long-term data analyzed in this dissertation. Chapters 2 and 4 were generated in collaboration with two former graduate students in the Holekamp lab, Drs. Joseph M. Kolowski and Russell C. Van Horn, respectively. An amazing team of undergraduates also assisted in enriching the conceptual frameworks tested throughout my dissertation and helped me to extract each of the relevant data sets from archived field notes. Many of these individuals served as on each of the co-authors the published chapters or will co-author of Chapter 5.

Because of the outstanding contributions of the aforementioned collaborators, I will use the term "we" in each of the following data chapters to indicate that my dissertation research was, in fact, a collaborative effort.

# Chapter 2

Smith JE, Kolowski JM, Graham KE, Dawes SE, Holekamp KE, 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. Animal Behaviour 76:619-636.

# Chapter 2

# SOCIAL AND ECOLOGICAL DETERMINANTS OF FISSION-FUSION DYNAMICS IN THE SPOTTED HYENA

## INTRODUCTION

Most mammalian carnivores are solitary, spending their lives alone except when breeding (Gittleman, 1989). Among the roughly 20% of carnivore species that are at least somewhat gregarious, a few species live in groups that are highly cohesive, such as wild dogs (*Lycaon pictus*) and various species of mongooses. However, like elephants (*Loxodonta* spp.), cetaceans (e.g. bottlenose dolphins, *Tursiops truncatus*), and certain primates, most gregarious carnivores live in groups commonly referred to as fission-fusion (FF) societies. FF societies are stable social units in which individual group members are often found alone or in small subgroups, and in which subgroup size and composition change frequently over time. In the FF societies of hamadryas (*Papio hamadryas*), gelada baboons (*Theropithecus gelada*), and elephants, stable subgroups that contain multiple individuals join (fusion) and break away from (fission) other stable subgroups belonging to the larger social unit (Kummer, 1971; Wittemyer et al., 2005). By contrast, the FF societies of gregarious carnivores are typically individual-based (Rodseth et al., 1991) such that individual group-members are commonly found alone, and individually make decisions to join or leave subgroups (Gittleman, 1989).

Gregarious carnivores living in FF societies typically know each other as individuals and defend a common territory, but all group members rarely occur together concurrently (reviewed by Holekamp et al. 2000). Although group members seldom exhibit signs of distress when separating from group-mates, they typically engage in reunion displays upon subgroup fusion (Holekamp et al. 2000). Terrestrial carnivores that live in societies with these characteristics include lions (*Panthera leo*), coatis (*Nasua* spp.), European badgers (*Meles meles*), dingoes (*Canis lupus dingo*), coyotes (*C. latrans*), dholes (*Cuon alpinus*), kinkajous (*Potos avus*), brown hyenas (*Parahyaena brunnea*) and spotted hyenas (*Crocuta crocuta*).

Spotted hyenas are long-lived carnivores that reside in permanent social groups, called clans, in which individual members travel, rest, and forage in subgroups (Kruuk, 1972; Mills, 1990) that change membership multiple times per day (Kolowski et al., 2007). Virtually all males permanently disperse from their natal clans after puberty, whereas females are philopatric (East and Hofer, 2001; Mills, 1990; Smale et al., 1997). Clans contain one to several matrilines of adult females and their offspring, as well as multiple adult immigrant males. Individuals choose to join subgroups containing particular clan members, and they vary in the extent to which they associate with conspecifics (Smith et al., 2007; Szykman et al., 2001). Hyenas associate most often with kin (Holekamp et al., 1997a; Wahaj et al., 2004). Among non-kin, hyenas prefer to join subgroups containing potential mates (Szykman et al., 2001) and same-sexed social companions who are higher-ranking than, but close in rank to, themselves (Smith et al., 2007). Although up to 80 individuals may belong to a single clan concurrently (Henschel and Skinner, 1991; Kruuk, 1972; Mills, 1990), all clan members are rarely, if ever, found together in one place (Holekamp et al., 2000). Here we provide the first detailed description of FF dynamics in the spotted hyena. Because social and ecological circumstances can promote or constrain the cohesiveness of animal societies (Chapman, 1990; Chapman et al., 1995; Wrangham et al., 1993), we first evaluate the extent to which specific circumstances promote the formation of hyena subgroups of various sizes, and the tendency for individual hyenas to be found alone or with conspecifics. We then test three hypotheses suggesting factors limiting subgroup size in this species.

First, the infant safety hypothesis (Otali and Gilchrist, 2006) predicts that reproduction is a disruptive force in FF societies in which offspring are vulnerable to infanticide, the direct killing of infants by older conspecifics. Because adult *Crocuta* are known to commit infanticide (East and Hofer, 2002; Kruuk, 1972; White, 2005), we test two predictions derived from this hypothesis. Mammalian offspring are especially vulnerable to infanticide immediately after parturition (Agrell et al., 1998), so we expected adult females to spend the most time away from other conspecifics during early lactation. We also expected young hyenas to be found most often with their mothers during early life history stages in which young are most vulnerable to infanticide.

Second, the dispersive conflict resolution hypothesis (Schino, 2000) proposes that costs associated with physical combat, such as energy expenditure and risk of injury or death, limit gregariousness among animals living in FF societies. *Crocuta* frequently direct aggression towards clan-mates to establish and maintain rank relationships even in the absence of food (Kruuk, 1972; Smale et al., 1993). Because *Crocuta* are well armed with massive teeth and jaws, victims of aggression risk injury resulting from continued or escalated fighting during within-group conflicts (Kruuk, 1972). Thus, individuals might reduce the short-term costs of conflict by relying on dispersive mechanisms to avoid or resolve fights. If this is the case, then hyenas should leave subgroups more often after receiving aggression than when conspecifics direct no aggression towards them. Further, hyenas sometimes resolve conflicts by engaging in conciliatory behaviors such as greetings and/or non-aggressive approaches (Hofer and East, 2000; Wahaj et al., 2001). If reconciliation promotes social cohesion in this species, then targets of aggression should remain in subgroups more often when they reconcile with former opponents than when no reconciliation occurs.

Finally, the ecological constraints hypothesis (Chapman et al., 1995) posits that resource competition, as affected by both short-term and seasonal fluctuations in resource availability, limits subgroup size among animals that otherwise benefit from grouping. This hypothesis explains FF dynamics in a number of non-human primates, but should also theoretically be able to explain grouping patterns in a broad range of gregarious taxa, including spotted hyenas. *Crocuta* benefit from grouping because multiple, often unrelated (Van Horn et al., 2004a), clan members cooperate to obtain and defend resources from kleptoparasitism by neighboring hyena clans and lions, and also to protect clanmates from direct killing by lions (Boydston et al., 2001; Henschel and Skinner, 1991; Kruuk, 1972). Nevertheless, hyenas compete intensely with group-mates for limited food, comprised mainly of ungulate prey they have killed themselves (Engh et al., 2000; Frank, 1986; Kruuk, 1972; Tilson and Hamilton, 1984). Ungulate carcasses represent energy-rich food patches that are both ephemeral and usurpable, and an individual's priority of access to food is determined by its social rank (Engh et al., 2000; Frank, 1986; Tilson and Hamilton, 1984). If the ecological constraints hypothesis is correct, then given their reduced priority of access to resources, low-ranking hyenas should spend more time alone than high-ranking ones. We also expected heterogeneity in the foraging environment to influence grouping patterns (Ramos-Fernandez et al., 2006). If feeding competition in particular constrains subgroup size, then hyenas should congregate at food patches in numbers proportional to the amount of energy contained within patches, and they should spend relatively more time with conspecifics than alone when prey are superabundant. Further, low-ranking hyenas should be particularly vulnerable to costs associated with feeding in large subgroups. To test this prediction, we replicate earlier work (Frank, 1986) by inquiring whether social rank determines feeding success in adult female *Crocuta,* and extend it by examining how a female's relative rank within her current subgroup influences her ability to feed. Finally, although energy gain increases with group size in some carnivores living in cohesive societies (e.g. wild dogs, Creel & Creel 1995; Creel 1997), the ecological constraints hypothesis predicts that per capita energy intake and the proportion of time individuals spend feeding should decline with increasing subgroup size among spotted hyenas.

## METHODS

### *Study Populations*

We monitored two large *Crocuta* clans inhabiting the Masai Mara National Reserve, Kenya. From July 1988 through December 2004, we monitored hyenas in the Talek clan. From August 2002 to March 2004, we also studied the Mara River clan, located 8 km west of Talek, in an area with habitat types and prey abundance that did not differ significantly from those in the Talek area (Kolowski et al., 2007). We identified individuals in both clans by their unique spots. From 1988 to 1999, the Talek clan defended a stable group territory covering an area of 62 $km^2$ (Boydston et al., 2001). Starting in 2000, the original Talek clan permanently split to form two new clans, Talek East and Talek West, defending adjacent territories of 19 $km^2$ and 28 $km^2$, respectively (Kolowski et al., 2007). Members of the Mara River clan defended a territory of 31 $km^2$. Subjects in the current study were members of the original Talek, the Talek West, and the Mara River clans.

Resident ungulates grazing year round in the study areas include Thomson's gazelle (*Gazella thomsonii*, average body mass: 25 kg), impala (*Aepyceros melampus*, 53 kg), and topi (*Damaliscus korrigum*, 119 kg). Large migratory herds of wildebeest (*Connochaetes taurinus*, 132 kg) and zebra (*Equus burchelli*, 235 kg) join resident ungulates annually between June and September; the superabundance of prey during these months relaxes feeding competition among hyenas (Holekamp et al. 1993, 1996). *Crocuta* in our study areas hunt all of these species and occasionally also scavenge carcasses of adult giraffe (*Giraffa camelopardalis*, 935 kg) and elephants (3550 kg). Mean masses reported here are from Kingdon (1997) and Oindo (2002).

Here we estimated (to ± 7 days) the ages of cubs upon first observing them above ground (Holekamp et al., 1996). We sexed hyenas based on the morphology of the erect phallus (Frank et al., 1990). Adult females bear young in isolated natal dens and transfer them to a communal den when cubs are 2 to 5 weeks old (East et al., 1989; Kruuk, 1972). There is no allonursing or communal care of young in this species (Mills, 1985). We considered cubs to be independent of dens when we found them more than 200 m from the current communal den on at least 4 consecutive occasions; this occurred when cubs were around 9 months of age (Boydston et al., 2005). On average, den-independent cubs nurse from their mothers until they are 14 months old (Holekamp et al., 1996). Here we assigned weaning dates (to ± 10 days) based on observed weaning conflicts and the cessation of nursing (Holekamp et al., 1996). We considered natal animals older than 24 months to be reproductively mature adults (Glickman et al., 1992).

We ranked adults in a linear dominance hierarchy, based on outcomes of dyadic agonistic interactions (Holekamp and Smale, 1993; Smale et al., 1993). All adult female spotted hyenas breed, but high-ranking females enjoy greater reproductive success than do low-ranking females (Frank et al., 1995; Hofer and East, 2003; Holekamp et al., 1996). All adult females are dominant to all immigrant males. Here we ranked immigrant males and adult females in separate hierarchies, with one being the highest possible rank in each. We assigned relative ranks to adult females at each kill based on their positions within the dominance hierarchy relative to those of the other females present at that kill.

### *Behavioral Data Collection*

We used two general methods to collect behavioral data: long-term focal animal 'follows,' and short-term observation 'sessions.' From 2002 to 2004, we conducted focal follows on 19 adults (11 females, 8 males) fitted with radiocollars (Telonics Inc., Mesa, Arizona). Focal animals were members of either the Talek West clan ($N = 9$) or the Mara River clan ($N = 10$). Focal animals spanned a wide range of social ranks. Follows were focal animal samples (Altmann, 1974) with continuous recording of behavior, lasting from 2-15 h. Using methods described by Kolowski et al. (2007), we conducted follows at all times of day and night with the aid of night-vision binoculars and infrared spotlights. In addition to continuous monitoring of behavior, every 10 minutes we recorded the total number of hyenas present in the subgroup of the focal hyena. We recorded the identity of every hyena in the subgroup whenever possible. Subgroups were comprised of one or more hyenas separated from other hyenas by at least 200 m. The 19 hyenas followed were in view of observers, on average, for 98 ± 0.56% of follow minutes ($N = 100$ follow segments). We terminated a follow when the focal animal remained out of sight for more than 30 minutes.

We were unable to follow hyenas for complete 24-hour periods due to constraints imposed by terrain and vegetation. Instead, we documented the 24-hour pattern of social activity for each individual hyena by observing it during shorter follow segments that together generated a composite 24-hour cycle. We attempted to complete this cycle as quickly as possible after its onset, with the average time necessary for completion being 31 days. All analyses below requiring equal sampling throughout the 24-hour period utilize only data from composite 24-hour cycles. However, other analyses utilize all recorded follow segments, 21% of which did not contribute to a composite 24-hour cycle (e.g. due to hyena death or collar failure before cycle completion). In all analyses based on follows, the sampling unit was the individual hyena. Averaged estimates represent any individual observed during more than one composite follow. Because females with den-dwelling cubs spend much of their time at the communal den (Holekamp et al., 1996), where subgroup size is often large, we only followed females without den-dwelling cubs to allow for appropriate comparisons between the sexes.

Fluidity is a measure of how often subgroup composition changes over time (Kummer, 1971). To describe the size and fluidity of subgroups here, we averaged subgroup size, subgroup duration, and minimum number of changes in subgroup size during each composite follow across all focal animals. In addition, we calculated the mean number of different clan members encountered per hour, and the total numbers of clan members encountered by focal animals during follow segments conducted between 1800 and 0900 hours. We used individual follow segments for these calculations because accurate estimation of these two variables required use of continuous monitoring. We focused exclusively on the 1800-0900 period here because Mara hyenas spend most of their daylight hours lying in cool, shaded spots, and move very little (Kolowski et al., 2007).

Our second method of data collection was based on short-term observation sessions involving members of the Talek and Talek West clans. We collected these data daily around dawn and dusk, between 0530 and 0900 hours and between 1700 and 2000 hours, respectively, throughout our 16-year study. We initiated a session each time we encountered one or more hyenas separated from others by at least 200 m. Sessions ranged in duration from 5 minutes to several hours, and ended when we left an individual or subgroup. Every 15-20 minutes throughout each session, we conducted a scan in which we recorded the identity and activity of every hyena present. We also recorded the geographic location, relative to known landmarks, at which subgroups were found, subgroup size (total number of hyenas observed in the session), the primary activity in which hyenas present were engaged, and whether or not food, alien hyenas, or lions were also present. In 2003 and 2004, we recorded subgroup locations using GPS units. From GPS data, we calculated distances between successive observation sessions occurring within the same morning or evening sampling period to estimate distances among subgroups in our study area.

### *Tendency to be Alone*

Based on session data, we evaluated how the tendency to be alone varied across the lifespan by calculating the percent of sessions in which natal males and females were found alone during each of the following life history stages: 1) natal den, 2) communal den, 3) den-independent but still nursing, 4) weaned but pre-reproductive, and 5) reproductively mature adults. To calculate the percent of observations alone, we divided the number of sessions in which an individual was found alone by the total number of sessions in which we observed that individual during a particular life history stage, and then multiplied by 100. We used this same method to calculate the percent of sessions in which immigrant males were found alone. We also assessed the relationship between an adult's intrasexual social rank and its tendency to be alone. For reasons detailed elsewhere (Holekamp et al., 1997a; Smith et al., 2007), we calculated an overall mean proportion of observations alone for each intrasexual rank position by summing proportions across all individuals holding that rank during the study, and divided this value by the total number of individuals holding that rank position. We limited analyses based on rank to years (July 1988 to July 1989, 1991 to 1999, and 2002 to 2004) in which rank relationships were known to be stable.

### *Social and Ecological Influences on Subgroup Size*

We assigned each session to one of nine behavioural contexts (Table 2.1) in order to evaluate the extent to which specific circumstances influence subgroup size and the tendency for individuals to be found alone or with conspecifics. To compare conflicts with lions or alien hyenas to situations in which lions or aliens were present but no conflict occurred, we also assigned sessions in which lions and aliens were present, but no between-group fighting occurred, to their own 'non-conflict' contexts. Conflicts occurred if we observed at least one agonistic interaction between our study animals and lions or alien hyenas, respectively. Conflict sessions occurring at kills were only assigned to the conflict context. The 'other' category (Table 2.1) provided a 'baseline'

**Table 2.1.** Each session was assigned to one of the following behavioural contexts.

| Behavioural context | Social and ecological circumstance |
|---|---|
| Hunting | one or more resident hyenas chased a selected prey animal for at least 50 m, regardless of the outcome of the hunting attempt[1,2]* |
| Natal den | one or more resident hyenas observed at an isolated den used by only one mother for shelter of a single litter until her cubs reach 2 to 5 weeks of age; no food present[1,3,4]* |
| Kill | one or more resident hyenas observed feeding on at least one fresh ungulate carcass[1,2,3]; no hunting observed* |
| Courtship/mating | immigrant male(s) engaged in mating tactics such as shadowing, defending, harassing, or mounting a sexually mature female[1,5,6]; no food present* |
| Communal den | one or more resident hyenas observed at a den or den complex used concurrently by several litters ranging up to 12 months of age[1,3,7,8]; no food present* |
| Border patrol | resident hyenas engaged in high rates of scent-marking and socially facilitated defecation along territory boundaries[1,9]; no food present* |
| Clan war | agonistic interactions observed between resident and alien hyenas at territory boundaries[1,9]; no lions present |
| Conflict with lion(s) | agonistic interactions observed between resident hyenas and at least one lion[1,10,11]; regardless of location or other activity |
| Other | one or more resident hyena(s) traveling or resting when no food present; none of the contexts above applied* |

*Asterisks* (*) represent contexts assigned only when both lions and alien hyenas were absent. Superscript numbers refer to published works explaining contexts in more detail than presented here. Kruuk 1972[1], Holekamp et al. 1997[2], Mills 1990[3], East et al. 1989[4], Hofer & East 2003[5], Szykman 2007[6], White 2007[7], Boydston et al. 2005[8], Boydston et al. 2001[9], Cooper 1991[10], Höner et al. 2005[11].

measure of social activity for *Crocuta* because neither resources (e.g. food or mates) nor threats (e.g. natural enemies or competitors) that might attract or repel conspecifics were present during these sessions. We considered subgroup sizes that differed from 'baseline' to represent the formation of smaller or larger subgroups. To ensure consistency in data collection across years, we limited our analyses to sessions in which hyenas were located without the aid of radio telemetry because radiocollars were not used in Talek until 1991.

### *Tests of Hypotheses Suggesting Forces Limiting Subgroup Size*

### Infant Safety Hypothesis

We compared the tendency for adult females to be alone, or only with their dependent offspring, across reproductive states; offspring were considered to be dependent until they were weaned. We divided the lactation interval into two parts: the first two weeks of lactation ('early lactation') and the remainder of the lactation interval ('late lactation'). We then assigned each female in each session to one of the following reproductive states: the first, second, or third trimesters of pregnancy, early lactation, or late lactation. We divided the total number of sessions during which a female in a particular reproductive state was found alone, or with only her dependent offspring, by the total number of sessions in which we observed that adult female in that reproductive state, and multiplied by 100. Next, we evaluated the relative impacts of reproductive state and prey abundance on the tendency for adult females to be alone or only with their dependent offspring. Focusing here on the subset of females observed at three or more observation sessions across all five reproductive states, we compared female behaviour between months when migratory prey were present and absent. Finally, focusing on offspring, we evaluated how the tendency to be with one's mother varied across the lifespan by calculating the percent of sessions each hyena spent with its mothers during each life history stage.

### Dispersive Conflict Resolution Hypothesis

From 1988 to 2001, we conducted 30-minute focal animal 'surveys' on natal animals of both sexes that were no longer living at dens to evaluate the effect of within-group conflict on subgroup cohesion. During surveys in which the focal animal was the target of at least one dyadic aggression (e.g. lunge, snap, bite, chase, displace, push, stand over, and intention movement to bite), we recorded whether focal animals engaged in conciliatory behaviors in response to aggression within 15 minutes after each fight. We ended all surveys when the focal animal moved at least 200 m away from its subgroup or 15 minutes passed after the fight started, whichever occurred first. We then compared the tendency for a focal animal to leave its subgroup between surveys in which it received aggression (but did not reconcile) and surveys in which that same animal received no aggression. We also compared the tendency for a victim of aggression to remain within its current subgroup between surveys in which it initiated a conciliatory interaction with a former opponent and surveys in which it failed to reconcile its fights with that same opponent. We required that sessions containing matched surveys occur within 45 days of one another, that they contain similar numbers (± 4) of individuals, and that either both occur at kills or both occur away from kills. Due to small sample size, surveys assigned to other behavioural contexts were excluded (Table 2.1).

### Ecological Constraints Hypothesis

We estimated local abundance of prey and assessed the extent to which this influenced the tendency for hyenas to be with conspecifics (versus alone) and to hunt with particular numbers of conspecifics. To do this, we performed biweekly counts between 08:00 and 10:00 hours of all prey animals found within 100 m of two 4-km transect lines in different parts of the Talek area, and averaged biweekly counts to determine mean monthly prey counts. We also inquired whether the mass of the ungulate carcass available in each kill session predicted the numbers of hyenas present. Here we focused only on sessions in which the prey species was known or where only 'scraps' (e.g. scattered bones, horns, and/or small pieces of skin) were present that contained little nutritional or energetic value. We used mean mass values for each prey species (Kingdon, 1997; Oindo, 2002) to estimate food amounts available at kill sessions. Following Henschel & Tilson (1988), we assumed scraps weighed 2 kg.

Because hunting success is significantly higher when hyenas hunt in groups than when they hunt alone (Holekamp et al., 1997b), we also asked whether hunting and feeding subgroup sizes were related. We did this to evaluate the relative costs and benefits associated with feeding or hunting with conspecifics. The addition of a second hunter increases hunting success by 19%, but the addition of subsequent hunters does not significantly increase hunting success further (Holekamp et al., 1997b). Therefore, we compared numbers of new arrivals and total competitors present 5, 10, and 15 minutes after solo hunters or pairs of hunters successfully captured prey. To control for effects of prey size, we limited this analysis to matched sessions in which solo hunters and pairs of hunters acquired ungulates of similar size. Lone hyenas regularly kill antelope as large as wildebeest or topi in this population (Holekamp et al., 1997b).

We inquired about the effects of intraspecific competition on feeding success using two types of data from adult females. We first assessed how per capita energy gain varied among females as a function of subgroup size. We also asked how the proportion of scans in which females fed varied as function of subgroup size and social rank. Using methods developed by Creel & Creel (2002), we determined the energetic value of each prey animal consumed by each hyena subgroup of known size based on the species, sex, and age class of that prey animal. Here we used only sessions in which the amount of food (e.g. proportions of flesh, viscera, and skin) consumed by known individuals was visually quantifiable. We considered amounts to be quantifiable only when our field notes indicated exact changes in the amount of food (e.g. forelimbs, hind limbs, pelvis, lumbar spine, ribcage, neck, and head) consumed over time. These amounts corresponded directly to published data on the masses of East African prey (Blumenschine and Caro, 1986; Sachs, 1967). We subtracted the amount of edible biomass present at the end of the session or when no meat remained on the carcass, whichever occurred first, from that present when the food was first acquired, or when the session began if we arrived on the scene after the prey animal had been captured.

We standardized subgroups containing hyenas of various ages by calculating rates of energy gain by juveniles relative to those of adult females, as has been done for other carnivores (Baird and Dill, 1996; Mills and Biggs, 1993; Packer et al., 1990). Frank (1986) found that cubs less than five months of age and immigrant males rarely feed at kills with adult females. Therefore, we ignored food intake by animals in the former two categories in our calculations. We assumed that individuals 6 to 24 months of age consumed only half as much food mass per unit time as did adult females (Frank, 1986). When changes in feeding subgroup sizes occurred, we calculated a weighted average of the number of adults present as: {Σ (# of minutes each subgroup size lasted)*[(# of adult females in each subgroup) + (0.5 * # of subadults present in each subgroup)]}/(# of minutes each session lasted). We calculated per capita energy intake per minute by dividing the number of kilojoules the entire subgroup consumed by the number of adult females present and the number of minutes in which feeding was observed. Kolowski et al. (2007) found that adult females in the Masai Mara spend, on average, 9.2 minutes feeding at fresh kills during each 24-hour period. Therefore, we multiplied energy intake per minute for each session by 9.2 minutes to convert to daily rates, allowing for comparison with values reported elsewhere.

Within each scan made at each kill session, we quantified the proportion of the adult females present that were actually feeding from the carcass, and asked whether this proportion varied as a function of the numbers of adult females present. In each kill session between 1988 and 1999 at which neither alien hyenas nor lions were present, we averaged the proportion of adult females feeding over all scans within each session and multiplied this value by 100. Because food is unequally divided among adult females (Frank, 1986), we also assessed how the proportion of time adult females fed at kills varied with their absolute social ranks within the clan, and with their relative ranks within their current subgroups. This was based on the number of scans in which each adult female fed at kills, divided by the number of scans in which that female was present at kills while she held a particular rank position, and then multiplied by 100. Here again, we used values averaged over all individuals that held each particular rank position.

### *Statistical Analyses*

We employed non-parametric statistics throughout most of this study due to low sample sizes, the inability to transform non-normally distributed data, or both. We used Mann-Whitney *U* tests to compare means between two independent samples, and Kruskal-Wallis ANOVAs to compare means among multiple groups. We used Wilcoxon-signed rank tests and Friedman's ANOVA for repeated measures when comparing the means of two or more than two dependent groups, respectively. We calculated correlation coefficients, Spearman's *R*, to examine correlational relationships. We compared effects of multiple independent variables using Analysis of Covariance (ANCOVA) on log-transformed, normally distributed data. We report partial eta-squared values as measures of effect size. We performed all statistical tests using STATISTICA 6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.). We used only two-tailed tests, and considered differences to be statistically significant at alpha < 0.05. We corrected for multiple testing using the sequential Bonferroni adjustment (Rice, 1989). We report *P*-values in their adjusted form and critical values following (Mundry and Fischer, 1998). Wherever appropriate, we report means ± standard error (SE).

## RESULTS

### *Fluidity, Duration, and Size of Subgroups*

During long-term focal follows, we monitored the behavior of 19 hyenas for a total of 624 hours, and completed composite 24-hour follow cycles for 16 hyenas ($N$ = 5 males, $N$ = 11 females). Of those hyenas, we followed six hyenas for two complete cycles. Variation in subgroup size experienced by one typical adult female spotted hyena during her two composite long-term follows is shown in Figure 2.1. Hyenas from both Talek West and Mara River clans encountered similar numbers of different conspecifics during each hour followed (1.7 ± 0.3 and 1.7 ± 0.2 individuals/hour, respectively, Mann-Whitney U test: $U = 38.0$, $P = 0.825$). Because we detected no significant differences for this, or any other variables, based on clan membership, we pooled follow data from both clans (Mann-Whitney U tests, $U \geq 0.20$ and $P > 0.20$ for all variables). We detected no sex differences in any measure calculated from follow data (Mann-Whitney U tests, $U \geq 18.0$ and $P \geq 0.28$ in all cases, Table 2.2).

Although clan sizes ranged from 47 to 55 for Talek West and from 28 to 41 for Mara River during the period in which we conducted long-term follows, subgroup size averaged only 3.6 ± 0.4 individuals over all 24-hour composite

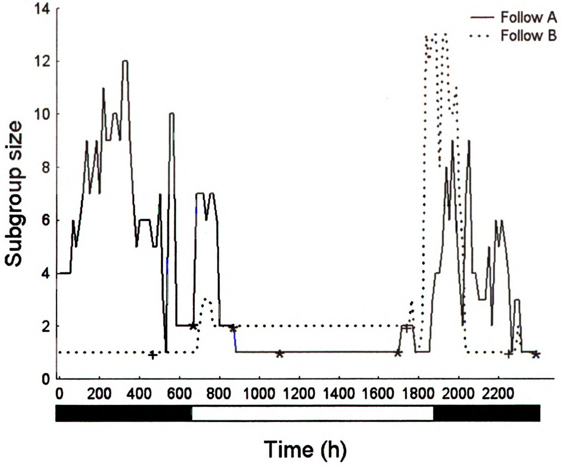

**Figure 2.1.** Variation in subgroup size experienced by one adult female spotted hyena during two long-term follows, A and B, conducted at different times. Follow A consisted of 5 segments lasting an average of 4.8 hours each. Follow B consisted of 3 segments, lasting an average of 8.0 hours each. Breaks between continuous follow segments are indicated by asterisks (follow A) and plus signs (follow B). Plotted values include the focal animal, and represent subgroup size recorded every 10 min; a subgroup size of one indicates the focal animal was alone. Shaded and open bars indicate hours of darkness and daylight, respectively.

**Table 2.2.** Mean ± SE subgroup sizes and estimates of fluidity for males (*N* = 5) and females (*N* = 11) based on entire 24-hour composite follows

| | Females | Males | *U*-statistic | *P*-value |
|---|---|---|---|---|
| Subgroup Size | 3.9 ± 0.6 | 3.1 ± 0.3 | 24.0 | 0.692 |
| # Subgroup Size Δs | 26.7 ± 3.3 | 23.5 ± 3.3 | 20.5 | 0.427 |
| Subgroup Duration (min) | 54.3 ± 7.4 | 60.7 ± 10.1 | 18.0 | 0.282 |
| % Time Spent Alone | 27.2 ± 7.2 | 35.1 ± 10.7 | 24.0 | 0.692 |

follows. The largest subgroup size recorded during any of the follows was 23 hyenas (44% of the clan) during a conflict with lions. Subgroup size was highly fluid such that focal hyenas, on average, experienced a minimum of 25.7 ± 2.5 changes in subgroup size during the course of a 24-hour period. Subgroup sizes experienced by each focal individual varied dramatically both within and between days (e.g. Figure 2.1). The maximum number of observed changes in subgroup size during a 24-hour period was 48. During follows, subgroup compositions lasted for an average of 56.3 ± 5.9 minutes, and adults spent approximately one third (29.6 ± 5.8 %) of their time alone. On average, adults ($N = 19$) encountered a minimum of 8.2 ± 0.7 other clan members (19.7 ± 1.6 % of the entire clan) within a single follow segment during the active period; these segments lasted an average of 5.4 ± 0.4 hours. Thus, each hyena encountered roughly 1.5 new conspecifics per hour during the active period.

Observation session data generated patterns that were generally consistent with data from long-term follows. On average, the distance between subgroups occurring at two different observation sessions observed sequentially within the same morning or evening sampling period was 1.11 ± 0.03 km ($N =$ 1291 distances; ranging from 201 m to 9.8 km). Mean subgroup size was 3.70 ± 0.02 hyenas ($N = 34{,}848$ sessions). Modal subgroup size, however, was only one hyena, and almost half of our observation sessions (45.3%) involved lone hyenas (Figure 2.2). Excluding transient males (immigrants remaining in the clan for less than six months), our clan in the Talek area contained 39 to 74 members, and the mean size of the clan during the entire study was 57 ± 3 hyenas, based on

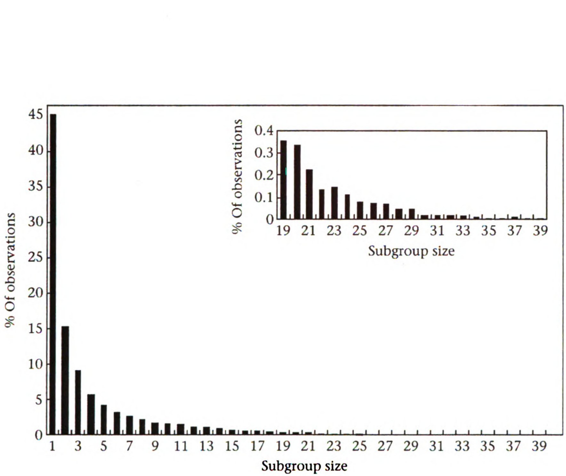

**Figure 2.2.** Frequency distribution of subgroup sizes in which we found members of the Talek clan throughout our longitudinal study ($N$ = 34,848 observation sessions). The inset box shows a magnified view of the frequency of subgroup sizes ranging from 19 to 39.

monthly population estimates. Subgroups ranged in size from 1 to 39 individuals (Figure 2.2) and were always less than current clan sizes. For example, when we observed 39 hyenas together, the current clan size was 67 individuals. We never observed the entire clan together concurrently during a single session. The frequency with which we encountered subgroups of specific sizes decreased as subgroup size increased (Spearman rank correlation: $R_S = -0.997$, $P < 0.00001$, $N = 39$ sizes, Figure 2.2).

### *Variation in the Tendency to be Alone*

The tendency for hyenas to be alone increased significantly with each successive life history stage (Kruskal-Wallis test: $H_{4,695} = 421.3$, $P < 0.00001$; Figure 2.3A). Cubs were alone significantly more often at communal than at natal dens (Mann-Whitney *U* test: $Z = -2.62$, $P < 0.009$). Cubs independent of the communal den were alone more often than were those still residing at the communal den, but less often than weaned, pre-reproductive animals ($Z = -11.1$ and $-8.29$, respectively, $P < 0.00001$ for both). We detected no sex differences in the proportion of sessions spent alone within any life history stage before adulthood (Mann-Whitney *U* tests: $Z_1 = 0.00$, $Z_2 = -0.60$, $Z_3 = -1.59$, $Z_4 = -0.73$, $P \geq 0.56$ in all cases, Figure 2.3A). However, reproductively mature natal males were significantly more likely to be alone than were either adult females ($Z = -3.31$, $P = 0.006$) or weaned, pre-reproductive natal males ($N = 85$, $Z = -2.99$, $P = 0.014$). By contrast, adult females were no more likely to be alone than were weaned, pre-reproductive females ($Z = -1.13$, $P = 0.52$). On average, immigrant males ($N = 67$) were found alone during a significantly greater proportion of their

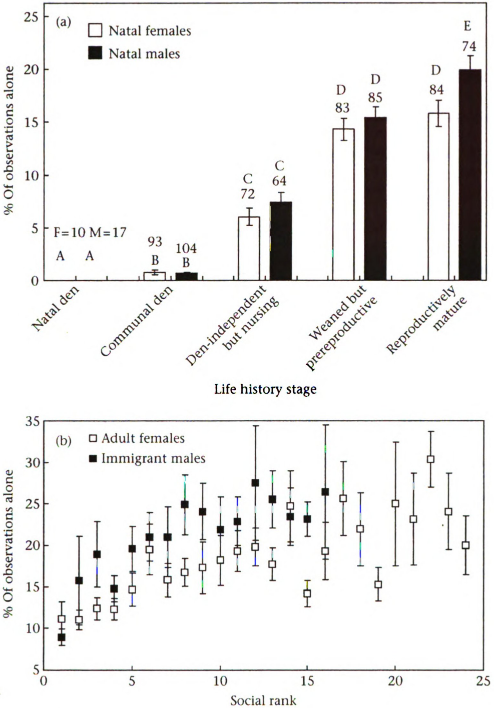

**Figure 2.3.** Mean ± SE percentage of observation sessions in which A) natal animals were found alone during each life history stage, and B) adult females (*N* = 45) and immigrant males (*N* = 40) were found alone as a function of intrasexual social rank. By convention, the highest possible rank is one. Sample sizes in A) shown above each bar represent numbers of individuals. Different letters above bars indicate significant differences after correcting for multiple testing.

sessions (21.2 ± 1.5 %) than were adult females ($N = 84$, 15.8 ± 1.3 %, Mann-Whitney $U$ test: $Z = 3.21$, $P = 0.001$). Within each sex, low-ranking adults were also found alone significantly more often than were high-ranking individuals (Spearman rank correlation: $R_S = 0.77$ and 0.85, $N = 24$ and 18 rank positions, for adult females and immigrant males, respectively, $P < 0.00001$ for both; Figure 2.3B).

*Social and Ecological Influences on Subgroup Size*

The total numbers of hyenas present during sessions varied significantly with the contexts in which hyenas were observed (Kruskal-Wallis test: $H_{8,34847} = 11030.49$, $P < 0.0001$, Figure 2.4). During baseline sessions, mean subgroup size was only 2.2 ± 0.2 hyenas. Hunting subgroups were significantly smaller than baseline (Mann-Whitney $U$ test: $Z = 5.00$ and $P = 0.0002$), indicating that hyenas typically leave subgroups to hunt alone or with a single companion. In fact, solo hunters and pairs of hunters conducted 87.3 % of 393 hunts observed here. Subgroups observed at natal dens were also generally small, but did not differ significantly from baseline ($Z = 0.12$, $P = 0.91$). Courtship interactions, communal dens, kills, border patrols, conflicts with lions, and clan wars attracted significantly larger numbers of individuals than did baseline sessions ($Z = -34.08$, $-87.59$, $-47.74$, $-8.92$, $-9.92$, $-6.08$, respectively, $P < 0.0002$ in all cases, Figure 2.4). Hyenas were observed with conspecifics in 81.5% of sessions where lions were present but no interspecific agonistic interactions were observed; mean subgroup size here (8.6 ± 0.4, $N = 390$ sessions) was significantly smaller than in sessions in which agonistic interactions occurred between lions and hyenas ($Z =$

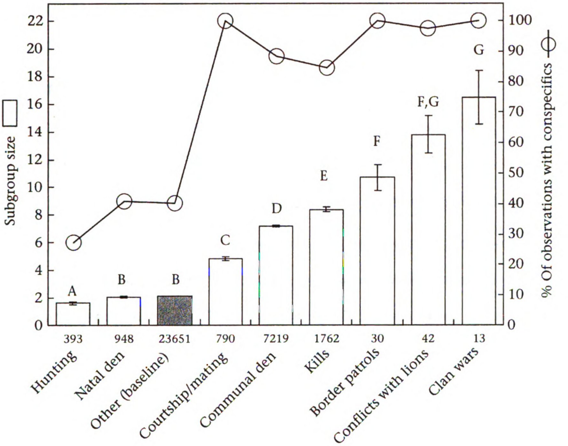

**Figure 2.4.** Mean ± SE subgroup size (left vertical axis and histogram bars) and proportion of observations in which *Crocuta* were found in subgroups containing more than one individual (right vertical axis and open circles) as a function of the context in which groups formed. Sample sizes, shown below each bar, represent numbers of observation sessions assigned to each context. Different letters indicate statistically significant differences between contexts after correcting for multiple testing. The shaded bar represents the baseline value of subgroup sizes occurring in 'other' sessions, against which other groups were compared.

4.06, $P < 0.0001$). Mean subgroup size in sessions in which alien hyenas were present, but no clan wars occurred, was 5.0 ± 0.5 hyenas ($N = 101$ sessions), a value significantly lower than that observed during clan wars ($Z = -4.87$, $P < 0.0001$). Overall, both intra- and interspecific between-group conflicts promoted the formation of large subgroups.

*Testing the Infant Safety Hypothesis*

In general, the tendency for adult females to be alone or only with their dependent offspring varied significantly among reproductive states (Friedman's ANOVA: $F_{4,38} = 66.4$, $P < 0.00001$, Figure 2.5A). Females were seen alone or with only their dependent offspring significantly more often during late pregnancy and early lactation than during any of the other phases of the reproductive cycle (Wilcoxon signed-ranks tests: $Z \geq 3.24$ and $P \leq 0.016$ in all cases). As predicted by the infant safety hypothesis, females were seen alone with their dependent offspring significantly more often during early lactation than during other reproductive states ($Z = 4.87$, $P = 0.0001$). However, the increasing tendency for females to be found alone as pregnancy progressed (Figure 2.5A) was not predicted by the infant safety hypothesis.

Our model containing the subset of females ($N = 16$) observed across all reproductive states during both months of prey scarcity and abundance, with social rank as a covariate ($F_{1,149} = 3.685$, Partial eta-squared = 0.024, $P = 0.057$), explained a significant amount of variation ($r^2 = 0.316$) in the tendency for females to be alone or only with their dependent offspring (ANCOVA, $F_{10,149} = 6.879$, $P < 0.00001$). As before (Figure 2.5A), the tendency for females to be

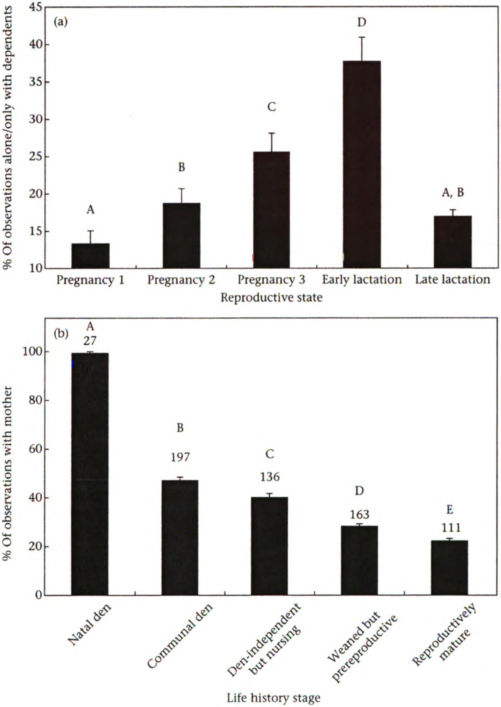

**Figure 2.5.** Mean ± SE percentage of observations in which A) adult females (*N* = 38) were found alone or only with their dependent offspring as a function of the female's reproductive state, and B) natal animals were found with their mothers during each life history stage. Sample sizes, shown above each bar in B), represent numbers of individuals observed in each life history stage. Different letters indicate statistically significant differences between categories after correcting for multiple testing.

alone, or only with dependent offspring, varied significantly among reproductive states ($F_{4,149}$ = 15.089, Partial eta-squared = 0.288, $P < 0.00001$). Prey abundance, however, did not significantly predict this aspect of female behaviour ($F_{1,149}$ = 0.028, Partial eta-squared = 0.0001, $P = 0.867$) nor did it interact with the effect of reproductive state ($F_{4,149}$ = 1.181, Partial eta-squared = 0.031, $P$ = 0.321). These results indicate that social rank and reproductive state are better predictors of a female's tendency to be alone, or only with dependent offspring, than is local prey abundance.

Mothers were most likely to be present with their offspring during the life history stages in which their offspring were most vulnerable to infanticidal conspecifics. Mothers and infants spent progressively smaller proportions of their time together as offspring matured (Kruskal-Wallis test: $H_{4,633}$ = 237.3, $P <$ 0.0001; Figure 2.5B). Mothers and cubs were observed together more often at natal den than communal dens (Mann-Whitney *U* test: $Z = -8.35$, $P < 0.0001$) because newborn cubs rarely appeared above ground when their mothers were absent. We observed mothers and cubs together more often when cubs resided at communal dens than when cubs were den-independent but still nursing, or weaned but pre-pubertal ($Z = -4.00$ and 5.52, respectively, $P < 0.001$ for both). Mothers and offspring were also seen together more often when offspring were weaned but pre-pubertal than when offspring were reproductively mature ($Z$ = 3.67, $P = 0.001$). We found no sex differences in this measure within any life history stage ($Z_1 = -0.43$, $Z_2 = 0.15$, $Z_3 = 1.36$, $Z_4 = 1.58$, $Z_5 = -0.71$, $P \geq 0.575$ for all).

*Testing the Dispersive Conflict Resolution Hypothesis*

Overall, we conducted a total of 211 focal animal surveys, 162 of which were in the absence of food and 49 of which were at kill scenes, in which clan members directed aggression towards 68 different focal animals in the absence of lions, aliens, and courtship/mating. Within a single survey, a particular animal never responded to aggression by both reconciling with a former opponent and departing from its current subgroup. In response to aggression, focal hyenas left their current subgroup after 19.8% of fights away from kills and 2.2 % of fights at kills (*N* = 33 fights involving 21 focal animals). Focal animals were never observed reconciling at kills, but did reconcile with former opponents after 11.7 % of fights away from kills (*N* = 19 fights involving 17 focal animals).

We completed 145 pairs of matched surveys, occurring within 13 ± 1 days of one another, in which the same animal was present with conspecifics and received aggression in one survey but not the other. None of these fights were reconciled. Matched surveys differed in subgroup sizes by only 0.9 ± 0.1 hyenas. In the absence of food, as predicted by the dispersive conflict resolution hypothesis, the probability of immediate departure from the scenes was significantly higher when focal animals received aggression (23.8 ± 5.2 %) than when they did not (2.2 ± 1.0 %; Wilcoxon signed-ranks test: $Z = 3.68$, $P = 0.0002$, $N = 47$ focal animals). However, victims of aggression were significantly less likely to depart from their current subgroups at kills than from subgroups in which no food was present (Mann-Whitney *U* test: $Z = -2.20$, $P = 0.028$, $N = 20$ and 47 focal animals, respectively). Victims of aggression virtually always remained in feeding subgroups; focal animals were no more likely to depart from feeding subgroups after receiving aggression (5.0 ± 5.0 %) than when they did not receive aggression (5.0 ± 5.0 %, $N = 20$ focal animals). Our sample did not permit us to run a Wilcoxon signed-ranks test on these data because only two focal animals differed in their responses between matched surveys at kills.

We completed 13 matched surveys during which the same victim of aggression responded by initiating a conciliatory interaction with its former opponent during one survey but failed to do so during the other. These matched surveys were collected away from food within 20 ± 5 days of one another, and pairs of surveys differed in subgroup sizes by only 1.4 ± 0.3 hyenas. As predicted by this hypothesis, reconciliation promoted subgroup cohesion. The tendency for focal animals to remain in subgroups following fights was significantly greater when victims of aggression reconciled with former opponents (100 ± 0 %; no departures) than when they did not (61.5 ± 14.0 %; Wilcoxon signed-ranks test: $T = 0$, $P = 0.043$, $N = 13$ focal animals).

### *Testing the Ecological Constraints Hypothesis*

Consistent with the ecological constraints hypothesis, *Crocuta* adjusted grouping patterns to match seasonal variation in local prey abundance and the energy available at food sources. *Crocuta* were significantly more likely to be found with conspecifics during months when migratory prey were present ($N = 60$ months) than when migratory prey were absent ($N = 122$, Mann-Whitney $U$ test: $Z = -3.36$, $P < 0.0001$, Figure 2.6A). Variation in hunting subgroup size was unable to explain this seasonal change in the tendency to be with conspecifics

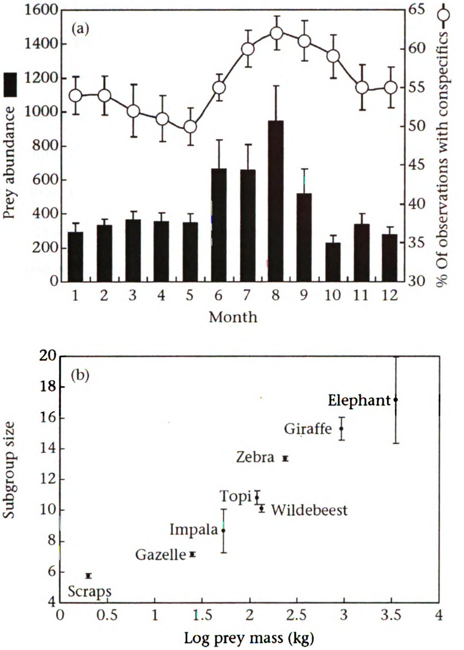

**Figure 2.6.** A) Monthly mean ± SE numbers of prey animals counted each month during biweekly ungulate censuses (left vertical axis and histogram bars) and percentage of observation sessions in which *Crocuta* were found in subgroups containing more than one individual (right vertical axis and open circles). B) Mean ± SE subgroup size as a function of prey mass [logs of values reported by (Kingdon, 1997) and (Oindo, 2002)] available at sessions with scraps (*N* = 1315) or fresh kills. Sample sizes for kills were: Thomson's gazelle (*N* = 382), impala (*N* = 53), wildebeest (*N* = 706), topi (*N* = 108), zebra (*N* = 193), giraffe (*N* = 29), and elephant (*N* = 13). because mean numbers of individuals found hunting together did not differ.

significantly between months when migratory prey were present and those in which ungulate prey were absent ($N = 393$ hunting subgroups, Mann-Whitney $U$ test: $Z = -0.38$, $P = 0.703$). Overall numbers of hyenas present at kills increased with the mass of the prey carcass available within each session, even at scavenged carcasses such as adult giraffe and elephants (Spearman rank correlation: $R_S = 0.98$, $N = 8$ prey types, $P < 0.0001$, Figure 2.6B).

The total numbers of competitors present at kills increased significantly over time within 15 minutes after successful hunts ended (Friedman's ANOVA: $F_{2,18} = 11.27$, $P = 0.0001$, Figure 2.7), but only when multiple hyenas made kills. During the first 5 min, on average, two more competitors arrived at kills made by pairs than at kills made by solo hunters (Wilcoxon signed-ranks test: $T = -1.50$, $P = 0.035$). On average, 10 minutes after prey capture, more than six competitors were present at kills made by two hunters, whereas lone hunters virtually always continued to feed alone ($T = -1.00$, $P = 0.028$). Very few new conspecifics arrived at any of the kills sampled here more than 10 minutes after prey capture.

*Crocuta* consumed quantifiable amounts of fresh biomass at 41 different kill sessions lasting an average of 26 ± 3 minutes each (range: 6 to 98 min). On average, each adult female consumed 44,161 ± 6,737 kJ (6.4 ± 1.0 kg) in a single day. However, per capita energy intake was highly variable at fresh ungulate carcasses, and decreased significantly as the number of adult females present increased (Spearman rank correlation: $R_S = -0.63$, $P < 0.0001$, Figure 2.8A). The lowest rate of per capita energy gain (527 kJ/hyena/day) was experienced by 5.5 hyenas feeding on a single juvenile Thomson's gazelle,

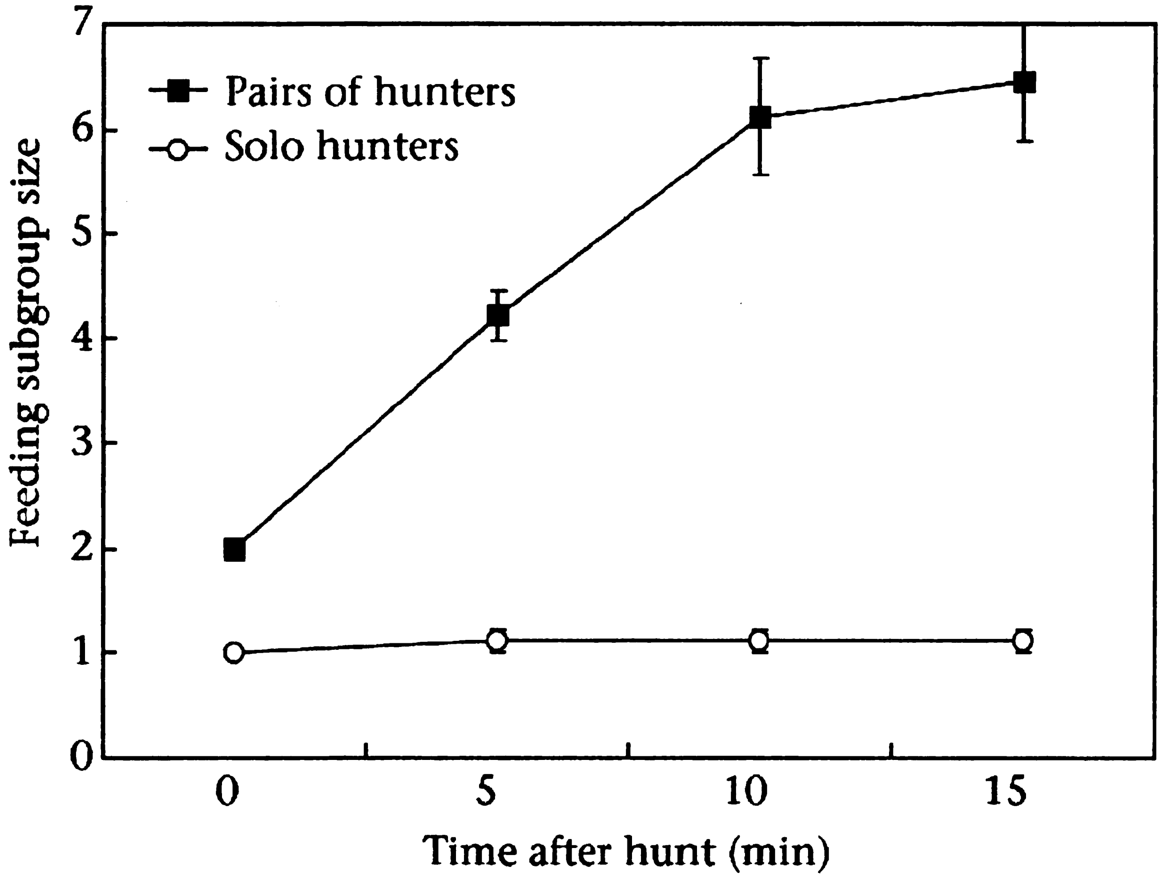

**Figure 2.7.** Feeding subgroup size during the first 15 minutes after solo hunters or pairs of hunters killed ungulates of similar size (*N* = 9 matched pairs of hunts).

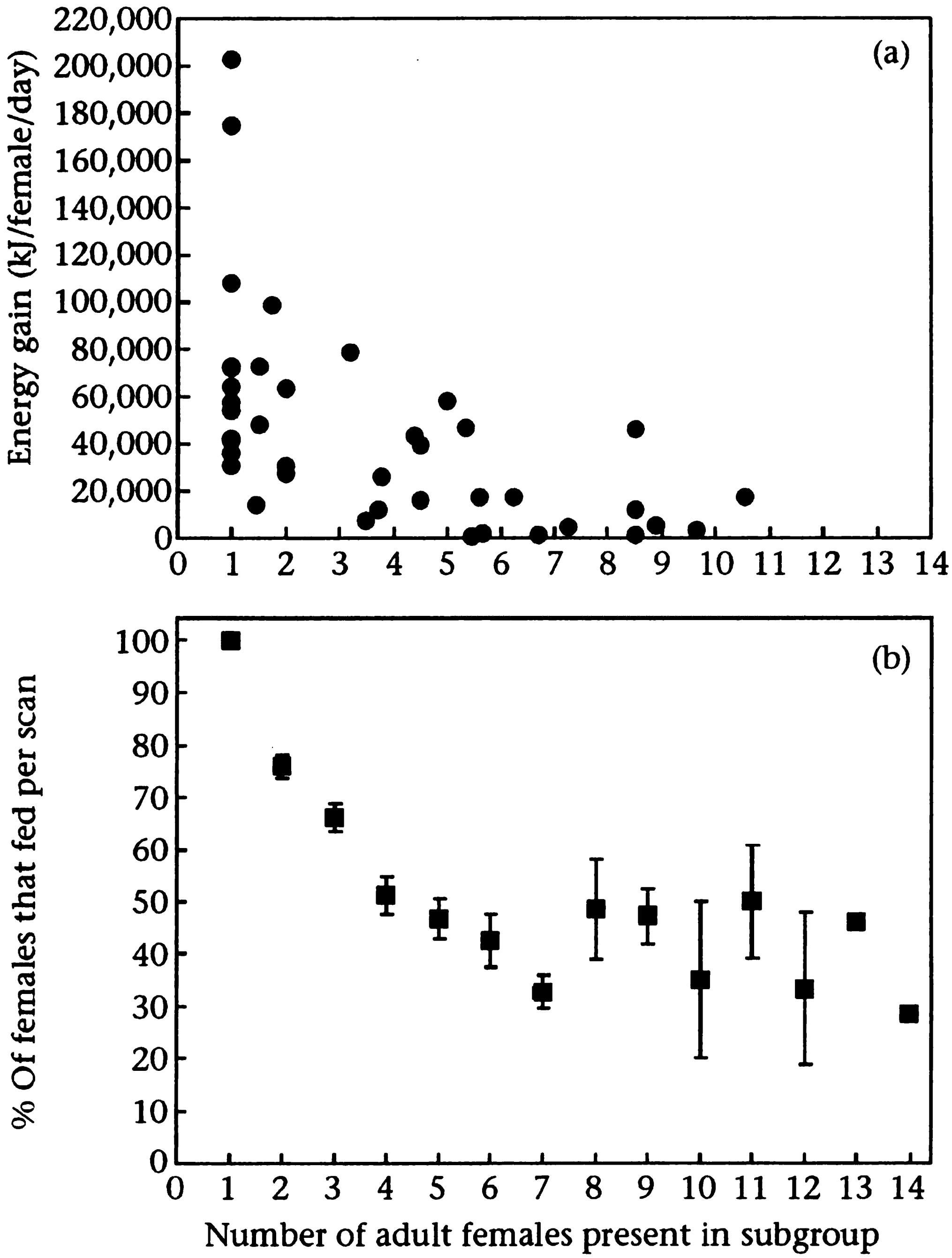

**Figure 2.8.** A) Per capita daily energy gain as a function of the number of adult females present at fresh ungulate kills (*N* = 41). B) Mean ± SE percentage of adult females observed feeding per scan as a function of the number of adult females present within each subgroup at kills (*N* = 426 sessions).

whereas the highest rate (202,509 kJ/hyena/day) occurred when a hyena fed alone on an adult wildebeest.

The proportion of scans in which adult females were able to feed at kills also declined significantly as the number of adult female competitors increased (Spearman rank correlation: $R_S = -0.62$, $P < 0.00001$, $N = 426$ sessions, Figure 2.8B). On average, high-ranking females were significantly more likely to feed at kills than were low-ranking females ($R_S = -0.60$, $P = 0.002$, $N = 24$ rank positions, Figure 2.9A). Females outranking others within their current subgroup also gained better access to kills than did those with low relative ranks ($R_S = -0.70$, $P = 0.006$, $N = 14$ relative ranks, Figure 2.9B).

## DISCUSSION

### *Fluidity of Spotted Hyena Societies*

Spotted hyena clans are dynamic, fluid societies in which subgroup composition changes frequently over time. Although Mara hyenas spent the majority of their time with conspecifics, our data demonstrate that *Crocuta* clans are atomistic, individual-based societies (Rodseth et al., 1991). The mean subgroup size for hyenas ($\bar{X} = 4$) was similar to that reported for other species living in individual-based FF societies including lions ($\bar{X} = 2$ to 5; Packer et al. 1990), chimpanzees (*Pan troglodytes,* $\bar{X} = 7$ to 9; Symington 1990), spider monkeys (*Ateles geoffroyi,* $\bar{X} = 4$; Symington 1990), and bottlenose dolphins in Western Australia ($\bar{X} = 4$ and 6; Connor et al. 1999) and Sarasota, Florida ($\bar{X} = 5$; Irvine et al. 1981) but

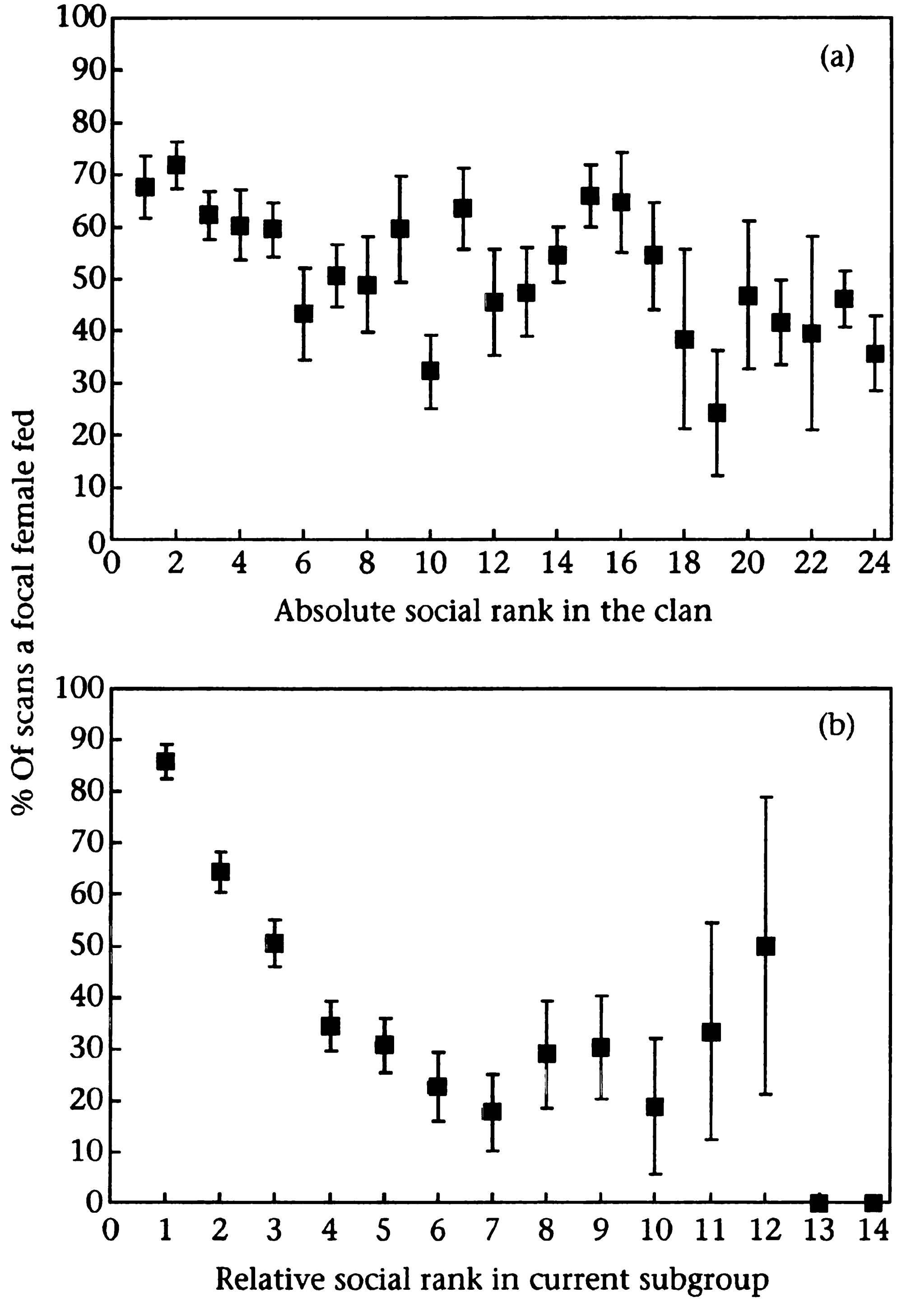

**Figure 2.9.** Mean ± SE percentage of scans in which focal females were observed feeding at kills while holding A) an absolute social rank position within the clan (*N* = 24 absolute ranks), or B) a relative social rank position within the current subgroup (*N* = 14 relative ranks).

not those in Doubtful Sound, New Zealand ($\bar{X}$ = 17; Connor et al. 1999; Lusseau et al. 2003). Subgroups lasted longer for hyenas ($\bar{X}$ = 56 min) than for chimpanzees ($\bar{X}$ = 25 min; Lehmann & Boesch 2004), but were shorter than those observed for Doubtful Sound dolphins ($\bar{X}$ > 24 hours; Lusseau et al. 2003) or lions ($\bar{X}$ = 48 to 75 hours; Packer et al. 1990). Mara hyenas spent roughly the same amount of time alone ($\bar{X}$ = 30%) as did spider monkeys ($\bar{X}$ = 13 to 37%) or chimpanzees ($\bar{X}$ = 14 to 65%; reviewed by Symington 1990), but more time than Doubtful Sound dolphins ($\bar{X}$ < 1%; Lusseau et al. 2003) or lions ($\bar{X}$ = 10 to 15%; Packer et al. 1990).

### *Variables Promoting Subgroup Fission and Fusion*

Life history stage, sex, social rank, and current activity all influenced the likelihood of finding hyenas of both sexes alone, as did reproductive state among adult females. Spotted hyenas tended to occur in larger subgroups when they were active than during hours when they were resting. Intriguingly, this pattern appears to differ from that observed among certain other mammalian carnivores, including both brown and striped (*Hyena hyena*) hyenas and European badgers (Mills, 1990; Wagner, 2006; Woodroffe and Macdonald, 1993), which are all usually found in larger subgroups when resting than when active. We also found that adult spotted hyenas spent more time alone than did younger individuals. Adult males were generally found alone more often than adult females, but adult females with neonatal cubs were away from other clan members most often.

Our current finding that, within each sex, low-ranking hyenas were alone more frequently than high-ranking individuals supplements previous research indicating that low-ranking adults spend more time further from the den (Boydston et al., 2003) and associate less often with same-sexed conspecifics (Holekamp et al., 1997a; Smith et al., 2007) than do high-ranking animals. Rank-related variation in subgroup composition contributes to these patterns. Hyenas generally prefer to associate with members of their own matriline, and high-ranking matrilines contain more individuals than do low-ranking matrilines (Holekamp et al., 1997a; Van Horn et al., 2004a; Wahaj et al., 2004). Among non-kin, hyenas actively join subgroups containing social companions higher-ranking than themselves; this gains them social and feeding tolerance from the dominant animals with which they associate most with often (Smith et al., 2007).

Our finding that multiple animals ($\bar{X}$ = 5 hyenas) congregate during courtship and mating is consistent with previous work showing that numbers of males observed with females increase as females approach estrus (East et al., 2003; Szykman et al., 2007). Given the importance of the communal den as a focal point for social activity (Boydston et al., 2005; White, 2007), including cooperative and affiliative behaviors among kin (Engh et al., 2000; Smale et al., 1993; Wahaj et al., 2004), we were not surprised to find large subgroups ($\bar{X}$ = 7 hyenas) at these locations.

Overall, our data suggest that cooperative defense of shared resources during between-group competition (e.g. clan wars, lion-hyena interactions) is a strong cohesive force in hyena societies, promoting the formation of large subgroups. Most interestingly, we found that large numbers of hyenas ($\bar{X}$ = 11 to 17 hyenas) joined forces during intra- and interspecific between-group conflicts.

Clan members gathered during cooperative marking and defense of territory boundaries, during defense of carcasses from either alien hyenas or lions, and in response to predation attempts by lions.

*Crocuta* can only successfully defend food from lions when the ratio of hyenas to lions is high (e.g. 4:1 when adult male lions are absent; Kruuk 1972; Cooper 1991). Because lions are three to five times larger than hyenas, the resource holding power of a single lion exceeds that of a single hyena (Cooper, 1991; Höner et al., 2002; Kruuk, 1972). In addition to being their direct competitors, lions also represent a leading mortality source for spotted hyenas (Kruuk, 1972; Mills, 1990; Watts, 2007). Therefore, individual hyenas cannot effectively compete with lions for possession of a carcass or defend themselves from predation by lions without aid from conspecifics. Effective maintenance of group territories also requires that individuals from multiple matrilines, with low mean relatedness (Van Horn et al., 2004a), join forces during cooperative defense against neighboring hyena clans. Loss of a clan war can result in substantial reduction in the area of a clan's territory, and repeated losses can further result in overall loss of the territory to a neighboring clan (K.E. Holekamp, unpublished data). Cooperative defense of territories appears to offer a similarly important advantage during intraspecific between-group conflicts in a variety of other carnivores such as dwarf mongooses (*Helogale parvula*), meerkats (*Suricata suricatta*), and Ethiopian wolves (*Canis simensis*, reviewed by Creel & Macdonald 1995), with the larger of two groups typically winning disputes.

### *Factors Limiting Subgroup Size*

Our data were consistent with all three of the hypotheses suggesting factors limiting subgroup size in spotted hyenas. First, as predicted by the infant safety hypothesis (Otali and Gilchrist, 2006), adult females spent the most time alone with dependent offspring during early lactation, when they stayed near isolated natal dens. Mother-cub associations were especially close at the natal den, and declined as cubs matured. Similarly, lion and chimpanzee mothers are also most solitary during early lactation (Otali and Gilchrist, 2006; Packer et al., 1990; Symington, 1990). In fact, lionesses keep cubs hidden in thick vegetation for the entire first month of life. Like lions (Packer et al., 1990), female hyenas were also frequently found alone during late pregnancy, a finding not predicted by the infant safety hypothesis. Reproductive suppression associated with attacks by conspecifics is unlikely to explain this pattern because female mammals are less physiologically vulnerable to pregnancy loss resulting from attacks during late than during early pregnancy (Wasser and Barash, 1983). However, females late in pregnancy may be least constrained by demands of prior offspring, and therefore prefer to forage alone to maximize energy intake in preparation for the substantial energetic demands imposed on them by neonatal cubs.

The immediate threat of aggression disrupted subgroups in the absence of food, a finding consistent with predictions of the dispersive conflict resolution hypothesis (Schino, 2000). In contrast, victims of aggression rarely reconciled at, nor departed from, feeding subgroups. This suggests that, whereas hyenas sometimes retreat a few steps away from food in response to receiving aggression (Frank, 1986; Kruuk, 1972), individuals rarely leave feeding subgroups when food of high quality is present. Away from kills, however, targets of aggression always remained in subgroups after reconciling fights with former opponents, and targeted hyenas frequently left their subgroups if fights were not reconciled. These data suggest that reconciliation promotes social cohesion by reducing the potential for escalated aggression among individuals that remain in their current subgroups. In the absence of conciliatory interactions, subgroup fission reduced the risk of continued conflict, and the potentially lethal consequences of escalated aggression. In captivity, hyenas fight intensively, and severely wound group-mates when denied opportunities to depart (Jacobi, 1975). However, within-group conflict rarely leads to mortality of adult hyenas in natural populations (Kruuk, 1972). Therefore, the ability of *Crocuta* to resolve conflicts by separating from former opponents appears to provide a second mechanism, along with reconciliation (Hofer and East, 2000; Wahaj et al., 2001), by which hyenas reduce the immediate costs of intra-group conflict.

Finally, our results were consistent with all predictions of the ecological constraints hypothesis (Chapman et al., 1995). This hypothesis was able to explain grouping patterns of all animals in the population, not just those of reproductive females or hyenas recently attacked, over multiple time scales. Our data show that feeding competition constrains grouping behaviour in the short-term at kills, and in the long-term during periods of food scarcity lasting several months. Our findings, together with data from previous studies (Frank, 1986; Holekamp et al., 1996; Höner et al., 2005), imply that ecological constraints operate at virtually all times in the lives of spotted hyenas. It appears the only situations that can trump the disruptive force of feeding competition in hyena societies are those occurring when females have highly vulnerable offspring.

As in other animal societies characterized by FF dynamics (Aureli et al., 2008; Chapman et al., 1995; Kummer, 1971; Lehmann et al., 2007a; Lusseau et al., 2004; van Schaik, 1999), the flexible FF structure of *Crocuta* clans permits individuals to adjust grouping patterns in response to fluctuations in local resource abundance. In Tanzania and Namibia, hyenas redistribute themselves from less profitable areas to more profitable areas in response to long-term changes in prey abundance (Höner et al., 2005; Trinkel et al., 2004). Similarly, *Crocuta* in our study were most gregarious when ecological constraints were relaxed during periods when prey, particularly large-bodied ungulates, were abundant. Because hunting subgroup size did not vary seasonally, the benefits of cooperative hunting could not explain this variation in gregariousness. Instead, this dynamic pattern may be driven by increased within-group aggression at kills during the extended period each year in Talek when prey are scarce (Holekamp et al., 1993).

Over shorter time scales, we showed that hyenas quickly congregated at kills in numbers correlated with the size and energetic value of captured prey. As predicted by the ecological constraints hypothesis, reduced feeding competition permitted the formation of larger subgroups and greater per capita food intake at large than small carcasses. The relative costs of joining feeding groups varied with rank such that low-ranking hyenas, which enjoyed little resource holding power, were least likely to feed in large subgroups. Our data are consistent with earlier research showing priority of access to food is determined by rank in this species (Frank, 1986; Tilson and Hamilton, 1984). In addition, here we show for the first time that an individual's relative rank within its current subgroup directly predicts its immediate rate of food consumption, which likely influences staying and leaving decisions in feeding subgroups. Our work, therefore, extends previous findings indicating that low-ranking individuals hunt significantly more often, and in smaller subgroups than do high-ranking hyenas (Holekamp et al., 1997b). More generally, our data support the hypothesis that resource limitation constrains subgroup size.

On average, adult females consumed 44,161 ± 6,737 kJ (6.4 kg) per hyena per day. This mean daily energy intake value is within the range of values reported for wild spotted hyenas elsewhere in Africa: 2.5 kg (Kruuk, 1972), 3.6 kg (Henschel and Skinner, 1990), 3.8 kg (Green et al., 1984), 6.2 kg (Mills, 1990), 7.4 kg (Whateley, 1980), and 9 kg (Gasaway et al., 1991). They also match the value reported for hungry captive hyenas housed in a group of five individuals (4 kg per hyena, Henschel & Tilson 1988); here Mara hyenas in subgroup sizes of 4.5 to 5.5 each consumed 27,865 ± 7,674 kJ (4.1 kg) per hyena per day.

A number of authors (e.g. Kruuk 1972; Tilson & Hamilton 1984) have suggested that group living evolved in *Crocuta* to facilitate cooperative hunting of large ungulates. Many carnivores including wild dogs, jackals (*Canis* spp.), coyotes, and lions (reviewed by Creel & Macdonald 1995) gain some advantages from cooperative hunting. Similarly, *Crocuta* enjoy increased hunting success and capture a larger array of prey species when hunting in groups than when hunting alone (Holekamp et al., 1997b; Kruuk, 1972). However, our current results, like those from earlier work (Holekamp et al., 1997b), suggest hyenas typically hunt either alone or in pairs, such that the average subgroup size during hunting is significantly smaller than the mean subgroup size documented in any other context.

We suggest that *Crocuta* often hunt alone because individuals who leave their group-mates to hunt are likely to be able to feed from any carcass they acquire for at least a few minutes before other competitors arrive. Here we found that Mara hyenas often fed alone before additional competitors arrived following prey capture. Hyenas are able to detect sounds associated with kills from at least 2.4 km away (Mills, 1989). Noise generated by pairs of hunters competing over kills (e.g. giggles in response to aggression) attracts additional competitors to kills made by groups; by contrast, hyenas feed silently when alone. Spotted hyenas can ingest meat and bone at a rate of 1.3 kg/minute (Kruuk 1972) and lone hunters in our study typically enjoyed much longer periods of solitary feeding than did hyenas hunting in groups. Each lone hunter should be able to ingest approximately 6.5 kg of food during only the first 5 minutes after making a kill. This amount is as much or more than the average adult spotted hyena consumes in a 24-hour period in many parts of Africa (Green et al., 1984; Henschel and Skinner, 1990; Kruuk, 1972).

Although group hunters are 19% more likely than solo hunters to succeed in capturing prey, even the addition of a second hunter dramatically increases ensuing subgroup size. Here, on average, within 10 minutes of prey capture, over six hyenas competed for kills made by pairs of hunters whereas solo hunters almost always still fed alone. We found that hyenas fed nearly the entire time they were alone at fresh kills, but hyenas in subgroups of six at kills spent less than half their time (43%) feeding. Moreover, per capita energy gain declined rapidly with increasing subgroup size such that the majority of individuals feeding in large subgroups consumed very little food. Taken together, these results suggest that hyenas hunting alone enjoy more time feeding, and thus consume more food mass, than individuals hunting with conspecifics. Overall, the initial benefits of increased hunting success are more than offset by the costs of increased competition in the larger subgroups that form after group hunts. Rather than functioning as a cohesive force in *Crocuta* societies, our data suggest that hunting actually promotes subgroup fission. In this regard spotted hyenas differ from societies of wild dogs (Creel, 1997), but are similar to those of many other gregarious carnivores [e.g. coatis (Gompper, 1996), European badgers (Kruuk and Parish, 1982), brown and striped hyenas (Kruuk, 1976; Mills, 1990; Wagner, 2006), and kinkajous (Kays and Gittleman, 2001)] in which individuals reduce feeding competition by leaving group-mates to forage alone or in small subgroups.

### *Conclusions*

Unlike animals living in cohesive social groups, individuals living in FF societies are able to make decisions without the consensus of the entire group (Conradt and Roper, 2005). Our current study demonstrates that *Crocuta* choose to associate with particular numbers of conspecifics based upon their own current state, and in response to fluctuations in the local resource base. Although our data are consistent with predictions of all three of the hypotheses we tested here, only the ecological constraints hypothesis can explain variation in grouping patterns involving all clan members over both short and long time scales.

Extant spotted hyenas apparently descended within the past 900,000 years from a carrion-feeding ancestor with a solitary lifestyle much like that of the modern striped hyena (Lewis and Werdelin, 2000). Our data suggest that selection favoring cooperative hunting did not shape gregariousness during the evolution of this species. However, the ability to capture a larger array of prey animals more successfully might have emerged as a secondary consequence of group living favored by other selection pressures. In many different species, flexible FF lifestyles limit the costs of group living while allowing group members to aggregate when the benefits of sociality are high or the costs of grouping are low (Chapman et al., 1995; Wrangham et al., 1993). Here we found that within-group competition tended to drive individuals apart, whereas intra- and interspecific between-group competition was a strong cohesive force within *Crocuta* clans. Our data, therefore, suggest that group living might have evolved in spotted hyenas to permit cooperation among conspecifics during defense of shared resources, including both space and food. However, constraints imposed by limited food resources might account for retention of the tendency for *Crocuta* to spend large amounts of time alone, rather than the evolution of a more cohesive social structure.

# Chapter 3

Smith JE, Memenis SK, Holekamp KE, 2007. Rank-related partner choice in the fission-fusion society of spotted hyenas (*Crocuta crocuta*). Behavioral Ecology and Sociobiology 61:753-765.

## Chapter 3

# RANK-RELATED PARTNER CHOICE IN THE FISSION-FUSION SOCIETY OF SPOTTED HYENAS

## INTRODUCTION

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

Like monkeys, *Crocuta* frequently compete over limited resources and cooperate by joining forces to direct coalitionary aggression towards conspecifics

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

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

Here, we inquired whether social rank or rank distance influences intrasexual partner choice among unrelated adult *Crocuta* of both sexes. We also investigated the potential benefits of rank-related partner choice among females. In particular, we asked whether dominant or subordinate females initiate associations by promoting group formation. Dominant *Crocuta* benefit from the presence of other clan members in that they enjoy priority of access to resources cooperatively obtained and defended by multiple group members (Cooper 1991; Holekamp et al. 1997b; Boydston et al. 2001; Boydston et al. 2003), but the benefits of such partnerships to subordinates are unknown. We tested three hypotheses, each suggesting a potential benefit to be gained by subordinates from rank-related partner choice. Specifically, we asked whether subordinate females benefit from: 1) reduced harassment (or increased social tolerance) by conspecifics, 2) increased tolerance during feeding, or 3) increased coalitionary support during aggressive interactions. The reduced harassment hypothesis predicts that subordinate females should receive less frequent dyadic aggression and better access to monopolized space from unrelated dominant females with which they associate more often. We examined this in situations in which no food was involved. The feeding tolerance hypothesis predicts that, during feeding competition, females should receive less frequent dyadic aggression from unrelated dominant females with which they associate more often, they should be permitted better access to monopolized food, or both. Finally, the coalitionary support hypothesis predicts that subordinate females should receive more frequent coalitionary support during aggressive interactions from unrelated dominant females with which they associate more often.

## METHODS

### *Study site and subject animals*

From 1988 to 1999, we studied members of one large clan of *Crocuta* inhabiting a territory of $62km^2$ in the Talek region of the Masai Mara National Reserve, Kenya (Boydston et al., 2001). Excluding transient males (immigrants remaining in the clan for less than six months), clan size during the study period ranged from 45 to 78 residents. Each resident was known individually by its unique spots, and sexed based on the dimorphic morphology of its erect phallus (Frank et al., 1990). We estimated birth dates (to ± 7 days) using methods described previously (Holekamp et al., 1996). We classified natal females as adults at 36 months of age or at their first known date of conception, whichever occurred first. Whereas female *Crocuta* are philopatric, males disperse 1-76 months after puberty (Smale et al., 1997; Van Horn et al., 2003), which occurs at approximately 24 months of age in this species (Dloniak et al., 2006; Glickman et al., 1992). On average, genetic relatedness among natal members of a clan is extremely low (Queller-Goodnight $R = -0.05 \pm 0.007$), as is mean relatedness among adult immigrant males (Queller-Goodnight R = 0.009 ± 0.007; Van Horn et al. 2004). Because we were interested here in partner choices involving unrelated adult females, we excluded all dyads containing grandmothers and adult granddaughters, mothers and adult daughters, and adult maternal sisters, based on known maternal relationships and genotyping. We considered all males immigrating into the Talek clan to be unrelated adults.

### *Behavioral data collection*

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

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

### *Measures of intrasexual association*

We estimated the degree of affiliation between members of each dyad using the Twice-Weight Association Index (AI) of Cairns and Schwager (1987), as done previously (Holekamp et al., 1997a; Szykman et al., 2001). We employed this method because it was appropriate for *Crocuta* and because it enabled us to compare our current data to earlier association data for *Crocuta*. We elected not to use the fission-fusion decision index (Cross et al., 2005) because *Crocuta* do not satisfy its key assumption that travel costs are high when individuals move among subgroups within the territory (Holekamp et al., 2000; Kruuk, 1972). We calculated intrasexual AIs for immigrant males for the first time here, and extended earlier analyses of female-female association by including data collected from 15 February 1994 through 31 December 1999, not available in our earlier study (Holekamp et al., 1997a). An AI was calculated for each same-sex dyad of unrelated adults, hyenas A and B, for each year during which they were concurrently present in the clan as adults for at least six months. We calculated $AI_{A,B}$ as: $(A+B_{together}) / [(A_{without\ B}) + (B_{without\ A}) + (A+B_{together})]$ where $(A+B_{together})$ represents the number of observation sessions in which A and B were both present, $(A_{without\ B})$ represents the number of sessions in which A was observed but B was not present, and $(B_{without\ A})$ represents the number of sessions in which B was observed but A was not present.

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

High-ranking females have offspring at the communal den more frequently than do low-ranking females because high-ranking adult females wean their young faster and enjoy shorter interbirth intervals than do low-ranking females (Frank et al., 1995; Holekamp et al., 1996). To avoid this factor as a confounding variable, sessions at the communal den were excluded from all calculations of AIs. Because immigrant males search for mating opportunities by actively joining subgroups containing sexually receptive females (Szykman et al., 2001), we conservatively used only sessions in which potentially fertile females, those over 24 months of age, were absent to evaluate patterns of male-male partner choice while controlling for the effects of mate choice.

*Decisions to join subgroups containing other adult females*

To determine whether subgroups containing each focal female were more likely to be joined by subordinate or dominant females during subgroup fusion events within the clan, we conducted focal animal surveys, totaling at least 2 hours per animal, on eight adult females from our study clan holding ranks of 7, 8, 9, 11, 12, 13, 18, and 21. Adult females ranking above 7 were from the alpha matriline and those ranking below 21 were from the lowest-ranking matriline. Individuals within these two matrilines were excluded from this analysis because no unrelated dominant females were available to join the former and no unrelated subordinate females were available to join the latter. We ended surveys when the focal female went out of view for more than 5 consecutive minutes. We recorded all unrelated females that actively joined each focal female during fusion events throughout the focal animal survey. To control for kinship, a prospective joining animal was only counted if none of her kin were present in the subgroup containing the focal female. We conducted surveys in the absence of food and away from the den to exclude other factors that might promote group formation, and possibly confound joining rates.

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

### *Tests of hypotheses suggesting benefits of rank-related partner choice*

Within each dyad where female A outranked female B, we calculated an hourly rate of aggression observed in each of two contexts, when food was absent and when it was present. We calculated rates of aggression within each dyad by dividing the total number of aggressive acts female A directed towards female B in a particular context by the total number of hours A and B spent together in that context. We required that both members of each dyad be observed together in each context for at least 6 hours during their adult lives. We measured feeding tolerance by dividing the number of scans in which female B fed when female A was present by the number of scans in which both A and B were recorded together during their adult lives in sessions where food was present, and then multiplied by 100. The only dyads included in this analysis were those in which both members were present concurrently as adults at sessions with food during at least 15 scans.

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

### *Statistical analyses*

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

## RESULTS

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

Unrelated adult females associated significantly more closely with each other (AI = 0.037 ± 0.002, $N = 50$ females) than did unrelated adult males (AI = 0.018 ± 0.002; Mann Whitney $U = 2467.00$, $N = 57$ males; $P < 0.001$). For both sexes, mean intrasexual AIs increased with social rank (Figure 3.1A). This relationship was statistically significant among females but not among males (Spearman rank correlation for females: $R_S = -0.88$, $N = 24$ rank positions, $P < 0.001$; for males: $R_S = -0.39$, $N = 18$ rank positions, $P = 0.098$). Both sexes of *Crocuta* associated most often with non-kin holding social ranks similar to their own, as indicated by significant negative relationships between intrasexual AIs and rank distance (Spearman rank correlation for females: $R_S = -0.97$, $N = 24$ rank distances, $P < 0.001$; males: $R_S = -0.86$, $N = 18$ rank distances, $P < 0.001$; Figure 3.1B).

When we controlled for rank distance, females associated significantly more often with females occupying rank positions immediately above them than they did with females occupying rank positions immediately below them (Wilcoxon signed ranks test; $Z = -1.99$, $N = 33$ females, $P = 0.046$; Figure 3.2). However, the relationship between rank and AIs among immigrant males was not statistically significant after we controlled for rank distance (Wilcoxon signed ranks test; $Z = 0.16$, $N = 49$ males, $P = 0.87$; Figure 3.2). That is, the AIs of focal immigrant males with adjacent-ranking, subordinate males did not differ from the

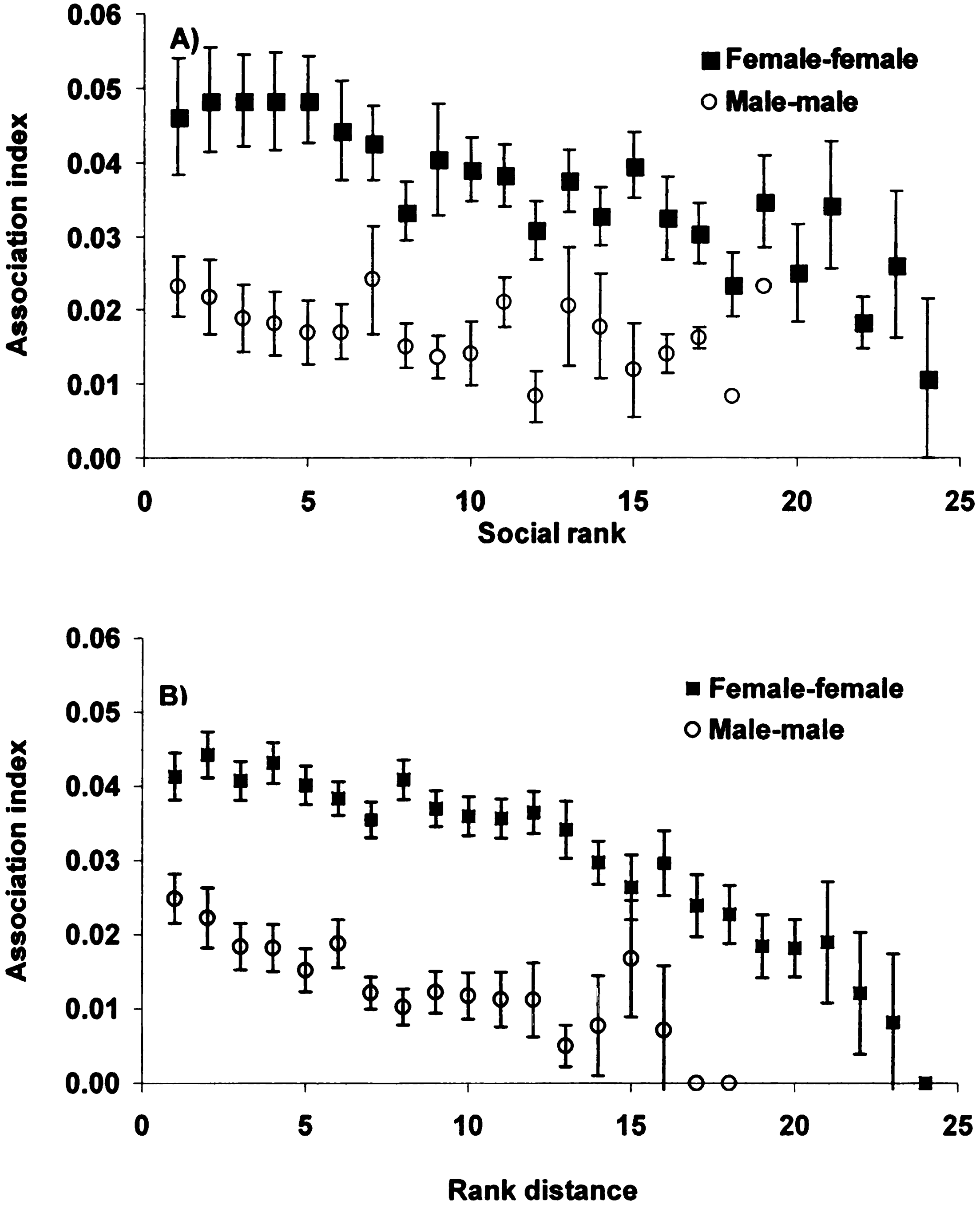

**Figure 3.1.** Mean ± SE intrasexual association indices plotted as a function of A) intrasexual social rank and B) intrasexual rank distance for unrelated adult *Crocuta*. Squares represent adult females and circles represent adult males that held a particular rank while observed with an unrelated adult of the same sex. By convention, the highest rank possible is 1.

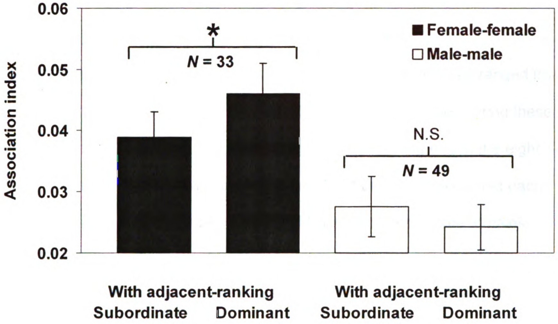

**Figure 3.2.** Mean ± SE association indices of *Crocuta* of each sex with animals of the same sex occupying rank positions either immediately above, or immediately below, them in the hierarchy of the clan. The asterisk over the bracket indicates $P < 0.05$, and N.S. indicates $P > 0.87$.

AIs of focal immigrant males with adjacent-ranking, dominant males. We, therefore, focused our subsequent analyses exclusively on AIs among unrelated adult females, the more selective sex in the context of rank-related, intrasexual partner choice.

*Decisions to join subgroups containing other adult females*

The total time of focal animal surveys for each of the 8 focal females ranged from 2.13 hours to 6.30 hours, averaging 4.39 ± 0.46 hours per female. During these surveys, unrelated adult females joined subgroups containing one of the eight focal females a total of 18 times such that unrelated adult females joined each focal female at an average rate of 0.54 ± 0.11 times/h. Subordinate females joined focal females 15 times (83.3% of fusion events), whereas dominant females joined focal females only three times (16.7% of fusion events). After correcting for the number of potential subordinate and dominant joiners available in the population for each focal female, we found that the percentage of available subordinate females joining focal females per hour was significantly greater than the percentage of available dominant females joining focal females per hour (Wilcoxon signed ranks test, $T = 36$, $N = 8$ females, $P < 0.008$; Figure 3.3). This result was not simply an artifact of the number of unrelated subordinates ($N = 9 \pm 2$) and dominants ($N = 11 \pm 2$) available to join focal females because numbers of individuals from each category did not differ significantly (Wilcoxon signed ranks test; $T- = 19$, $N = 8$ females, $P = 0.95$). Overall, subordinate females selectively joined subgroups containing dominant females significantly more often than vice versa.

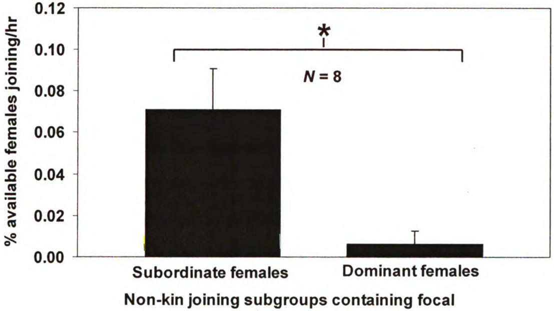

**Figure 3.3.** Proportion of unrelated subordinate and dominant adult females available to join that actively joined subgroups containing focal females, divided by the number of hours during which we monitored each focal female. The asterisk over the bracket indicates $P < 0.05$.

### *Tests of hypotheses suggesting benefits of rank-related partner choice*

Among dyads of unrelated adult females, the majority (95.2%) of all aggressive acts ($N = 2374$) were directed by dominants towards subordinates. Therefore, all rates of aggression reported here refer to aggressions directed by dominants towards subordinates within dyads. The mean rate of dyadic aggression was slightly higher at sessions in the presence of food (0.06 ± 0.005 aggressions/hour) than in its absence (0.05 ± 0.003 aggressions/hour), but this difference was not statistically significant (Wilcoxon signed ranks test, $Z = 1.51$, $N = 367$ dyads, $P = 0.13$). The benefits received by subordinates from dominants were more strongly related to AIs than to rank distance for all measures of aggression when we considered AIs and rank distance as explanatory variables (Table 3.1). In every case, the effect of rank distance was substantially weaker than that of AIs. As predicted by the reduced harassment hypothesis, rates of dyadic aggression were significantly negatively related to AIs within dyads when food was absent (Spearman rank correlation, $R_S = -0.33$, $N = 367$ dyads, $P < 0.001$; Figure 3.4A). The same relationship emerged when food was present, supporting the first prediction of the feeding tolerance hypothesis (Spearman rank correlation, $R_S = -0.12$, $N = 367$ dyads, $P < 0.001$; Figure 3.4B). Tolerance by dominants of subordinates during feeding was significantly higher within dyads that associated more often than within dyads that associated less often, supporting the second prediction of the feeding tolerance hypothesis (Spearman rank correlation, $R_S = 0.33$, $N = 37$ dyads, $P = 0.045$; Figure 3.4C).

**Table 3.1.** Spearman rank correlations between association indices or rank distances and hourly rates of A) non-food and B) food-related dyadic aggression directed by dominants towards subordinates, C) feeding tolerance of subordinates by dominates, and D) hourly rates at which dominants provided coalitionary support to subordinates within dyads of unrelated adult females.

| Dependent variable | Independent variable | | | |
|---|---|---|---|---|
| | Association index (AI) | | Rank distance | |
| | $R_s$ | *P*-value | $R_s$ | *P*-value |
| A) Non-food aggressions/hour | -0.33 | <0.001*** | 0.14 | < 0.006*** |
| B) Food-related aggressions/hour | -0.12 | <0.001*** | -0.003 | 0.96 |
| C) Feeding tolerance (% scans) | -0.33 | 0.045* | -0.13 | 0.44 |
| D) Fights supported/hour | 0.093 | 0.078 | -0.033 | 0.53 |

Asterisks indicate significant relationships at $P < 0.001^{(***)}$ and $P < 0.05^{(*)}$.

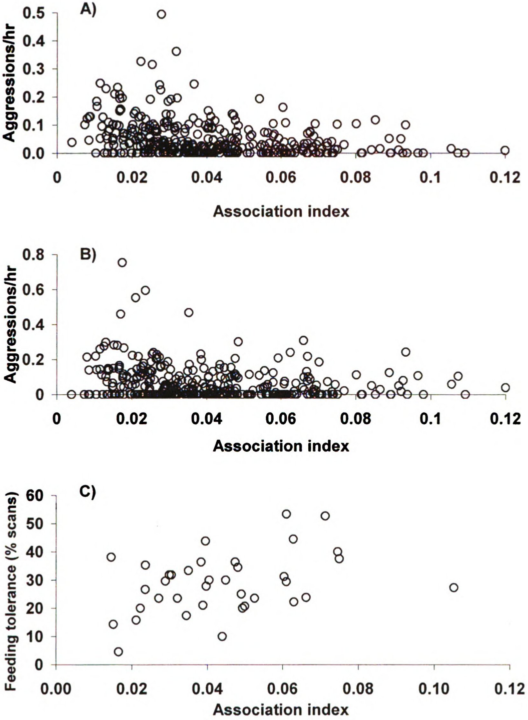

**Figure 3.4.** Hourly rates of dyadic aggression directed by dominant females towards subordinate females when food was A) absent and B) present (*N* = 367 dyads for both). C) Feeding tolerance, measured as the percent of scans in which a dominant female tolerated a subordinate female feeding at a kill when both were concurrently present, plotted against association indices within 37 dyads.

Unrelated adult females provided coalitionary support to focal female aggressors during a total of 28 ongoing dyadic fights involving 12 adult female aggressors that started fights in sessions where both subordinate and dominant unrelated females were present. As expected, dominant females supported aggressors at a significantly higher mean hourly rate than did subordinates (Wilcoxon signed ranks test, $T = 66$, $P = 0.034$; Figure 3.5A). However, our data did not support the main prediction of the coalitionary support hypothesis; we detected no significant relationship between AIs and hourly rates at which dominant females provided coalitionary support to subordinate females within dyads (Spearman rank correlation, $R_S = 0.093$, $P = 0.078$, $N = 367$ dyads; Figure 3.5B).

## DISCUSSION

### *Sex differences in rank-related partner choice*

Overall, high-ranking animals of both sexes were more gregarious than low-ranking individuals. Our data suggest that *Crocuta* assess the ranks of same-sexed conspecifics and associate most often with the adjacent-ranking individuals based on those assessments. Females associated more often with same-sexed adults occupying rank positions directly above them than they did with individuals ranking immediately below them in the clan's dominance hierarchy. Unrelated adult female hyenas also generally associated with one another more closely than did immigrant males, reflecting the same patterns as those found during greeting ceremonies of *Crocuta* (East et al. 1993). Greeting is

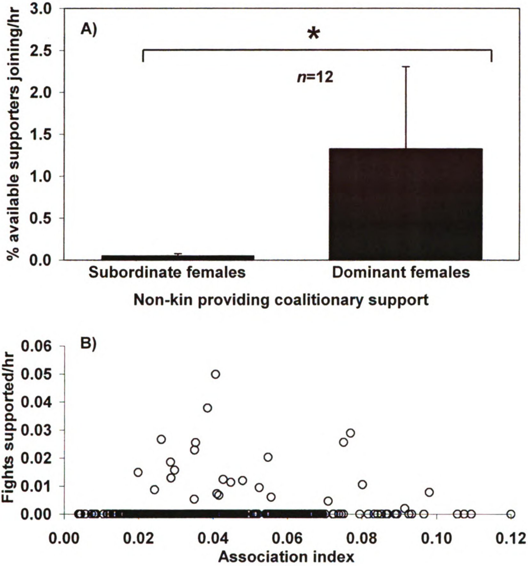

**Figure 3.5.** A) Proportion of subordinate and dominant females present during ongoing fights that intervened to provide coalitionary support to focal female aggressors per hour. The asterisk over the bracket indicates $P < 0.05$. B) The relationship between association indices and rates at which dominant females provided coalitionary support to subordinate females within 375 dyads.

an affiliative behavior exhibited during subgroup reunions (Kruuk, 1972); females initiate more greetings with same-sexed partners than do males, and subordinates initiate greetings more often than do dominants (East et al., 1993). Similarly here adult females associated more often with same-sexed partners than did adult males, and subordinates initiated associations more often than did dominants. Adult males in our study also associated less often with one another (AI = 0.018 ± 0.002) than with adult females (AI = 0.062 ± 0.002: reported by Szykman et al. 2001). The association patterns we observed among hyenas were generally consistent with those in female-bonded groups of cercopithecines (Isbell and Young, 2002; Sterck et al., 1997a; Wrangham, 1980), suggesting that sexually dimorphic patterns of reproduction and dispersal generate sex differences in association in hyenas as they do in primates.

### *Adaptive partner choice in fission-fusion societies*

Dominant hyenas benefit from cooperative partnerships with subordinates (Kruuk 1972; Cooper 1991; Boydston et al. 2001), but our current analysis suggests that low-ranking females actively join subgroups containing dominants. At first, this surprised us, given that dominants often usurp food from subordinates, and that animals are more likely to be targets of dyadic aggression in the presence than in the absence of dominants (Frank, 1986; Mills, 1990). However, the benefits gained by subordinates from joining subgroups containing dominant females may outweigh these potential costs. Subordinate females who associated more often with dominant females were the recipients of relatively low hourly rates of aggression both away from food and at kills, and they also gained relatively good access to food. These data suggest that females minimize the costs of group living by initiating social interactions with conspecifics that outrank them, and by forming relationships likely to offer them return benefits in a variety of ways. By refraining from driving close subordinate associates away from food, dominants allow subordinates to access a highly valued resource, which should enhance subordinates' fitness.

Life in a fission-fusion society appears to permit *Crocuta* to be more flexible in their decisions about partner choice than animals living in more cohesive social groups, including most cercopithecines (Conradt and Roper, 2000; Couzin, 2006). The salient features of fission-fusion societies likely to affect decisions about partner choice are that subgroups are highly labile, and that opportunities exist for dispersive conflict resolution (Wahaj et al., 2001). Patterns of social tolerance in *Crocuta* resemble those documented for other mammals living in fission-fusion societies. For example, African elephants (*Loxodonta africana*) avoid one another to minimize conflict (de Villiers and Kok, 1997). Moreover, red deer (*Cervus elaphus*) stags living in fission-fusion societies structured by stable linear dominance hierarchies (Clutton-Brock et al., 1982) direct the lowest rates of dyadic aggression towards close associates (Appleby, 1983a). Low rates of aggression result when subordinate stags actively avoid dominants, but low rates of aggression within *Crocuta* dyads appeared to be the product of partner solicitation, not avoidance, by subordinates.

### *Alternative theoretical frameworks in which to view partner choice*

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

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

Hamilton's (2000) model assumes that the presence of subordinates enhances the fitness of dominants, and this is true among *Crocuta;* dominants need subordinate allies during cooperative defense of the clan's territory and carcasses against lions or other hyenas (e.g., Boydston et al. 2001), and when hunting certain types of ungulates (Kruuk 1972; Holekamp et al. 1997b.). Furthermore, Hamilton's model correctly assumes that subordinate *Crocuta* will be less likely to leave a group if offered a proportion of the resources obtained by the group, and that dominants can control the division of at least some of the resources obtained by the group. However, this model further assumes that the subordinate's only choice to joining the group is to forage alone, and that subordinates cannot choose among alternative groups; neither of these assumptions hold in *Crocuta*. Most importantly, the skew model assumes that all subordinates will receive an equal share of the dominant's leftovers, an assumption not met in hyenas because subordinates themselves vary in rank. This highlights the more general inability of skew theory to predict patterns of association and partner choice in *Crocuta*. That is, skew models ignore individual variation within dominant or subordinate classes, and assume that all members of each class are identical. Whereas Hamilton's (2000) model successfully predicts that subordinates will join groups containing dominants, and that dominants will offer subordinates incentives to stay by permitting them to feed, it fails to predict that subordinates will choose to associate with dominants ranking just above them in the clan's social hierarchy. One type of model derived from skew theory that takes intra-class variation into account is referred to as a "bidding game (Reeve, 1998; Reeve and Emlen, 2000)." However, this is in effect a "biological market" model (Noë and Hammerstein, 1994; Noë and

Hammerstein, 1995; Noë et al., 2001). We suggest biological market and rank attractiveness (Seyfarth 1977) models are more consistent with our observations than are skew models.

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

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

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

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

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

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

# Chapter 4

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# Chapter 4

# EVOLUTIONARY FORCES FAVORING INTRAGROUP COALITIONS AMONG SPOTTED HYENAS AND OTHER ANIMALS

## INTRODUCTION

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

Agonistic aiding occurs when group members join forces to attack either members of their own social group (intragroup coalitions), or members of a different group (intergroup coalitions). A social group is "any set of organisms belonging to the same species that remain together,... interacting with one another to a distinctly greater degree than with other conspecific organisms" (p. 8, Wilson, 1975b). Whereas researchers have investigated patterns of intergroup coalition formation in many taxa (reviewed by Creel and Macdonald, 1995; Fashing, 2001; Harcourt, 1992), research on intragroup coalitions has historically focused on non-human primates. In fact, early workers suggested that complex patterns of intragroup coalition formation might be unique to primates. For example, Harcourt (1992) proposed that primate coalitions are more complex than non-primate coalitions. Specifically, he posited that intragroup coalitions among primates might occur at higher frequencies, involve larger numbers of coalition partners, and involve adult beneficiaries of support more often than do non-primate coalitions. Further, because the outcomes of coalitions can affect the social ranks of individual group members, and because rank often influences reproductive success, agonistic aiding should theoretically have profound fitness consequences for all participants (Isbell and Young, 2002; Seyfarth, 1977; Sterck et al., 1997a; Wrangham, 1980). Nonetheless, most studies have investigated adult male coalitions or interventions by adult females on behalf of their immature offspring (reviewed by de Waal and Harcourt, 1992; Olson and Blumstein, 2009). As a result, we currently understand little about the evolutionary forces promoting intragroup coalitions among adult females, especially in non-primates (Silk, 2007a;b).

In light of recent advances in our understanding of social complexity among non-primates, we first perform a comprehensive review of 49 species to evaluate the notion that intragroup coalitions formed by primates differ from those formed by non-primates. We then conduct a detailed investigation, documenting patterns of coalition formation in a non-primate, the spotted hyena (*Crocuta crocuta*). Spotted hyenas are gregarious carnivores that live in female-bonded groups (Holekamp et al., 1997a; Smith et al., 2007), called clans (Kruuk, 1972). Because hyena clans are strikingly similar in size and hierarchical structure to troops of cercopithecine primates (Drea and Frank, 2003; Holekamp et al., 2007), this provides a unique opportunity to compare the evolutionary forces favoring coalition formation in primates and carnivores, taxonomic groups that last shared a common ancestor 90-100 MYA (Springer et al., 2003). Specifically, here we describe patterns of coalition formation among various age-sex classes of spotted hyenas belonging to a single, large social group. We then explain these patterns by inquiring in particular why natural selection favors coalitionary support among adult female spotted hyenas.

Like troops of cercopithecine monkeys (Drea and Frank, 2003; Holekamp et al., 2007), hyena clans are multigenerational groups that usually contain multiple matrilines of adult females and their offspring, as well as multiple adult immigrant males born elsewhere (Kruuk, 1972). Further, as in many cercopithecines (Chapais, 1992), adult female spotted hyenas provide coalitionary support to their juvenile offspring to aid them in rank acquisition (East et al., 2009; Engh et al., 2000; Smale et al., 1993). Although it has been shown that hyena siblings generally form coalitions at higher hourly rates than do unrelated individuals (Wahaj et al., 2004), it is unknown to what extent kinship and other factors influence aiding decisions made by adult spotted hyenas.

Because the ultimate goal of this investigation is to elucidate the evolutionary forces shaping this decision-making process, here we test hypotheses suggesting that kin selection, reciprocal altruism, and direct benefits, respectively, drive intragroup coalition formation among adult female spotted hyenas, as detailed below.

*Predictions based on kin selection*

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

*Predictions based on reciprocal altruism*

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

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

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

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

*Predictions based on direct benefits*

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

Food access hypothesis

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

### Status quo hypothesis

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

## METHODS

### *Study site and subjects*

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

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

All adult female hyenas are socially dominant to all adult immigrant males (Frank, 1986). We ranked adult females in a linear dominance hierarchy for each month of the study (Holekamp and Smale, 1993; Smale et al., 1993). Adult females generally maintained stable dominance relations, and most ranks changed gradually over time due to maturation and deaths (Frank, 1986; Holekamp and Smale, 1993). However, two brief periods of social instability occurred during this study (Van Meter et al., 2009).

### *Terminology*

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

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

### *Behavioral data collection*

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

When multiple females joined the same fight, we recorded the sequence in which individuals intervened, and considered this to be a single coalitionary attack. We tabulated the hourly rate of coalition formation for each hyena belonging to a particular age-sex class category. To correct for variation in the amount of time we observed each hyena in situations during which it had opportunities to form coalitions, we based rates on sessions in which each focal animal was concurrently observed with at least one potential coalition partner and at least one potential target. Specifically, we calculated the rate at which hyena A engaged in coalitions as [(number of coalitions hyena A formed to attack any clan member)/(number of hours hyena A was observed with at least two clan members)]. We also calculated a rate of attack directed towards adult females as [(number of coalitions hyena A formed to attack any adult female)/(number of hours hyena A was observed with at least one adult female and at least one other clan member)].

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

### *Testing the kin selection hypothesis*

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

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

To simultaneously investigate patterns of support among multiple females, we constructed a representative, weighted network in NetDraw Version 2.064 for each kin group of adult females concurrently alive from January 1997 to December 1998. First, we constructed a directed graph to represent supportive interventions. Here arrows connecting females were called 'arcs'. Arcs originated from each donor of support, and terminated at each beneficiary of support.

Members of each dyad were connected by: 1) two arcs (reciprocal support), 2) one arc (unilateral support), or 3) zero arcs (no support). For each kinship group, we calculated the "density" of its support network as [(number of realized arcs)/(number of potential arcs)]. Density is a measure of network cohesion that describes how well connected group members are to one another (Wasserman and Faust, 1994; Wey et al., 2008). Second, we applied similar methods to construct an agonistic network for this same subset of adult females. In the coalitionary attack network, arcs originated from intervening females and terminated at victims of coalitionary attacks.

*Testing the reciprocal altruism hypothesis*

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

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

### *Testing the direct benefits hypotheses*

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

### *Statistical analyses*

We tested the effects of kinship, and variables indicating direct benefits, on intervention decisions using the generalized estimating equations (GEE) approach to logistic regression for fitting marginal generalized linear models

(Faraway, 2006; Hardin and Hilbe, 2003; Liang and Zeger, 1986). This procedure is particularly good at handling binary data, while including both fixed and random effects, when model residuals are non-independent and non-normally distributed (Hardin and Hilbe, 2003; Liang and Zeger, 1986). GEE models for binomial data are similar to, but extend, traditional logistic regression by controlling for pseudoreplication resulting from repeated measures (Carlin et al., 2001; Williams, 2000). We implemented these models using geepack (Halekoh et al., 2006) in R Version 2.6.2 (The R Foundation for Statistical Computing 2008).

Sample sizes, limited by knowledge of paternal kinship, did not permit us to build a single model. Instead, as done in similar studies (e.g. Schino et al., 2007b), we built two separate models to evaluate the effects of the explanatory variables on decisions made by females to 1) support beneficiaries and 2) direct coalitionary attacks towards targets when given the opportunity to do so. We used an information-theoretic approach to identify the most parsimonious models (Burnham and Anderson, 1998). We sequentially entered and dropped all potential explanatory terms, including all 2-way interactions, and deemed the candidate model with the smallest Quasilikelihood Information Criterion ($QIC_u$) value to the be the best model (Pan, 2001).

We used STATISTICA 6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.) to conduct post-hoc comparisons. Whenever possible, we used GPOWER (Faul et al., 2007) to perform post-hoc power calculations for non-significant, univariate analyses that were based on small sample sizes. We compared means for two, or among more than two, independent groups using the Mann-Whitney *U* and Kruskal-Wallis tests, respectively. We used matched pairs for post-hoc comparisons whenever this was permitted by our sample sizes. We used Wilcoxon-signed rank tests and Friedman's ANOVA for repeated measures when comparing the means of two, or more than two, dependent groups, respectively. We compared frequencies using the Chi-square test and tested correlations using Spearman's *R*. We applied the sequential Bonferroni adjustment to correct for multiple testing, and report p-values in their corrected form (Rice, 1989). Where appropriate, we report mean values ± 1 SE and sample proportions ± 1 SD for binomial trials (Agresti and Coull, 1998). We based Kendall's (*Kr*) matrix partial correlations on 2,000 random permutations and one-tailed probabilities because the reciprocal altruism hypothesis makes clear, directional predictions (de Vries, 1993; Hemelrijk, 1990a). All other tests were based on two-tailed probabilities and considered significant at alpha less than 0.05.

## RESULTS

### *Coalitions formed by primates and non-primates share similar characteristics*

Overall, the results from our literature review suggest that primates and non-primates fail to differ significantly with respect to the proportion of agonistic interactions that involve coalitions, rates at which individuals form coalitions, mean coalition size, or the proportion of coalitions involving only two allies (Table 4.1). The available data suggest that primates of both sexes are significantly more likely to form intragroup coalitions (87.5 % of 32 species studied) than are

**Table 4.1.** Patterns of coalition formation during intragroup conflicts.

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary | | % of aggressive acts | Coalitions/hr | | Coalition size: Mean w/2 allies | % of coalitions | Kinship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Age | Sex | | per group | per subject (range) | | | | | | |
| **A) Primates** | | | | | | | | | | | | |
| (1) ***Homo sapiens*** (humans) | $20^{W}$ | JJ | BB | 15 % | 5.2 | 0.3 | ---- | ---- | ---- | ---- | Y* | $Y^{R}$ |
| | ---- | BB | BB | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- |
| | Mean across studies: | | | 15 % | 5.2 | 0.3 | ---- | ---- | ---- | | | |
| (2) ***Pan troglodytes*** (chimpanzees)$^{a}$ | $20\text{-}23^{C}$ | BB | BB | 40 % | 1.7 | 0.09 | 3.6 (2-13) | 42 % | M | Y | Y | $Y^{CH,R}$ |
| | $9\ (20\text{-}30)^{C}$ | AA | MM | ---- | 0.4 | 0.04 | ---- | ---- | M | ---- | Y* | ---- |
| | $16\ (20\text{-}30)^{C}$ | AA | FF | ---- | 0.3 | 0.02 | ---- | ---- | M | ---- | Y* | ---- |
| | $9\ (82)^{W}$ | AA | MM | 19 % | 0.1 | 0.01 | ? (2-3) | ---- | ---- | ---- | ---- | $Y^{CH,R}$ |
| | $8\ (?)^{W}$ | AA | MM | 25 % | 0.1 | 0.01 | 2.7 (2-3) | 84 % | ---- | ---- | ---- | $Y^{R}$ |
| | $22\text{-}24\ (\sim 150)^{W}$ | AA | MM | ---- | 0.5 | 0.06 | ---- | ---- | M | N | Y* | $Y^{R}$ |
| | Mean across studies: | | | 25 % | ---- | 0.08 | 3.2 (2-13) | 63 % | | | | |
| (3) ***P. paniscus*** (bonobo) | $6\ (8)^{W}$ | AA | BB | 14 % | 0.6 | 0.1 | 2.4 (2-5) | 58 % | ---- | ---- | Y* | $Y^{R}$ |
| (4) ***Gorilla g. beringei*** (mountain gorilla) | $11\text{-}18\ (13\text{-}24)^{W}$ | AA | BF | 4 % | ---- | ---- | ---- | 77 % | M,P | Y | Y* | ---- |
| (5) ***Papio anubis*** (olive baboon)$^{b}$ | $3\text{-}11\ (?)^{W}$ | AA | MM | 69 % | ---- | ---- | ---- | ---- | ---- | ---- | Y* | ---- |
| (6) ***P. papio*** (Guinea baboon) | $30\ (34)^{C}$ | BB | BB | 15 % | 0.4 | 0.01 | ---- | ---- | M | ---- | ---- | ---- |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary Age | Sex | % of aggress-ive acts | Coalitions/hr per group | per subject (range) | Coalition size: Mean w/2 allies | % of coali-tions | Kin-ship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (7) ***P. cynocephalus*** | 8 (24)$^{W}$ | AA | FF | 7 % | ----- | ----- | ----- | ----- | ----- | ----- | Y* | ----- |
| (yellow baboon)$^{c,d}$ | 6 (41-46)$^{W}$ | BB | FF | 32 % | 0.1 | 0.02 | ----- | ----- | M | Y | ----- | Y$^{R}$ |
| | 6-7 (51-57)$^{W}$ | AA | MM | 8 % | 0.3 | 0.05 | ----- | ----- | ----- | ----- | N* | Y$^{CH}$ |
| | 12 (78-90)$^{W}$ | AA | MM | 17 % | 0.03 | 0.003 | 2.1 (2-3) | 89 % | ----- | ----- | N* | Y$^{CH}$ |
| | 7-17 (20-57)$^{W}$ | AA | FF | 8 % (6-9) | ----- | ----- | 2.7 (2-?) | ----- | M | Y | N | Y$^{R}$ |
| | <u>Mean across studies</u>: | | | 14 % | ----- | 0.02 | 2.4 (2-?) | 89 % | | | | |
| (8) ***P. hamadryas*** | 6 (12)$^{C}$ | AA | FF | 38% | 0.2 | 0.05 | ----- | ----- | ----- | ----- | ----- | Y$^{R}$ |
| (hamadryas baboon)$^{e}$ | | | | | | | | | | | | |
| (9) ***Theropithecus*** | 14$^{C}$ | BB | BB | 21 % | 4.4 | 0.3 | ----- | ----- | ----- | ----- | ----- | ----- |
| ***gelada*** | 3-6$^{W}$ | AA | FF | ----- | ----- | ----- | ----- | ----- | M | Y | Y* | Y$^{R}$ |
| (gelada baboon) | <u>Mean across studies</u>: | | | 21 % | ----- | 0.3 | ----- | ----- | | | | |
| (10) ***Mandrillus*** | 13$^{C}$ | BB | BB | 17 % | 1.5 | 0.1 | 2.3 (2-3) | 72 % | ----- | ----- | ----- | ----- |
| ***sphinx*** (mandrill) | | | | | | | | | | | | |
| (11) ***Macaca*** | 9 (68)$^{SC}$ | AA | BB | 4 % | ----- | 0.01 | ----- | ----- | ----- | ----- | N | Y$^{R}$ |
| ***arctiodes*** | 14 (25)$^{C}$ | AA | BB | ----- | ----- | ----- | ----- | ----- | M | ----- | Y | Y$^{R}$ |
| (stumptail macaque) | | | | | | | | | | | | |
| (12) ***M. assamensis*** | 25 (64)$^{SC}$ | AA | BB | 28 % | 0.3 | 0.01 | ----- | ----- | ----- | ----- | ----- | Y$^{R}$ |
| (Assamese macaque) | | | | | | | | | | | | |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary Age | Sex | % of aggressive acts | Coalitions/hr per group | per subject (range) | Coalition size: Mean w/2 allies | % of coalitions | Kinship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (13) ***M. radiata*** | 10 (72-80)$^{C}$ | AA | FF | ---- | 0.3 | 0.03 | ---- | ---- | M | Y | N | Y$^{R}$ |
| (bonnet macaque)$^{f}$ | 16 (54)$^{C}$ | AA | MM | 25 % | 1.5 | 0.09 | 3.0 (2-9) | 78 % | M | Y | Y | Y$^{R}$ |
| | <u>Mean across studies</u>: | | | 25 % | ---- | 0.06 | 3.0 (2-9) | 78 % | | | | |
| (14) ***M. fuscata*** | 17-24$^{C}$ | BB | BB | ---- | 0.1 | 0.01 | ---- | ---- | M | Y | N | Y$^{CH,R}$ |
| (Japanese | 14 (37)$^{C}$ | AA | FF | 6 % | 1.4 | 0.1 | ---- | ---- | M | ---- | ---- | Y$^{R,CH}$ |
| macaque)$^{d}$ | 22 (24)$^{C}$ | BB | BB | 14 % | 0.06 | 0.003 | ---- | ---- | M | ---- | ---- | ---- |
| | 8-20 (25-55)$^{W}$ | AA | FF | ---- | 0.1 | 0.01 | ---- | ---- | M | Y | N | ---- |
| | 57 (57)$^{C}$ | BB | BB | 16 % | 3.7 | 0.07 | ---- | 86 % | M | Y | Y | Y$^{R}$ |
| | <u>Mean across studies</u>: | | | 12 % | ---- | 0.04 | ---- | 86 % | | | | |
| (15) ***M. mulatta*** | 20-24 (50-62)$^{C}$ | AA | BB | ---- | ---- | ---- | ---- | ---- | M | Y | Y | Y$^{R}$ |
| (rhesus | 18 (~62)$^{SC}$ | BB | FF | ---- | 0.1 | 0.007 | ---- | ---- | M | ---- | ---- | Y$^{CH}$ |
| macaque)$^{g}$ | 12 (?)$^{W}$ | AA | FF | ---- | ---- | ---- | ---- | ---- | M | Y | N | Y$^{R}$ |
| | 39 (67-94)$^{C}$ | AA | BB | ---- | 0.6 | 0.1 | ---- | ---- | M | Y | N | ---- |
| | 34 (172)$^{W}$ | AA | FF | ---- | 1.1 | 0.03 | ---- | ---- | M,P | Y | ---- | Y$^{CH,R}$ |
| | <u>Mean across studies</u>: | | | ---- | ---- | 0.05 | ---- | ---- | | | | |
| (16) ***M. fascicularis*** | 14-17$^{C}$ | BB | BB | 28 % | 3.4 | 0.2 | 2.7 (2-7) | ---- | ---- | ---- | ---- | ---- |
| (long-tailed | 21 (30-40)$^{C}$ | AA | FF | ---- | ---- | ---- | ---- | ---- | M | Y | Y | Y$^{R}$ |
| macaque) | <u>Mean across studies</u>: | | | 28 % | ---- | 0.2 | 2.7 | ---- | | | | |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary Age | Sex | % of aggress-ive acts | Coalitions/hr per group | per subject (range) | Coalition size: Mean w/2 allies | % of coali-tions | Kin-ship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (17) ***M. name-strina*** (pig-tailed macaque) | 49$^{C}$ | BB | BB | 46 % | 4.2 | 0.09 | ----- | ----- | M | Y | N | Y$^{R}$ |
| (18) ***M. tonkeana*** (tonkean macaque) | 19-21$^{SC}$ | BB | BB | 10 % | 0.4 | 0.02 | ----- | ----- | M | Y | ----- | Y$^{R}$ |
| (19) ***M. nigra*** (crested macaque) | 20 (23)$^{C}$ | BB | BB | 16 % | 0.2 | 0.01 | ----- | ----- | M | ----- | ----- | ----- |
| (20) ***M. sylvanus*** | 51 (~250)$^{SC}$ | AA | FF | ----- | 0.1 | 0.002 | ----- | ----- | M | Y | ----- | Y$^{CH,R}$ |
| (barbary | 31 (81)$^{SC}$ | AA | MM | ----- | 0.5 | 0.02 | 3.0 (2-8) | 51% | M | Y | Y | Y$^{R}$ |
| macaque)$^{e}$ | Mean across studies: | | | ----- | ----- | 0.01 | 3.0 (2-8) | 51 % | | | | |
| (21) ***Presbytis*** | 5 (16-28)$^{W}$ | AA | MM | 15% | 0.04 | 0.008 | ----- | ----- | ----- | ----- | ----- | ----- |
| ***entellus*** | 13 (39)$^{W}$ | AA | FF | ----- | 0.02 | 0.002 | ----- | ----- | M | Y | ----- | ----- |
| (Hanuman langurs)$^{c}$ | Mean across studies: | | | 15 % | ----- | 0.005 | ----- | ----- | | | | |
| (22) ***Cercopith-*** | 17 (18)$^{W}$ | BB | BB | 21 % | 1.7 | 0.1 | ----- | ----- | M,P | Y | Y | Y$^{R}$ |
| ***ecus aethiops*** | 23 (10-29)$^{W}$ | AA | FF | ----- | ----- | ----- | ----- | ----- | ----- | ----- | Y* | ----- |
| (vervet monkey)$^{f,d}$ | Mean across studies: | | | 21 % | ----- | 0.1 | ----- | ----- | | | | |
| (23) ***Cercocebus*** | 24 (78-100)$^{W}$ | AA | FF | 3 % | 0.09 | 0.004 | ----- | ----- | ----- | ----- | ----- | Y$^{R}$ |
| ***torquatus atys*** | 12 (27-28)$^{W}$ | BJ | BB | ----- | 0.3 | 0.02 | ----- | ----- | M | Y | ----- | Y$^{R}$ |
| (sooty mangabey) | Mean across studies: | | | 3 % | ----- | 0.01 | ----- | ----- | | | | |

**Table 4.1.** (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary |  | % of aggressive acts | Coalitions/hr |  | Coalition size: Mean w/2 allies | % of coalitions | Kinship | Evidence for kin selection, reciprocity, or direct benefits? |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | Age | Sex |  | per group | per subject (range) |  |  |  |  |  |  |
| (24) ***Lemur catta*** (ring-tailed lemur)$^{d}$ | 10 (20)$^{SC}$ | AA | BB | 1 % | 0.2 | 0.02 | ----- | ----- | M | Y | ----- | ----- |
| (25) ***Eulemur fulvus rufus*** (red-fronted lemur)$^{d}$ | 8 (10)$^{SC}$ | AA | BB | 4 % | 0.8 | 0.1 | ----- | ----- | M | Y | N* | ----- |
| (26) ***Saimiri oerstedi*** (squirrel monkeys) | 23$^{W}$ | BB | BB | ----- | ----- | ----- | ? (2-12) | ----- | M | Y | ----- | ----- |
| (27) ***S. boliviensis*** (squirrel monkeys) | 45-75$^{W}$ | BB | BB | ----- | ----- | ----- | ----- | ----- | M | Y | ----- | ----- |
| (28) ***Cebus apella*** (brown/tufted capuchin) | 13$^{C}$ | BB | BB | 24 % | 0.3 | 0.02 | 2.6 (2-7) | 71 % | M | Y | N | ----- |
| (29) ***C. capucinus*** | 6 (21)$^{W}$ | AA | FF | ----- | 0.1 | 0.02 | 2.0 (2-3) | 96 % | ----- | ----- | N* | Y$^{R}$ |
| (white-faced | 4 (21)$^{W}$ | AA | MM | ----- | 0.09 | 0.02 | ----- | ----- | ----- | ----- | ----- | Y$^{R}$ |
| capuchin)$^{c,d}$ | 30-35$^{W}$ | BB | BB | 16 % | ----- | ----- | ----- | ----- | ----- | ----- | ----- | Y |
|  | <u>Mean across studies</u>: |  |  | 16 % | ----- | 0.02 | 2.0 (2-3) | 96 % |  |  |  |  |
| (30) ***C. olivaceus*** (wedge-capped capuchin) | 3-9 (7-26)$^{W}$ | AA | FF | ----- | ----- | ----- | ----- | ----- | M | ----- | Y* | ----- |
| (31) ***Alouatta palliata*** (mantled howler monkey) | 18 (?)$^{W}$ | AA | BB | ----- | 0.06 | 0.003 | 2.0 (2-3) | 96% | M | Y | ----- | Y$^{R}$ |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary | | % of aggressive acts | Coalitions/hr | | Coalition size: Mean w/2 allies | % of coalitions | Kinship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Age | Sex | | per group | per subject (range) | | | | | | |
| (32) ***Ateles*** | 4-11 (20-35)$^{W}$ | BB | MM | ---- | ---- | ---- | 4.3 (4-5) | 0 % | ---- | ---- | ---- | Y$^{CH}$ |
| ***geoffroyi*** | 5 (20)$^{W}$ | AA | MM | ---- | ---- | ---- | 3.4 (2-5) | 25 % | ---- | ---- | ---- | Y$^{CH}$ |
| (spider monkey)$^{h}$ | Mean across studies: | | | ---- | ---- | ---- | 3.9 (2-5) | 13 % | | | | |
| **B) Non-primates** | | | | | | | | | | | | |
| (33) ***Crocuta*** | 10$^{C}$ | JJ | BB | ---- | 2.6 | 0.3 | 3.2 (2-9) | 47 % | ---- | ---- | ---- | Y$^{R}$ |
| ***crocuta*** | 58-95$^{W}$ | BB | BB | 14 % | 0.4 | 0.1 | 2.4 (2-7) | 71 % | M,P | Y | N | Y$^{CH,R}$ |
| (spotted hyena)$^{a,d}$ | Mean across studies: | | | 14 % | ---- | 0.2 | 2.8 (2-9) | 59 % | | | | |
| (34) ***Panthera leo*** (African lion) | 3 (?)$^{W}$ | AA | FF | ---- | ---- | ---- | 3 | 0 % | M | Y | ---- | ---- |
| (35) ***Nasua nasua*** | 8-30$^{W}$ | BB | BB | 6 % | ---- | ---- | 2.5 (2-6) | 69 % | ---- | ---- | ---- | ---- |
| (ring-tailed coati)$^{d,i}$ | 13$^{C}$ | AA | FF | 38 % | 0.9 | 0.07 | 2.5 | 64 % | ---- | ---- | Y* | ---- |
| | Mean across studies: | | | 22 % | ---- | 0.07 | 2.5 (2-6) | 67 % | | | | |
| (36) ***N. narica*** (white-nosed coati) | 6-22$^{W}$ | BB | BB | 68 % | ---- | ---- | ---- | ---- | M,P | Y | ---- | ---- |
| (37) ***Canis lupus*** | 4-23$^{C}$ | BB | BB | ---- | ---- | ---- | ---- | ---- | ---- | ---- | ---- | Y$^{R}$ |
| (Grey wolf) | 10-12$^{C}$ | BB | BB | 2 % | 0.06 | 0.005 | 5.6 (2-11) | 4 % | ---- | ---- | ---- | ---- |
| | 15$^{C}$ | AA | BB | 4 % | 9.3 | 0.6 | ---- | ---- | M,P | ---- | ---- | Y$^{R}$ |
| | Mean across studies: | | | 3 % | ---- | 0.3 | 5.6 (2-11) | 4% | | | | |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary Age | Sex | % of aggress-ive acts | Coalitions/hr per group | per subject (range) | Coalition size: Mean w/2 allies | % of coali-tions | Kin-ship | Evidence for kin selection, reciprocity, or direct benefits? | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (38) ***Lycaon pictus*** (African wild dog) | $38^{W}$ | BB | BB | ----- | 0.2 | 0.006 | ----- | 50 % | M,P | ----- | ----- | $Y^{R}$ |
| (39) ***Tursiops aduncus*** (bottlenose dolphin)$^{a,c}$ | 21 (~300)$^{W}$ | AA | MM | ----- | 0.5 | 0.1 | 2.9 (2-5) | 68 % | M,P | Y | ----- | Y |
| (40) ***Loxodonta*** | 2-25$^{W}$ | AJ | FB | ----- | ----- | ----- | ----- | ----- | M | Y | ----- | ----- |
| ***africana*** (African elephant)$^{d}$ | 6-12 (18-39)$^{W}$ | AA | FF | 4 % | ----- | ----- | 2.2 (2-4) | 84 % | M,P | Y | ----- | ----- |
| (41) ***Equus quagga*** (plains zebra)$^{d}$ | 23-29$^{SC}$ | BB | BB | 11 % | ----- | ----- | ----- | ----- | M | Y | ----- | Y |
| (42) ***E. caballus*** (wild horse)$^{d}$ | 13 (94)$^{SC}$ | AA | MM | 3 % | 0.01 | 0.0008 | 2 (2) | 100 % | M,P | N | Y | Y |
| (43) ***Dama dama*** (fallow deer) | 34-42 (~570)$^{W}$ | AA | MM | 9 % | 0.04 | 0.001 | ----- | ----- | ----- | ----- | ----- | $Y^{R}$ |
| (44) ***Ovis aries*** (feral sheep)$^{a}$ | 8 (81)$^{SC}$ | AA | MM | ----- | 0.4 | 0.05 | ----- | ----- | ----- | ----- | ----- | ----- |
| (45) ***O. canadensis*** (bighorn sheep) | 24-28 (66-68)$^{W}$ | BB | MM | 10 % | ----- | ----- | 2.2 (2-3) | 80% | M,P | Y | ----- | $Y^{R}$ |
| (46) ***Anser anser*** (greylag geese)$^{j}$ | 53 (170)$^{SC}$ | BB | BB | 10 % | 18 | 0.3 | 2.2 (2-6) | 86 % | M,P | Y | ----- | $Y^{R}$ |

Table 4.1. (Continued)

| SPECIES | Subject # (Group size)$^{Type}$ | Donor & beneficiary Age | Donor & beneficiary Sex | % of aggressive acts | Coalitions/hr per group | Coalitions/hr per subject (range) | Coalition size: Mean w/2 allies | % of coalitions | Kinship | Evidence for kin selection, | reciprocity, or | direct benefits? |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (47) ***Cygnus bewickii*** (Bewick's swan) | ~ 250 (583)$^{W}$ | AJ | BB | 34 % | ----- | ----- | ? (2-3) | ----- | M,P | Y | ----- | Y$^{R}$ |
| (48) ***Corvus frugilegus*** (rook) | 12$^{C}$ | JJ | BB | ----- | ----- | ----- | ----- | ----- | M,P | N | Y* | Y$^{CH}$ |
| (49) ***C. monedula*** (jackdaw) | 26 (36)$^{C}$ | AA | BB | ----- | ----- | ----- | ----- | ----- | ----- | ----- | ----- | Y$^{CH}$ |

**Summary:**

| **Mean ± SE (range) (*N* = species w/data[k])** | **% of aggressive acts (that were coalitions)** | **Coalitions per hour per subject** | **Coalition size** | **% of coalitions w/ only 2 allies** |
|---|---|---|---|---|
| **A) Primates** | **19 ± 3 %**<br>(2-69 %, *N* = 25) | **0.07 ± 0.02**<br>(0.002-0.3, *N* = 26) | **2.9 ± 0.2**<br>(2-13, *N* = 11) | **71 ± 7 %** |
| **B) Non-primates** | **17 ± 8 %**<br>(3-68 %, *N* = 11) | **0.11 ± 0.04**<br>(0.0008-0.6, *N* = 9) | **2.7 ± 0.3**<br>(2-11, *N* = 10) | **63 ± 11 %**<br>(0-100, *N* = 11) |
| **Mann-Whitney U-tests** (Primates vs. Non-primates) | *Z* = 1.31, ***P* = 0.19**<br>Effect size: 0.134<br>Power = 0.072 | *Z* = 0.44, ***P* = 0.66**<br>Effect size: 0.447<br>Power = 0.285 | *Z* = -1.20, ***P* = 0.23**<br>Effect size: 0.166<br>Power = 0.074 | Effect size: 0.250<br>Power = 0.110 |
| **Overall** | **19 ± 3 %** | **0.08 ± 0.02** | **2.8 ± 0.2** | **67 ± 6 %** |

### **Table 4.1.** (Continued)

| (*N* = **species w/data**$^k$) | **% Of studies per species with evidence for:**<br>**Kin selection** | <br>**Reciprocal altruism** | <br>**Direct benefits** |
|---|---|---|---|
| **A) Primates** | **98 ± 2 %** (*N* = 20) | **52 ± 13 %** (*N* = 11) | **100 ± 0 %** (*N* = 20) |
| **B) Non-primates** | **83 ± 10 %** (*N* = 14) | **50 ± 50 %** (*N* = 2) | **100 ± 0 %** (*N* = 12) |
| **Mann-Whitney U-tests**<br>(Primates vs. Non-primates) | $Z = 1.25$, $P =$ **0.21**<br>Effect size: 0.528<br>Power = 0.438 | $Z = 0.10$, $P =$ **0.92**<br>Effect size: 0.028<br>Power = 0.050 | **(N/A)** |
| **Overall** | **92 ± 5 %** | **51 ± 12 %** | **100 ± 0 %** |

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

**Table 4.1.** (Continued)

**Specific notes about variation among studies:** [a]Hourly rates were divided by mean subgroup size to estimate rates on a per subject basis because not all members of the fission-fusion society were simultaneously available as potential coalition partners or targets. [b]Data based only on interventions in disputes in response to adult males soliciting help from donors. [c]Data suggest that donors gain direct benefits in the form of increased access to immediate feeding or mating opportunities rather than, or in addition to, influencing rank relationships per se. [d]Data generated from multiple study groups. [e]Data based on all occurrences of peaceful and aggressive interventions during ongoing interactions of any type between two other group members. [f]Data limited to interventions during conflicts among individuals belonging to different matrilines. [g]Data based only on interventions during ongoing disputes between two siblings. [h]Data based on coalitionary attacks by males during ultimately lethal, intragroup conflicts. [i]One female was immature during the study whereas all other data were collected on adult females. [j]Aggressions only recorded during feeding time. [k]Pair-bonded rock pigeons (*Columbia livia,* Lefebvre and Henderson, 1986) also join forces to direct coalitionary aggression towards conspecifics in their flocks, but comparable data were unavailable. **References:** (1) Humans: (Flinn et al., 2005; Grammer, 1992), (2) (Boesch and Boesch-Achermann, 2000; de Waal, 1984; de Waal and Luttrell, 1988; de Waal and van Hooff, 1981; Hemelrijk and Ek, 1991; Mitani et al., 2000; Mitani et al., 2002; Nishida and Hosaka, 1996; Uehara et al., 1994; Watts, 2002), (3) (Stevens et al., 2005; Vervaecke et al., 2000), (4) (Watts, 1997), (5) (Packer, 1977), (6) (Petit et al., 1997), (7) (Bercovitch, 1988; Noë, 1984; Noë, 1990; Seyfarth, 1976; Silk et al., 2004; Walters, 1980), (8) (Stammbach, 1978), (9) (Bramblett, 1970; Dunbar, 1980), (10) (Schino, unpublished data), (11) (de Waal and Luttrell, 1988; Richter et al., 2009), (12) (Cooper and Bernstein, 2008; Cooper et al., 2005), (13) (Silk, 1982; Silk, 1992; Silk, 1993), (14) (Chapais, 1988; Chapais et al., 1991), (15) (de Waal and Luttrell, 1986; de Waal and Luttrell, 1988), (16) (de Waal, 1977; Hemelrijk, 1994), (17) (Massey, 1977), (18) (Petit and Thierry, 1994), (19) (Petit et al., 1997), (20) (Prudhomme and Chapais, 1993; Widdig et al., 2000), (21) (Borries, 1993; Sommer, 1988), (22) (Hunte and Horrocks, 1987; Seyfarth, 1980), (23) (Range, 2006; Range and Noë, 2002), (24) (Pereira and Kappeler, 1997), (25) (Pereira and Kappeler, 1997; Pereira and McGlynn, 1997), (26) (Baldwin and Baldwin, 1972), (27) (Boinski et al., 2005), (28) (Schino et al., 2009), (29) (Perry, 1996; Perry, 1998; Vogel et al., 2007), (30) (O'Brien, 1993), (31) (Jones, 1980), (32) (Campbell, 2006; Valero et al., 2006), (33) (Engh et al., 2000; Smith et al., 2010; Wahaj et al., 2004; Zabel et al., 1992), (34) (Schaller, 1972), (35) (Hirsch, 2007; Romero and Aureli, 2008), (36) (Gompper et al., 1997), (37) (Derix et al., 1993; Fentress et al., 1987; Zimen, 1976), (38) (de Villiers et al., 2003), (39) (Connor et al., 2001; Connor et al., 1992; Krützen et al., 2003; Parsons et al., 2003), (40) (Lee, 1987)(Archie, Moss, and Alberts, unpublished data), (41) (Schilder, 1990), (42) (Feh, 1999), (43) (Jennings et al., 2009)(Jennings and Gammell, unpublished data), (44) (Rowell and Rowell, 1993), (45) (Pelchat, 2008), (46) (Scheiber et al., 2005, 2009), (47) (Scott, 1980), (48) (Emery et al., 2007), (49) (Wechsler, 1988).

non-primates of both sexes (58.8 % of 17 species, Chi-square test: $\chi^2 = 5.24$, *d.f.* = 1, $P = 0.022$). However, this pattern may be attributed to the literature bias, favoring studies on intragroup coalitions in primates (72 references available). Only 26 references on non-primates were found. Nonetheless, adult animals joined forces during intragroup conflicts in virtually all species reviewed, except for some species of pair-bonded birds for which limited data are currently available. Finally, we failed to detect any differences in the evolutionary forces favoring coalition formation between primates and non-primates. In fact, although evidence of reciprocal trading of coalitionary support among non-kin was generally rare, most species reviewed here gained both direct and indirect benefits from participating in coalitionary interventions.

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

#### Coalition formation among hyenas of all age-sex classes

On average, from 1996 to 2000, our study clan contained 75 ± 1 hyenas (Range: 58 to 95), including 23 ± 1 adult females, for each month of the study (Range: 21 to 25, Table 4.2). We observed 11,194 aggressive interactions and 6,944 greetings among all clan members. Coalitions formed during 14 % of aggressive interactions ($N = 1{,}589$ coalitions). Whereas affiliative greetings occurred at a rate of 1.7 greetings per hour, intragroup coalitions formed only once every 2.7 hours of observation (0.38 coalitions/hour). Based on these 1,589 coalitions, we calculated the frequency, percentage, hourly rate and mean size of coalitions for each clan member ($N = 185$ subjects, including 37 adult females).

**Table 4.2.** Patterns of coalition formation among spotted hyenas belonging to different age-sex classes within a single, large clan in the Masai Mara National Reserve, Kenya

| Demography study clan[a] | | Coalitionary attacks directed toward any member of the clan[b] | | | Coalitionary attacks directed toward any adult female victim[c] | | | Interventions in of female–female fights[d] |
|---|---|---|---|---|---|---|---|---|
| Age-sex class | $\bar{X}$ hyenas/ month (% of clan) (*N* = subjects) | Coalition# (% of all aggressive acts)[a] | Mean±SE hourly rate rate per subject | Mean±SE coalition size per subject | Coalition# (% of all aggressive acts)[a] | Mean±SE hourly rate per subject | Mean±SE coalition size per subject | Intervention # (% of all 3rd-party interventions)[b] |
| Adult females | $\bar{X}$ = 23 (30.7 %)<br>(*N* = 37) | 824<br>(52 %) | 0.16 ± 0.02 | 2.5 ± 0.03 | 480<br>(59 %) | 0.09 ± 0.01 | 2.7 ± 0.08 | 81 (54 %) |
| Juvenile females | $\bar{X}$ = 14 (18.7 %)<br>(*N* = 57) | 711<br>(45 %) | 0.16 ± 0.02 | 2.5 ± 0.03 | 388<br>(48 %) | 0.04 ± 0.005 | 2.8 ± 0.07 | 28 (18.5 %) |
| Juvenile males | $\bar{X}$ = 14 (18.7 %)<br>(*N* = 52) | 691<br>(43 %) | 0.19 ± 0.02 | 2.5 ± 0.03 | 321<br>(40 %) | 0.04 ± 0.006 | 2.8 ± 0.08 | 28 (18.5 %) |
| Natal adult males | $\bar{X}$ = 7 (9.3 %)<br>(*N* = 24) | 302<br>(19 %) | 0.13 ± 0.02 | 2.6 ± 0.05 | 128<br>(16 %) | 0.08 ± 0.02 | 2.7 ± 0.10 | 14 (9 %) |
| Immigrant adult males | $\bar{X}$ = 17 (22.6 %)<br>(*N* = 38) | 230<br>(15 %) | 0.09 ± 0.01 | 2.5 ± 0.01 | 67<br>(8 %) | 0.02 ± 0.004 | 3.1 ± 0.10 | 0 (0%) |
| Entire clan | $\bar{X}$ = 75 hyenas<br>(*N* = 185)[c] | | 0.14 ± 0.12<br>(range: 0-0.79)[d] | 2.6 ± 0.03<br>(range: 2-7) | | 0.04 ± 0.003<br>(range: 0-0.38)[e] | 2.8 ± 0.04<br>(range: 2-6) | 151 |

**Table 4.2.** (Continued)

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

Unless stated otherwise, sample sizes were the same as the number of subjects belonging to each age-sex category represented in Table 4.2.

Overall, the rates at which hyenas formed coalitions varied among age-sex classes (Kruskal-Wallis test: $H_{4,208} = 36.50$, $P = 0.023$, Table 4.2). Adult females ($N = 37$) directed coalitionary attacks towards clan members of any age-sex class at higher hourly rates than did immigrant males ($N = 38$, Mann-Whitney *U* tests: $Z = -2.84$, $P = 0.022$), but at rates similar to those of juvenile males ($N = 52$) or females ($N = 57$), and adult natal males ($N = 24$, $Z = 0.07$, 0.62, and -1.30, respectively; $P \geq 0.582$ for all cases). Modal coalition size (71 % of coalitions) was two hyenas, and coalition size did not vary significantly among age-sex classes (Kruskal-Wallis test: $H_{4,179} = 7.65$, $P = 0.11$, Table 4.2).

Coalition formation among adult female hyenas

Adult females ($N = 37$) were the victims of 51 % of all coalitionary attacks; this was disproportionately high based on their representation in the clan (31 % of clan). In fact, adult females received a greater proportion of attacks (27 ± 2 %, $N = 37$ victims) in the form of coalitionary aggression than did other members of the clan (10 ± 1 % of attacks, $N = 148$ victims, Mann-Whitney *U*-test: $Z = 6.941$, $P < 0.00001$). Moreover, the hourly rates at which hyenas directed coalitionary attacks towards adult female victims varied among age-sex classes of aggressors (Kruskal-Wallis test: $H_{4,208} = 36.5$, $P < 0.0001$, Table 4.2). Natal animals were significantly more likely to direct coalitionary attacks towards adult females than were immigrant males (Mann-Whitney *U*-tests: $U \leq -2.769$ and $P < 0.0006$ for all comparisons, see Table 4.2 for sample sizes). On average, adult females directed coalitionary attacks towards other females more often than did individuals belonging to any other age-sex category, but we detected no sex differences in the rates at which juveniles or natal adults directed coalitionary attacks towards adult females (Mann-Whitney *U*-tests: $U$ = 1468.5 and 352.0, $P$ = 0.934 and 0.528, respectively).

Overall, adult females participated in 480 coalitions attacking other adult females (Table 4.2). Of these attacks, 57 % involved juveniles joining forces with adult females and 29 % involved two or more adult females joining forces to attack a third adult female. Adult females never joined forces with immigrant males to attack adult females. Most (86 %) all-female coalitions contained two partners, 12 % contained three partners, and only 2 % contained more than three partners. Fifty four percent of third-party interventions in disputes between two adult females were by lone adult females. Thus, adult females intervened more often than expected based on their representation in the clan (31 % of clan). Adult females intervened in fights between adult females about three times more often than did juveniles of both sexes and almost six times more often than did adult natal males (Table 4.2).

### *Social and ecological contexts of interventions by adult female hyenas*

Lone adult females intervened in 81 of 1171 (7 %) ongoing dyadic fights between other adult females, and a context could be assigned to 63 of these interventions. Overall, these interventions were more frequent during unprovoked fights (56 %) than during fights in the contexts of food (22 %), maternal intervention (16 %), pesky (6 %), or scapegoating (0 %). After correcting for opportunities to join, we found that the tendency for adult females ($N = 24$) to intervene in ongoing fights varied significantly with the context of the original fight (Friedman's ANOVA: $F_{4,24} = 32.7$, $P < 0.00001$, Figure 4.1). Specifically, females were more likely to intervene in unprovoked dyadic fights than in fights involving scapegoating or food (Wilcoxon signed-ranks tests: $Z \geq 3.24$ and $P \leq 0.005$ in both cases). Females also intervened to a greater extent over food than during scapegoating ($Z = 3.059$ and $P = 0.016$).

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

*Modeling factors to explain interventions by adult female hyenas*

We used model selection to assess the effects of kinship, and variables indicating direct benefits, on the tendency for females to intervene in disputes between adult females. We only included those pairs of adult females for which we could unambiguously assign a coefficient of relatedness in our statistical models. Multiple females were often simultaneously available to intervene at each fight; each focal female ($N = 31$) represented in the statistical models, on

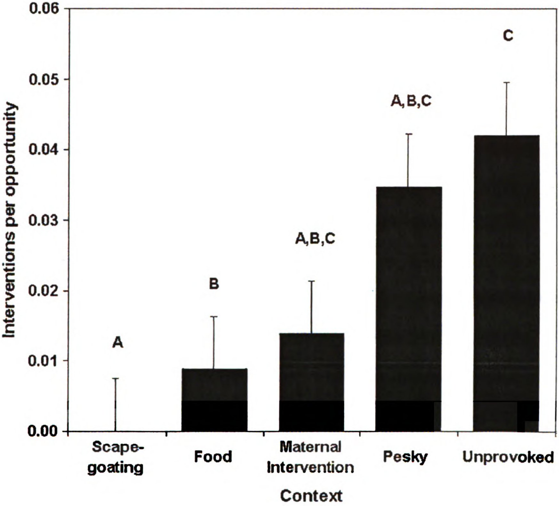


**Figure 4.1.** Mean ± SE interventions per opportunity in which the same adult females ($N$ = 24) intervened in fights between two other adult females based on the context of the original fight. Different letters above bars indicate statistically significant differences after correcting for multiple testing.

average, provided support or directed coalitionary attacks, respectively, in 2.7 ± 0.7 % and 1.9 ± 0.5 % of the cases in which she was available to do so. The same adult females ($N$ = 31) were included in both models, and the extent to which females intervened in fights was statistically equivalent for both data sets (Wilcoxon Signed-Ranks Test: $N$ = 31 females, $Z$ = 1.153, $P$ = 0.249, Effect size: 0.257, Power = 0.403). Final models identified the subset of candidate predictor variables that most strongly structure patterns of coalitionary support and attacks (Tables 4.3 and 4.4). Neither model retained strongly intercorrelated variables ($r^2 \leq 0.10$).

*Kin selection hypothesis*

Nepotistic coalitionary support among adult females

As predicted by the kin selection hypothesis, interventions by adult females were highly nepotistic (Table 4.3, Figure 4.2). Females biased support towards kin, and did so regardless of the intensity of the original fight (Kinship * Intensity interaction: -0.019 ± 0.150, Wald-Statistic = 0.015, $P$ = 0.902). This pattern is best illustrated by placing a subset of female dyads, all of known kinship and all present together as adults in the clan, into a weighted cooperation network (Figure 4.3). Network density increased with the level of relatedness among kinship groups. The density of the close kin network (realized arcs/total possible arcs = 0.38) was over three times that of distant kin (0.12) and over seven times that of non-kin (0.05, Figure 4.3). In addition to providing a concrete example of inter-individual dynamics and coalition formation within one "cohort"

**Table 4.3.** Independent variables predicting patterns of coalitionary support donated by adult females on behalf of adult female beneficiaries during interventions in dyadic fights.

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

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

**Table 4.4.** Independent variables predicting patterns of coalitionary attacks directed by adult females towards adult female victims during interventions in dyadic fights.

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

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

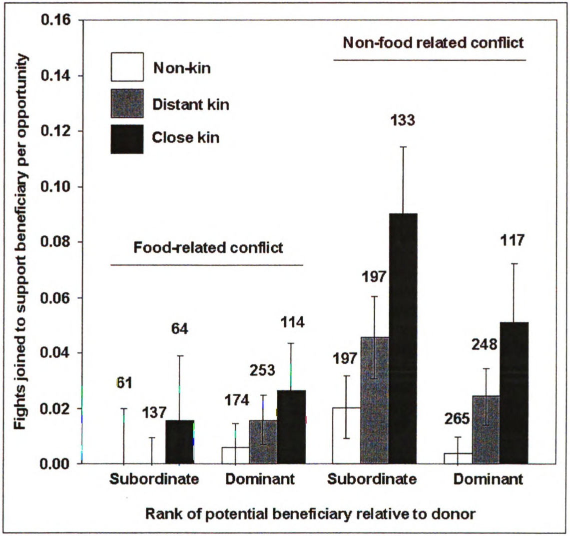


**Figure 4.2.** Proportion of fights in which adult females supported beneficiaries subordinate or dominant to themselves, out of all opportunities to intervene in the presence or absence of food. Bar color indicates kinship of each dyad as non-kin (white), distant kin (gray), and close kin (black). Sample sizes over each bar indicate the number of opportunities potential donors had to support potential beneficiaries. Error bars represent ± 1 standard deviation for binomial trials.

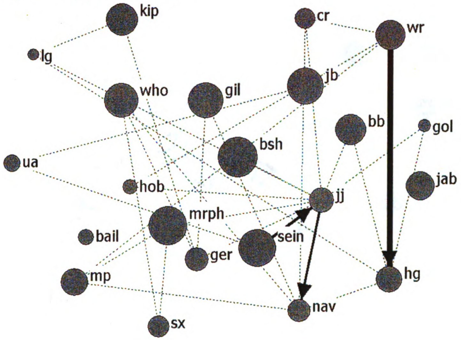
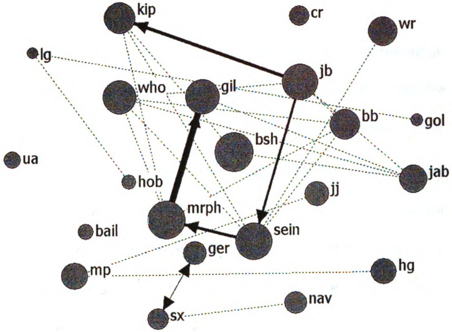

A) Non-kin:
Density of support = 0.05

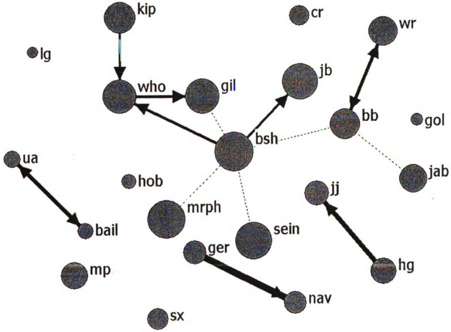
**Figure 4.3.** Cooperation networks among females present concurrently as adults from 1997 to 1998 that were A) non-kin, B) distant kin, and C) close kin. Each circle (node) represents an adult female. Node size is proportional to the social rank held by that female (e.g. alpha female is largest). Connected dyads within each network represent dyads belonging to a particular kinship group based on maternal and paternal kinship. Whereas dyads connected by solid black arcs formed coalitions, dyads connected by dashed gray lines failed to support one another in fights despite the fact that both dyad members had opportunities to do so. Solid, black arrows (arcs) originate at donors of support, and arrowheads point towards beneficiaries of support. Double-headed arcs represent reciprocal support within dyads, whereas single-headed arcs represent unilateral support. Densities reflect the number of realized arcs (number of solid black lines) divided by the total number of possible connections (number of dashed gray lines and solid black lines for each kin group). Line thickness (weighted edges) indicates the proportion of times adult females intervened out of all opportunities to do so

**Figure 4.3.** (Continued)

B) Distant kin:
Density of support = 0.12



C) Close kin:
Density of support = 0.38



of adult females, these diagrams show how female dyads are embedded in the larger network of female social relationships. They also highlight our particularly striking finding that, despite the relative paucity of close kin as potential allies, close kin were clearly the likeliest allies.

Overall, the extent to which adult females intervened on behalf of their sisters varied with their genetic relationship to those sisters (Kruskall-Wallis ANOVA: $H_{2,34} = 7.025$, $P = 0.030$). First, adult females supported their full sisters (10.1 ± 3.6 %, $N = 8$ donors) three or four times more often than they supported their maternal half sisters (2.9 ± 1.3 %, $N = 9$ donors) or paternal half sisters (1.5 ± 1.0 %, $N = 17$ donors), respectively. This bias in support towards full sisters remained statistically significant for paternal half sisters after correcting for multiple testing (Mann-Whitney U-test: $Z = 2.462$, $P = 0.014$, Effect size: 1.093, Power: 0.859). However, the difference between full siblings and maternal half sisters did not remain statistically significant after the correction (Mann-Whitney U-test: $Z = -1.000$, $P = 0.317$, Effect size: 0.925, Power: 0.608). Although females were twice as likely to donate support to maternal than paternal half sisters, this difference failed to reach statistical significance (Mann-Whitney U-test: $Z = 1.812$, $P = 0.070$), perhaps because of our low statistical power (Effect Size: 0.080, Power: 0.056). On average, mothers supported their adult daughters roughly twice as often as those same adult daughters supported their mothers in fights, but this difference was not statistically significant (9.6 ± 4.2 % and 4.7 ± 2.6 % of opportunities, respectively; Wilcoxon signed-ranks test: $T = 19$, $P = 0.678$, $N = 13$ matched pairs, Effect size: 0.291, Power: 0.231). Interestingly, however, females supported their full sisters ($N = 8$ donors, 10.1 ± 3.6 % of opportunities) more often than they supported their mothers or daughters ($N = 18$ donors; 6.3 ± 2.4 % of opportunities; Mann-Whitney *U*-test: $Z = 2.060$, $P = 0.039$).

### Audience effects modulated by kinship

Donating support was costly in the presence of higher-ranking bystanders. Donors of support were attacked by an adult female bystander immediately after 14 ± 6 % of their interventions occurring in the presence of at least one higher-ranking adult female bystander ($N = 30$ donors), whereas none of the 18 donors were subsequently attacked when higher-ranking bystanders were absent (Mann-Whitney *U*-test: $Z = 2.186$, $P = 0.029$). The effects of higher-ranking bystanders were modulated by kinship, as predicted by Hamilton's rule (Table 4.3). That is, adult females were significantly less likely to intervene on behalf of distant kin or non-kin victims of aggression as the number of higher-ranking bystanders increased (Spearman rank correlations: $R_S = -0.719$ and $-0.840$, $P < 0.004$ and $0.005$, $N = 14$ and 9 audience sizes, respectively). Interestingly, however, females intervened on behalf of close kin regardless of the increased risk of doing so near large numbers of dominant bystanders ($R_S = -0.431$, $P = 0.213$, $N = 9$ audience sizes). Because the number of higher-ranking bystanders was correlated with the absolute number of adult females present ($r^2 = 0.25$), we investigated the prospect that the latter variable explained the apparent bystander effects. However, our data allowed us to rule out this possibility because the fit of our best statistical model of coalitionary support was not improved by either the addition of the absolute number of adult females present

(-0.019 ± 0.031, Wald-Statistic = 0.374, *P* = 0.540) or the interaction between this number and kinship (-0.044 ± 0.074, Wald-Statistic = 0.352, *P* = 0.553).

### Kinship fails to protect females from coalitionary attacks

Although adult females strongly biased their supportive interventions towards kin, kinship failed to protect potential victims from becoming targets of coalitionary attacks (Estimate: 0.074 ± 1.155, Wald-Statistic = 0.004, $P < 0.949$). Our best model revealed that coalitionary attacks were significantly more likely when the intensity of the fight was low than when it was high (Table 4.4), independent of kinship (Intensity * Kinship interaction: 1.693 ± 1.970, Wald-Statistic = 0.738, *P* = 0.390). For the subset of dyadic fights in which triadic genetic relationships were known, adult females (*N* = 25) were slightly more likely to intervene in fights when their kinship to each of the contestants differed (3 ± 1 %) than when females were equally related to both contestants (1 ± 1 %), but this difference was not statistically significant (Wilcoxon signed-ranks test: *T* = 5, *P* = 0.500, Effect size: 0.143, Power: 0.136). When intervening in fights in which they were more closely related to one of the two contestants, female aggressors (*N* = 8) were significantly more likely to attack the more distantly related (94 ± 6 %) than the more closely related of the contestants (6 ± 6 %, Wilcoxon signed-ranks test: *T* = 0, *P* = 0.018). Although kinship generally failed to protect females from attacks, this final result is consistent with predictions of kin selection theory because females biased attacks away from the more closely related contestant.

### *Reciprocal altruism hypothesis*

#### No evidence of reciprocity or interchange trading among non-kin

To test for reciprocal trading, we examined the correlation between support given and services received within dyads of non-kin. After controlling for effects of kinship, no significant relationship emerged between support donated and received by adult females (Partial rowwise matrix correlations: *TauKr* = -0.155, *P* = 0.860). We also found no evidence of interchange trading. Non-kin failed to trade support in exchange for help during hunting (*TauKr* = 0.012, *P* = 0.420), opportunities to greet (*TauKr* = -0.079, P = 0.861), or social tolerance (*TauKr* = 0.327, *P* = 1.000). Our data also fail to indicate that natural selection favors agonistic aiding on the basis of indirect reciprocity; females provided the least support when the number of dominant bystanders in the audience was high (Table 4.3).

#### No evidence of stable alliances among non-kin

Unrelated adult females failed to form stable coalitionary alliances. This could be most clearly seen in the support networks, where double-headed arcs, representing reciprocal support, were limited to kin (Figure 4.3B and 4.3C). Moreover, the support network among non-kin was extremely sparse, and non-kin capitalized upon only 5 % of the possible network connections (Figure 4.3A). When we focused on all 106 dyads in which kinship category could be assigned and in which both members had opportunities to provide support, dyads engaging in reciprocal support (6 %) were far less common than dyads providing unilateral support (25 %) or no support (69 %) on behalf of either member of the dyad (Figure 4.4). Reciprocal support was only observed between genetically related adult females (Figure 4.3B and 4.3C) such that dyads of kin participated in reciprocal support more often than did non-kin dyads. Repeated interventions by the same donor on behalf of the same beneficiary were rare. No adult female was ever observed supporting the same unrelated adult female in more than one fight (*N* = 31 females involved in 115 dyads). Even among kin, multiple instances of interventions by the same donor on behalf of the same beneficiary only occurred in 2.2 % of 90 distant kin dyads and 11.1 % of 36 close kin dyads.

### *Direct benefits hypothesis*

#### Coalitionary interventions fail to increase immediate access to food

Three lines of evidence indicate that intervening females do not accrue direct benefits in the form of immediate, enhanced intake of food. First, females were significantly less to likely to intervene during fights involving food than in fights unrelated to food (Table 4.3 and 4.4, Figure 4.2 and 4.5). Whereas females were significantly more likely to support subordinates (6.2 ± 1.7 %) than dominants (1.7 ± 0.5 %) in the non-food context (Wilcoxon signed-ranks test: *Z* = 2.20, *P* = 0.028, *N* = 22 females), females were unlikely to provide support during fights over food, regardless of their rank relative to that of potential beneficiaries (*Z* = 1.05, *P* = 0.294, *N* = 21 females, Effect size: 0.169, Power: 0.151). Second, coalitionary aggression was no more effective in displacing competitors from kills (52.6 ± 11.8 %) than was dyadic aggression (51.6 ± 9.2 %) by the same aggressor (*Z* = 44.50, *P* = 0.944, *N* = 19 females, Effect size: 0.059, Power: 0.606). Finally, local prey abundance failed to predict female interventions in

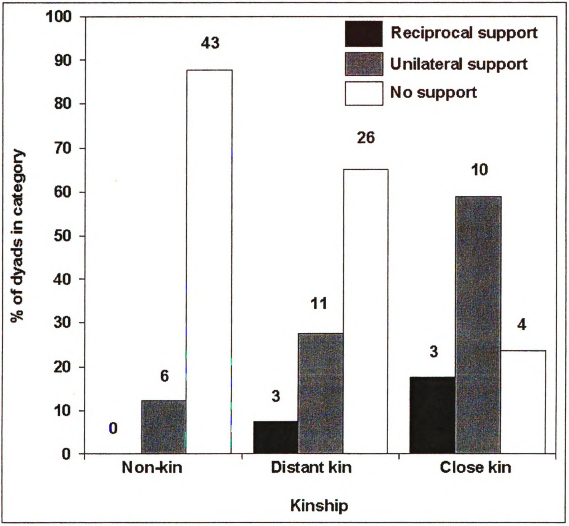


**Figure 4.4.** Variation among kinship categories regarding the proportion of dyads in which both members supported one another (reciprocal support: black), only one member supported the other member (unilateral support: gray), or neither member provided support to the other (no support: white). Sample sizes over bars indicate the number of dyads in which both members had opportunities to provide reciprocal support ($N$ = 106 dyads).

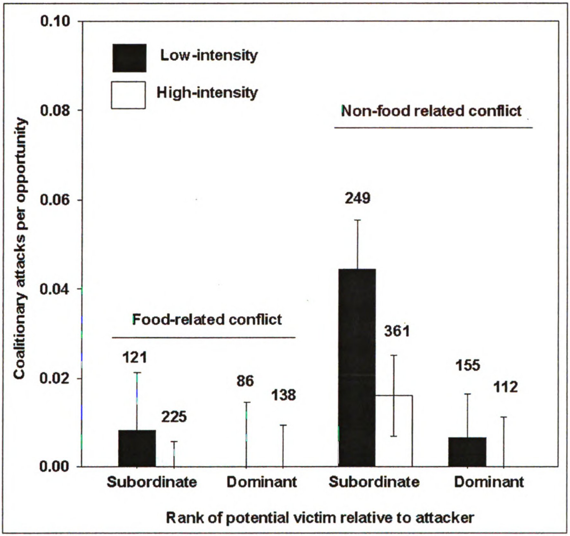


**Figure 4.5.** Proportion of fights in which adult females attacked victims subordinate or dominant to themselves, given the opportunity to intervene in the presence or absence of food. Bar colors indicate whether females intervened in ongoing dyadic fights of low (black) or high (white) intensity. Dyads belonging to all kinship categories are pooled because kinship failed to protect victims from attacks. Sample sizes over bars indicate the number of opportunities females had to attack targets already under attack by another adult female. Error bars represent ± 1 standard deviation for binomial trials.

fights (Tables 4.3 and Table 4.4).

### Coalitionary interventions reinforce the status quo

Our data are generally consistent with the idea that females benefit directly from reinforcing the status quo. A univariate approach revealed that high-ranking females, with comparable opportunities to intervene, on average, did so significantly more often than did low-ranking females (Spearman rank correlations: $R_S = -0.733$, $P < 0.0001$, $N = 25$ rank positions, Figure 4.6). Nonetheless, relative ranks within dyads (e.g. beneficiary subordinate to potential donor in Table 4.3 and victim subordinate to potential attacker in Table 4.4) were better predictors of whether adult females intervened than were the absolute ranks of potential donors (Table 4.3) or attackers (Table 4.4). Females directed the majority of coalitionary attacks towards subordinate victims (Table 4.4, Figure 4.5 and 4.7), and in most fights (93.9 ± 2.5 %) supported the higher-ranking of the two contestants (Wilcoxon signed-ranks test: $Z = 5.012$, $P < 0.00001$, $N = 36$ donors). Cooperation and agonistic networks reflect these rank effects. High-ranking females, indicated by large node sizes (Figure 4.3), provided the most support in cooperation networks. Because females directed most attacks down the hierarchy towards victims subordinate to themselves, arrows originated at nodes larger than those at which they terminated in the agonistic network (Figure 4.7). The density of the agonistic network (0.08 realized arcs/potential arcs) was low in part because these females only attacked subordinates (Figure 4.7).

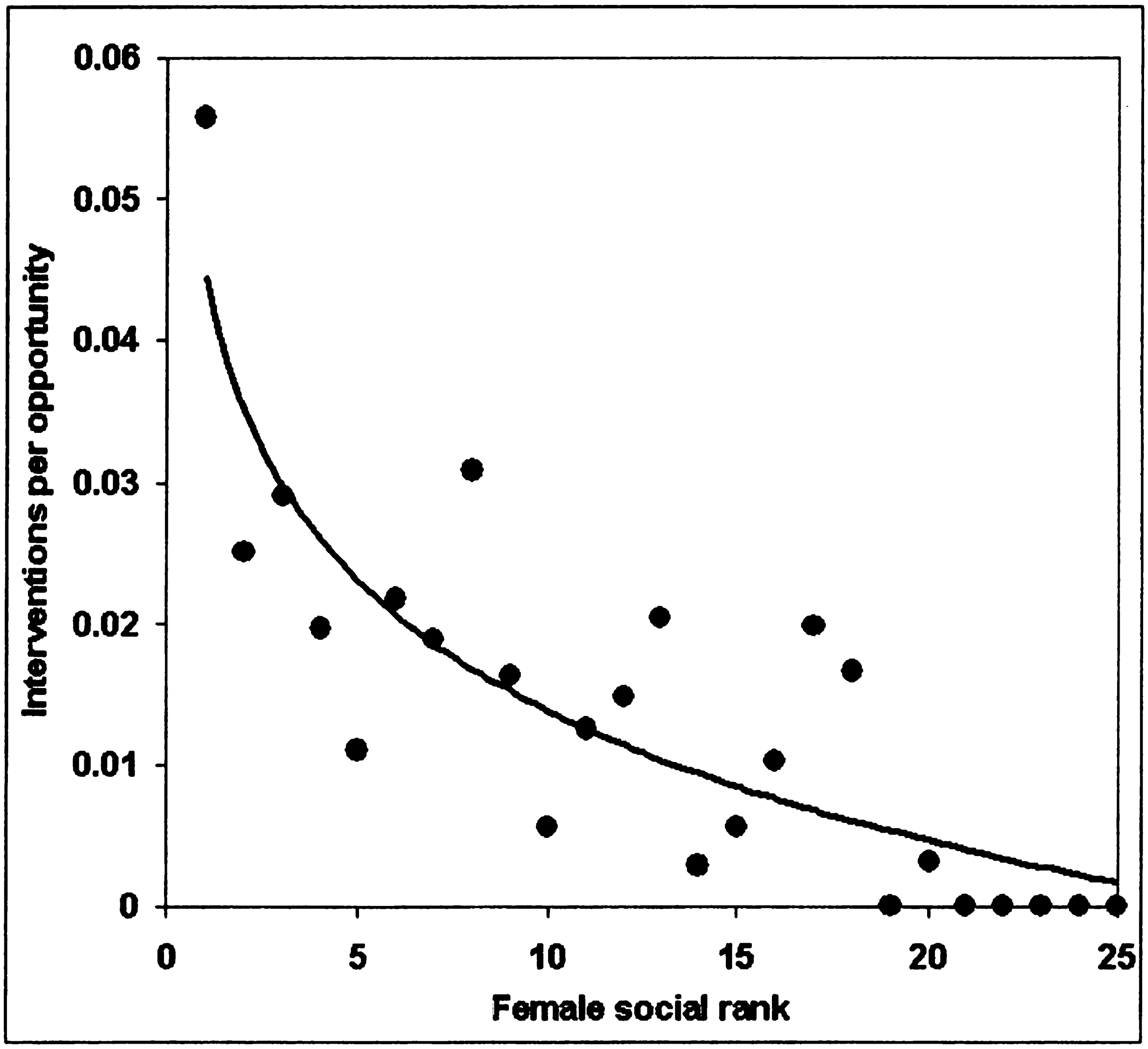


**Figure 4.6.** The effect of absolute social rank on the proportion of fights in which females intervened on behalf of other adult females out of all opportunities in which females holding a particular social rank might have supported potential beneficiaries. By convention, the highest possible rank is one (e.g., the alpha female).

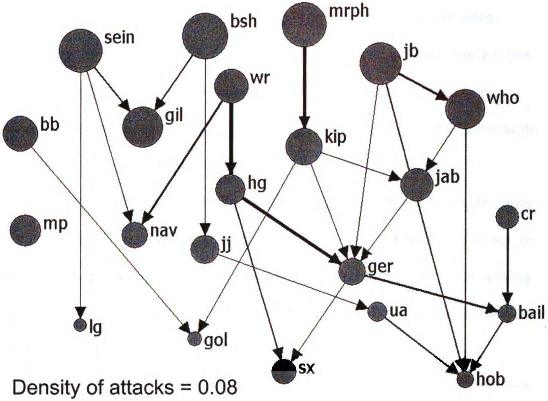


**Figure 4.7.** Agonistic network: A directed, weighted attack network structured by the same adult females as in Figure 4.3. Solid, black arrows (arcs) originate at intervening aggressors, and arrowheads terminate at victims of coalitionary attack. Line thickness (weighted edges) indicates the proportion of times adult females targeted the other member of the dyad out of all opportunities to do so. All dyads are shown on a single network because kinship failed to protect females from coalitionary attacks.

## DISCUSSION

### *Intragroup coalitions in spotted hyenas compared to those in other taxa*

Overall, we failed to detect any differences in the salient characteristics of intragroup coalitions formed by primates and non-primates. Moreover, the evolutionary forces favoring intragroup coalitions in spotted hyenas were strikingly similar to those found for many cercopithecines. Indeed, many monkeys simultaneously direct coalitionary support towards kin while limiting their individual costs by directing attacks towards subordinates to reinforce the status quo. For example, this pattern occurs among female baboons (*Papio cynocephalus*) as well as male stumptail (*Macaca arctiodes*), bonnet (*M. radiata*), and barbary (*M. sylvanus*) macaques (see Table 4.1 for references). In fact, our findings that nepotism and direct benefits shape intervention decisions among adult female hyenas parallels findings from most vertebrate species for which comparable data are available.

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

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

### *Nepotism among adult female spotted hyenas*

As in most adult mammals reviewed here (Table 4.1) and earlier (e.g. Silk, 2002; Widdig, 2007), intragroup coalitions among adult female spotted hyenas were generally nepotistic. Consistent with the predictions of kin selection theory (Lehmann et al., 2007b), the density of cooperation networks clearly increased with the degree of genetic relatedness among adult female hyenas. Moreover, mothers received support from their adult daughters as often as adult daughters received support from their mothers. These data support the hypothesis proposed by Holekamp and Smale (1995) suggesting that, in addition to gaining indirect benefits by helping their young daughters acquire their dominance status, mothers directly benefit by gaining new adult allies when their daughters mature.

Females preferentially supported full sisters over half sisters, biasing more support towards maternal than paternal half sisters. Although the latter result was not statistically significant, we suspect that our low statistical power may have kept us from detecting a biologically meaningful difference. This proved to be the case, for example, when Silk et al. (2006) discovered that the inability of Smith et al. (2003) to distinguish between nepotism directed towards maternal and paternal kin in baboons was an artifact of small sample sizes. More broadly, our results indicate that nepotism directed by adult females towards both maternal and paternal kin resemble patterns observed among adult female mountain gorillas (*Gorilla g. beringei*, Watts, 1997), adult female rhesus macaques (Widdig et al., 2006), and juvenile spotted hyenas (Wahaj et al., 2004). Despite its seemingly important influence on coalition formation, paternal kinship was rarely considered in the vast majority of studies reviewed here, underscoring the need for future studies that evaluate the role of paternal kinship in structuring cooperative decisions in animals.

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

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

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

### *No evidence of reciprocity among unrelated adult female hyenas*

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

### *Feeding competition limits coalition formation among adult female hyenas*

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

### *Adult female hyenas gain direct benefits from reinforcing the status quo*

Although females forming coalitions at a carcass apparently do not improve their immediate access to food, females that direct coalitionary attacks towards subordinates away from food should nevertheless benefit directly in feeding situations. That is, because dominance relationships are stable across contexts in this species (Frank, 1986), by using coalitions to reinforce the status quo away from food, females guarantee their priority of access to resources during subsequent competitive interactions at carcasses. Indeed, coalitions appear central to the maintenance of rank relations long after adult female spotted hyenas establish their ranks as juveniles (Holekamp and Smale, 1993; Smale et al., 1993; Engh et al., 2000). Consistent with our findings here, a number of other mammals living in despotic groups similarly use coalitionary attacks to reinforce the status quo (see Table 4.1 for details and references).

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

### *Do members of highly cooperative groups enjoy enhanced fitness?*

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

### *To cooperate or not: a complex decision*

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

# Chapter 5

Smith JE, Powning KS, Dawes SE, Estrada JR, Hopper AL, Piotrowski SL, Holekamp KE, To be submitted, June 2010. Gestural communication reinforces alliances among greeting partners in the spotted hyena. Animal Behaviour.

## Chapter 5

# GESTURAL COMMUNICATION REINFORCES ALLIANCES AMONG GREETING PARTNERS IN THE SPOTTED HYENA

## INTRODUCTION

Societies characterized by fission-fusion dynamics consist of subgroups of variable size and composition in which group members regularly join (fusion) or separate from (fission) each other (Kummer, 1971). This flexible lifestyle characterizes the societies of humans, chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles* spp.), elephants (*Loxodonta* spp.), many cetaceans (e.g. bottlenose dolphins, *Tursiops truncatus*), and most terrestrial carnivores. This social structure permits individuals to separate temporarily from one another when the costs of grouping are high, and to aggregate when the costs of grouping are low or the benefits of sociality are high (Aureli et al., 2008; Lehmann et al., 2007; Rodseth et al., 1991; Schino, 2000; Smith et al., 2008; Wrangham et al., 1993). Although life in a fission-fusion society permits individuals to reduce conflicts of interest (Conradt and Roper, 2005), this lifestyle imposes a unique set of challenges upon group members that are often separated from one another for long durations (Aureli et al., 2008). As a result, individuals must cope with uncertain relationship status after temporary separations (Barrett et al., 2003).

Theory predicts that ritualized signals should evolve that quickly communicate the intent of senders to receivers when relationship status is uncertain (Endler, 1993; Maynard Smith and Price, 1973; Zahavi, 1980). Consistent with this prediction, many animals use visual displays, called gestures, to communicate their intent to conspecifics (Hewes, 1973; Pollick and de Waal, 2007). Greetings, or meeting ceremonies, are important non-aggressive gestures that often involve risky and intimate contact. Ritualized greetings can function to reconcile fights (Aureli and de Waal, 2000), signal acknowledgement of relative social status (de Waal, 1986; de Waal and Luttrell, 1985; Preuschoft and van Schaik, 2000), reduce tension among individuals with insecure social relationships (Aureli and Schaffner, 2007; Dias et al., 2008; Kutsukake et al., 2006), or reinforce social bonds (Smuts, 2002; Smuts and Watanabe, 1990).

Spotted hyenas (*Crocuta crocuta*) engage in greetings when two partners stand parallel to each other and face in opposite directions to sniff each other's anogenital region (East et al., 1993; Glickman et al., 1997; Kruuk, 1972). The importance of the erect phallus in both sexes makes these greetings particularly intriguing. Females erect their penile clitoris and males erect their penis during greetings. Symmetric greetings occur when both members engage in the same set of behaviors, such as both lifting their leg during mutual investigation of the genitalia (East et al., 1993). In asymmetric greetings, only one partner exhibits the behavior. Greetings that serve as a form of reconciliation only account for roughly 8-9% of all greetings in this species (East et al., 1993). Although previous studies (Hofer and East, 2000; Wahaj et al., 2001) demonstrated that these conciliatory greetings are useful in preventing escalated aggression between former opponents, the vast majority of greetings occur in other contexts, suggesting that these signals may serve other important functions.

Early workers found that spotted hyenas in the Serengeti National Park typically initiate greetings with social partners dominant to, or older than, themselves (East et al., 1993; Kruuk, 1972). Although both of these earlier studies agreed that low-ranking hyenas were most likely to initiate greetings, the interpretation of these results differed. Kruuk (1972) hypothesized that greetings likely function to reestablish social bonds at reunions because hyenas "expose the most vulnerable area of their bodies to the teeth of their opponents (p. 229)". In contrast, East et al. (1993) concluded that "greetings are a ritualized, active form of submission that confirm asymmetries in status between greeting partners (p. 364)", and referred to the erect phallus as a "flag of submission".

Although greetings might signal submission, East et al. (1993) failed to rule out alternative hypotheses that appeared in the literature after 1993, or to use contemporary multivariate statistics to account for correlations among potential predictor variables. Here, we take advantage of modern conceptual frameworks and quantitative methods to extend earlier work, and to resolve discrepancies in the interpretation of early studies. Adopting the methods of East et al. (1993), we first replicate their work by documenting the occurrence of greetings among members of a single, large social group of spotted hyenas in the Masai Mara National Reserve. Next, we confirm that reconciliation only accounts for a small fraction of greetings in our population and, for the first time, reveal how conciliatory and non-conciliatory greetings differ. Finally, we test three competing hypotheses, each of which aims to elucidate the type of information communicated during non-conciliatory greetings among spotted hyenas.

Spotted hyenas are long-lived carnivores that reside in complex fission-fusion societies, called clans, containing up to 80 individuals that defend a common territory (Kruuk, 1972). Individual members travel, rest, and forage in subgroups that change membership roughly every hour (Kruuk, 1972; Mills, 1990; Smith et al., 2008). Clans are structured by linear dominance hierarchies (Frank, 1986), and contain one to several matrilines of adult females and their offspring, as well as multiple adult immigrant males. Virtually all males permanently disperse from their natal clans after puberty, but females are philopatric (East and Hofer, 2001; Mills, 1990; Smale et al., 1997).

Our main goal here was to investigate the function of non-conciliatory greetings among adult females. Hyenas belonging to this age-sex category greet each other at the highest frequencies (East et al., 1993). Moreover, although rank relationships are extremely stable among adult females (Engh et al., 2000), those of juveniles are often not yet firmly established (Holekamp and Smale, 1993; Smale et al., 1993). Further, although adult females maintain long-term social bonds (Holekamp et al., 1997a), associations among adult males are often weak (Smith et al., 2007) or short-lived (Van Horn et al., 2003). Adult females make active decisions to join temporary subgroups containing their kin (Holekamp et al., 1997a). Among non-kin, adult females associate most often with females ranked directly above them in the dominance hierarchy and, by doing so, gain enhanced tolerance from dominants (Smith et al., 2007).

### *Predictions based on the submission hypothesis*

To minimize the costs of competition, dominance hierarchies structure societies in which individuals use transient signals to communicate their knowledge of power asymmetries among group members (Lu et al., 2008; Preuschoft, 1999;

Preuschoft and van Schaik, 2000). Because spotted hyenas use multiple status indicators to reliably signal submission in a variety of contexts (Frank, 1986; Kruuk, 1972), the initiation of greetings might represent another formalized status signal. Although this hypothesis generally predicts that low-ranking females should solicit greetings more often than high-ranking females, as found by East et al. (1993), it importantly predicts that initiation of greetings should be strictly *unidirectional* within dyads across ecological contexts (de Waal and Luttrell, 1985; de Waal and Luttrell, 1989). Therefore, the degree of directional consistency and transitive properties of greeting initiation should coincide precisely with those found in a dominance hierarchy based on fight outcomes. Moreover, because animals closest in rank possess the greatest need to clarify dominance (de Waal, 1991), females should greet most often and engage in the least symmetric greetings with females holding ranks similar to their own.

#### *Predictions based on the tension reduction hypothesis*

The tension-reduction hypothesis posits that, to reduce the probability of costly fighting, natural selection should favor the evolution of ritualized gestures that signal peaceful intent, and, thus, reduce fighting among individuals with insecure relationships, especially in contexts in which tensions might otherwise be elevated (Aureli and Schaffner, 2007; Colmenares et al., 2000; Dias et al., 2008; Hohmann and Fruth, 2000; Kutsukake et al., 2006). If greetings evolved to reduce tensions, then adult females should greet most often, and engage in the most symmetric greetings, with those females with whom their social relationships are least secure, such as non-kin, distantly associating kin, or hyenas with which they rarely form coalitions. Further, feeding competition is intense in this species; hyenas feed at kills that are energetically rich and highly ephemeral (Frank, 1986; Kruuk, 1972; Mills, 1990; Smith et al., 2008). Thus, if greetings reduce tensions over food, then females should greet most often per opportunity when kills are immediately present, especially during those months when prey abundance is locally scarce. Finally, if greetings reduce immediate tensions, or substitute for aggression in tense contexts, then greeting partners should direct less aggression towards one another in the minutes directly after reunions than do non-greeting partners.

### *Predictions based on the social bonding hypothesis*

The social bonding hypothesis posits that group-living animals should use risky interactions to routinely test and reinforce affiliative relationships (Kummer, 1978; Smuts, 2002; Zahavi, 1977b). Specifically, senders and receivers should theoretically use costly signals to exchange honest information about social bonds (Gintis et al., 2001; Zahavi, 1977a). Because hyena greetings are potentially costly if they result in severe genital wounding (Kruuk, 1972), greetings might facilitate the development and maintenance of social bonds. If greetings reflect affiliative ties, then hyenas should greet their preferred social partners most often, and these greetings should be the most symmetric. Further, if greetings reinforce bonds, then they should occur most often in contexts in which tensions are reduced (Smuts and Watanabe, 1990), as in the absence of direct feeding competition, and might facilitate cooperative hunting (Creel and Creel, 2002) or coalition formation (Smuts, 2002).

## METHODS

### *Study site and subjects*

From June 1988 through December 2004, we monitored spotted hyenas from a large clan that defended a stable group territory in the Masai Mara National Reserve, Kenya (Boydston et al., 2001). Spotted hyenas feed primarily on antelope they hunt themselves, but local prey abundance varies seasonally (Holekamp et al., 1997b). Feeding competition is reduced and social cohesion is enhanced among clan mates when migratory ungulates are present with resident herds (Holekamp et al., 1996; Smith et al., 2008).

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

Here we determined the social rank of each individual hyena based on the outcomes of dyadic agonistic interactions; all adult females were dominant to all immigrant males (Holekamp and Smale, 1993; Smale et al., 1993). We ranked adult males and females in separate hierarchies, with the highest possible rank in each being one. We calculated rank distance as the absolute value of the difference in intrasexual ranks between the members of each dyad.

### *Behavioral data collection*

Using our field vehicles as mobile blinds, we observed hyenas daily. We initiated an observation session each time we encountered one or more hyenas separated from other clan members by at least 200 meters; hyenas in different sessions were typically separated by at least 1 km (Smith et al., 2008). Upon arrival at each session, and during subsequent scans performed every 15-20 minutes, we recorded the identity and activity of every hyena in that focal subgroup. We recorded as critical incidents all occurrences of agonistic interactions, greetings, and hunting (Altmann, 1974). Aggressive behaviors included head waves, lunges, chasing, displacements, standing over, biting, pushing, and aggressive postures.

Following Wahaj et al. (2001), we considered a greeting to serve a conciliatory function between former opponents if it occurred within 10 minutes immediately after a fight. Based on this definition, we categorized each greeting as either conciliatory or non-conciliatory. Dyadic aggression involved only one aggressor, whereas coalitionary aggression involved at least two hyenas joining forces to direct aggression towards the same target animal (Smith et al., 2010). Intragroup coalition partners were those females that formed at least one aggressive coalition directed towards one or more members of their clan.

Resident females also joined forces to attack alien hyenas during intergroup conflicts at territory boundaries, called clan wars, or to attack lions during conflicts over food (Kruuk, 1972). Hunting partners were those females that hunted together. Thus, within each session, each pair could potentially cooperate as intragroup coalition partners, as hunting partners, as participants in a clan war, and/or as coalition partners in joint attacks directed towards lions.

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

We also timed a subset of greetings using a stopwatch, starting when the initiator lifted its hind leg and ending when the terminating hyena put its hind leg back down on the ground. Most of these greetings were timed during a single year of our study. From these data, we calculated the duration of each greeting for which a clear initiator, start time, and end time could be discerned.

Whenever possible, in addition to recording the stereotypic behavior of leg-lifting, we also recorded all well-recognized submissive signals (e.g. head-bobbing, submissive posture, groveling (carpel crawling), and open mouth appeasement), including unsolicited appeasements, and all affiliative behaviors (e.g. nuzzling, rubbing-against, sniffing, friendly approaches or presenting of the hindquarters) emitted by hyenas during greetings.

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

### *Testing the submission hypothesis*

First, we confirmed that juveniles and lower-ranking hyenas in our study clan initiate greetings most often, as observed by East et al. (1993). Then we extended this finding by testing the null hypothesis that the hierarchical orders of adult females winning fights and receiving greetings were equivalent (de Vries et al., 1993). We also calculated the directional consistency index (DC, van Hooff and Wensing, 1987), linearity index (*h'*, de Vries, 1995), and Kendall's coefficient of linearity (*K*, Appleby, 1983) for dominance and greeting matrices constructed for the same adult females, all of which had the opportunity to interact with each other as adults both at and away from kills.

DC was based on the number of times that a behavior was performed in the direction of higher frequency within each dyad (H) minus the number of times it occurred in the direction of the lower frequency within each dyad (L), divided by the number of times it was performed by all individuals: DC = (H - L)/(H + L). DC ranges from zero, for completely bidirectional exchanges, to one for completely unidirectional exchanges (van Hooff and Wensing, 1987). Because this measure is a proportion, it allows for meaningful comparisons between matrices containing unequal numbers of interactions. It also provides equivalent information to indices used by previous authors (e.g. Noë et al., 1980; Rowell, 1966).

We evaluated the linearity and transitive properties of both matrices using two methods. Linearity is a measure of how consistently individuals positioned higher in the hierarchy outrank all individuals ranked lower than themselves (Whitehead, 2008). If such relationships are transitive, then when A outranks B, and B outranks C, A must also outrank C. We used an improved version of Landau's h index of linearity (Appleby, 1983b; Landau, 1951), called *h'*, which corrects for unknown relationships. This corrected measure allowed us to make comparisons between matrices in which relationships within some dyads were unknown. This measure ranges from zero, for a completely non-linear system, to one for a completely linear system (de Vries, 1995). Second, we calculated *K* to assess linearity based on transitivity of triads in each matrix (Appleby, 1983).

### *Testing the tension reduction and social bonding hypotheses*

Because greetings may occur either at subgroup fusion when individuals reunite after being separated, or among hyenas that have been present together in a subgroup for several hours (Kruuk, 1972), we first quantified the distribution of greetings over time after reunions. Because the vast majority of greetings occurred within the first 10 minutes after fusion events (see Results), we constructed statistical models to assess the effects of social and ecological variables on the propensity for adult females to greet, given the opportunity to do so, within 10 minutes after fusion. Models based on greetings occurring within 5 minutes after fusion produced equivalent results. Thus, for the sake of brevity, we report only the former results. We entered subgroup size at fusion (number of possible greeting partners available to each arriving female) as a covariate to control for the possibility that greeting queues might form at fusion events.

Although the mean genetic relatedness among natal members of our clan is extremely low, adult females belonging to the same matriline are all closely related to one another (Van Horn et al., 2004a). Here, we modeled the effects of kinship on greeting interactions by entering two measures of relatedness directly into our models as continuous predictor variables. First, following Wahaj et al. (2001), we assigned coefficients of relatedness based only on known maternal relationships from pedigree data. Second, following Smith et al. (2010), we assigned coefficients of relatedness to female pairs based on knowledge of maternal pedigrees and genetic assignment of paternal relationships.

Statistical models explaining the tendency to greet at fusion were based on detailed records extracted for all fusion events from 1996 to 2000. Although data on greeting symmetry were available throughout our longitudinal study, we limited our statistical models explaining symmetry to those greetings observed before 2001 to ensure that social ranks were stable; our study clan permanently split into two clans by 2001 (Smith and Holekamp, unpublished data).

Because patterns of association reflect social preferences among hyenas (Holekamp et al., 1997a; Smith et al., 2007; Wahaj et al., 2004), we calculated the Twice-Weight Association Index (AI) of Cairns and Schwager (1987) to investigate the strength of social bonds within dyads. An AI was calculated for each pair of females, hyenas A and B, during which they were concurrently present in the clan as adults. We calculated $AI_{A,B}$ as: $(A+B_{together}) / [(A_{without\ B}) + (B_{without\ A}) + (A+B_{together})]$ where $(A+B_{together})$ represents the number of sessions in which A and B were both present, $(A_{without\ B})$ represents the number of sessions in which A was observed but B was not present, and $(B_{without\ A})$ represents the number of sessions in which B was observed but A was not present.

### *Statistical analyses*

We implemented all matrix analyses in MatMan 1.0 (Noldus Information Technology, Wageningen, The Netherlands). For measures of linearity, we used a two-step test with 10,000 randomizations (de Vries 1995). Matrix analyses were based on one-tailed probabilities because these hypotheses make clear, directional predictions (de Vries, 1993; Hemelrijk, 1990a). All other tests were based on two-tailed probabilities. Differences were considered significant at alpha less than 0.05. We applied the sequential Bonferroni adjustment to correct for multiple testing, and report all *P*-values in their corrected form (Rice, 1989). Where appropriate, we report mean ± 1 SE and sample proportions ± 1 SD for binomial trials (Agresti and Coull, 1998).

We built generalized linear mixed models (GLMM) to evaluate the effects of the predictor variables using lme4 (Bates and Maechler, 2010) in R Version 2.6.2 (The R Foundation for Statistical Computing 2008). We entered the identity of each hyena as a random effect to avoid potential pseudoreplication, and tested the significance of its inclusion in each model using likelihood-ratio tests (Pinheiro and Bates, 2000). For each data set, we sequentially entered and dropped all potential explanatory terms, including all 2-way interactions, and deemed the candidate model with the smallest Akaike's information criterion (AIC) value to the be the best model (Burnham and Anderson, 2002). No strongly intercorrelated variables were retained in any of the final models ($r^2 \leq 0.15$). We obtained statistics for terms removed from our best model by adding each term individually to the minimal model. We modeled the duration data assuming a Gaussian family because these data were normally distributed. To predict decisions made by adult females to: 1) greet with potential adult female partners within 10 minutes after fusion events and 2) engage in symmetric gestures when greeting other adult females, we modeled data using binomial response variables. Otherwise, we used *STATISTICA* 6.1 (StatSoft, Inc., Tulsa, OK, U.S.A.) to analyze data failing to meet assumptions of normality and/or homoscedasticity of variances. We compared means for two, or more than two, independent groups using Mann-Whitney $U$ and Kruskal-Wallis tests, respectively. We compared means from dependent groups using Wilcoxon-signed rank tests and tested correlations using Spearman's $R$.

## RESULTS

### *Distribution and patterning of conciliatory and non-conciliatory greetings*

We recorded a total of 15,852 greetings involving 414 individual hyenas during 15,288 observation hours. Only 0.3 % ($N = 52$) of all greetings involved more than two partners, such that the mean number of hyenas involved in each greeting was 2.0 ± 0.0 hyenas (Range: 2 to 7 partners). Greetings were generally spontaneous, and rarely occurred in response to overt aggression. In fact, only 8.9 % of greetings were conciliatory and the rest were non-conciliatory (91.1 %). Interestingly, focal hyenas ($N = 387$) were more almost twice as likely to engage in one or more affiliative behaviors (35.9 ± 2.0 % of greetings) than to display submissive signals when soliciting greetings (18.2 ± 1.0 % of greetings, Wilcoxon Sign-Ranks Test: $Z = 11.00$, $P < 0.00001$). Similarly, recipients ($N = 395$) of invitations to greet were twice as likely to engage in affiliative behaviors (21.9 ± 1.1 % of greetings) than to display submissive signals (10.6 ± 0.9 % of greetings, Wilcoxon Sign-Ranks Test: $Z = 10.13$, $P < 0.00001$). Hyenas never attempted to greet with heterospecifics, and natal hyenas only greeted with clan members. Only on 7 occasions did immigrant males greet with males from a neighboring clan; it is possible that these males previously belonged the same clan.

### Duration of all greeting ceremonies

Greetings were similar in duration to those measured by East et al. (1993), lasting, on average, 20.9 ± 0.7 sec. (range = 1 to 95 sec., $N = 283$ greetings). We first confirmed the singular finding on duration from this earlier study. Specifically, when we used the methods of East et al. (1993), we also found that intrasexual greetings were longer between adult females (24.6 ± 1.1 sec., $N = 27$ adults) than adult males (18.7 ± 2.0 sec, $N = 17$ adults, Mann-Whitney *U*-test: $Z = 2.194$ and $P = 0.028$). We then extended this result by modeling other factors that might influence the duration of greetings among different age-sex classes. Interestingly, adult females ($N = 31$, 22.8 ± 1.0 sec.) participated in greetings that lasted longer than those involving juvenile females ($N = 20$, 21.0 ± 1.1 sec.), juvenile males ($N = 32$, 17.4 ± 1.1 sec.), or immigrant males ($N = 18$ males, 19.4 ± 2.0 sec., Table 5.1). The duration of greetings was also influenced by the relationship between the hyenas involved. That is, our best model revealed that greetings between adults (24.7 ± 1.4 sec.) lasted longer than those involving one or more juveniles (19.2 ± 1.4 sec., Age composition: Table 5.2). Further, greetings initiated by females (23.4 ± 1.1 sec.) lasted longer than those initiated by males (18.4 ± 0.9 sec., Sex of initiator: Table 5.2). Interestingly, conciliatory greetings lasted roughly 50 % longer (30.7 ± 4.8 sec.) than did non-conciliatory greetings (20.2 ± 0.7 sec., Table 5.2). Finally, greetings initiated by dominants (22.4 ± 1.4 sec.) lasted longer than those initiated by subordinates (20.1 ± 0.8 sec., Table 5.2).

**Table 5.1.** Independent variables predicting the duration of greetings in which focal hyenas participated.

| Coefficients: | Estimate ± S.E. | *Z*-value | *P*-value |
|---|---|---|---|
| (Intercept) | 18.517 ± 0.807 | 22.947 | <0.000001 |
| Age (adult) | 2.584 ± 1.122 | 2.303 | 0.022 |
| Sex (female) | 1.720 ± 1.144 | 1.503 | 0.134 |

The effects of age and sex were additive (Interaction: -0.769 ± 2.344, *Z* = -0.328, *P* = 0.743). Neither the main effect of social rank (-0.005 ± 0.032, Z = -0.141, P = 0.888), nor its interaction with age (0.052 ± 0.063, *Z* = 0.828, *P* = 0.409) or sex (-0.056 ± 0.064, *Z* = -0.877, *P* = 0.382) improved the fit of the model. Including the random effect of hyena identity improved the best model (Likelihood ratio test: $\chi^2$ = 4.3, *d.f.* = 1, *P* = 0.038), which was based on 283 greetings involving 32 juvenile males, 18 adult males, 20 juvenile females and 31 adult females.

**Table 5.2.** Independent variables predicting the duration of greetings based on the relationships between initiators and recipients of greetings.

| Coefficients: | Estimate ± S.E. | *Z*-value | *P*-value |
|---|---|---|---|
| (Intercept) | 16.706 ± 1.100 | 15.193 | < 0.0000001 |
| Conciliatory greetings | 10.254 ± 2.667 | 3.844 | 0.0001 |
| Age composition (both adults) | 3.793 ± 1.589 | 2.388 | 0.018 |
| Sex of initiator (female) | 2.820 ± 1.478 | 1.908 | 0.058 |
| Initiator outranks recipient | 2.770 ± 1.412 | 1.962 | 0.051 |

The inclusion of the following additional factors as predictors of the duration of greetings within female pairs failed to further improve the fit of our best model: kinship (0.876 ± 1.4980, $Z = 0.585$, $P = 0.559$), rank distance (-0.045 ± 0.065, $Z = -0.697$, $P = 0.487$), absolute rank of initiator (0.026 ± 0.047, $Z = 0.546$, $P = 0.586$), and absolute rank of recipient (-0.007 ± 0.047, $Z = -0.159$, $P = 0.874$). Including the random effect of hyena identity improved the model (Likelihood ratio test: $\chi^2 = 15.1$, *d.f.* = 1, $P = 0.0001$), which was based on 283 greetings involving 32 juvenile males, 18 adult males, 20 juvenile females and 31 adult females. Conciliatory greetings involving former opponents lasted longer than non-conciliatory greetings. Age composition influenced duration; greetings between adults lasted longer than greetings involving one or more juveniles.

Hourly rates of greetings vary with life history stage and context

East et al. (1993) reported the frequencies of greetings (but not hourly rates) between different age and sex categories observed exclusively at the communal den. By contrast, we report here the hourly rates at which different classes of animals participated in greetings not only at dens but also at kills and locations away from kills and away from dens (called "other contexts"). Overall, the hourly rate at which hyenas participated in greetings varied among life history stages (Kruskal-Wallis test: $H_{2,649} = 102.7$, $P < 0.0001$). In general, adult females ($N = 75$) and subadults ($N = 209$) participated in greetings at similarly high hourly rates (Mann-Whitney U-test: $Z = 0.276$, $P = 1.0000$). Both adult females and subadults greeted at significantly higher rates than did den cubs ($N = 289$ cubs, $Z \geq 8.101$, $P \leq 0.000001$). We detected no sex differences in the rates of greeting at which den cubs ($Z = -0.690$, $P = 1.0000$, $N_F = 137$, $N_M = 152$) or subadults ($Z = 0.270$, $P = 1.0000$, $N_F = 97$, $N_M = 112$) greeted. Immigrant males ($N = 76$) greeted with clan members at lower rates than did subadults or adult females ($Z \geq 2.979$, $P \leq 0.014$), but at rates similar to those of den cubs ($Z = 0.702$, $P = 1.0000$).

Next we inquired whether hourly rates of greeting varied among contexts. Here we combined subadults and adult females into a single category, called den-independent hyenas, because these natal hyenas participated in greetings at indistinguishable rates within each context. Den cubs were only observed at the den, but we compared rates at which den independent hyenas ($N = 232$) and immigrant males ($N = 76$) greeted in all three contexts. Overall, the hourly rates at which hyenas participated in greetings varied significantly among life history stages and among contexts (Kruskal-Wallis test: $F_{6,1299} = 234.3$, $P < 0.0001$, Figure 5.1). In contrast to the predictions of the submission and tension-reduction hypotheses, hyenas participated in greetings at the lowest hourly rates at kills.

Initiation of greetings by juveniles and subordinates

Adopting the methods of East et al. (1993), we analyzed patterns of initiation for all greetings such that our initial analysis included both conciliatory and non-conciliatory greetings. As found by East et al. (1993), the younger or socially subordinate of the two partners here typically solicited greetings by lifting their leg first. The extent to which juveniles initiated greetings with adults depended upon on the age–sex category of the partners involved (Kruskal-Wallis ANOVA: $H_{3,610} = 10.873$, $P = 0.0124$, Figure 5.2). When greeting partners differed in age, the younger hyena lifted its leg first significantly more often (76.6 ± 2.2 %) than did the older partner ($N = 304$ focal hyenas, Wilcoxon Signed-Ranks Test: $Z = 8.25$, $P < 0.000001$). Both den cubs ($N = 259$) and subadults ($N = 178$) initiated a significant majority of their greetings with adult females ($Z \geq 6.921$ and $P \leq 0.000001$). However, the initiation of greeting was generally symmetric when den cubs ($N = 85$) or subadults ($N = 108$) greeted with adult males ($Z \leq 0.856$, $P \geq 0.398$). Focal den cubs ($N = 79$) and subadults ($N = 103$) initiated a greater proportion of greetings involving adult females than they did when greeting adult males ($Z < 3.922$, $P \leq 0.007$). However, we found no sex difference in the extent to which den cubs initiated greetings with adult females ($N_F = 111$, $N_M = 129$) or males ($N_F = 40$, $N_M = 44$, Mann-Whitney $U$-test: $Z \leq 0.994$, $P \geq 0.960$ for both). Strikingly, although both sexes of subadults ($N_M = 58$, $N_F = 50$) initiated greetings

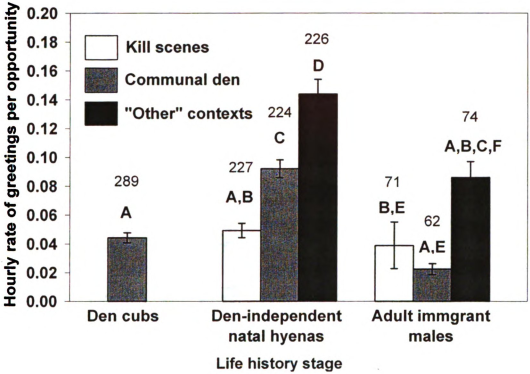


**Figure 5.1.** Mean ± SE hourly rates at which hyenas in each life history stage participated in greeting ceremonies at kills, dens, and "other" contexts (both away from kills and away from dens). Because we detected no sex differences in the rates at which den cubs or den-independent natal animals greeted, we pooled the values within each life history stage. Sample sizes shown above each bar represent numbers of individuals in each category. Letters above bars indicate statistically significant differences after correcting for multiple testing at $P < 0.05$.

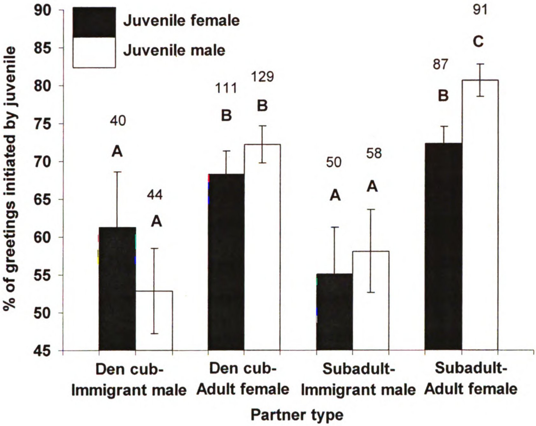


**Figure 5.2.** Percentage of greetings with adults initiated by juveniles. Den cubs were those juveniles still residing at the den whereas subadults were those juveniles that were independent of the den but not yet adults. Sample sizes shown above each bar represent numbers of individuals involved in greetings with partners in each adult category. Letters above bars indicate statistically significant differences after correcting for multiple testing.

with adult males to similar extents (Mann-Whitney U-test: $Z = -0.231$, $P = 1.000$), male subadults ($N = 91$) were significantly more likely than female subadults ($N = 87$) to initiate greetings with adult females ($Z = -2.903$, $P = 0.0185$). Among same-sexed dyads of adults, the subordinate partner was significantly more likely to lift its leg first in both sexes than was the dominant greeting partner ($N_M = 42$, $N_F = 59$, 75.1 ± 4.9 and 73.7 ± 3.2 %, $Z \geq 4.19$, $P \leq 0.00003$). Therefore, as before, when we used the same methods used by East et al. (1993), we observed the same patterns they did.

*Linearity and directional consistency among adult females*

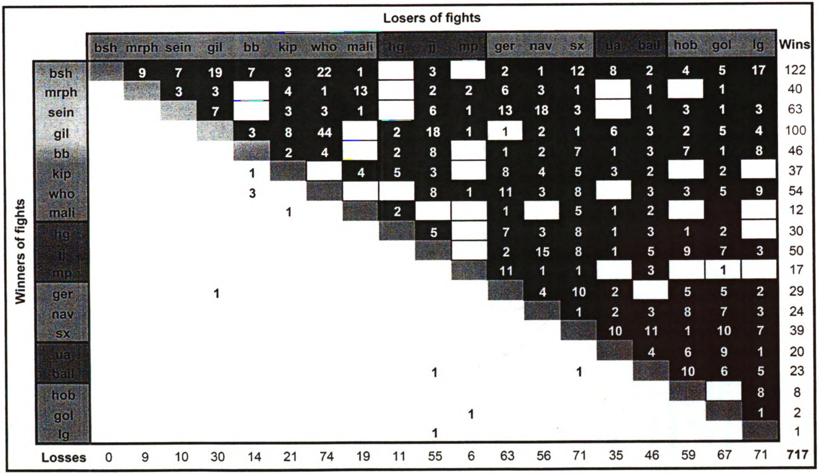
Although the results reported above are consistent with those of East et al. (1993), to qualify as a formal status indicator, non-conciliatory greetings should exhibit a degree of linearity and directional consistency similar to that produced by fight outcomes. To test the submission hypothesis, we focused on 8 years of pairwise interactions among a subset of adult females ($N = 19$), all of which had opportunities to greet and fight one another as adults, both at kills and away from kills. A dominance matrix containing these 19 females was generated based on outcomes of dyadic fights; the "winner" was the hyena being appeased and the "loser" displayed appeasement when the fight ended (Engh et al., 2005). A greeting matrix involving those same 19 females was based on interactions in which the "initiator" lifted her leg first to solicit greeting from a "recipient".

After correcting for the number of interactions observed for each dyad ($TauKr = 0.329$), a partial rowwise matrix correlation revealed a weak, but significant, tendency for losers of fights to also be the member of each dyad responsible for initiating non-conciliatory greetings (*TauKr* = 0.186, $P < 0.05$, Figures 5.3 and 5.4). Nonetheless, in contrast to the results predicted by the submission hypothesis, we found multiple striking discrepancies between dominance and greeting matrices. First, only 15.8 % of the rankings generated by fight outcomes and those generated by the initiation of greetings were in agreement. Second, the directional consistency of fight outcomes was high overall and nearly perfectly asymmetric, indicating an extreme imbalance in competitive ability within dyads of adult females (DC = 0.97). This value remained virtually the same when calculated for these 19 adult females at food (DC = 0.98) and away from food (DC = 0.97). In stark contrast, the directional consistency of greeting interactions was low overall (DC = 0.65) and varied among contexts. Although greetings were generally rare at kills, when they did occur, the DC (0.83) at kills was greater than the DC (0.66) away from kills. Thus, contrary to the predictions of the submission hypothesis, the initiation of greetings is neither unidirectional nor is the extent to which initiation is unidirectional 'context-free'.

We also found another striking discrepancy between the two matrices. Fight outcomes produced a rigid and significantly transitive linear dominance hierarchy (Improved Linearity Test: $h' = 0.59$, $P = 0.0001$, Figure 5.3). This structure remained statistically significant when based on fights occurring only over food ($h' = 0.35$, $P = 0.014$) or only in non-food contexts ($h' = 0.47$, $P = 0.0001$). In contrast, greeting initiation failed to produce a linear rank order ($P = 0.136$, Figure 5.4), with a linearity index ($h' = 0.26$) that was less than half of that

**Figure 5.3.** A dominance matrix based on the outcomes of 717 dyadic fights, each of which had a clear winner and loser. Each row of the matrix represents a different adult female (*N* = 19 hyenas), all of which were present together as adults both at food and away from food. At the intersection of each row (the winner) and column (the loser), a cell shows the number of fights won against the loser. We listed individuals based on their rank order, with the alpha female (bsh) represented in the top row and the left most column of the matrix. Similarly shaded adjacent cells within the first row and the left most column represent adult females belonging to the same matriline. For example, the alpha matriline contains bsh, mrph, sein, gil, bb, kip, who, and mali. A total of five matrilines are represented within the matrix. Dyadic relationships were either unidirectional (71.9 %, *N* = 123), bidirectional (4.1 %, *N* = 7), or unknown (24.0 %, *N* = 41). Black squares indicate that one adult female member of the dyad won the majority of fights within that dyad. White squares indicate dyads for which an equal number or no agonistic interactions were observed.

**Figure 5.3.**



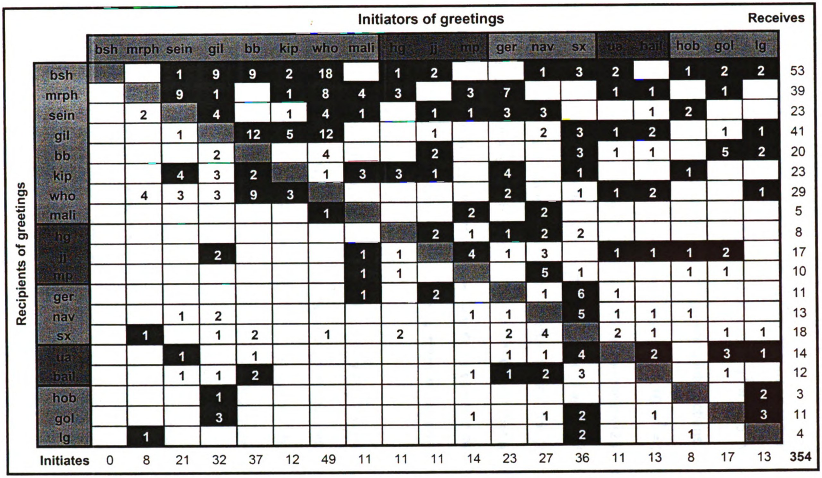
Losers of fights

Winners of fights

| | bsh | mrph | sein | gil | bb | kip | who | mali | hg | ji | mp | ger | nav | sx | ua | bail | hob | gol | lg | Wins |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| bsh | | 9 | 7 | 19 | 7 | 3 | 22 | 1 | | 3 | | 2 | 1 | 12 | 8 | 2 | 4 | 5 | 17 | 122 |
| mrph | | | 3 | 3 | | 4 | 1 | 13 | | 2 | 2 | 6 | 3 | 1 | | 1 | | 1 | | 40 |
| sein | | | | 7 | | 3 | 3 | 1 | | 6 | 1 | 13 | 18 | 3 | | 1 | 3 | 1 | 3 | 63 |
| gil | | | | | 3 | 8 | 44 | | 2 | 18 | 1 | 1 | 2 | 1 | 6 | 3 | 2 | 5 | 4 | 100 |
| bb | | | | | | 2 | 4 | | 2 | 8 | | 1 | 2 | 7 | 1 | 3 | 7 | 1 | 8 | 46 |
| kip | | | | | 1 | | | 4 | 5 | 3 | | 8 | 4 | 5 | 3 | 2 | | 2 | | 37 |
| who | | | | | 3 | | | | | 8 | 1 | 11 | 3 | 8 | | 3 | 3 | 5 | 9 | 54 |
| mali | | | | | | 1 | | | 2 | | | 1 | | 5 | 1 | 2 | | | | 12 |
| hg | | | | | | | | | | 5 | | 7 | 3 | 8 | 1 | 3 | 1 | 2 | | 30 |
| ji | | | | | | | | | | | | 2 | 15 | 8 | 1 | 5 | 9 | 7 | 3 | 50 |
| mp | | | | | | | | | | | | 11 | 1 | 1 | | 3 | | 1 | | 17 |
| ger | | | | 1 | | | | | | | | | 4 | 10 | 2 | | 5 | 5 | 2 | 29 |
| nav | | | | | | | | | | | | | | 1 | 2 | 3 | 8 | 7 | 3 | 24 |
| sx | | | | | | | | | | | | | | | 10 | 11 | 1 | 10 | 7 | 39 |
| ua | | | | | | | | | | | | | | | | 4 | 6 | 9 | 1 | 20 |
| bail | | | | | | | | | | 1 | | | | 1 | | | 10 | 6 | 5 | 23 |
| hob | | | | | | | | | | | | | | | | | | | 8 | 8 |
| gol | | | | | | | | | | | 1 | | | | | | | | 1 | 2 |
| lg | | | | | | | | | | 1 | | | | | | | | | | 1 |
| **Losses** | 0 | 9 | 10 | 30 | 14 | 21 | 74 | 19 | 11 | 55 | 6 | 63 | 56 | 71 | 35 | 46 | 59 | 67 | 71 | **717** |

**Figure 5.4.** A greeting interaction matrix based on 354 greetings, each of which had a clear initiator and recipient. Because the individuals included here (*N* = 19 hyenas) were the same adult females shown in Figure 5.3, and because the act of initiating greetings failed to produce a significantly non-random ordering of relationships, we ranked females based on the dominance rank order established in Figure 5.3. As before, adult females belonging to the same matriline are shown in adjacent cells in the top row and left-most column are shaded in the same color. At the intersection of each row (the recipient of greetings) and column (the solicitor of greetings), a cell shows the number of greeting interactions received by a particular individual from the initiating hyena. Dyadic relationships were either unidirectional (39.7 %, *N* = 68), bidirectional (21.1 %, *N* = 36), or unknown (39.2 %, *N* = 67). Black squares indicate that one member of the dyad preferentially received greetings more often than it initiated greetings with the other adult female within that dyad. White squares indicate dyads for which an equal number of greetings or no initiations were observed.

Figure 5.4.



Initiators of greetings

| Recipients of greetings | bsh | mrph | sein | gil | bb | kip | who | mali | hg | jj | mp | ger | nav | sx | ua | bail | hob | gol | lg | Receives |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| bsh | | | 1 | 9 | 9 | 2 | 18 | | 1 | 2 | | | 1 | 3 | 2 | | 1 | 2 | 2 | 53 |
| mrph | | | 9 | 1 | | 1 | 8 | 4 | 3 | | 3 | 7 | | | 1 | 1 | | 1 | | 39 |
| sein | | 2 | | 4 | | 1 | 4 | 1 | | 1 | 1 | 3 | 3 | | | 1 | 2 | | | 23 |
| gil | | | 1 | | 12 | 5 | 12 | | | 1 | | | 2 | 3 | 1 | 2 | | 1 | 1 | 41 |
| bb | | | | 2 | | | 4 | | | 2 | | | | 3 | 1 | 1 | | 5 | 2 | 20 |
| kip | | | 4 | 3 | 2 | | 1 | 3 | 3 | 1 | | 4 | | 1 | | | 1 | | | 23 |
| who | | 4 | 3 | 3 | 9 | 3 | | | | | | 2 | | 1 | 1 | 2 | | | 1 | 29 |
| mali | | | | | | | 1 | | | | 2 | | 2 | | | | | | | 5 |
| hg | | | | | | | | | | 2 | 1 | 1 | 2 | 2 | | | | | | 8 |
| jj | | | | 2 | | | | 1 | 1 | | 4 | 1 | 3 | | 1 | 1 | 1 | 2 | | 17 |
| mp | | | | | | | | 1 | 1 | | | | 5 | 1 | | | 1 | 1 | | 10 |
| ger | | | | | | | | 1 | | 2 | | | 1 | 6 | 1 | | | | | 11 |
| nav | | | 1 | 2 | | | | | | | 1 | 1 | | 5 | 1 | 1 | 1 | | | 13 |
| sx | | 1 | | 1 | 2 | | 1 | | 2 | | | 2 | 4 | | 2 | 1 | | 1 | 1 | 18 |
| ua | | | 1 | | 1 | | | | | | | 1 | 1 | 4 | | 2 | | 3 | 1 | 14 |
| bail | | | 1 | 1 | 2 | | | | | | 1 | 1 | 2 | 3 | | | | 1 | | 12 |
| hob | | | | 1 | | | | | | | | | | | | | | | 2 | 3 |
| gol | | | | 3 | | | | | | | 1 | | 1 | 2 | | 1 | | | 3 | 11 |
| lg | | 1 | | | | | | | | | | | | 2 | | | 1 | | | 4 |
| Initiates | 0 | 8 | 21 | 32 | 37 | 12 | 49 | 11 | 11 | 11 | 14 | 23 | 27 | 36 | 11 | 13 | 8 | 17 | 13 | **354** |

produced by fight outcomes. Moreover, greeting interactions failed to produce a linear structure within a single context (Food: $h' = 0.18$, $P = 0.967$, Non-food: $h' = 0.23$, $P = 0.397$). Kendall's coefficient of linearity further confirmed these results; fight outcomes (Overall: $K = 0.55$, $\chi^2 = 87.2$, Food: $K = 0.27$, $\chi^2 = 44.5$, Non-food: $K = 0.42$, $\chi^2 = 67.4$, $P \leq 0.022$ in all cases), but not greeting interactions (Overall: $K = 0.20$, $\chi^2 = 34.1$, Food: $K = 0.08$, $\chi^2 = 14.9$, Non-food: $K = 0.16$, $\chi^2 = 27.6$, $P \geq 0.201$ in all cases), produced significant, transitive rank relationships (25.8 *d.f.* for each test). Whereas all dyads for which one member won the majority of fights (black squares) were above the diagonal in the dominance matrix, the greeting matrix contained multiple dyads for which the member of the dyad that received the most greetings (black squares) was the female situated below the diagonal. Overall, the majority of these data fail to support the submission hypothesis.

*Most greetings occurred directly after fusion events*

Timing relative to the proceeding fusion event was known for 13,074 greetings, involving 449 different hyenas. Hyenas generally initiated greetings immediately after reuniting with individuals from whom they had been separated. The modal number of minutes to pass between fusion events and the onset of greeting was one. On average, hyenas greeted within 6.3 ± 0.2 minutes of fusion events (Range: 1 to 137 minutes post-fusion). Interestingly, however, focal hyenas ($N = 267$) engaged in conciliatory greetings significantly later in the post-fusion interval (7.4 ± 0.4 minutes) than they engaged in non-conciliatory greetings (5.9 ± 0.1 minutes; Wilcoxon-Signed Ranks Test: $Z = 2.866$, $P = 0.004$).

Because our main goal here was to explain the function of non-conciliatory greetings, we next removed conciliatory greetings from the data set. Non-conciliatory greetings ($N$ = 11,759) typically occurred within 5.8 ± 0.2 minutes after fusion ($N$ = 448 hyenas), and became less frequent as time passed after fusion (Spearman rank correlation: $R_S = -0.958$, $P < 0.00001$, Figure 5.5). More than half of these greetings (57.7%) occurred within the first minute, 77.7% within 5 minutes, and 86.6 % within 10 minutes after fusion.

### *Females were selective when greeting after fusion events*

Away from kills, focal adult females ($N$ = 33) were significantly more likely to be responsible for initiating non-conciliatory greetings when they were responsible for initiating fusion (58.2 ± 4.0 %) than when they were joined by another female (41.8 ± 4.0 %, Wilcoxon-Signed Ranks Test: $Z = 2.16$, $P = 0.031$). In contrast, the initiation of greetings at kills was less structured; focal females ($N$ = 24) were no more likely to initiate greetings upon arriving at subgroups (47.9 ± 8.3 %) than when they were joined by other females (52.1 ± 8.3 %, Wilcoxon-Signed Ranks Test: $Z = 0.355$, $P = 0.723$). Arriving females ($N$ = 37) typically joined subgroups on their own such that, on average, adult females arrived with less than one (0.8 ± 0.1) companion. These females joined subgroups containing, on average, 7.9 ± 0.2 hyenas, of which 2.8 ± 0.5 were also adult females. Females were therefore selective with respect to greeting decisions, greeting, on average, only 7.1 ± 0.6 % of the adult females available to them after fusion events.

### *Modeling factors to explain greeting decisions after fusion events*

Next we identified the subset of candidate predictor variables that significantly

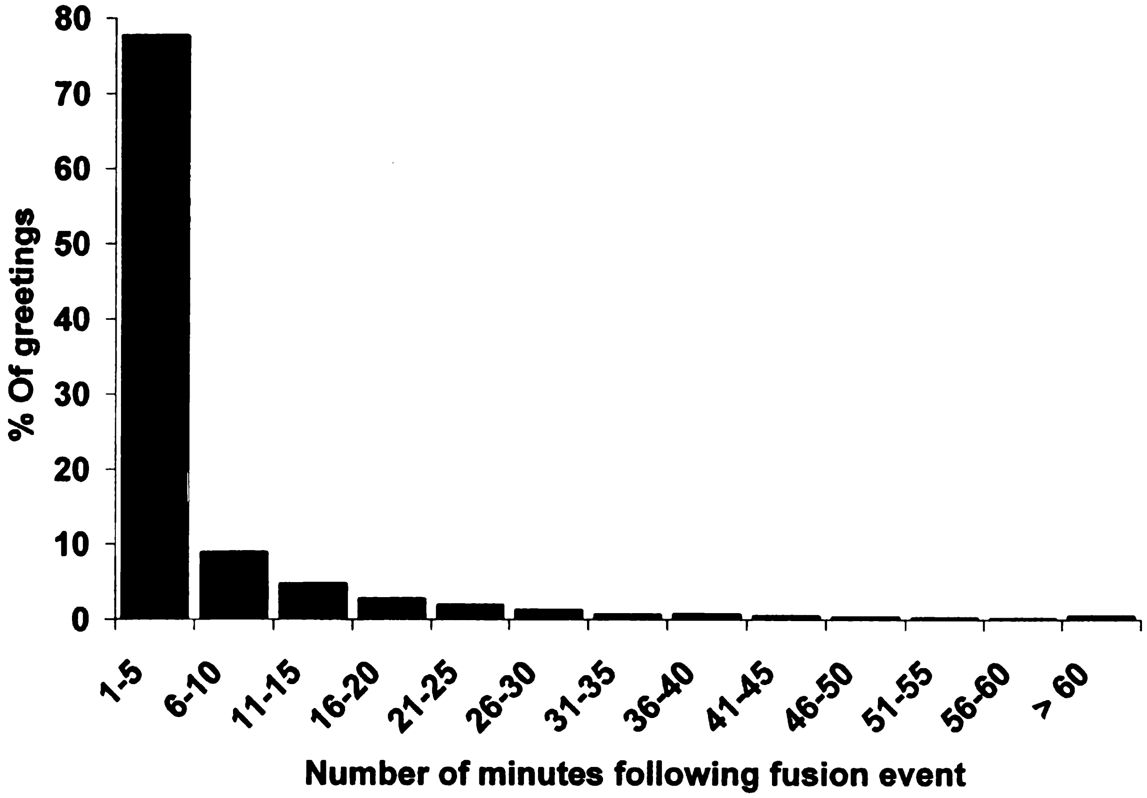


**Figure 5.5.** Percentage of all non-conciliatory greetings (*N* = 11,759) that occurred among spotted hyenas within the 5 minute-intervals directly after subgroup reunions ("fusion events") throughout our longitudinal study.

explained: 1) decisions to participate in non-conciliatory greetings with adult females after fusion and 2) the symmetry of non-conciliatory greetings between adult females. Whereas both models were consistent with the predictions of the social bonding hypothesis, neither model strongly supported the submission or tension reduction hypotheses.

### Limited support for the submission or tension reduction hypotheses

Overall, our statistical models failed to support the main predictions of the submission or tension reduction hypotheses. In contrast to the submission hypothesis, neither the relative social rank nor the rank distance of the arriving female to potential greeting partners explained whether females greeted after fusion (Table 5.3). Contrary to the predictions of the tension reduction hypothesis, females were actually least likely to greet per opportunity at kills (Table 5.3, Figure 5.6). Moreover, the act of greeting in non-conciliatory contexts also failed to protect hyenas from receiving aggression immediately after fusion (Table 5.3). Specifically, females greeting hyenas with whom they had not previous fought during the same session were just as likely to fight with them after participating in non-conciliatory greetings as were those females who failed to greet after fusion. Interesting, however, arriving females greeted high-ranking females most often per opportunity (Table 5.3). This final result suggests that, irrespective of their relative rank to potential partners, choosy females prefer to greet high-ranking social allies.

### Evidence supporting the social bonding hypothesis

As predicted by the social bonding hypothesis, but in direct contrast to the

**Table 5.3.** Independent variables predicting whether or not arriving adult females greeted particular females present in joined groups at each opportunity to do so.

| Coefficients: | Estimate ± S.E. | *Z*-value | *P*-value |
|---|---|---|---|
| (Intercept) | -1.747 ± 0.233 | -7.495 | < 0.0000001 |
| Subgroup size (at fusion) | -0.086 ± 0.013 | -6.609 | < 0.0000001 |
| Intragroup coalition partners | 1.038 ± 0.258 | 4.023 | 0.000057 |
| Food present (kill scene) | -0.556 ± 0.150 | -3.713 | 0.000205 |
| Clan war participants | 2.477 ± 0.843 | 2.939 | 0.003290 |
| Absolute rank of partner | -0.030 ± 0.011 | -2.681 | 0.007344 |
| Association index | 3.605 ± 1.925 | 1.873 | 0.061059 |
| Cooperatively attack lions | 0.795 ± 0.451 | 1.765 | 0.077638 |
| Coefficient of relatedness | 1.926 ± 0.558 | 3.453 | 0.000555 |
| Prey abundance | 0.096 ± 0.151 | 0.636 | 0.524833 |
| Relatedness * Prey abundance | -2.502 ± 0.752 | -3.326 | 0.000880 |

The following additional factors failed to improve the fit of the best model predicting whether or not females greeted after fusion events: Maternal kinship (0.341 ± 0.270, $Z = 1.262$, $P = 0.207$), Relative rank (arriving female subordinate to potential partner, 0.174 ± 0.142, $Z = 1.231$, $P = 0.218$), rank distance between potential partners (-0.020 ± 0.017, $Z = -1.172$, $P = 0.241$), absolute social rank of the arriving female (0.003 ± 0.011, $Z = 0.305$, $P = 0.761$), whether females cooperatively hunted (-0.467 ± 0.635, $Z = -0.735$, $P = 0.462$) or fought each other after fusion (0.035 ± 0.186, $Z = 0.190$, $P = 0.850$). Including hyena identity as a random effect improved the fit of our best (Likelihood ratio test: $\chi^2 = 14.6$, *d.f.* = 1, $P = 0.0001$), which was based on a total of 433 possible greeting pairs of adult females. Adult females ($N = 37$) only participated in a total of 369 greetings out of 4,448 potential opportunities after fusion. The negative relationship between the absolute rank of available partners and greetings per opportunity reflects a preference by adult females to greet with high-ranking females (e.g. the highest possible social rank was one).

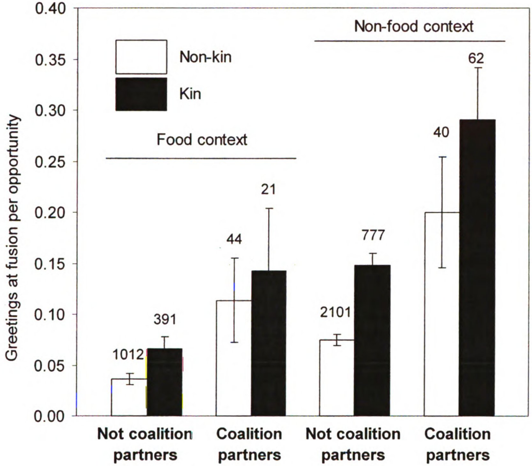


**Figure 5.6.** Proportion of fusion events in which adult females greeted other adult females within 10 minutes of subgroup fusion, out of all opportunities to do so, at kills (food context) and away from kills (non-food context). Coalition partners formed at least one aggressive coalition directed towards another hyena or towards a lion during the minutes after a fusion event, non-coalition partners failed to form a coalition in the minutes after a fusion event. Although bar color here indicates whether members of each dyad were non-kin (white) and kin (black), we entered the coefficient of relatedness for each dyad as a continuous variable in our statistical model (Table 5.2). Sample sizes over each bar indicate the number of opportunities available to arriving females to greet potential adult female partners. Error bars represent ± 1 standard deviation for binomial trials.

predictions of the tension reduction hypothesis, adult females preferentially greeted kin (Table 5.3, Figure 5.6) and closely associating non-kin (Table 5.3, Figure 5.7) most often per opportunity after each fusion event. After controlling for the influence of kinship, close associates greeted significantly more often at each fusion event than did distant associates regardless of local prey abundance (Association * Prey Abundance: -2.048 ± 3.138, $Z = -0.737$, $P = 0.461$). However, the effects of kinship significantly interacted with the effects of local prey abundance (Table 5.3). Whereas non-kin greeted at similarly low rates throughout the year (Prey abundance: 0.030 ± 0.154, $Z = 0.197$, $P = 0.844$), kin were most likely to greet per opportunity during months when prey were scarce (Prey abundance: -0.562 ± 0.185, $Z = -3.041$, $P = 0.004$). Nonetheless, kin were generally more likely than non-kin to greet during months of low prey (0.642 ± 0.198, $Z = 3.241$, $P = 0.002$) and high prey (0.362 ± 0.219, $Z = 1.656$, $P = 0.098$). Overall, these results are most consistent with predictions of the social bonding hypothesis; females greeted kin most often at fusion during those times of year when prey scarcity most reduces social cohesion among clan mates.

After controlling for the effects of kinship and patterns of association, females that joined forces to form aggressive coalitions after fusion were significantly more likely to greet per opportunity than were non-coalition partners (Table 5.3, Figure 5.6). This was the case when adult females directed intragroup coalitions towards other clan members and when females cooperatively attacked alien intruders at clan wars or when mobbing lions during cooperative defense of food. However, we detected no relationship between the acts of greeting and

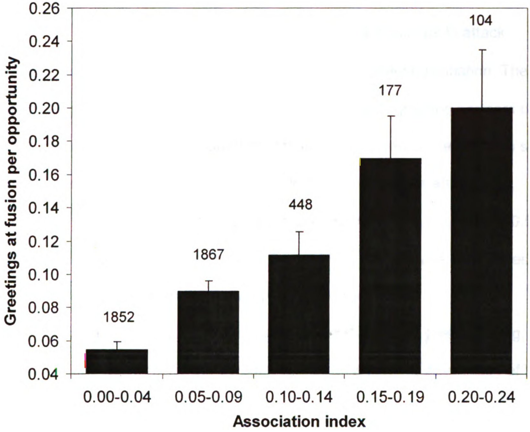


**Figure 5.7.** Proportion of fusion events in which adult females greeted other adult females within 10 minutes of subgroup fusion, out of all opportunities to do so, as a function of how often pairs of adult females associated with each other. For the purposes of visual representation only, we present patterns of association binned into discrete categories, but entered values as a continuous variable into our statistical model (Table 5.2). Sample sizes over each bar indicate the number of opportunities arriving adult females had to greet potential adult female partners at fusion events. Error bars represent ± 1 standard deviation for binomial trials.

cooperative hunting (Table 5.3). When females formed coalitions with greeting partners after fusion (Fig. 5.6), they were more likely to do so in the minutes immediately after greeting (78.5 ± 7.8 %) than in the minutes directly before greeting (21.5 ± 7.8 %, Wilcoxon-Signed Ranks Test: $Z = 2.520$, $P = 0.012$, $N =$ 21 females). On average, when these females formed coalitions to attack another hyena, they did so within 2.7 ± 0.9 minutes of greeting initiation. The tendency for females to preferentially form coalitions with greeting partners could not be explained simply by the amount of time females were observed with social partners. Females remained in subgroups for similar durations after fusion, regardless of whether or not they formed a coalition (35.7 ± 2.7 vs. 31.4 ± 0.5 minutes, Wilcoxon-Signed Ranks Test: $Z = 1.547$, $P = 0.123$, $N = 21$ females).

*Modeling factors to explain the symmetry of greetings*

Following East et al. (1993), a single univariate analysis of all greetings (e.g. conciliatory and non-conciliatory combined) indicated that the asymmetry of leg lifting increased as the rank distance between adult females increased (Spearman Rank Correlation: $N = 22$ rank distances; $R_S = 0.553$, $P = 0.007$). Interestingly, conciliatory greetings involving focal females ($N = 52$) were significantly more asymmetric (63.3 ± 4.3 %) than were non-conciliatory greetings (48.3 ± 2.7 %, Wilcoxon-Signed Ranks Test: $Z = 4.049$, $P = 0.00005$). After we accounted association and relatedness, in contrast to the predictions of submission hypothesis, rank distance was excluded from our best model explaining the symmetry of non-conciliatory greetings (Table 5.4). Also in contrast to the tension reduction hypothesis, but as predicted by the social bonding hypothesis, closely associating females generally engaged in the most symmetric greetings. However, after accounting for patterns of association, non-kin generally participated in more symmetric greetings than kin, suggesting that socially bonded non-kin might rely more heavily upon reciprocal greetings to reinforce bonds than do kin. Overall, our findings are more consistent with predictions of the social bonding hypothesis than those of the submission and tension reduction hypotheses.

## DISCUSSION

### *Conciliatory versus non-conciliatory greetings*

Overall, the meaning and distribution of greetings varied among contexts, suggesting that greetings represent complex signals. First, as found in early studies, here the vast majority of greetings served a non-conciliatory function (East et al., 1993; Hofer and East, 2000). The low frequency of conciliatory greeting (e.g. occurring immediately after fights) is presumably because hyenas rely most heavily upon dispersive conflict resolution to settle disputes (Smith et al., 2008; Wahaj et al., 2001). Second, whereas conciliatory greetings transpire primarily among non-kin and are initiated mostly by losers of fights (Wahaj et al., 2001), we found here that non-conciliatory greetings mainly involved kin, even after correcting for opportunities to greet. Third, non-conciliatory greetings were more symmetric and occurred earlier in the interval directly after fusion events than did conciliatory greetings. Finally, conciliatory greetings lasted longer than non-conciliatory greetings; this finding is consistent with the idea that it takes more time to renegotiate damaged relationships after fights than it does to

**Table 5.4.** Independent variables predicting the symmetry of non-conciliatory greetings among adult females.

| Coefficients: | Estimate ± S.E. | *Z* Statistic | *P*-value |
|---|---|---|---|
| (Intercept) | -0.246 ± 0.115 | -2.142 | 0.032 |
| Association index (AI) | 4.037 ± 1.472 | 2.742 | 0.006 |
| Coefficient of relatedness | -1.108 ± 0.418 | -2.650 | 0.008 |

The additional predictor variables failed to improve the fit of our best model: Rank distance: -0.016 ± 0.014, *Z* = -1.106, *P* = 0.269, Maternal kinship: -0.255 ± 0.267, *Z* = -0.955, *P* = 0.339, Cooperative hunting: 0.701 ± 0.463, *Z* = 1.514, *P* = 0.130, Intragroup coalition partners: -0.137 ± 0.232, *Z* = -0.592, *P* = 0.554, Intergroup coalition partners (clan war): 0.878 ± 0.894, *Z* = 0.982, *P* = 0.326, Prey abundance: -0.093 ± 0.105, *Z* = -0.885, *P* = 0.376, Food: -0.051 ± 0.130, *Z* = -0.396, *P* = 0.692). The interaction between association and kinship (AI * Kinship: -7.657 ± 7.153, *Z* = -1.070 *P* = 0.284), or that of any other terms, failed to improve the fit our model. A Likelihood ratio test confirmed that the inclusion of the random effect, "hyena identity", improved the model's fit ($\chi^2$ = 11.6, *d.f.* = 1, *P* = 0.0007), which included 1,750 non-conciliatory greetings involving 456 different pairs of adult females from 1988 to 2000 (*N* = 57 adult females).

reinforce existing social bonds (Aureli et al., 2002).

### *Non-conciliatory greetings fail to signal submission*

Although spotted hyena greetings are still cited as one of the key examples of "reliable ritualized expressions of formal rank" (see p. 444, Cafazzo et al., 2010), our critical test of the submission hypothesis revealed that this does not in fact appear to be the case. In general, our study produced results that were consistent with data obtained in earlier studies when we used the same methods. Specifically, younger or subordinate spotted hyenas generally initiated greetings more often than did older or socially dominant hyenas, as found by East et al. (1993) and Kruuk (1972). However, when we focused only on non-conciliatory greetings and simultaneously accounted for potential confounding factors using a multivariate approach not yet widely available when the earlier studies were conducted (e.g. Carlin et al., 2001; Faraway, 2006; Halekoh et al., 2006; Hardin and Hilbe, 2003), we obtained results that differed from those of East et al. (1993). Importantly, our work revealed that the strength of social bonds is a better predictor, than rank relationships, in explaining non-conciliatory greetings among adult females. Interestingly, this finding is consistent with the hypothesis originally proposed by Kruuk (1972).

The availability of new matrix permutation tools allowed us to quantify the linearity of greeting initiation while explicitly correcting for unknown relationships (e.g. de Vries, 1995). These analyses revealed that fight outcomes clearly adhered to the expectations of a linear hierarchy (*en sensu* Drews, 1993), but that greetings failed to do so. Directional consistency (DC) is the most reliable measure for comparing the strength of competition among taxonomic groups in part because it is informative even in species for which some group members interact at relatively low rates (Archie et al., 2006; Isbell and Pruetz, 1998; Isbell and Young, 2002). Here the initiation of greetings was far more balanced within dyads (DC = 0.65) than were fight outcomes (DC = 0.98). Further, although fight outcomes were unidirectional across contexts, the extent to which signaling during greetings was unidirectional varied among contexts. Our results represent particularly strong evidence against the submission hypothesis because we found here that the directional consistency (DC) of dominance interactions within dyads of adult female spotted hyenas was generally similar to or greater than DCs based on fight outcomes among other adult female mammals (Table 5.5). In contrast, the DC based on hyena greetings is more akin to DC values based on affiliative behaviors in other species (Table 5.5). Whereas these findings might seem surprising, use of these new quantitative methods has similarly revealed misconceptions about signaling in other species (reviewed by Kutsukake, 2009).

Although grooming among primates is often preferentially directed towards higher and adjacently ranked coalition partners (Schino, 2001; Seyfarth, 1977; Seyfarth and Cheney, 1984), grooming clearly does not signal submission. In addition to its hygienic and hedonistic values, grooming also provides important "political" information to social partners (Cheney et al., 1986; Dunbar, 1991; Dunbar and Sharman, 1984). The pivotal role of grooming in social bond maintenance is well documented among non-human primates living in cohesive

**Table 5.5.** Directional consistency (DC) of behavioral interactions among gregarious mammals.

| Species: | Interaction Type | DC | References |
|---|---|---|---|
| Wedge-capped capuchins (*Cebus olivaceus*) | Allogrooming | 0.43 | (O'Brien, 1993) |
| Spider monkeys (*Ateles belzebuth hybridus*) | Allogrooming | 0.51 | (Leiva et al., 2008) |
| Chimpanzees (*Pan troglodytes schweinfurthii*) | Friendly approaches | 0.57 | (Murray, 2007) |
| Bonobos (*Pan paniscus*) | Fight outcomes | 0.63 | (Vervaecke et al., 1999) |
| Black-and-white colobus (*Colobus guereza*) | Allogrooming | 0.65 | (Kutsukake et al., 2006) |
| **Spotted hyenas (*Crocuta crocuta*)** | **Greeting initiation** | **0.65** | **(current study)** |
| Wolves (*Vulpes familiarus*) | Tail-wagging | 0.66 | (van Hooff and Wensing, 1987) |
| Cows (*Bos Taurus*) | Fight outcomes | 0.68 | (Val-Laillet et al., 2009) |
| Wolves (*Vulpes familiarus*) | Genital sniffing | 0.72 | (van Hooff and Wensing, 1987) |
| Patas monkeys (*Erythrocebus patas)* | Fight outcomes | 0.78 | (Isbell and Pruetz, 1998) |
| Olive baboons (*P. anubis*) | Fight outcomes | 0.89 | (McMahan and Morris, 1984) |
|  | Fight outcomes | 0.96 | (Barton and Whiten, 1993)] |
| Hanuman langurs (*Semnopithecus entellus*) | Fight outcomes | 0.90 | (Lu et al., 2008) |
| Gray-cheeked mangabeys (*Lophocebus albigena*) | Fight outcomes | 0.90 | (Chancellor and Isbell, 2009) |
| American bison (*Bison bison)* | Fight outcomes | 0.94 | (Vervaecke et al., 2005) |
| African elephants (*Loxodonta africana)* | Fight outcomes | 0.94 | (Archie et al., 2006) |
| Pigs (*Sus domestica)* | Fight outcomes | 0.92 | (Hoy and Bauer, 2005) |
| Orangutans (*Pongo borneo*) | Fight outcomes | 0.97 | (de Vries, 1995), |
| Chimpanzees (*Pan troglodytes schweinfurthii*) | Fight outcomes | 0.97 | (Murray, 2007), |
| **Spotted hyenas (*Crocuta crocuta*)** | **Fight outcomes** | **0.97** | **(current study)** |
| Hamadryas (*Papio hamadryas hamadryas*) | Fight outcomes | 0.98 | Leinfelder et al., 2001) |
| Vervet monkeys (*Cercopithecus aethiops*) | Fight outcomes | 1.00 | (Isbell and Pruetz, 1998) |

Fight outcome data were restricted to those found for adult female mammals. Because measures of DC on affiliative interactions were less prevalent in the literature, these data were not restricted to adult females.

groups (e.g. Gomes et al., 2009; Lazaro-Perea et al., 2004; Matheson and Bernstein, 2000; Silk et al., 2006), especially when the values of partners are dynamic (Barrett et al., 2002; Henzi and Barrett, 1999; Henzi and Barrett, 2002). Although adult female hyenas rarely allogroom, our data are consistent with the idea that greetings might function to quickly update social bonds among hyenas. Interestingly, spider monkeys (*A. geoffroyi*) also exchange greetings, but not allogrooming, at fusion (Schaffner and Aureli, 2005). In fact, Aureli and Schaffner (2007) theorized that individuals living in societies characterized by high rates of fission-fusion dynamics should greet to quickly update relationships. As predicted, we found here that friendly greetings among preferred companions were extremely brief and typically occurred immediately after fusion.

### *Non-conciliatory greetings fail to reduce tension*

Our data generally failed to support the hypothesis that non-conciliatory greetings reduce tensions. In fact, greetings were least likely to occur when meeting up after fusion events with distant associates, including non-kin, which presumably have the least secure social relationships (Wahaj et al., 2001). Moreover, most greetings occurred in neutral contexts in which tensions are low compared to situations in which resource competition is most likely (Frank, 1986). Finally, the act of greeting in non-aggressive contexts failed to protect hyenas from immediately receiving aggression. This last finding is consistent with earlier studies. Even though kin are each other's the best allies, kinship fails to protect hyenas (Smith et al., 2010; Wahaj et al., 2004) and many primates (reviewed by Widdig, 2007) from becoming targets of aggression.

Like hyena greetings, genital contacts among adult female bonobos (*P. paniscus)* serve multiple functions, and are sometimes used to reconcile fights (Hohmann and Fruth, 2000). Non-conciliatory genital contacts reduce tensions over food among bonobos (Hohmann and Fruth, 2000). In contrast, non-conciliatory greetings here reinforced alliances among hyenas away from food. Although genital contacts facilitate food sharing within the egalitarian societies of bonobos (de Waal, 1997a), hyena greetings appear to promote coalition formation among adult females that function to reinforce the status quo in contexts away from food (Smith et al., 2010).

*Non-conciliatory greetings reinforce social bonds*

Overall, our findings are most consistent with the social bonding hypothesis. Indeed, adult females only exchanged greetings at fusion events with a small subset of the adult females present, and they selectively directed these gestures towards their preferred social companions. Specifically, females greeted coalition partners, relatives and close associates most often per opportunity. Thus, the finding that females often initiate greetings with high-ranking females (East et al., 1993 and Table 5.3) likely reflects social preferences for powerful allies rather than functioning to signal submission.

Although mutual inspection of the highly vulnerable genitalia might improve the efficacy of gestures signaling bond strength (Smuts, 2002; Zahavi, 1977b), hyenas generally minimized this risk by selecting greeting partners who posed the least risk to them, and by greeting these partners most often away from contexts in which aggression is most common. First, because the reproductive careers of maternal kin are closely linked to one another, through direct and indirect fitness benefits (Hamilton, 1964), females should theoretically be disinclined to damage the reproductive organs of their maternal kin. Second, we found here that hyenas generally greeted in neutral contexts in the absence of direct feeding competition. Similarly, male baboons (*Papio cynocephalus anubis*) and domestic dogs (*Canis lupus familiaris*) greet most often when there are no immediate resources at stake (Smuts, 2002; Smuts and Watanabe, 1990). In peaceful contexts, greetings might permit group members to assess the intentions of their partners when the risk of injury to the genitalia is greatly reduced. Within their highly competitive, female-dominated society, greetings among adult female spotted hyenas appear to offer a behavioral mechanism by which females can assess the cooperative tendencies of potential allies.

### *Non-conciliatory greetings promote collective action*

Although greetings failed to play an important role in preparing hyenas for cooperative hunting, African wild dogs (*Lycaon pictus*) almost always engage in greetings prior to hunting (Creel and Creel, 2002). Wild dogs live in cohesive groups and increase their per capita energy intake by hunting in large groups (Creel, 1997). In contrast, spotted hyenas typically hunt alone or in pairs because individuals often suffer reduced energy gains when hunting in large parties (Smith et al., 2008). Thus, hyenas might be subject to opposing selection pressures contraindicating the use of greetings to coordinate group hunting.

Importantly, we found strong evidence suggesting that greetings facilitate coalition formation; this was true even after controlling for effects of kinship, association patterns, and immediate ecological context. Although many workers theorize that greetings promote coalition formation, direct empirical evidence for this is limited. Smuts (2002) noted that a pair of male olive baboons engaged in more risky and more symmetric genital touching than did non-coalition partners. Ritualized embracing and mutual genital inspection appear to mediate social relationships in many non-human primates (Alfaro, 2008; Colmenares, 1991; Okamoto et al., 2001; Perry, 1998; Perry et al., 2003; Smuts and Watanabe, 1990; Wang and Milton, 2003; Whitham and Maestripieri, 2003). Our work importantly extends these findings by demonstrating for the first time a temporal link between the patterning of greetings and coalition formation.

### *Cognitive demands of bond maintenance in dispersed societies*

Whereas shifting ecological environments are known to favor enhanced cognitive abilities in animals (e.g. Braithwaite and Salvanes, 2005; Kotrschal and Taborsky, 2010), dynamic variation in social group composition should theoretically also impose cognitive demands upon species in which individuals recognize the relationships among group mates from whom they are often separated (Amici et al., 2008; Aureli et al., 2008; Barrett et al., 2003; Connor, 2007). Because resource competition often forces members of fission-fusion societies to spend much of their time in fragmented subgroups (Aureli et al., 2008; Schino, 2000; Smith et al., 2008; Wrangham et al., 1993), many social animals, including spotted hyenas (East and Hofer, 1991; Theis et al., 2007), have evolved contact calls to “stay in touch” over long distances (e.g. McComb et al., 2000; McComb et al., 2003; McCowan and Reiss, 2001; Ramos-Fernandez, 2005; Smolker et al., 1993; Spillmann et al., 2010). Moreover, hyenas maintain cohesion within their social network by depositing individually distinct scent marks (Burgener et al., 2009; Drea et al., 2002; Theis, 2008).

Although vocal and olfactory cues effectively communicate a hyena's identity when clan members are spatially separated, and although adult female spotted hyenas understand third-party relationships among group mates (Engh et al., 2005), experiments suggest that vocal cues fail to communicate information about third-party relationships (Holekamp et al., 1999a). Our findings suggest that greetings represent reliable signals with which hyenas can quickly confirm relationship status in a society in which group members spend much of their time apart. These signals appear to be especially important in maintaining bonds among kin during those times of year when resource limitation most strongly constrains sociality (Smith et al., 2008).

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

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