SOCIAL DEVELOPMENT AND ITS INFLUENCE ON ADULT TRAITS IN THE SPOTTED HYENA

By

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ABSTRACT

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Patterns of social development have proven to vary widely within species, and to have important long-term effects on adult traits and fitness. This is especially true in species that have complex societies, such as spotted hyenas (*Crocuta crocuta*). These animals have been well-studied over their entire lives, their ontogenetic development can be partitioned into distinct stages, and these hyenas are strongly affected by anthropogenic disturbance. My research uses social network analysis (SNA) to explore the social development of spotted hyenas in the Masai Mara National Reserve, Kenya. Furthermore, I test how social development affects the fitness of individuals, and how human disturbance affects their development and adult traits.

My research has demonstrated that male and female hyenas develop their social positions along different ontogenetic trajectories. Social rank affects the social development of females more than it affects that of males in this species. Their dimorphic patterns of social development also appear to prepare male and female hyenas for their different life-history trajectories of dispersal by males versus female philopatry in the natal clan. Furthermore, the longevity of females is affected by the social positions they hold as juveniles, particularly the positions they hold during the period before puberty but after they become independent of the communal den. My research has also shown that human disturbance is affecting spotted hyena development and behavior. Individuals who grow up in areas characterized by low anthropogenic disturbance are bolder than those from areas of high disturbance. This is consistent across ontogeny and different contexts, and boldness has significant effects on their survival. Additionally, human disturbance affects the overall social structure of entire clans, with clan members from areas of lowdisturbance being more strongly and indirectly connected than those in high-disturbance areas, indicating that the high-disturbance clan is less cohesive than clans in low-disturbance area. Human disturbance also affects the social development of juveniles in ways that influence their survivorship.

These findings elucidate the complexities of social development and its life-long consequences, something that has rarely been done for long-lived animals in the wild. Furthermore, they highlight how anthropogenic disturbance is affecting behavior in a highly plastic, gregarious carnivore, and my results could thus have important implications for carnivore conservation.

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CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Social networks, which are patterns of social bonds with group-mates or other conspecifics, offer a powerful way to explore group dynamics. Social networks support myriad behaviors critical to individual fitness, from mate choice and cooperative relationships to foraging and anti-predator behavior (Croft, James, & Krause, 2008). An animal social network involves more than two individual animals, called nodes, connected by behavioral interactions or co-occurrences in space, called ties or links, and portrayed as a graph or a matrix. Ties can be directed, if the behavior has an initiator and a receiver, or undirected when there is no clear direction in the relationship. Additionally, ties can be weighted when there is a certain number or probability of occurrence of the behavior, or they can be unweighted such that their occurrence is binary.

Social network analysis (SNA) enables researchers to quantify and analyze specific metrics of sociality, such as centrality, strength of relationships, etc., in ways that were not previously possible, and at levels of analysis ranging from an individual's position or role in its social environment to the social structure of entire populations. SNA has been developed and used in fields ranging from sociology to physics for decades, but has only recently come into use in the biological sciences (J. Krause & Lusseau, 2009; Pinter-Wollman et al., 2014). Looking at networks dynamically, as they change over time, can add considerable realism to network models of how social relationships are developed and maintained, both during ontogeny and over the course of evolution (Pinter-Wollman et al., 2014; Skyrms & Pemantle, 2000). Currently in non-human animals, we know virtually nothing about the development of social networks or the

individual's social position within its network on either time scale, nor do we know how environmental variation during early ontogeny affects the development and fitness consequences of social network position.

Here, I study the ontogenetic development of social networks. Using spotted hyenas (*Crocuta crocuta*) as subjects that live under contrasting ecological conditions of either high or low habitat disturbance due to human activity, my dissertation research follows the positions of individuals within their networks as these emerge over the course of ontogenetic development. Spotted hyenas are found throughout sub-Saharan Africa, including many areas currently undergoing rapid change due to anthropogenic disturbance. In the Masai Mara National Reserve, Kenya, I followed cohorts of cubs from birth until maturity in clans living in habitats with low or high levels of anthropogenic disturbance and assessed their social network positions during discrete stages of development. Existing knowledge about their development and social structure makes hyenas a good model for the study of the ontogeny of social network position. Hyena societies are much like those of cercopithecine primates in terms of their structure, size and complexity (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012). However, in contrast to development in primates, hyen development is divisible into discrete stages marked by unambiguous life-history milestones: 1) at the natal den (ND), 2) at the communal den (CD), 3) den independence to weaning (DI), 4) weaning to sexual maturity, and 5) adulthood after sexual maturity (Holekamp & Smale, 1998a). These stages, together with the fact that spotted hyenas live in fission-fusion societies, make it possible to construct detailed social networks based on association patterns among individuals observed during each life history stage (J. E. Smith, Memenis, & Holekamp, 2007). This detailed knowledge of hyena development, in conjunction with the use of SNA, allowed me to study the social development of individual hyenas, including

how a cub's social position changes and develops into its adult social role during its ontogeny, at a finer scale than has been done before (McDonald, 2007; Stanton, Gibson, & Mann, 2011).

My dissertation is composed of four chapters. In the first chapter, I describe how the social position or role, defined by social network metrics, of a hyena changes dynamically over three developmental stages (CD, DI, and adult), and how developmental patterns differ between the sexes. For this analysis, I made association, aggression, and affiliation networks. Association networks represented when individuals were in proximity to each other, aggression networks were when individuals initiated aggressive interactions with each other, and affiliation networks characterized initiating affiliative greeting interactions with others. I found that there were striking differences over development between males and females. Furthermore, females were more strongly affected by rank than were males.

The second chapter of my dissertation tests hypotheses suggesting that the characteristics of an individual's network position during two early development (CD and DI stages) predict fitness measures in adulthood, specifically longevity and reproductive success. Here, I found that females' longevity in particular was influenced by their early social positions, especially during the DI stage.

My third chapter tests hypotheses about how anthropogenic disturbance affects risktaking responses of hyenas to a model intruder and inquires whether different methods of testing personality yield consistent results within spotted hyenas. These results indicated that hyenas in low-disturbance areas were bolder than those in areas of high-disturbance, and these risk-taking behaviors affected individuals' survival. Additionally, different measures of boldness were consistent across contexts and age classes.

The last chapter in my dissertation inquires how anthropogenic disturbance affects social position development during the CD and DI stages in spotted hyenas. Human disturbance did indeed affect social structure, particularly strength of relationships and indirect connections, within clans as well as the social development of individual juveniles.

Overall, these chapters address questions about how sociality develops as well as how development shapes the traits and fitness of adult individuals. Addressing critical gaps in our knowledge about social position development, its sensitivity to environmental disturbance, and its fitness consequences, should lead to a better understanding of the significance of the early social bonds and networks that are virtually ubiquitous features of complex animal societies, while simultaneously providing information useful to wildlife conservation.

WRITING STYLE OF THIS DISSERTATION

Each chapter in this dissertation was written as a manuscript for publication and is the result of collaborative efforts involving multiple people and building on data collected by numerous others over the history of the Mara Hyena Project since 1988. Thus, I will use "we" instead of "I" to represent this collaborative work.

CHAPTER 2

ONTOGENETIC CHANGE IN DETERMINANTS OF SOCIAL NETWORK POSITION IN THE SPOTTED HYENA

Turner, J. W., Bills, P. S., & Holekamp, K. E. (2018). Ontogenetic change in determinants of social network position in the spotted hyena. *Behavioral Ecology* and Sociobiology, 72, 10.

ABSTRACT

Social development is crucial in the ontogeny of animals living in complex societies and has lasting consequences in adulthood. Spotted hyenas (Crocuta crocuta) live in fission-fusion societies as complex as those of cercopithecine primates. The social positions adult hyenas hold within their groups are complex and varied, but little is known about how those positions emerge and change over the course of development. Using social network analysis (SNA), we tested predictions of hypotheses suggesting that sex and dominance status affect the social network positions of young hyenas across three stages of ontogeny: 1) while living at the communal den, 2) den independent but pre-reproductive, and 3) early adulthood. By examining rates at which hyenas were found alone and their association networks, aggression networks, and affiliation networks, we observed striking changes in individuals' network positions across ontogeny, as well as pronounced sex differences. With the exception of rates at which individuals were found alone, which increased over ontogeny, most social network position metrics decreased greatly from infancy to adulthood. However, females showed considerably more rank-related variation in this trajectory than did males. Overall, social rank had stronger effects on the development of social network positions in females than males. Thus, females and males have different social development trajectories that appear to prepare them for their different respective futures of integrating into their natal clan or dispersing to a new one.

Keywords: Spotted Hyena, Social Network, Social Position, Social Development, Ontogeny, Social Bonds

Significance statement: Social development is difficult to study, particularly in long-lived gregarious mammals, so little is known about the variables shaping the emergence during ontogeny of social roles played by adults. We used social network analysis to investigate how sex and rank affect the social positions of maturing spotted hyenas as their positions change across ontogenetic development. Females develop more complex social positions than males early in life, with strategies that vary with their dominance status. Although males are just as well connected to group-mates as females when they are cubs, they generally disengage from the natal clan as they mature; males clearly do not disperse because they are aggressively expelled from their natal group. Our data suggest for the first time that social development appears to prepare females and males for their alternative futures of philopatry or dispersal.

INTRODUCTION

Just as the surroundings in which a child grows up are critical to its development, early environments are also important to non-human animals (Belsky, Steinberg, & Draper, 1991; Belsky et al., 2007; McDonald, 2007; Moffitt, Caspi, Belsky, & Silva, 1992; Stanton & Mann, 2012). For species living in highly complex societies like those of primates, bottlenose dolphins (*Tursiops* sp.), or elephants (*Loxodonta africana*), it is critical for individuals to develop the skills and relationships needed to function effectively as members of their social group and to maximize their fitness. An individual's behavior and fitness appear to be strongly affected by both the structure of its social network and its position within that network, especially in

complex societies (e.g., Chiyo, Moss, & Alberts, 2012; Silk, 2003; Silk et al., 2010; Stanton & Mann, 2012).

There is a long history in the primate literature, in particular, of documenting how and why early development is important to the long-term welfare of individual animals (e.g., Mason, 1968). Robert Hinde found that proper social development was necessary for individual primates to become fully functioning adults in their social group (Hinde, 1976; Hinde & Atkinson, 1970). Hinde was one of the first primatologists to use social networks to describe the structure of animal groups and the positions of individuals within those groups, based on their interactions. However, since Hinde conducted his work in the 1960s and '70s, computational resources have improved tremendously, allowing us to use detailed network metrics to go beyond mere descriptions of association patterns or analysis of rates of interactions, as Hinde did, to document the positions or roles of individuals within their social networks. Behavioral biologists are now using social network analysis (SNA) to elucidate the roles of individuals in complex mammalian societies (e.g., Archie & Chiyo, 2012; Hobson & DeDeo, 2015; Hock, Ng, & Fefferman, 2010; Wilson, Krause, Dingemanse, & Krause, 2013). Network analysis has a long history of use in disciplines ranging from mathematics to sociology, but has only recently been utilized by behavioral biologists (Barabasi & Albert, 1999; Croft et al., 2008; Granovetter, 1973; Newman, 2003). SNA enables us to document the ontogenetic development of the roles played by individual adults in their societies.

Many factors have been shown to affect behavioral development in general and social development in particular. For example, many primates show sexually dimorphic social roles in adulthood, but it is unclear how or why those patterns develop (Campbell, Fuentes, MacKinnon, Bearder, & Stumpf, 2011). In both juvenile and adult bonnet macaques (*Macaca radiata*), sex,

rank, and kinship differentially predict rates of affiliation and aggression interactions (Silk, Samuels, & Rodman, 1981). By puberty, the social networks of rhesus macaques (*Macaca mulatta*) become sexually dimorphic, such that males play almost exclusively with other males, and females with other females (Suomi, 2005), but see (Berman, 1982). These sex-specific patterns of social interaction continue to diverge, setting males and females on different trajectories into the future (Suomi, 2005).

Recent applications of SNA to bottlenose dolphins similarly show that males and females develop along different trajectories. Males tend to form the strongest social bonds with other young males whereas females tend to develop the strongest bonds with their mothers (Stanton et al., 2011; Stanton & Mann, 2012). These are among the few studies exploring early social position in wild mammals. To our knowledge, studies using SNA to examine social development in mammals with complex societies have been restricted to dolphins and primates, although social development can be crucial to long-term success in many other taxa as well (Hobson, Avery, & Wright, 2013; Makagon, McCowan, & Mench, 2012; Pinter-Wollman et al., 2014).

Another factor that frequently affects the roles of individuals in complex hierarchical societies, such as those of cercopithecine primates, is social dominance status. High-ranking individuals may lead social lives that are fundamentally different from those of their group-mates because they enjoy priority of access to resources, and this has lasting consequences for their reproductive success, longevity, and stress levels (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Ellis, 1995; Holekamp, Smale, & Szykman, 1996; Silk, 2003). In baboons (*Papio hamadryas ursinus*), for instance, high-ranking females are groomed preferentially, whereas lower-ranking females are attacked more frequently, and this in turn affects the differential social stress they experience (Crockford et al., 2008).

Here we use SNA to test predictions of hypotheses suggesting that sex and dominance status affect patterns of social development in free-living spotted hyenas (Crocuta crocuta) as they do in primates. Spotted hyenas offer a particularly good model system in which to study effects of these variables on social development for two reasons. First, in contrast to primates, dolphins, and most other mammals living in complex societies, spotted hyenas develop by advancing through life-history stages that are clearly demarcated by such unambiguous milestones as cessation of dependence on dens for shelter (Holekamp & Smale, 1998a). These milestones allow us to partition development into clear stages and compare effects of sex and rank among stages. Second, spotted hyenas live in societies, called clans, that are as large and complex as troops of baboons or macaques (Holekamp, Dantzer, Stricker, Yoshida, & Benson-Amram, 2015). Furthermore, as in these primates, dispersal behavior in hyenas is strongly sexually dimorphic, with most males emigrating to new groups shortly after reaching sexual maturity and females remaining for life in their natal groups (Smale, Nunes, & Holekamp, 1997). As in the societies of many cercopithecine primates, hyena social rank determines priority of access to key resources, such that it has profound effects on fitness (e.g., Holekamp et al., 1996; Swanson, Dworkin, & Holekamp, 2011). However, in contrast to cercopithecine primates, spotted hyenas live in fission-fusion societies in which individuals are often found alone or with small subgroups of clan-mates (Kruuk, 1972). The fission-fusion nature of hyena sociality allows us to complement social network metrics with measures of time spent alone and relationship strength among clan-mates, as reflected in association indices. Here, after assessing ontogenetic change in the percentage of their time individuals spent alone, we compare positions of high-, mid- and low-ranking hyenas of both sexes in three types of ego networks across three life stages. We first assess association networks, which indicate the extent to which individuals in

each sex and rank category spend time with particular clan-mates. We also assess aggression networks, which indicate which individuals are aggressors and which are targets during dyadic agonistic interactions. Finally, we assess affiliation networks based upon patterns of greeting behavior observed among clan-mates.

METHODS

Study site and subject animals

This study took place in the Masai Mara National Reserve, Kenya. Subjects were members of a single large clan of spotted hyenas that defend a group territory in the Talek region (Boydston, Morelli, & Holekamp, 2001). Detailed behavioral data (described in detail below) were collected via daily, year-round monitoring from June 1988 through September 2013. We identified individual hyenas by their unique spots, determined the sex of each animal based on its phallic morphology (Frank, Glickman, & Licht, 1991), and determined its birthdate to ± 7 days based on its appearance when first observed (Holekamp et al., 1996). Because our study involved focal animals in the field, it was not possible to record data blind.

Spotted hyenas live in mixed-sex, matrilineal societies organized by linear dominance hierarchies (Frank, 1986; Holekamp et al., 2012), and they acquire their social ranks via a learning process typical of old-world monkeys called "maternal rank inheritance" (Holekamp & Smale, 1991; 1993). Young hyenas of both sexes acquire social ranks immediately below those of their mothers during the first two years of life. Clans contain multiple matrilines of adult natal females and their young, but most breeding males are immigrants born elsewhere. Females are socially dominant to males among adults because males enter the hierarchy of their new clan at the bottom when they immigrate to join a new social group (East & Hofer, 2001). Adult females

and their young tend to be core figures in hyena societies, but adult males are more peripheral (Holekamp et al., 1997a; Kruuk, 1972; Szykman et al., 2001). Rank relationships among adult females are quite stable over long periods (Holekamp et al., 2012). High-ranking females enjoy significantly greater reproductive success than do low-ranking hyenas (Hofer & East, 2003; Holekamp et al., 1996; Swanson et al., 2011), which are also more strongly affected by fluctuations in prey abundance than are high-ranking hyenas (Holekamp et al., 1996). Here we assigned each individual a social rank based on its wins and losses in dyadic agonistic interactions, then we further assigned each subject to one of three rank categories by standardizing the ranks from -1 to 1 (lowest rank to highest rank) in each year of our study, and categorizing any ranks -1 to -0.33 as low-ranking, -0.33 to 0.33 as mid-ranking, and 0.33 to 1 as high-ranking. Until cubs acquired their own ranks, they were assigned the social ranks of their mothers.

To explore the social development of our subjects, we used the distinctive milestone markers in hyena development to partition ontogenetic development into three stages (Table 2.1). Young hyenas in our study area live at a communal den with other members of their cohort until they are 9-10 months old. During this stage, social interactions are more limited than during later stages because cubs' choices of social partners are restricted to members of their cohorts and whichever den-independent hyenas choose to visit the den. Thus, the first stage of development on which we focus in this paper was the communal den stage (CD), lasting from the date on which each cub was first seen until its date of den independence. All subjects were first seen within the first three months of life and were restricted to animals with known dates at which they became independent of the communal den. We determined that a juvenile was independent of the den when it was found away from the den on at least three consecutive occasions.

Developmental Stage	Abbreviation	Beginning	End
Communal Den	CD	Date first seen	Date of den independence
Den Independent	DI	Date of den independence	Period equal in length to CD period for that hyena
Adulthood	Adult	Date 24 months old	Period equal in length to CD period for that hyena

Table 2.1 Definitions of the developmental stages assessed in this paper

During the second stage of development, juveniles are independent of the den, and potentially able to interact with all their clan-mates, but they remain dependent on their mothers for food until they wean, on average, at 14 months of age (Holekamp & Smale, 1998a). During this second stage of development, juveniles learn their ranks in relation to clan members with whom they did not interact at the communal den. The second stage of development here was thus the stage of den independence (DI), defined for each individual to start when the cub became den-independent, and to be equal in length to the length of its CD stage for SNA. Although juveniles could be weaned at any time during the DI stage, and although this might conceivably influence network metrics during this stage, youngsters continue to rely heavily on their mothers for assistance in feeding throughout the DI stage because their skulls and skull musculature are far from fully developed (Swanson et al., 2013; Tanner, Zelditch, Lundrigan, & Holekamp, 2009; Watts, Tanner, Lundrigan, & Holekamp, 2009). Thus, it seemed unlikely that DI metrics would be strongly affected by variable weaning ages among juveniles. Furthermore, our analyses required that all three developmental stages be of the same duration within each juvenile's ontogeny, so instead of ending the DI stage at weaning, we made the DI stage the same length as the CD stage.

Male and female spotted hyenas both reach sexual maturity at approximately 24 months of age; males disperse to new clans 1-76 months after reaching sexual maturity, whereas females

remain in their natal clans for life (Höner et al., 2010; Smale et al., 1997; Van Horn, McElhinny, & Holekamp, 2003). Here, all natal animals under 24 months old were considered juveniles, and older animals were considered adults. We defined the adult stage of development as starting on the day on which an individual reached 24 months of age and extending from that date for a period equal in length to that of its CD stage. The adult stage for each hyena was thus standardized to represent its adult social world before it died or dispersed; all subjects had disappearance or dispersal dates after the end of their adult stages, as defined here. Within individuals, all three stages of development were of the same length for consistent comparisons, and each individual subject was observed during all three stages of development, so sample sizes were the same across all developmental stages. Mean stage length was 7.17±0.13 months for females (n=108; 52 high-ranking, 34 mid-ranking, 22 low-ranking) and 7.45±0.22 months for males (n=109; 52 high-ranking, 28 mid-ranking, 29 low-ranking).

Behavioral data collection

Behavioral observations were conducted year-round over the 25-year study period, from our vehicles, which we used as mobile blinds. Observations were made daily between 0530 and 0900 h, and again between 1700 and 2000 h. Each observation session was initiated when we found one or more hyenas separated from others by at least 200 m and terminated when we left that individual or group. In the absence of vocal communication, hyenas appear to be completely unaware of one another when separated by more than 200 m (J. E. Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). Although no focal hyenas were radio-collared here, subgroups of hyenas were located either via use of radio telemetry or while observers drove daily circuits in which all highpoints within the study clan's home range were visited. By making 360 degree

visual scans with binoculars from each highpoint, we were able to sample all parts of the clan's territory every day for presence of subgroups of hyenas. Each subgroup sighted or found via telemetry was then visited to determine its composition. On average, subgroups were found 1.11 ± 0.03 km apart (N = 1291 distances, ranging from 201 m to 9.8 km) (J. E. Smith et al., 2008).

To maximize independence of observations, we used only the first session in which an individual was seen during morning or evening observation periods. At the beginning of each observation session and subsequently at 15-20 minute intervals, we performed scan samples in which we recorded all individuals present (Altmann, 1974). From our session data, we determined association patterns based on the twice-weight index of association (Cairns & Schwager, 1987), as used previously (Holekamp et al., 1997a; 2012; Szykman et al., 2001). Because some subgroups were easier to find than others, given their size or the presence of one or more individuals fitted with radio collars, the twice-weight index was the association index most appropriate for our sampling methods (Cairns & Schwager, 1987); dyadic twice-weight association indices are robust and accurate indicators of social bond strength in spotted hyenas (Holekamp et al. 1997, 2012; Smith et al 2007). We also used all-occurrence sampling (Altmann, 1974) to record all agonistic and affiliation interactions. We built networks based only upon aggressive interactions in which we could see which individual initiated the attack and which individual was its recipient. Because greeting ceremonies, in which individuals raise their legs to one another to sniff the other's ano-genital region, were previously shown to promote and maintain social bonds (J. E. Smith et al., 2011), we used greeting behaviors to construct affiliation networks. We created affiliation networks using only interactions in which we knew which individual initiated each greeting by lifting its leg first.

Network construction

Social networks consist of groups of more than two individual animals (nodes) connected by behavioral interactions or co-occurrences in space (ties or links) and portrayed as graphs or matrices. Ties can be directed if the behavior has an initiator and a receiver, or undirected when there is no clear direction in the relationship. Here networks based on associations were undirected, as they indicated co-occurrence, but both aggression and affiliation networks were directed. We used only ego networks in this study; these are networks containing only those individuals directly connected to a focal animal.

We used the R package, 'network' version 1.13.0 (Butts, 2008; 2015) to build three social networks per subject per network type, each based on data collected during one of the three stages of development. The focal individual had to be seen at least ten times during each developmental stage for its network to be calculated, and each of its partners also had to be seen at least ten times during a particular stage to be included in the ego network. Each tie in each association network occurred when individuals meeting our selection criteria were seen together in one or more observation sessions. Ties in aggression networks occurred when an individual initiated, or received an aggression from, a group-mate during the developmental stage in question. Similarly, ties in affiliation networks were added when an individual initiated or received a greeting ceremony from a group-mate during that developmental stage. In this study, we chose to use binary networks with strong criteria for inclusion so that we could make a robust baseline assessment of social position development.

Network metrics and statistical analysis

For each focal individual, during each stage of development (CD, DI, and adulthood), for each network type, we calculated several measures of social network position. First, we calculated the proportion of observation sessions in which the focal individual was found alone, when it clearly could not be interacting with other animals, as the number of sessions in which the individual was seen alone divided by the total number of sessions in which the individual was observed during that developmental stage. We next calculated degree centrality, here called "degree", which is the number of other individuals to which the focal individual is connected. Degree is an important metric in social networks, as having a higher degree can indicate that an individual is more of a social hub, which in turn can affect its fitness and its exposure to both information and pathogens (e.g., Barocas, Ilany, Koren, Kam, & Geffen, 2011; Hamede, Bashford, McCallum, & Jones, 2009; Royle, Pike, Heeb, Richner, & Kolliker, 2012). In directed networks, we calculated both in-degree centrality, which represents the number of individuals that directed actions at the focal individual, and out-degree centrality, representing the number of individuals with which the focal animal initiated interactions. We also determined ego density, which is the number of ties that occur in the ego network, excluding the ego, out of all possible ties that could potentially be formed with all hyenas in the ego network. In ego networks, density indicates how much the individuals in the focal animal's network interact with one another; this can be important for learning and disease exposure in animal societies, as more dense networks enable more efficient information flow, and spread of pathogens, within the group (Croft et al., 2008; Hanneman & Riddle, 2005; Kurvers, Adamczyk, van Wieren, & Prins, 2011). Social network metrics were calculated using the 'statnet' package (v.2016.4) in R (Handcock, Hunter, Butts, Goodreau, & Morris, 2008).

Once the network metrics were calculated, we then ran each metric in its own mixed effects model using R (v. 3.2.3) and glmmADMB (Fournier et al., 2012; Skaug, Fournier, Bolker, Nielsen, & Magnusson, 2016). For all degree metrics, we used a Poisson error distribution, and for alone rates and density metrics, we used a logistic error distribution. Because the metrics calculated for one individual in a network are dependent on the other animals in the network, network data often violate assumptions of independence, requiring randomization tests to generate p-values that reflect independence among subjects. However, that was unnecessary here because we were working with 1953 different ego networks, with only 7% structural and 9.6% temporal overlap among networks. Three different ego networks were calculated for each of 108 females and 109 male subjects in each of three different developmental stages, drawing from hyenas studied over a period of 25 years. Thus, the ego networks studied here were almost entirely independent of one another due to rare overlap with respect to both the periods during which individuals were observed and the individuals comprising the networks.

To test our hypotheses that sex and rank affect network position over ontogeny, we predicted each metric with sex, developmental stage, rank, and specific interactions among these three key variables. We have previously documented sexually dimorphic development in other aspects of the behavior of spotted hyenas (e.g., Boydston, Kapheim, Van Horn, Smale, & Holekamp, 2005), and we expected that rank might have different effects on females and males here because females retain their rank by remaining in their natal clan whereas males lose their natal rank when they disperse. Therefore, we included two-way interactions between (sex and developmental stage) and (sex and rank), as well as the three-way interaction of (sex, developmental stage, and rank). Each model also included the identity of the focal individual as a

random effect. During the periods of study, clan size ranged from 36 to 125, and contained, on average, 77.31±0.57 hyenas. Therefore, we included an offset for clan size during the stage in question; this value was log transformed to make the scale more closely comparable to our response measures. Group size is known to affect network metrics because it limits the number of individuals with which a focal animal can interact. Thus, the equation for each GLMM run was: Metric ~ sex + stage + rank + sex*stage + sex*rank + sex*stage*rank [+ id + clan size]. We considered differences among groups to be significant when P < 0.05. All reported mean values are shown ±SE.

RESULTS

Data describing observations per individual and interaction frequency for focal hyenas in each stage of development are summarized in Table 2.2. The social network metrics of individuals exhibited striking variation over the course of ontogeny, generally decreasing with age and social rank. Fig. 2.1 shows representative examples of affiliation networks for one highranking, one mid-ranking, and one low-ranking female across our three ontogenetic stages; metrics calculated for each of these networks are shown in Table 2.3. Fig 2.1 clearly shows that the high-ranking female had more individuals and interactions in her networks than did the midor low-ranking females. However, we observed considerable variation among network types, and not all of them looked exactly like these.

	CD	DI	Adult
Total # observation sessions	93.2±2.95	80.9±2.94	60.0 ± 2.40
	(12-241)	(2-196)	(1-172)
# observation sessions per day	0.44 ± 0.014	0.39±0.015	0.28±0.011
	(0.055 - 1.2)	(0.0078 - 1.0)	(0.0034-0.79)
# huonas soon non sossion	11.5±0.18	9.28±0.16	9.50±0.23
# nyenas seen per session	(5-20)	(3-19)	(1-22)
# • • • •-	13.1±0.60	12.2±0.59	12.1±0.7
# aggressive interactions	(0-47)	(0-45)	(0-45)
# affiliative interactions	10.6±0.63	8.10±0.45	8.25±0.56
# annative interactions	(0-52)	(0-36)	(0-33)

Table 2.2 Mean±SE values describing observability and interaction frequency for focal hyenas in each stage of development. Ranges are in parentheses



(jab

CD





b) Mid-ranking





Fig. 2.1 Examples of typical affiliation ego networks of a) high-ranking (ego = GIL), b) mid-ranking (ego = HML), and c) low-ranking (ego = BERN) females across ontogeny (see Table 2.4 for the specific network metrics of each ego)

	CD		DI		Adult	
Metric	Degree	Density	Degree	Density	Degree	Density
GIL	12	0.14	7	0.1	33	0.16
HML	6	0.3	8	0.13	11	0.16
BERN	10	0.14	5	0	8	0.089

Table 2.3 Network metrics of the representative affiliative ego networks shown in Fig. 2.1 over the course of ontogeny. GIL is high-ranking, HML is mid-ranking, and BERN is low-ranking

Table 2.4 Mean \pm SE network metrics for females and males over the course of ontogeny using "degree" to indicate the number of individuals comprising each ego network. For example, females (N=108) engaged in agonistic interactions with 12.7 \pm 0.84 individuals in their networks, and males (N=109) engaged in agonistic interactions with 13.5 \pm 0.87 individuals during the CD stage

		CD		DI		Adult	
Network Type	Metric	F	Μ	F	Μ	F	Μ
	Alone proportion	0.007±0.001	0.007±0.001	0.06±0.004	0.067±0.01	0.1±0.01	0.1±0.01
Association	Degree	58.9±1.3	59.4±1.4	60.6±1.63	58.8±1.81	53.1±3.2	37.8±3.1
	Density	0.92±0.004	0.91±0.005	0.89±0.01	0.88 ± 0.02	0.7±0.04	$0.55 \pm .04$
Aggression	Degree	12.7±0.8	13.5±0.9	12.5±0.81	11.3±0.85	11.4±0.93	4.83±0.63
	Density	0.22±0.01	0.23±0.01	0.19±0.01	0.19±0.01	0.13±0.01	0.1±0.01
Affiliation	Degree	9.03±0.76	12.3±1.0	7.73±0.61	8.25±0.65	7.84±0.8	3.18±0.4
	Density	0.14±0.01	0.17±0.01	0.11±0.01	0.13±0.01	0.1±0.01	0.07±0.01

Changes in Network Position Across Developmental Stages

Although cubs were rarely seen alone during the communal den (CD) stage, hyenas of both sexes were seen alone significantly more often as they matured (Table 2.4; Fig. 2.2). In association networks, both degree centrality and density decreased significantly between the CD stage and adulthood (Table 2.4; Figs. 2.3 & 2.4). In aggression networks, we observed that indegree, out-degree, and density of individuals' ego networks significantly decreased over ontogeny (Table 2.4; Figs. 2.5-2.7). As with most other network metrics, greeting in-degree and out-degree also decreased significantly over the course of development in affiliation networks (Table 2.4; Figs. 2.8 & 2.9). Similarly, we found that affiliation densities also decreased significantly over the course of ontogeny (Table 2.4; Fig. 2.10). Note that our analyses of degree and density, which were unweighted, assumed that a pair of individuals found together once during a developmental stage had the same value as a pair often found together. However, given the rigor of our criteria for inclusion of individuals in these analyses, as described above, we are nevertheless confident that our results are robust.



Figure 2.2 Effects of social rank on proportion of time found alone. Mean proportion of observation sessions in which animals were found alone, based on rank level for a) females and b) males across three developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes were as follows: high-rank (\bullet , f=52, m=52), mid-rank (\circ , f=34, m=28), and low-rank (\bullet , f=22, m=29). Sample sizes represent numbers of focal individuals and error bars indicate ±SE



Figure 2.3 Effects of social rank on association network metrics. Mean **degree** in the association networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Degree indicates the number of other individuals in the focal animal's network. Sample sizes and error bars are as in Fig. 2.2



Figure 2.4 Effects of social rank on association network metrics: Mean **density** in the affiliation networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.2


Developmental Stage

Developmental Stage





Figure 2.6 Effects of social rank on aggression networks metrics: Mean **in-degree** in the aggression networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.2



Figure 2.7 Effects of social rank on aggression network metrics: Mean **density** in the affiliation networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.2



Figure 2.8 Effects of sex on affiliation network metrics: Mean a) **in-degree vs. b) out-degree** in the affiliation networks of female and male spotted hyenas across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.5



Developmental Stage

Developmental Stage

Figure 2.9 Effects of social rank on affiliation network metrics: Mean **in-degree** in the affiliation networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.2



Figure 2.10 Effects of social rank on affiliation network metrics: Mean **density** in the affiliation networks of a) females and b) males by rank level across developmental stages: communal den (CD), den independent (DI), and adulthood. Sample sizes and error bars are as in Fig. 2.2

Effects of Sex on Network Position

We found no significant differences between males and females with respect to the proportion of time spent alone (Table 2.4; Fig. 2.2). We did however observe a significant interaction between sex and developmental stage, with males being seen alone more than females by the time they reached adulthood (Table 2.5).

Degree centrality of association networks was significantly higher for females than males during the adult stage; thus, females associated with more individuals than did males by adulthood (Tables 2.5 & 2.6; Fig. 2.3), which supports our hypothesis that sex affects social network positions. The mean ego density of association networks for both males and females also generally declined across ontogeny (Table 2.3), but sex had no significant effect on this metric (Table 2.6; Fig. 2.3).

		sex F x	ex F x stage DI se			sex F x stage Adult			sex F x rank Mid			sex F x rank Low		
Network type	Metric	Est.	SE	р	Est.	SE	р	Est.	SE	р	Est.	SE	р	
	alone	-0.017	0.032	0.60	-0.090	0.035	0.0094	-0.020	0.056	0.71	0.012	0.061	0.84	
Association	degree	0.031	0.035	0.39	0.11	0.035	0.0063	-0.053	0.063	0.40	-0.021	0.069	0.76	
	density	-0.012	0.061	0.85	0.11	0.070	0.12	-0.091	0.083	0.27	0.036	0.089	0.69	
Aggression	in-degree	0.054	0.12	0.65	0.61	0.14	<0.0001	-0.62	0.21	0.0027	0.15	0.22	0.49	
	out-degree	0.22	0.098	0.025	1.04	0.098	<0.0001	-0.47	0.23	0.046	-0.17	0.28	0.54	
	density	0.025	0.037	0.51	-0.037	0.039	0.34	-0.054	0.064	0.40	0.011	0.070	0.88	
Affiliation	in-degree	0.52	0.13	<0.0001	1.2	0.13	<0.0001	-0.56	0.24	0.023	-0.081	0.26	0.76	
	out-degree	0.37	0.13	0.0044	1.3	0.16	<0.0001	-0.71	0.22	0.0012	-0.43	0.23	0.067	
	density	-0.038	0.044	0.38	-0.024	0.044	0.58	-0.14	0.065	0.031	-0.068	0.070	0.34	

Table 2.5 GLMM output describing each metric, including parameter estimates and SE, for two-way interactions between 1) sex and developmental stage, and 2) sex and rank. Bolded p-values are significant

		sex F (Compa males)	sex F (Compared to males)		stage DI (Compared to CD stage)		stage Adult (Compared to CD stage)		rank Mid (Compared to High rank)		rank Low (Compared to High rank)					
Network type	Metric	Est.	SE	р	Est.	SE	р	Est.	SE	р	Est.	SE	р	Est.	SE	р
	alone	0.04	0.1	0.3	0.05	0.02	0.03	0.1	0.03	<0.01	0.002	0.1	0.7	-0.03	0.1	0.5
Association	degree	0.05	0.1	0.2	-0.01	0.02	0.71	-0.1	0.03	0.03	-0.02	0.1	0.7	-0.04	0.1	0.5
	density	0.06	0.1	0.2	-0.03	0.1	0.57	-0.4	0.05	<0.01	0.03	0.1	0.6	-0.06	0.1	0.3
Aggression	in- degree	0.16	0.1	0.3	-0.29	0.1	<0.01	-1.0	0.11	<0.01	0.35	0.2	0.02	0.10	0.2	0.6
	out- degree	0.16	0.2	0.3	-0.17	0.1	0.02	-0.9	0.1	<0.01	-0.26	0.2	0.1	-0.27	0.2	0.15
	density	0.05	0.1	0.2	-0.04	0.03	0.11	-0.2	0.03	<0.01	0.03	0.1	0.53	-0.07	0.1	0.17
Affiliation	in- degree	-0.001	0.2	0.9	-0.70	0.1	<0.01	-1.3	0.13	<0.01	-0.01	0.2	0.94	-0.02	0.2	0.93
	out- degree	0.01	0.1	0.9	-0.40	0.1	<0.01	-1.3	0.13	<0.01	0.25	0.2	0.10	0.54	0.2	<0.01
	density	0.08	0.1	0.1	-0.02	0.03	0.62	-0.1	0.03	<0.01	0.09	0.1	0.07	-0.001	0.1	0.98

Table 2.6 GLMM output describing each metric, including parameter estimates and SE, for the effects of sex, developmental stage, and rank on network position in wild spotted hyenas. Bolded p-values are significant

In aggression networks, the degree centrality of each focal animal indicated the total number of individuals in its aggression ego network, which generally declined differently over time between the sexes (Table 2.4). By the time hyenas reached adulthood, the number of individuals aggressing upon them was significantly higher for females than males, even though in-degree still generally decreased over development in both sexes (Tables 2.4 & 2.5; Fig. 2.5a). There was no overall sex difference in mean out-degree in aggression networks, but the average out-degree centrality among females was significantly higher than that among males during adulthood. The mean number of individuals aggressed upon by males declined across ontogeny, but this was not true for females, in which this metric remained relatively constant over development (Tables 2.4 & 2.5; Fig. 2.5b). The average aggression network density, indicating how connected all animals were within the ego network, declined over ontogeny, but we observed no significant difference in this between the sexes (Tables 2.4 & 2.6; Fig. 2.7).

In affiliation networks, the decreasing in-degree over the course of ontogeny appeared to be largely driven by values for males declining more steeply than those for females, whose values varied more during ontogeny (Table 2.4); here we observed a significant effect of the interaction between sex and developmental stage on in-degree centrality (Tables 2.5 & 2.6; Fig. 2.5a). We also found an interaction between sex and developmental stage in which females had higher mean affiliation out-degree than males during DI and adult stages (Tables 2.5 & 2.6; Fig. 2.5b). Furthermore, similar to the patterns seen in aggression networks, out-degree in the greeting networks of females remained relatively consistent as they matured. By contrast, males greeted with significantly more individuals than did females during the CD stage, but with relatively few clan-mates during adulthood (Fig. 2.5b). Affiliation network densities decreased over the course of development in both sexes (Table 2.4), although network densities decreased

less sharply for females than did those for males, and females tended to have higher densities in general (Tables 2.5 & 2.6; Fig. 2.10).

Effects of Rank on Network Position

In support of the hypothesis that dominance status affected network positions, we observed a significant interaction in females between rank and developmental stage where, by adulthood, mid-ranking females tended to be alone more often than were either high- or lowranking females (Table 2.7). Social rank did not significantly affect degree centrality or density for either females or males in their association networks (Tables 2.6 & 2.7; Figs. 2.3 & 2.4). However, in aggression networks, mid-ranking hyenas had significantly higher in-degree centrality than did either high- or low-ranking individuals, indicating that the former were the targets of more aggression (Table 2.4). The in-degree of mid-ranking females was higher during the DI stage than during either CD or adult stages (Fig. 2.6a; Table 2.7). Additionally, there was a significant interaction in males between developmental stage and rank, in which low-ranking males had lower in-degree centrality than did males in other rank categories during adulthood (Fig. 2.6b; Table 2.7). High-ranking females had a significantly higher out-degree than midranking and low-ranking females, indicating that higher ranking females aggressed on more individuals than did lower-ranked female hyenas, particularly in adulthood (Table 2.7). On the other hand, high- and mid-ranking males aggressed on more individuals than did low-ranking males, as indicated by out-degree measures, but this difference was only significant in adulthood (Table 2.7). Social rank had no significant effect on the aggression network densities of focal individuals, and we observed no significant interactions among any of the factors (Table 2.6; Fig. 2.7).

		sex F x s Mid	ex F x stage DI x rank ⁄Iid			sex F x stage Adult x rank Mid			sex F x stage DI x rank Low			sex F x stage Adult x rank Low		
Network														
type	Metric	Est.	SE	Р	Est.	SE	р	Est.	SE	р	Est.	SE	р	
	alone	0.006	0.037	0.86	0.066	0.041	0.07	-0.02	0.04	0.61	0.011	0.044	0.80	
Association	degree	0.03	0.040	0.41	0.074	0.042	0.08	-0.07	0.04	0.13	-0.047	0.048	0.33	
	density	-0.0002	0.068	0.99	0.033	0.076	0.66	0.001	0.07	0.99	-0.083	0.087	0.34	
	in-													
Aggression	degree	0.49	0.13	0.0001	0.39	0.13	0.003	0.09	0.13	0.46	0.057	0.14	0.69	
	out-													
	degree	0.13	0.13	0.32	-0.28	0.13	0.034	-0.36	0.17	0.032	-0.85	0.18	<0.0001	
	density	-0.049	0.042	0.25	0.051	0.045	0.25	-0.06	0.05	0.22	0.0052	0.048	0.91	
	in-													
Affiliation	degree	-0.26	0.17	0.13	-0.67	0.17	0.0001	-0.64	0.20	0.0012	-0.69	0.20	0.0003	
	out-													
	degree	0.24	0.15	0.10	-0.21	0.15	0.17	-0.25	0.16	0.13	-0.49	0.17	0.0035	
	density	0.013	0.048	0.78	0.055	0.049	0.26	0.03	0.05	0.59	-0.0043	0.056	0.94	

Table 2.7 GLMM output describing each metric, including parameter estimates and SE, for the three-way interactions in our model between sex, developmental stage, and rank. Bolded p-values are significant

Table 2.7 (cont'd)

		sex M x rank M	sex M x stage DI x rank Mid			sex M x stage Adult x rank Mid			sex M x stage DI x rank Low			sex M x stage Adult x rank Low		
Network														
type	Metric	Est.	SE	р	Est.	SE	р	Est.	SE	р	Est.	SE	р	
	alone	-0.008	0.040	0.85	-0.020	0.043	0.64	0.023	0.040	0.56	-0.03	0.04	0.53	
Association	degree	0.047	0.043	0.28	-0.018	0.050	0.72	-0.013	0.044	0.77	-0.04	0.05	0.42	
	density	-0.004	0.074	0.95	0.078	0.086	0.36	0.0014	0.076	0.98	-0.08	0.09	0.38	
	in-													
Aggression	degree	0.28	0.13	0.040	0.14	0.18	0.44	0.21	0.13	0.11	-0.38	0.19	0.042	
	out-													
	degree	0.17	0.14	0.22	-0.20	0.19	0.29	-0.35	0.14	0.014	-0.92	0.21	<0.0001	
	density	-0.011	0.045	0.80	0.0057	0.047	0.90	0.0068	0.046	0.88	-0.01	0.05	0.78	
	in-													
Affiliation	degree	0.068	0.17	0.69	-0.19	0.21	0.37	-0.033	0.18	0.85	-0.29	0.23	0.21	
	out-													
	degree	0.31	0.14	0.029	-0.10	0.19	0.59	0.20	0.13	0.15	-0.46	0.21	0.027	
	density	-0.092	0.051	0.071	-0.11	0.053	0.030	-0.015	0.052	0.77	-0.02	0.05	0.79	

Social rank did not significantly affect affiliation network in-degree in either sex, but there was a significant interaction between rank and developmental stage. That is, significantly fewer clan-mates initiated greetings with mid- and low-ranking females than with high-ranking females except during the CD stage (Fig. 2.9; Table 2.7). Low-ranking individuals, however, initiated greetings with significantly more individuals than did higher ranking individuals (Table 2.6). The significant interaction between sex and rank indicated that mid-ranking females had lower out-degree centrality than did mid-ranking males (Table 2.5). Low-ranking males also initiated greetings with significantly fewer individuals than did high- or mid-ranking males in adulthood (Table 2.7).

Lastly, mid-ranking individuals tended to have higher affiliation densities than did hyenas in other rank categories, but this appeared to be driven partially by mid-ranking males, who had higher network densities than high- or low-ranking males during the CD stage, but whose densities then dropped below values for the other rank groups during the DI stage (Tables 2.6 & 2.7; Fig. 2.10). Mid-ranking males also had significantly higher densities than did mid-ranking females, but this also appeared to be driven mainly by interactions during the CD stage (Table 2.5; Fig. 2.10).

DISCUSSION

Changes in Network Position Across Developmental Stages

Hyenas generally spent more time alone, and their social interactions diminished overall, as they matured. Because the communal den is the clan's social hub, cubs living there rarely have opportunities to be alone, and they tend to have more individuals with which to interact, and more often, than during later stages of development. Most females with den-dwelling cubs

visit daily to nurse them, older siblings come to visit their mothers and younger siblings, and other clan members come to socialize and investigate their new clan-mates (Holekamp et al., 1997a). Once youngsters were no longer dependent on dens here, they were seen alone more often, their social interactions diminished, and this trend increased even further in adulthood, as the fission-fusion character of the hyenas' society became more fully apparent.

The numbers of individuals toward which females directed aggressive and affiliative acts, and from which they received such acts, did not change significantly across ontogeny. There was, however, a great deal of variation within these metrics, suggesting that individual personality traits might affect network positions, as also occurs among Trinidadian guppies (*Poecilia reticulata*) (Croft, Krause, & Darden, 2009), great tits (*Parus major*) (Aplin et al., 2013), rhesus macaques (*M. mulatta*) (McCowan et al., 2011), chimpanzees (*Pan troglodites*) (Massen & Koski, 2014), and other species in which personality and network position are related.

Effects of Sex on Network Position

An individual's sex only directly affected affiliation density (Table 2.6), but sex interacted significantly with developmental stage to affect several other network metrics (Table 2.6), supporting our hypothesis that sex affects the development of social network position. Even though the two sexes exhibited similar values early in life, females had larger, more dense association and aggression networks than males by adulthood, indicating that they were more central and better connected than maturing males. This pattern is also seen in primates, although SNA has seldom been used to document these changes (Lehmann & Ross, 2011; Pereira, 1988). It is interesting that male and female hyenas did not differ with respect either to the proportion of

time spent alone or in their positions in affiliation networks. Frequently in matriarchal mammalian societies, males are alone more often and have different, usually smaller, less connected affiliation network positions than do females (e.g., K. E. Evans & Harris, 2008; Onyango, Gesquiere, Altmann, & Alberts, 2013); this pattern only appeared in adulthood among hyenas, and was not observed among juveniles. Juvenile patterns tend to be understudied in primates and other mammals growing up in complex societies.

In contrast to those of female hyenas, male social position metrics in directed networks showed a consistent pattern of decreasing significantly across the course of ontogeny. As seen in both in-degree and out-degree centrality metrics in both types of directed networks, males were both initiating interactions with fewer clan-mates and receiving interactions from fewer clanmates than were their female peers (Figs 4, 7). As they mature, females are more interactive and involved in more agonistic interactions than males, as both attackers and recipients of attacks. By contrast, females are relatively stable in their levels of affiliation compared to males, whose values start higher than females during the CD stage but then drop significantly by adulthood. Male ego networks were also frequently less dense than those of females, indicating that males were interacting with other individuals that interacted with one another less than did females. Anecdotally, in the field we observe males nearing dispersal age tending to associate almost exclusively with immigrant males or other maturing males who are also about to disperse. This pattern has also been seen in primates (Onyango et al., 2013; Onyango, Gesquiere, Altmann, & Alberts, 2012).

Interestingly, our data clearly demonstrate that male spotted hyenas are not forced out of their natal clan at dispersal (Holekamp & Smale, 1998b; Kruuk, 1972; Smale et al., 1997; Van Horn et al., 2003). Numbers of clan-mates directing aggressive acts towards males decreased

greatly as they reached adulthood, which would not be expected if males were aggressively expelled from their natal groups (Figs 4a, 5b). Instead, we saw that males generally spontaneously disengaged from interactions within the natal clan as they prepared to disperse.

Effects of Rank on Network Position

We observed what appears to be the emergence during ontogeny of different social strategies based on rank among females but not among males (e.g., Figs 2, 5, 7), which supports hypotheses suggesting that both sex and dominance status affect the network positions of individual hyenas as they develop. Males mainly only showed rank-related variation in their affiliation networks, with high-ranking individuals initiating greetings with more individual, and having higher affiliation network densities, by adulthood than did lower-ranking males (Table 2.6). These rank differences among young adult natal males may be related to the rank-related variation documented in the success enjoyed by males in their new clans after dispersal; sons of high-ranking females enjoy greater reproductive success in their new clans than do lower-ranking males (Höner et al., 2010).

Females showed a much more complicated pattern than males of rank-related variation across network types. Generally high- or low-ranking females each adopted a particular strategy, with the pattern observed among mid-ranking individuals resembling that of one of those other rank classes, depending on the metric being assessed. However, mid-ranking females were the only ones who had significantly more individuals aggressing upon them after the CD stage than did either high- or low-ranking females, whose in-degree values decreased over ontogeny (Fig. 2.6). Furthermore, mid-ranking females strongly tended to be alone more often than did either high- or low-ranking females as they matured (Fig. 2.2a). Mid-ranking hyenas must remember

more individuals both above and below their own rank positions than either high-ranking females, who know that most others are ranked below them, or low-ranking females, who know that most clan-mates out-rank them. This middle position in the hierarchy may be why mid-ranking females are aggressed upon more than other ranks, as they may have a harder time learning their ranks; this might explain why they tend to be seen alone more often by adulthood. Uncertainty in the status of mid-ranking individuals can have adverse health effects, as seen in rhesus macaques (Vandeleest et al., 2016). Furthermore, primates have been shown to utilize different social strategies to compensate for rank-related disadvantages to gain better access to resources and improve reproductive success (Anderson & Mason, 1978; Bercovitch, 1991), which may be occurring here, although we would need to look at later adulthood to determine whether the tendency to be alone more often strengthens over time.

Our findings also highlight the fact that high-ranking females lead strikingly different social lives from those of either low- or mid-ranking females in this species, starting early in ontogeny. In the field, we often see that high-ranking females are accompanied by an entourage of "groupies" (J. E. Smith et al., 2007). Although we found no significant effects of female rank on position in association networks, which would be expected because lower-ranking "groupies" are associating with higher-ranking females (Smith et al. 2007), high-ranking females did appear to be more directly socially active, indicating that they were developing into social hubs in their networks. High-ranking females initiated more aggressive acts and received more affiliative acts than did females of other ranks (Fig. 2.9, Table 2.7). Many other mammals, especially primates, also have societies in which high-ranking individuals function as social hubs (Pereira, 1988; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012; J. E. Smith et al., 2007). However, high-ranking females greatings with more individuals than did mid- or low-ranking

females, perhaps because it is equally important for females of all ranks to help maintain social cohesion within the clan (J. E. Smith et al., 2011).

Low-ranking female hyenas may cultivate fewer, but nonetheless important, direct ties with specific clan-mates rather than maintaining relationships with many different conspecifics, as high-ranking females appear to do. Here high- and low-ranking females spent similar amounts of time alone, and they had similar association patterns. Previous research has shown that highand low-ranking hyenas have significantly different association patterns (Holekamp et al., 1997a), but earlier workers used mean association indices in their analyses whereas we used the social network positions of degree centrality and density, which account for numbers of associates and connectedness within networks. Together, our findings indicate that, although their positions in the network have similar structures, low-ranking females have weaker associations overall than do high-ranking females (Holekamp et al., 1997a). Furthermore, with the sole exception of aggressive acts directed towards them, in social network position metrics where we observed significant rank effects (aggressions directed by and at them; affiliations directed by and at them), low-ranking female hyenas exhibited lower values than did high-ranked individuals, on average (Tables 2c; Figs 5a, 7a). The fact that low-ranking females directly interacted with fewer individuals than the number with which they associated suggests that they may be actively choosing their preferred social partners while associating less strongly with, or actively avoiding, other group-mates.

CONCLUSIONS

Our results suggest that spotted hyenas adopt social strategies during development that vary with their age, sex, and rank. Such strategies have previously been most reported in

primates. For instance, although high rank is frequently hypothesized to enhance reproductive success, some have found that primates may use other social skills and strategies to circumvent their rank limitations and manage to achieve high reproductive success despite those limitations (reviewed in Bercovitch, 1991).

The prolonged juvenile period in primates is known to be driven in part by the time needed to learn how to live in their complex societies (Joffe, 1997; Walker, Burger, Wagner, & Rueden, 2006). Our data suggest that, even though the prolonged juvenile stage in spotted hyenas is required largely by the time needed to develop a feeding morphology specialized for bone-cracking (Holekamp, Swanson, & Van Meter, 2013; Watts et al., 2009), it also provides spotted hyenas with opportunities to learn to live in their primate-like social groups. However, social development is a largely unexplored aspect of the behavior of non-primate mammals. There is a pressing need to explore social development in other taxa, and this paper represents a first step toward elucidating social development in a highly gregarious carnivore. The findings presented here raise many new questions. For example, we will be fascinated to see whether the different social positions and strategies indicated by our data have fitness consequences for individuals, as have been documented in adult primates (Archie, Tung, Clark, Altmann, & Alberts, 2014; Brent, Ruiz-Lambides, & Platt, 2017; Silk, 2003; Silk et al., 2010). It will also be critical to determine whether there are sensitive periods in social development that are crucial to becoming a functioning member of society and affect future longevity or reproductive success.

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CHAPTER 3

EARLY LIFE RELATIONSHIPS MATTER: SOCIAL POSITION DURING EARLY LIFE AFFECTS FITNESS AMONG FEMALE SPOTTED HYENAS

Turner, J. W., Bills, P. S., & Holekamp, K. E. (under review). Early life relationships matter: Social position during early life affects fitness among female spotted hyenas. *Proceedings B.*

ABSTRACT

How social development in early life affects fitness remains poorly understood. Recent improvements in computational abilities enable us to exploit the power of social network analysis to explore how variation in social network position during early ontogeny affects adult fitness outcomes. Here, we explore how social network positions during two stages of early ontogeny affect annual reproductive success (ARS) and longevity among adult female spotted hyenas (*Crocuta crocuta*). Specifically, we test the social bonds hypothesis, which suggests that social relationships made during early development prepare youngsters for adult success. We found that the social positions held by juveniles do indeed affect their fitness measures also differed between stages of early development. Network parameters when youngsters were denindependent better predicted longevity than when they were confined to the communal den. Our study is unique in that it assesses how social bonds formed during multiple early stages of social development affect lifetime fitness outcomes.

Keywords: Social development, Social bonds, Fitness, Spotted hyena, Ontogeny

INTRODUCTION

The early development of both humans and non-human animals affects later-life phenotypes and fitness outcomes (e.g., Belsky et al., 1991; Kasumovic, 2013)). Much empirical evidence shows that favorable early environments, ranging from quality of parental care to the general physical and social environment, improve fitness whereas unfavorable ones reduce it (e.g., Branchi & Cirulli, 2014; Douhard et al., 2014; Lee, Bussiere, Webber, Poole, & Moss, 2013). However, despite a growing understanding of the relationship between sociality and fitness during adulthood (e.g., Lee et al., 2013; Silk, 2003)), the long-term fitness consequences of the individual's early social network, and its position within that network, have seldom been explored. The few cases in which these social metrics have been investigated suggest that earlylife social networks can have important fitness consequences. For instance, centrality among juvenile long-tailed manakins (Chiroxiphia linearis) significantly affects their later reproductive success (McDonald, 2007). Social networks in great tit (Parus major) broods predict the future success of families, with more connected individuals gaining more reproductive opportunities and producing more surviving offspring (Royle et al., 2012). Among Alpine marmots (Marmota *marmota*), early and adult social environments both independently and additively affect the longevity and reproductive success of dominant females (Berger, Lemaître, Allainé, Gaillard, & Cohas, 2015).

In long-lived species, the more complex the social environment, the more likely it is that variations in social development may have subtle, far-reaching consequences. Some stages of development may be more important than others with respect to their influence on adult traits (Bateson, 1979). For instance, there are sensitive periods in early life for the development of secure attachments (Bateson & Gluckman, 2011; Bateson & Hinde, 1987; H. F. Harlow &

Harlow, 1962). Rhesus macaques (*Macaca mulatta*) that do not develop secure attachments during infancy experience negative long-term health consequences for which later normal socialization cannot compensate (Conti et al., 2012). In general, adolescence represents an important stage in many species, perhaps because it represents a last chance to modify the phenotype in response to the current environment before reaching adulthood (Sachser, Kaiser, & Hennessy, 2013). Although studies such as these focus on a single stage of development during infancy or adolescence, we know of no prior research looking at multiple stages of juvenile social development and their respective influences on adult traits among free-living animals. The dearth of such studies may be due to the fact that there are seldom obvious ways in which to identify discrete developmental stages in most gregarious vertebrates.

Here, we use social network analysis (SNA) and a long-term dataset collected from freeliving spotted hyenas (*Crocuta crocuta*) to test the social bond hypothesis (Fairbanks, 1993; Stanton et al., 2011), which suggests that young animals develop relationships or social skills necessary for their success later in life. Spotted hyenas offer a particularly good model system in which to use SNA to test the social bonds hypothesis for two reasons. First, in contrast to primates and most other mammals living in complex societies, spotted hyenas advance through life-history stages that are clearly demarcated by unambiguous milestones, such as cessation of dependence on dens for shelter (Holekamp & Smale, 1998a). These milestones allow us to partition early development into clear stages. Second, spotted hyenas live in societies, called clans, that are no smaller or less complex than those of baboons or macaques (Holekamp et al., 2015). Furthermore, as in these primates, dispersal behavior in hyenas is strongly sexually dimorphic; most males emigrate to new groups shortly after puberty, whereas females remain in their natal groups for life (Smale et al., 1997). Hyena social rank determines priority of access to

key resources, which has profound effects on fitness measures, including both longevity and reproductive success (e.g., Holekamp et al., 1996; Swanson et al., 2011)). However, in contrast to cercopithecine primates, spotted hyenas live in fission-fusion societies in which individuals are often found alone or with small subgroups of clan-mates (Kruuk, 1972). The fission-fusion nature of hyena sociality allows us to complement social network metrics with measures of time spent alone and relationship strength among clan-mates as reflected in association indices. Our extensive knowledge of hyenas' lineages, development, and social ranks allows us to control for other factors that might affect individuals' adult fitness aside from their social position early in life.

Our 25-year dataset enables us to inquire whether early social network positions have long-term fitness consequences for female hyenas. The social bonds hypothesis predicts that the positions individual hyenas hold in their social networks before they reach maturity should affect their reproductive success or longevity. Furthermore, we inquire whether social network metrics in one stage of development have more important fitness consequences than those in another developmental stage. We anticipate that bonds formed during specific stages of development may differentially affect long-term success among adult females. Specifically, we expect to see different adult outcomes based on the social positions held by individual females when they are confined to living at dens compared to their social positions once they are no longer dendependent.

METHODS

Study site and subject animals

This study took place in the Masai Mara National Reserve, Kenya. Our subjects were female members of a single large clan of spotted hyenas that defend a common territory in the Talek region (Boydston et al., 2001). We only monitored females in this study, as we could follow them throughout their lives to obtain fitness measures, which was not possible for many males that dispersed to unstudied clans. Data were collected via daily monitoring from June 1988 through September 2013. We identified individual hyenas by their unique spots, determined their sex based on phallic morphology (Frank et al., 1991), and determined their birthdates to ± 7 days based on their appearance when first observed (Holekamp et al., 1996).

Spotted hyenas live in matrilineal societies organized by linear dominance hierarchies (Frank, 1986; Holekamp et al., 2012), and they acquire their social ranks via a learning process common in old-world monkeys called "maternal rank inheritance" (Holekamp & Smale, 1991; 1993). Clans are composed of multiple matrilines of adult females and their young, but most breeding males are immigrants born elsewhere. Young hyenas of both sexes acquire social ranks immediately below those of their mothers during the first two years of life, but the ranks of males drop precipitously after they disperse, as females and their cubs are socially dominant to all immigrants. Adult females and their young tend to be core figures in hyena societies, whereas adult males occupy more peripheral positions (Holekamp et al., 1997a; Kruuk, 1972; Szykman et al., 2001). Rank relationships among adult females are quite stable over long periods (Holekamp et al., 2012). High-ranking females enjoy markedly greater reproductive success than do low-ranking hyenas (Holekamp et al., 1996; Swanson et al., 2011), which are also more strongly affected by fluctuations in prey abundance than are high-ranking hyenas (Holekamp et al., 1996).

Because females are only assigned their own ranks once they reach sexual maturity, those in the two ontogenetic stages analyzed here were assigned the social ranks of their mothers which were based on their wins and losses in dyadic agonistic interactions.

To explore the social development of our subjects, we partitioned ontogeny into two prepubertal stages, the Communal Den (CD) stage and the Den Independent (DI) stage, which were divided by the distinct milestone of becoming independent of the communal den. Young hyenas in our study area live at a communal den with other members of their cohort until they are 9-10 months old. During this stage, social interactions are more limited than during later stages because cubs' choices of social partners are restricted to members of their cohorts and whichever den-independent hyenas choose to visit the den. Thus, the first stage of development on which we focused in this paper was the CD stage, lasting from the date first seen for each cub, until its date of den independence. All subjects were first seen within the first three months of life and we restricted study subjects to animals with known dates at which they became independent of the communal den. A juvenile was considered independent of the den when it was found away from the den on at least three consecutive occasions.

During the DI stage of development, juveniles are independent of the den, and potentially able to interact with all their clan-mates, but they remain dependent on their mothers for food until weaning, which occurs at an average age of 14 months (Holekamp & Smale, 1998a). During this second stage of development, juveniles learn their ranks in relation to clan members with which they did not interact at the communal den. The DI stage started here when a cub became den-independent, and it was equal in length to the length of its CD stage for purposes of SNA. Hyenas reach puberty at approximately 24 months of age, so here all natal animals under 24 months were considered juveniles. For each individual, both stages of development were of

the same length for consistent comparisons, and each individual subject was observed during both stages of development. Mean stage length was 7.17±0.13 months.

Behavioral data collection

Behavioral observations were conducted year-round from our vehicles, which we used as mobile blinds, throughout the 25-year study period. Observations were made daily between 0530 and 0900 h, and between 1700 and 2000 h. Each observation session was initiated when we found one or more hyenas separated from others by at least 200 m and terminated when we left that individual or group. In the absence of vocal communication, hyenas appear to be unaware of one another when separated by more than 200 m. Although no focal hyenas were radio-collared here, subgroups of hyenas were located either via use of radio telemetry or while observers drove daily circuits in which all highpoints within the study clan's home range were visited. By making 360 degree visual scans with binoculars from each highpoint, we were able to sample all parts of the clan's territory every day for presence of subgroups of hyenas. Each subgroup sighted or found via telemetry was then visited to determine its composition.

To maximize independence of observations, we used only the first session in which an individual was seen during morning or evening observation periods. At the beginning of each observation session and subsequently at 15-20 minute intervals, we performed scan samples in which we recorded the identities of all individuals present (Altmann, 1974). From our session data, we determined association patterns using the twice-weight index of association. Because some subgroups were easier to find than others, given their size or the presence of one or more individuals fitted with radio collars, the twice-weight index was the association index most appropriate for our sampling methods (Cairns & Schwager, 1987). We also used all-occurrence

sampling (Altmann, 1974) to record all agonistic and affiliative interactions occurring within each observation session.

We built three types of whole networks for each focal individual: association, aggression, and affiliation. We built association networks based on association indices, and we built aggression networks based only on aggressive interactions in which we could see which individual initiated the attack and which individual was its recipient. Furthermore, because greeting ceremonies, in which individuals raise their legs to one another to sniff the other's anogenital region, were previously shown to promote and maintain social bonds (J. E. Smith et al., 2011), we used greeting behaviors to construct affiliation networks. We created affiliation networks using only interactions in which we knew which individual initiated each greeting by lifting its leg first.

Network construction

Social networks are composed of groups of more than two individual animals (nodes) connected by behavioral interactions or co-occurrences in space and time (ties) and portrayed as networks. Ties can be directed if the behavior has an initiator and a receiver, or undirected when there is no clear direction in the relationship. Here networks based on associations were undirected, as they merely indicated co-occurrence, but both aggression and affiliation networks were directed. Additionally, ties can be weighted when there is a certain number or probability of occurrence of the behavior, or they can be unweighted. Here all our networks were weighted such that ties reflected the number of observed associations or interactions.

Using the R package, 'network' version 1.13.0 (Butts, 2008; 2015), we built two social networks per subject per network type, each network based on data collected during either the

CD or DI stage of development. The focal individual had to be seen at least ten times during each developmental stage for its network to be calculated, and each of its partners also had to be seen at least ten times during a particular stage to be included in the network. Seventy-nine females met the criteria for being included as focal individuals. Each tie in each association network was calculated as a twice-weight association index (AI), which represented the number of times individuals A and B were seen together divided by the total number of times A and B were seen together plus the total number of times A was seen without B plus the total number of times B was seen without A (Cairns & Schwager, 1987). AIs have been shown to be robust and accurate indicators of social bond strength in spotted hyenas (Holekamp et al., 1997a; 2012; J. E. Smith et al., 2007). Ties in aggression networks were calculated as the number of aggressive acts an individual initiated or received within each dyad during the relevant developmental stage, weighted by the intensity of said aggression (1-3, lowest-highest), and divided by the AI for that dyad during that developmental stage to control for opportunity (Szykman et al., 2003). Similarly, each tie in each affiliation network was weighted based on rates of greeting between the focal individual and its group-mates during the specified developmental stage, divided by AI.

Network metrics

For each focal individual, during both stages of early development (CD & DI), in each network type (association, aggression, or affiliation networks), we calculated several measures of social network position. First, we calculated the proportion of observation sessions during each stage of development in which the focal individual was found alone ("alone rate"), when it clearly could not be interacting with other animals, as the number of sessions in which the individual was found alone divided by the total number of sessions in which that individual was

observed during that developmental stage. We next calculated degree centrality, here called "degree", which is the number of other individuals to which the focal individual was connected. Degree is an important metric in social networks, as having a higher degree can indicate that an individual is more of a social hub, which in turn can affect its fitness via its exposure to both information and pathogens (e.g., Hamede et al., 2009; Royle et al., 2012)). In directed networks, we calculated both out-degree centrality, which represents the number of individuals with which the focal animal initiated interactions, and in-degree centrality, which represents the number of individuals that directed actions at the focal individual. We also calculated network "strength" as the sum of the weights of all connections to the focal individual. Strength indicates the quality of interactions by accounting for how often or intensely dyads interact, which can have long-lasting social and fitness consequences (Stanton & Mann, 2012; Wey, Burger, Ebensperger, & Hayes, 2013). Lastly, we calculated "betweenness," a measure of indirect interactions, which is the number of shortest paths between members of any dyad in the network that run through the focal individual. Thus, individuals with higher betweenness, often referred to as "brokers," link more individuals that are otherwise unconnected (Lehmann & Dunbar, 2009a). Indirect ties, like betweenness, are frequently hypothesized to help maintain the cohesion of complex societies (Lehmann & Dunbar, 2009a). Social network metrics were calculated using the 'statnet' package (v.2016.4) in R (Handcock et al., 2008).

Models and statistical analyses

We explored two different fitness outcomes to test how they were affected by various aspects of juvenile social positions. Specifically, we focused on average annual reproductive success (ARS) and longevity, two measures known to be important for lifetime fitness in spotted

hyenas (Swanson et al., 2011). ARS was calculated as the mean number of cubs borne by the focal female per year over its reproductive lifetime to control for longevity. Only females who lived to at least four years of age were used in this analysis to ensure they had a chance to reproduce. Longevity was calculated as the age at which females were found dead or the last date on which they were seen alive before disappearing. Here individuals had to live at least three years to have an adult longevity measure. Ultimately, 67 females met our criteria for which we also had ARS data, and we had longevity measures for 65 females that met our inclusion criteria.

We employed generalized linear mixed models (GLMM) to predict how alone rate and specific social position metrics affected either ARS or longevity. We examined the focal animal's degree centrality, strength, and betweenness in its association, aggression, and affiliation networks. In directed networks, aggression and affiliation, we explored both the outand in-degree centrality. All predictor variables were scaled alike for easier comparisons. We also included the social rank of each individual as a fixed effect in all models. We fit these models using Markov chain Monte Carlo (MCMC) routines, to account for violation of assumptions of independence among relational data, using the 'MCMCglmm' package in R (Hadfield, 2010). We used uninformative priors for 1000 iterations with a thinning interval of 10. All reported p-values are pseudo p-values calculated in the 'MCMCglmm' package, and differences between groups were considered significant when these p-values were ≤ 0.05 . Because network metrics are often correlated, we used variance inflation factors (VIFs) to assess multicollinearity among the predictor variables. VIFs of 10 and higher usually indicate severe collinearity (O'brien, 2007), but the VIF values in all our models were between 1.1 and 5.5. Additionally, we log-transformed our fitness outcomes to normalize their distributions.

We ran separate models for CD and DI stages to determine whether the social position of an individual in either stage, represented by the network metrics calculated for that individual in each stage, affected its adult success. During the study period, clan size ranged from 36 to 125 individuals, and on average, the study clan contained 77.31±0.57 hyenas. Therefore, we included an offset for clan size during the stage in question for each individual; this value was logtransformed to make the scale more closely comparable to those of our response measures. Group size is known to affect network metrics because it limits the number of individuals with which a focal animal can interact. We also included as a random effect the identity of the mother of the focal individual. Mothers may have specific parenting styles that affect their offspring, and cubs "inherit" their mothers' social networks as they mature (Ilany & Akcay, 2016). We then used deviance information criteria (DIC) for model selection to determine which network metrics during each stage best predicted the fitness outcomes. Henceforth, we present the best model determined by DIC for each fitness measure in each developmental stage.

RESULTS

Female hyenas in this study were observed, on average, in 93.2 ± 2.95 sessions during the CD stage and 80.9 ± 2.94 sessions during the DI stage. They were seen in 0.44 ± 0.014 sessions per day during the CD stage and 0.39 ± 0.015 sessions per day during the DI stage. On average, focal females were observed participating in 13.1 ± 0.60 aggressive and 10.6 ± 0.63 affiliative interactions during the CD stage, and 12.2 ± 0.59 aggressive and 8.10 ± 0.45 affiliative interactions during the DI stage. Means (\pm SE) for all network metrics during each stage of development appear in Table 3.1. The mean ARS for the females in this study was 1.4 ± 0.05 (range: 0.71-2.9) cubs per year, and their mean longevity was 7.6 ± 0.46 (range: 3.2-19) years. The CD model for

ARS was a better fit than the DI model (dDIC = 10.5), although no metrics in either stage had a significant relationship with ARS. However, the DI model was a better fit for longevity than was the CD model (dDIC = 4.8).

		CD	DI
		Mean±SE	Mean±SE
	Alone	0.0068 ± 0.0013	0.054 ± 0.004
Association	Degree	58.94±1.27	60.57±1.63
	Strength	6.23±0.18	4.08±0.14
	Betweenness	4.68±0.45	5.84 ± 0.52
Aggression	Out-degree	6.46±0.52	6.52±0.50
	In-degree	6.21±0.43	6.02±0.46
	Strength	133.36±13.56	178.80 ± 14.70
	Betweenness	77.23±9.79	72.51±9.68
Affiliation	Out-degree	4.53±0.40	4.51±0.35
	In-degree	4.49±0.42	3.23±0.33
	Strength	101.14±17.57	98.85±9.53
	Betweenness	91.96±11.12	93.92±12.17

Table 3.1 Mean±SE of all network metrics calculated for 79 females during each stage of development.

Testing the social bonds hypothesis

We found that social relationships formed during early ontogeny did in fact predict the later-life fitness of female hyenas, but only in regard to longevity. The best model from the CD stage predicting ARS included only degree metrics in all network types; it did not include alone rate, strength, or betweenness. In this model, there were no metrics that significantly predicted adult ARS (Table 3.2a, Fig. 3.1a). When female hyenas were in the DI stage, ARS was again best predicted by degree in association networks, and by out-degree and in-degree in aggression and affiliation networks, but no network metrics were significantly associated with adult ARS (Table 3.2b, Fig. 3.1b).

Table 3.2. Posterior summaries for model variables explaining ARS among 67 adult females based on social network positions during the communal den (CD) and den independent (DI) stages.

		post.mean	l-95% CI	u-95% CI	eff.samp	рМСМС
	(Intercept)	0.263	0.147	0.371	1008	0.001
	Rank	-0.020	-0.201	0.162	764.7	0.852
Association	Degree	-0.205	-0.452	0.017	762.4	0.082
Aggression	Out-degree	0.045	-0.059	0.143	595.2	0.368
	In-degree	0.012	-0.093	0.103	1097	0.812
Affiliation	Out-degree	0.033	-0.150	0.199	548.7	0.726
	In-degree	0.000	-0.091	0.113	1000	0.982

a) CD

b) DI

		post.mean	l-95% CI	u-95% CI	eff.samp	рМСМС
	(Intercept)	0.271	0.183	0.366	1000	0.001
	Rank	0.004	-0.161	0.190	1022	0.972
Association	Degree	-0.010	-0.198	0.216	1000	0.894
Aggression	Out-degree	0.004	-0.116	0.130	1000	0.972
	In-degree	-0.015	-0.114	0.076	1241	0.788
Affiliation	Out-degree	-0.008	-0.161	0.139	1000	0.906
	In-degree	0.026	-0.106	0.128	1000	0.63



Figure 3.1. Posterior means with 95% credible intervals for social network metrics predicting females' ARS (n=67 individuals) during a) the communal den (CD) stage and b) den independent (DI) stage of development when model parameters were measured for the best model. "Deg.," "Out," and "In" indicate degree, out-degree, and in-degree respectively.

The best model for the CD stage predicting longevity included alone rate, degree in association networks and both out-degree and in-degree in aggression and affiliation networks; it did not include strength or betweenness metrics. Those individuals lived significantly longer who were alone less often, associated with fewer individuals and initiated greetings with fewer individuals, but who had more individuals who initiated greetings with them (Table 3.3a, Fig. 3.1a). The eventual longevity of female hyenas was best predicted by degree in association networks, out-degree and in-degree in aggression and affiliation networks, and by strength in all network types; alone rate and betweenness were not part of this model. Associating with fewer individuals more strongly and being in positions of greater strength in both aggression and affiliation networks during the DI stage, were both significantly associated with greater longevity

(Table 3.3b, Fig. 3.1b). Juveniles' social ranks, during both CD and DI stages, had no significant effects on either their ARS or longevity.

Table 3.3 Posterior summaries for model variables explaining longevity among 65 adult females based on social network positions during the communal den (CD) and den independent (DI) stages.

a)	CD
/	-

		post.mean	l-95% CI	u-95% CI	eff.samp	рМСМС
	(Intercept)	1.428	0.994	1.849	1000	0.001
	Rank	-0.063	-0.269	0.155	1000	0.526
	Alone	-0.760	-1.482	-0.063	1000	0.038
Association	Degree	-0.223	-0.456	-0.017	1742	0.048
Aggression	Out-degree	0.054	-0.076	0.167	1000	0.364
	In-degree	-0.068	-0.199	0.063	1000	0.368
Affiliation	Out-degree	-0.205	-0.397	0.009	1000	0.046
	In-degree	0.247	0.115	0.373	1000	0.001

b) DI

		post.mean	l-95% CI	u-95% CI	eff.samp	рМСМС
	(Intercept)	1.987	1.842	2.121	1058	0.001
	Rank	-0.015	-0.289	0.275	1000	0.938
Association	Degree	-0.481	-0.706	-0.236	1000	0.001
	Strength	0.434	0.074	0.757	1000	0.018
Aggression	Out-degree	-0.084	-0.310	0.150	1000	0.476
	In-degree	0.001	-0.121	0.118	1000	0.98
	Strength	0.234	0.019	0.465	1000	0.042
Affiliation	Out-degree	-0.101	-0.370	0.222	898.8	0.468
	In-degree	-0.005	-0.154	0.133	1000	0.93
	Strength	0.430	0.102	0.755	1000	0.016



Figure 3.2 Posterior means with 95% credible intervals for social network metrics predicting females' longevity (n=65 individuals) during a) the communal den (CD) stage and b) den independent (DI) stage of development when model parameters were measured for the best model. "Deg.," "Out," "In," and "Str." indicate degree, out-degree, in-degree, and strength respectively.

DISCUSSION

Support for the social bonds hypothesis and important developmental periods

We found that juvenile social network metrics predicted longevity but not ARS among adult female spotted hyenas, partially supporting the social bonds hypothesis. Some early network metrics had positive effects on longevity whereas others affected it negatively. Which specific metrics affected longevity changed over the course of early development. Early in life, direct, central network positions had a bigger influence on longevity than did indirect measures like betweenness, which did not appear in any of the best models.

Model selection revealed that the DI stage was an important stage affecting female longevity. The DI stage represents a phase of development when juvenile female hyenas are becoming acquainted with all the members of their clan, and with the clan's territory, on their own terms, as they are no longer restricted to dens, or to associating only with their mothers and their preferred companions. Earlier researchers found the adolescent period to be a sensitive period in other species (Sachser, Kaiser, & Hennessy, 2013), as it may be for female hyenas with respect to their longevity. Furthermore, among baboons, long-term, stable bonds enhance longevity, and the DI period in the lives of hyenas may be when females first have the independent agency to form these important bonds (Silk et al., 2010). As in baboons, stronger positions, where individuals spend more time together or interact more, in all network types emerged as a significant predictor of longevity during the DI stage among female hyenas.

Previously, Yoshida et al. (2016) found that longevity among adult female spotted hyenas was positively affected by lifetime group-joining rates, but they also found that lifetime greeting rates had no influence on longevity. However, in that study, the effects of either behavior paled in comparison to the effects of average lifetime social rank (K. Yoshida, Van Meter, & Holekamp, 2016). Thus, the earlier finding on group joining rates was consistent with our finding of association strength improving longevity, but our affiliation results differ from those obtained by Yoshida et al (2016). This difference may be due to the fact that Yoshida et al. (2016) were looking at overall mean lifetime greeting rates whereas here we specifically assessed network positions within affiliation networks during brief stages of early development. In other species, social positions can have stronger effects on fitness during certain life stages than others. For example, patterns of affiliation among female macaques are more important to their survival during prime reproducing years than later in life (Brent et al., 2017). Thus, in both hyenas and macaques, social network positions appear to have different influences in different phases of the lifespan. In hyenas it may be that the affiliation network position of a female is
more important to longevity during her early life, particularly during the DI stage, than during adulthood.

Longevity among female hyenas was better predicted by early social positions than was ARS. Our study is one of only a few that inquire how juvenile sociality affects multiple measures of fitness. Berger et al. (2015) found that early social environments positively affect both longevity and reproductive success among female Alpine marmots. Furthermore, they found that the early social environment was a stronger driver of longevity in marmots, whereas the adult social environment was a stronger driver of reproductive success (Berger et al., 2015). Hyenas may be similar to Alpine marmots insofar as relationships during adulthood have a far stronger impact on their ARS than do relationships during the juvenile period (Berger et al., 2015). This notion is supported by the earlier finding that adult social rank is a strong predictor of ARS among adult spotted hyenas (Holekamp et al., 1996; Swanson et al., 2011). Among adult female baboons, the survival of their infants is significantly predicted by adult eigenvector centrality and a composite sociality score, which is a metric most closely related to positions in hyena association and affiliation networks (Cheney, Silk, & Seyfarth, 2016; Silk, 2003); we need to study adult social network positions further to ascertain whether this also occurs among female hyenas. However, it is more likely that adult rank itself is having a large effect that overwhelms effects of early social bonds in determining ARS in spotted hyena (Holekamp et al., 1996).

Contrary to our expectations, the individual's social rank position during the earliest stage of postnatal development, during the CD stage, did not affect either its ARS or its longevity. Although it has been well-documented that maternal rank affects juvenile survivorship (Greenberg & Holekamp, 2017; Holekamp et al., 1996), of those individuals who survived past three years of age here, their ranks early in life did not affect their ARS in adulthood. However,

regardless of the rank an individual held early in life, its early social position within its network had a significant influence on its longevity. Young hyenas learn their ranks at the communal den and do not fully solidify their rank relationships with the adults in the clan as a whole until they are approximately 18 months old (Smale, Frank, & Holekamp, 1999), so perhaps it should not surprise us that the social bonds they develop here during the CD and DI stages had a greater impact on their eventual longevity than did their juvenile ranks.

Positions in association and affiliation networks had more significant influences on longevity among female hyenas than did positions in aggression network. This is an interesting finding in a species where the dominance hierarchy, which is maintained by aggression, structures its society (Holekamp et al., 2012). However, it might be that the rank acquisition process is so predictable or stable that variation in aggression network position during early ontogeny does not matter in predicting the fitness of adult females (Holekamp & Smale, 1991).

Costs and benefits of early social bonds

In general, female hyenas lived longer who had fewer associates overall during both CD and DI stages. This pattern indicates a clear cost of sociality. However, during the CD stage, those females who were alone less often also enjoyed greater longevity. Although cubs are seldom found alone at the den, some were alone at the den during that stage considerably more often than others, spending less time with their mothers and being less well-socialized with their peers. As an extreme example, we observed a mid-ranking female cub (TAST), which her mother kept alone at a den, who was so poorly socialized when she finally became independent of the den that she walked straight up to the alpha female's youngest son and attacked him. These inappropriate aggressive behaviors continued, and perhaps in retaliation, this particular

female was often attacked by other clan members, and she died young. Thus, it appears there is a fitness cost to cubs who do not establish the necessary social relationships early in life, although it also costs them to associate with a large number of clan-mates. Furthermore, those young females who initiated greetings with fewer individuals, but who also had more individuals initiate greetings with them, tended to live longer. These data suggest the hyenas benefit by being selective regarding with which clan mates they directly interact. They cannot necessarily control which clan-mates choose to associate with them, but they can control those with whom they initiate greetings, and young females that were more selective in this regard lived longer.

Being in a social position with a few strong bonds, as seen here among juvenile female hyenas during the DI stage, may be an example of social buffering, where close bonds are known to improve fitness and ameliorate stressful situations. For instance, stronger adult social bonds have previously been shown to enhance longevity among baboons (Silk et al., 2010), to improve reproductive success (Silk et al., 2009), and alleviate stress (Wittig et al., 2008). Studies of many primate species show that strong grooming networks, in particular, improve stress responses and longevity, but these studies all focus on adults (Brent et al., 2017; Silk et al., 2010; Wittig et al., 2008).

Stress may mediate network effects on adult success, as the social environment is known to influence stress levels and vice versa in other mammals (R. G. Hunter & McEwen, 2013; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). Although we have not yet assessed stress-coping mechanisms in regard to network positions among spotted hyenas, it is possible that stress mediates the effects of early network positions on longevity in our study animals as well. In any case, hyenas apparently suffer costs of socializing with too many individuals and derive benefits from interacting more strongly with only a few close associates.

It is interesting to see these patterns emerging very early in life in hyenas, as this has not yet been reported before in other species. However, work looking at effects of early stress and adversity increasingly demonstrates that the social environment and stress experienced during early life can affect adult fitness via epigenetic mediation in other species (R. G. Hunter & McEwen, 2013; Tung, Archie, Altmann, & Alberts, 2016). We see this as a fascinating avenue for further study, to better understand which variables affect fitness, and how they do so, as fitness in hyenas is clearly not only determined by rank or genetic inheritance.

Our study enhances our understanding of how early social development affects adult fitness. Most studies, whether exploring the influences of social position during early ontogeny or adulthood, measure fitness in terms of reproductive success, but studies that address how social position affects longevity are rare. To date, there have only been a handful of studies linking social positions to longevity in non-human animals (Archie et al., 2014; Berger et al., 2015; Blumstein, Williams, Lim, Kroeger, & Martin, 2018; Brent et al., 2017; Silk et al., 2010; Stanton & Mann, 2012; Yee, Cavigelli, Delgado, & McClintock, 2008), of which, only two (Berger et al., 2015; Stanton & Mann, 2012) consider juvenile social development. Thus, although this research area is growing, there are still critical gaps in our understanding, especially in regard to effects of early social position on longevity.

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CHAPTER 4

ANTHROPOGENIC DISTURBACE AFFECTS RESPONSES TO MODEL INTRUDERS BY FREE-LIVING SPOTTED HYENAS

Turner, J. W., LaFleur, R. M., Richardson, A. T., & Holekamp, K. E. Anthropogenic disturbance affects responses to model intruders by free-living spotted hyenas. To be submitted to *Animal Behaviour*.

ABSTRACT

Anthropogenic disturbance can have tremendous influence on the behaviors of wild animals, including their boldness when exposed to risky conditions. To examine whether human disturbance affects risk-taking behaviors in large carnivores, we exposed spotted hyenas (Crocuta crocuta) from one population that was highly disturbed and another that had very little exposure to humans to a life-size model hyena representing an intruder from another clan. The high disturbance population lived very near adjacent human settlements and the low disturbance population inhabited a relatively pristine part of the Reserve. A mock intruder was presented to individual hyenas to assess their reactions to a foreign hyena, and to determine whether their exposure to anthropogenic activity had any effect on those reactions. We found that human disturbance did indeed affect hyena risk-taking behavior. Hyenas tested in the low disturbance area exhibited more risk-taking behaviors by approaching the mock intruder more closely and spending more time investigating it than did their counterparts living with high disturbance. How much time a hyena spent in close proximity to the model intruder predicted their survival. Furthermore, the individual differences in measures of boldness assessed here were consistent with those obtained previously from the same animals using both experimental manipulations and naturally-occurring behaviors, indicating that risk-taking behaviors are consistent within individuals across development and contexts. Although our results are consistent with those from earlier tests of anthropogenic disturbance and boldness in spotted hyenas, they differ from results obtained from birds and small mammals, which are generally bolder in areas characterized by human disturbance. This indicates that large mammalian carnivores may have opposite personality-related responses to disturbance from those emitted by birds and small mammals.

Keywords: spotted hyena, risk-taking, boldness, anthropogenic disturbance

INTRODUCTION

Anthropogenic disturbance can strongly influence animal behavior, with some of the most profound effects seen on temperament traits (Miranda, Schielzeth, Sonntag, & Partecke, 2013). These effects can occur via either individual plasticity or microevolutionary change (Miranda et al., 2013). Birds and small mammals living in areas characterized by human disturbance show more proactive temperaments than do animals living in undisturbed areas which are more reactive; that is, animals in disturbed areas are more bold, exploratory, and aggressive than animals not exposed to human disturbance (Miranda et al., 2013; Sol, Lapiedra, & González-Lagos, 2013). However, to date there have only been two studies looking at effects of anthropogenic disturbance on predatory animals (Greenberg & Holekamp, 2017; Stewart et al., 2016). Because predators are frequently found to structure ecosystems via top-down processes, behavioral changes induced in them by human activity could potentially have widespread consequences (Estes et al., 2011). Furthermore, large carnivores that live in close proximity to humans can cause considerable damage to livestock. This damage can result in significant repercussions for local carnivores via such retaliatory actions as mass poisonings; these actions, in turn, put carnivores at increased risk as human population density increases (Ripple et al., 2014). Therefore, gaining a better understanding of temperament responses

exhibited by large carnivores to human disturbance could potentially contribute to conservation efforts (Greggor et al., 2016).

Boldness, defined as an individual's tendency to take risks, is a key temperament trait in the wild (Réale, Reader, Sol, McDougall, & Dingemanse, 2007) because it affects how animals forage, respond to predators, and cope with environmental perturbations in ways that have important fitness consequences (e.g., Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Jolles, Ostojić, & Clayton, 2013; Miranda et al., 2013; Wilson, Godin, & Ward, 2010). Boldness is frequently measured as a response to a predator, threat stimulus or trap, and has important implications for the survival, reproductive success, and social status of individual animals (reviewed in Réale et al., 2007). Although birds and small mammals are frequently bolder in areas characterized by anthropogenic activity (Miranda et al., 2013), wolverines (*Gulo gulo*) spend less time taking part in risky behaviors as human presence increases (Stewart et al., 2016). Thus, predators might exhibit different responses to anthropogenic disturbance than do small mammals or birds.

Here we experimentally tested boldness among wild spotted hyenas (*Crocuta crocuta*) in response to a mock intruder and compared boldness responses between hyenas living in disturbed and undisturbed areas within a single wildlife reserve in Kenya. Previous research revealed that individual spotted hyenas vary in their boldness. First, observers were asked to rate captive hyenas on several personality traits, and boldness was rated with very high reliability, but no shy-bold continuum was indicated in the captive population based on a principal components analysis (Gosling, 1998). Second, earlier studies of free-living hyenas suggested that consistent inter-individual differences in boldness exist in this species, based on the closest distances hyenas approached to lions during lion-hyena interactions; lions can easily kill or maim hyenas,

so approaching them closely is dangerous (K. Yoshida et al., 2016). Hyenas also varied with respect to whether or not they avoided lion roar playbacks, and in the strength of their behavioral response to the playbacks (Watts, Blankenship, Dawes, & Holekamp, 2010). Yoshida et al. (2016) found evidence of stabilizing selection on boldness among female hyenas, with the greatest longevity observed with intermediate boldness ratings; bold females may take too many dangerous risks, and shy females may not reap the benefits of risky behavior. Finally, to assess effects of anthropogenic disturbance on boldness in free-living juvenile hyenas, Greenberg and Holekamp (2017) recently measured the propensity of den-dwelling cubs to enter a wire-mesh box to obtain food. They found that juveniles living in low-disturbance areas were bolder than individuals living in high-disturbance areas. Thus, data from both wolverines and spotted hyenas suggest that predatory mammals may exhibit different boldness responses to anthropogenic disturbance than do birds and small mammals.

The spotted hyena is a good model carnivore in which to study the effects of anthropogenic disturbance on temperament. The species' range covers most of sub-Saharan Africa and they are top predators, along with lions, in most African ecosystems (Kruuk, 1972). Human disturbance is known to affect their stress hormone concentrations and several aspects of their behavior, including daily activity rhythms, den use, vigilance and habitat preferences (Boydston, Kapheim, Watts, Szykman, & Holekamp, 2003; Kolowski & Holekamp, 2009; Van Meter et al., 2009). Furthermore, earlier research suggests a high degree of variation in boldness traits in this species, both within and between populations; this variation is apparent even among very young individuals and occurs both when hyenas encounter lions and interact with novel stimuli at the communal den (Greenberg & Holekamp, 2017; K. Yoshida et al., 2016). However, to date no one has yet systematically assessed consistency among these different ways of

assessing boldness in spotted hyenas or inquired whether this consistency holds across lifehistory stages, or across vastly different contexts, for example, by comparing results from experimental manipulations with those obtained in natural contexts.

Here we focused on experimental assessment of risk-taking among adult hyenas and subadults no longer dependent on dens for shelter. Hyena clans are strongly territorial in southern Kenya, and they do not tolerate intruders in their territory; thus, a hyena in an unfamiliar territory may be attacked (Kruuk, 1972). Based on earlier findings, we hypothesized that human disturbance would affect hyena risk-taking behavior during interactions with a mock intruder. If the boldness of adult hyenas conforms to the well-established patterns seen in birds and small mammals, we expected to see hyenas inhabiting areas characterized by anthropogenic disturbance engaging in more risk-taking behaviors in response to a model intruder than hyenas from undisturbed areas. However, if older hyenas conform to patterns observed in den-dwelling hyena cubs (Greenberg & Holekamp, 2017) and adult wolverines (Stewart et al., 2016), we expected to obtain the opposite results, such that hyenas inhabiting disturbed areas would engage in less risk-taking behaviors than those inhabiting undisturbed parts of the Reserve. In either case, our findings should help establish whether responses to anthropogenic disturbance differ between carnivorous mammals and small mammals or birds. In addition, we inquired whether risk-taking behaviors in response to a model intruder predict survivorship. Lastly, by comparing our data to those obtained in earlier hyena studies using different methods, we inquired whether there is consistency among different measures of boldness obtained during successive lifehistory stages, obtained either by experimental manipulation or by observations of naturallyoccurring behavior.

METHODS

Subjects and study sites

We conducted this experiment during two periods, the first from June through August of 2012, and the second from June 2013 through May 2014. Study subjects were 93 spotted hyenas inhabiting disturbed and undisturbed regions within the Masai Mara National Reserve (henceforth, the Reserve), in southwestern Kenya. We identified individual hyenas by their unique spots, determined the sex of each animal based on its phallic morphology (Frank et al., 1991), and determined its birthdate to ± 7 days based on its appearance when it was first observed (Holekamp et al., 1996). For immigrant males and female hyenas we did not see when they were cubs, we based their age (± 6 months) on tooth wear measured during immobilizations or necropsies (Van Horn et al., 2003).

Spotted hyenas live in mixed-sex, matrilineal societies, called clans, organized by linear dominance hierarchies (Frank, 1986; Holekamp et al., 2012), and they acquire their social ranks via a learning process typical of old-world monkeys called "maternal rank inheritance" (Holekamp & Smale, 1991; 1993). Young hyenas of both sexes acquire social ranks immediately below those of their mothers during the first two years of life. Clans contain multiple matrilines of adult natal females and their young, but most breeding males are immigrants born elsewhere. Females are socially dominant to males among adults because males enter the hierarchy of their new clan at the very bottom when they emigrate from their natal clans to join new social groups (East & Hofer, 2001; Smale et al., 1997). Adult females and their young tend to be core figures in hyena societies, but adult males are more peripheral (Holekamp et al., 1997a; Kruuk, 1972; Szykman et al., 2001). Rank relationships among adult females are usually stable over long periods (Holekamp et al., 2012). Here we assigned each individual a social rank based on its

wins and losses in dyadic agonistic interactions then stratified them into thirds for high-, mid-, and low-rankings. Until juveniles acquired their own ranks when they reached maturity at 24 months of age, they were assigned the social ranks of their mothers.

Roughly half (44) of the 93 subjects lived in three clans whose territories were located in The Mara Conservancy (TMC), a relatively pristine area in the western portion of the Reserve and managed by a private nonprofit organization that strictly prohibits cattle grazing and human presence except in tour vehicles. We will therefore refer to this as our 'low disturbance' area. TMC clans have been monitored daily since 2008. The remaining 49 subjects were from the Talek clan, which has been continuously monitored since 1988, and defends a territory just inside the northeastern border of the Reserve beside the burgeoning town of Talek. We refer to this as our 'high disturbance' area because, since the late 1990s, there has been exponential human population growth along the border of the reserve (Watts & Holekamp, 2009), unrestricted development of tourism infrastructure (Boydston et al., 2003; Green, 2015; Kolowski & Holekamp, 2009; Van Meter et al., 2009), humans are active with their livestock both day and night inside the Reserve here, and direct conflict between hyenas and livestock is common both inside and outside the Reserve in this area (Kolowski & Holekamp, 2006). Since 2005, humans have been responsible for the majority of hyena deaths in the Talek area (through spearing, snaring and poisoning) for which mortality sources can be determined (Holekamp & Dloniak, 2010). Through historical analyses and comparative studies with populations living in more pristine areas, numerous behavioral effects of increased human activity have been documented in this population, including increased nocturnality, greater distances travelled daily, lower rates of den attendance by mothers, active avoidance of livestock and herders, and a preference for areas with dense vegetative cover (Boydston et al., 2003; Green, Johnson-Ulrich,

Couraud, & Holekamp, 2017; Kolowski & Holekamp, 2009; Kolowski, Katan, Theis, & Holekamp, 2007). The Talek clan contained approximately 125 hyenas during the study period. Of the 49 Talek subjects, 35 were females and 14 were males. We also kept track of whether focal hyenas were adults or subadults in case age affected boldness; subadults were any females who were not reproductively mature (having given birth at least once) or natal males who had not yet emigrated. Adults were females who had already given birth and immigrant males. In Talek, 29 subjects were adults and 20 were subadults. Of the 44 subjects tested from TMC clans, 25 were females, 19 were males, and 26 were adults and 18 were sub-adults. The three TMC clans contained approximately 43, 47, and 57 hyenas, respectively, during the study period. All procedures performed in this study were in accordance with the ethical standards of Michigan State University and following all applicable guidelines in Kenya. Ethical approval for use of animals in this study was issued by Michigan State University under IACUC approval # 05/11-110-00 on 22 August 2013.

Boldness trials and data collection

Boldness trials were conducted exclusively on individuals found alone who were far from any active communal den to eliminate social effects on boldness. A commercially available lifesize archery target, made of dense foam in the shape of a full-grown spotted hyena (Fig. 4.1), was deployed as a mock intruder within sight of an alert focal individual. We used our vehicle to block the view of the focal hyena while the model was deployed so the subject could not see us setting up the mock intruder. Then we drove approximately 30 m away from the mock intruder, and parked parallel to it. A Canon PowerShot SX260 and Canon Vixia HF R30 camcorder were both used to record each trial; one camera was zoomed in on the focal individual to capture finescale changes in its behavior, and the other was zoomed out to capture the position of the focal hyena relative to that of the model. The wide-angle camera was mounted on the car door with a magnetic tripod. The trial commenced when the focal hyena noticed the mock intruder, indicated by a startle response that was usually accompanied by a pause in its current activity. A trial ended when the subject either walked away to a distance greater than 50 m from the model or lay down closer to it for at least 5 minutes. Four sessions were terminated early because the focal hyena was damaging the mock intruder, and one ended early when an agitated topi (*Damaliscus korrigum*) chased off the focal individual.

At the end of each trial, we scored the hyena on its general performance. Hyenas were scored as fearful, neutral, bold/exploratory, or attacking (1-4). Fearful hyenas were those that detected the model and then immediately left or avoided it completely; they did not approach and seemed very nervous or disturbed by the situation. Neutral scores were given to hyenas that detected the model but appeared uninterested, and just walked by, or they studied the model a bit from afar but did not appear either fearful or curious. Bold or exploratory individuals were those that detected the model and approached closely or spent a long time (>10 minutes) studying the model from 20 m or more away. Lastly, subjects were coded as attacking when they approached and bit the model. To determine if there was a significant difference in boldness scores between disturbance levels, we use an ordinal logistic regression model with disturbance level as a predictor of score. Ordinal logistic regressions assume an order for categorical scores, which was least to most bold (1 to 4) in this study. These analyses were done with the 'MASS' package in R (version 3.4.1) (R Core Team, 2017; Venables & Ripley, 2002).

All videos were analyzed by at least two different observers for reliability of measured behaviors. All behaviors analyzed in this study were at least 95% correlated between the two

observers (distance from the model at which the trial started: 95%, closest distance the subject approached to the model: 95%, time taken to reach closest distance from the model: 95%, total duration of trial: 99%). We kept track of distances between the subject and the mock intruder in 5 m increments between 0-30 m, and we also tracked whether the subject was within 50 m of the model at all times. Furthermore, we took note of the specific distance from the model at which the focal hyena noticed it, and the closest distance to which each subject approached the model. Distances were measured in two ways. First, when the focal hyena was not in the same plane as the model, distances were dictated onto each videotape by a human observer equipped with a range finder. Second, when the focal hyena was walking in the same plane as the mock intruder, distances were measured from the video recording using a pixel measuring tool (PixelStick) by comparing the distance between the focal hyena and the mock intruder to the known length of the mock intruder (1 m). We also used this measuring tool to confirm dictated distances when hyenas were in the same plane as the model to make sure the dictated and measured distances were consistent, with particular attention to measurement of the closest distance to which a subject approached the model.

Three measures of risk-taking behavior were recorded in this study. One was the closest distance each focal hyena approached to the mock intruder. Second, we recorded the time elapsed between the instant when the focal hyena noticed the model and the time point when it made its closest approach to the model. Third, we calculated the percentage of total trial time during which the focal hyena was within 30 m of the mock intruder. The duration of the trial was the time between when the subject first noticed the mock intruder and the moment at which it lost interest, as indicated by leaving or lying down. We picked 30 m because this seemed to be the distance from the model at which focal hyenas appeared to start picking up olfactory cues

from it, indicated by the subjects positioning themselves downwind of the model and sniffing the air blowing toward them from the model.

Boldness analyses

Because there were no significant differences among hyenas in the three TMC clans with respect to any of the dependent measures considered here (Table 4.1), they were pooled for analysis purposes. We also pooled the age classes (adults and subadults) within disturbed and undisturbed areas because we found no differences between subadults and adults in either study population (Table 4.2). We log-transformed two of our risk-taking measures (closest distance approached and time taken to arrive at the closest distance to the model) to produce normal distributions. The percentage of trial time spent within 30 m of the mock intruder was normally distributed. We then ran three two-tailed ANOVAs with each risk-taking behavior as the response variable. Riskier behaviors are generally considered to include approaching more closely to the potential threat (i.e., the model), spending more time in close proximity to the threatening stimulus, and spending more time investigating the threatening stimulus (Blaszczyk, 2017; Godin & Dugatkin, 1996; Réale et al., 2007). Accordingly, these were represented, respectively, in our own response variables as the closest distance to which a subject approached the model, the percentage of total trial time spent within 30 m of the model, and the time taken to reach the subject's closest distance to the model. Our predictor variables were disturbance level (high or low), sex, and rank category (high-, mid- or low-ranking), with an offset for the distance between the focal hyena and the model at which trial started to control for variation in start distances (range: 25-200 m). We included sex and rank category as fixed effects because they

have previously been shown to affect other aspects of boldness in spotted hyenas (Greenberg &

Holekamp, 2017; K. Yoshida et al., 2016).

Table 4.1 Results from one-way ANOVAs to test if there were clan differences in any of our risk-taking measures within our low-disturbance area (N = 43, 47, and 57 hyenas per clan).

		Time to	% time	
	Closest	closest	within	
	distance	distance	30m	duration
F _(2,41)	1.404	1.708	0.244	0.593
p-value	0.257	0.194	0.785	0.557

Table 4.2 Results from one-way ANOVAs to test if there were clan differences in any of our risk-taking measures within our low-disturbance area (N= 38 subadults and 55 adults).

	Closest	Time to closest	% time within	
	distance	distance	30m	duration
F _(1,91)	0.936	1.102	0.932	1.04
p-value	0.338	0.297	0.337	0.311

Survival analysis

To inquire how risk-taking behavior in response to the mock intruder affected survival, we employed a Cox proportional hazards model for right-censored data. Only individuals with known birthdates were included in this analysis. We also limited this analysis to females, as we can follow them their entire lives unlike males who disperse to new clans at maturity. We ran separate models for each risk-taking metric recorded in regard to the model intruder. Each model was also stratified by disturbance and rank levels. We also controlled for the age the individual was at the time of testing. We used the 'survival' package in R to conduct these analyses (Therneau, 2015; Therneau & Grambsch, 2013).

Comparisons of boldness measures

The measures of boldness previously recorded for spotted hyenas included latency to approach a baited box among den-dwelling cubs (Greenberg & Holekamp, 2017) and the closest distances to which individual hyenas approached lions during naturally-occurring interspecific interactions (K. Yoshida et al., 2016). Here, we inquired whether different ways of testing risktaking behavior, including our mock intruder assays, were measuring the same aspects of boldness, indicating that this truly is a personality trait that is both consistent across time and diverse circumstances. There were a total of 12 hyenas, 4 from Talek and 8 from TMC, for which we had data from both mock intruder presentations and baited box trials. There were 40 hyenas, all from Talek, for which we had both data from mock intruder trials and lion proximity data. We had data for only two hyenas that experienced all types of boldness tests, so unfortunately, we could not compare all three methods at once but instead compared mock intruder data separately with data from baited box trials and lion proximity data.

To determine whether measures were consistent within individuals across tests, we ran mixed effects models using the 'glmmADMB' package in R (Fournier et al., 2012; Skaug et al., 2016). All models included rank category as a fixed effect. When comparing juvenile boldness measures obtained by Greenberg and Holekamp (2017) to the mock intruder risk-taking responses assessed here, we used latency to touch the baited box and the subject's latency to approach to its closest distance from the mock intruder. In this mixed effects models, we used a Poisson distribution. To evaluate consistency in risk-taking measures between closest approach to lions and responses to the mock intruder, we modeled 1) average lifetime minimum closest distance to lions (K. Yoshida et al., 2016) and closest distance approached to the model intruder, 2) average relative minimum distance to lions, standardized by the number of hyenas present,

and percentage of time spent within 30 m of the mock intruder, as these both represent relative risk-taking, and 3) average lifetime minimum closest distance to lions and percentage of time spent within 30 m of the mock intruder, as this metric tended to have a significant influence on survival. In these models, we used logistic, Gaussian, and Poisson distributions, respectively. Based on these models, we ran one model with individual ID as a random effect and one without. We then used Akaike's Information Criterion corrected for small sample sizes (AICc) to determine whether model fit was better when the individual's identity was included or omitted. A smaller AICc value indicated a better fit. We also calculated a parameter estimate for the effect of subject identity using a likelihood ratio test.

RESULTS



Figure 4.1 A subadult hyena in the low disturbance area investigates the mock intruder.

Effects of anthropogenic disturbance

Overall, hyenas directed a wide range of responses towards the mock intruder. At one extreme, one female subject detected the intruder, immediately backed up approximately 1 m, then started to circle around the mock intruder while putting approximately 200 m and our car between herself and the model, constantly keeping an eye on the model, until she reached approximately 200 m directly behind the mock intruder and continued in the same direction she was traveling before she spotted the model. At the other extreme, a different female hyena spotted the model, and after a 10 second pause, walked directly up to the mock intruder and bit its face. She would not stop attacking the model's face and buttocks, despite us driving at her to chase her off after the first bite, until one of us jumped out of the car and slammed the door. In our longest trial, a subadult male circled the model from 20 to 30 m away for 30 minutes pausing to stare at it from behind bushes and sniff the air downwind frequently. However, when most subjects spotted the mock intruder, they positioned themselves down-wind from the model right away and sniffed the air from various distances away. The average trial length was 6.8±0.45 minutes in the high disturbance area and 9.3 ± 0.87 minutes in the low disturbance area. Many subjects also visually scanned between the mock intruder and either the car or a nearby prey animal, looking back and forth between the two. Only 11 hyenas out of 93 actually came into contact with the model, four from Talek and seven from TMC, and most of those sniffed the model or touched it without biting it; only two hyenas, one on each side of the Reserve, aggressively attacked the model by biting its face and posterior surfaces (Figs. 1 & 2).



Figure 4.2 Proportion of hyenas in areas of high and low disturbance that received boldness scores of fearful, neutral, bold/exploratory, or attack (N=93, p=0.086).

Overall, TMC hyenas, which were exposed to less anthropogenic disturbance, were bolder than those exposed to high levels of disturbance. Hyenas from low disturbance areas tended to have higher boldness scores than did those from the area of high disturbance (β =0.70, SE=0.4, t=1.72, p=0.084, Fig. 4.2). Furthermore, TMC hyenas were slower to approach the mock intruder, but eventually approached it more closely and spent more time within 30 m of the model (Fig. 4.3). We found significant differences between hyenas from high- and lowdisturbance areas in all three of the measured risk-taking behaviors (Fig. 4.3). Hyenas from highdisturbance areas, on average approached to 26.9±4.2 m from the model whereas hyenas from low-disturbance areas approached to 17.8±4.0 m from the mock intruder (Table 4.3, Fig. 4.3). Talek hyenas also spent less time investigating as they approached the mock intruder. On average, they took 3.4±0.3 minutes to approach to their closest distance whereas TMC hyenas took 4.3±0.6 minutes to approach to their closest distance from the model (Table 4.3, Fig. 4.3). Furthermore, hyenas in high-disturbance areas spent only $32\pm4\%$ of their total trial time within 30 m of the model where they could more easily investigate it, compared to low-disturbance hyenas, which spent $46\pm5\%$ of their time within 30 m (Table 4.3, Fig. 4.3). Sex and rank category did not appear to have any influence on any of our measures of boldness (Table 4.3).



Figure 4.3 Average closest distances to which subjects approached the mock intruder, percentage of time within 30 m, and time to closest distance (\pm SE), compared between hyenas inhabiting areas of high-disturbance (Talek, N=49) and low-disturbance (TMC, N=44). Distance (m) and percent of time are represented on the left axis, and time (mins) is represented on the right axis. All risk-taking measures were significantly different between high and low disturbance areas (p<0.05).

Table 4.3 Results of an ANOVA describing the log of the closest distance to which subjects approached the mock intruder, log time a hyena subject took to reach its point of closest distance to the mock intruder after the trial started, and percentage of total trial time a hyena spent within 30 m of the mock intruder.

	Disturbance		sex		rank level	
	F _(1,88)	Р	$F_{(1,88)}$	р	$F_{(2,88)}$	р
closest distance approached	4.62	0.0343	0.322	0.572	0.155	0.856
time to closest distance	4.85	0.0303	0.252	0.617	0.157	0.855
proportion of time w/in 30m	4.842	0.0304	0.255	0.615	0.182	0.834

Boldness affects survival

Forty-seven female hyenas met the criteria for inclusion in our survival model, thirteen of which died by the end of 2016. How close female hyenas approached the mock intruder did not affect their survivorship (β =-0.014, SE=0.015, χ^2_3 =2.07, p=0.56). The time a female took to approach to its closest distance also had no effect on survival (β =0.00009, SE=0.0027, χ^2_3 =4.62, p=0.20). Lastly, those females that spent a smaller percentage of time within 30 m of the model had significantly better survival (β =1.89, SE=0.81, χ^2_3 =9.08, p=0.028, Fig. 4.4).



Figure 4.4 Proportion of female hyenas surviving who spent more than the mean proportion of time within 30 m of the model ("close") compared to females that spent a lesser proportion of time near the model ("far"). Mean proportion of time within 30 m = 0.33.

Different measures of boldness are consistent within individuals

Our analysis revealed consistency among risk-taking behaviors measured in different contexts and life stages. First, the model testing consistency in latency to approach a baited box between when hyenas were den-dwelling cubs (Greenberg & Holekamp, 2017)and their latency to approach our model hyena when those same individuals were independent of the den was a significantly better fit when ID was included than when it was not (χ^2 =29.28, p<0.0001). Thus, risk-taking was consistent across life stages and contexts.

The closest distances to which hyenas approached lions (K. Yoshida et al., 2016) were not consistent within individuals with their responses to the mock intruder ($\chi^2 < 0.0001$, p=0.999). However, the average standardized minimum approach distance to lions and the percentage of time spent within 30 m of the mock intruder tended to be consistent within individuals when comparing models that included ID with those that did not include ID (χ^2 =33.34, p=0.068). Furthermore, the model including average lifetime minimum closest distance to lions and percentage of time spent within 30 m of the mock intruder was significantly better when ID was included in the model than when it was not (χ^2 =207.76, p<0.0001).

DISCUSSION

Hyenas appeared to treat the mock intruder as though it was a strange hyena, at least from a distance. When the model was attacked, subjects attacked it as if it was a real intruder, targeting its face and buttocks. How long the ruse lasted appeared to vary among subjects, and depended on how closely the subject approached, and how it worked in relation to wind direction to pick up olfactory cues. We are still not entirely sure one high-ranking hyena who approached relatively closely to the model ever realized it was not a real hyena. With this exception, most subjects clearly realized the model was not an actual hyena, even if only when they started biting it. After the realization, their behaviors switched from approaching a threatening conspecific to approaching a strange, potentially dangerous, object to explore or avoid. Boldness and exploration have been shown to be correlated in hyenas (Greenberg & Holekamp, 2017), as was the case here.

Anthropogenic disturbance affects boldness

Our data supported the hypothesis that human disturbance affects the risk-taking behaviors exhibited by spotted hyenas. Hyenas living in undisturbed areas took more risks than those who were exposed to higher levels of anthropogenic disturbance. Spotted hyenas in areas of low anthropogenic disturbance approached more closely to the mock intruder and spent a more time investigating it than did hyenas in areas of high disturbance. These results are similar to those previously obtained in studies of boldness in den-dwelling juvenile spotted hyenas (Greenberg & Holekamp, 2017) and in wolverines, where animals in areas of low human disturbance took more risks than those from more disturbed areas (Stewart et al., 2016). This result differs markedly from boldness findings in birds and small mammals (Miranda et al., 2013; Sol et al., 2013). This difference might be because most small mammals and birds are released from predation pressures in urban environments and other habitats heavily disturbed by humans; clearly that is not the case for predators, who become more exposed to threats from humans in such environments due to conflicts over resources desired by both parties (A. V. Bell, Rader, Peck, & Sih, 2009; Ripple et al., 2014). For instance, urbanized coyotes (*Canis latrans*) and bobcats (Lynx rufus) explicitly try to avoid these conflicts by primarily entering urban areas during the night and spending daylight hours in more "natural" settings (reviewed in Lowry, Lill, & Wong, 2012).

It is perhaps surprising that we found no significant effects of rank or sex on risk-taking behavior in the presence of the mock intruder; only disturbance level affected these risk-taking behaviors. This indicates that disturbance is having a strong effect on the boldness of these hyenas. Previous research on adult spotted hyenas revealed that rank significantly affected boldness in responses to lions, with high-ranking individuals being bolder than low-ranking

individuals among females but not males (K. Yoshida et al., 2016); however, juvenile hyenas showed no rank-related variation in their boldness in regard to entering a wire mesh box to obtain a food reward (Greenberg & Holekamp, 2017). It might be that rank has different effects in different contexts. For example, hyenas of all ranks experience may equal risks from intruders, whereas risks imposed by lions may vary based on rank. An intruder is not likely to kill a resident hyena approaching it closely, whereas a lion could easily do so.

Among den-dwelling juvenile spotted hyenas, there was a trend for females to be bolder than males (Greenberg & Holekamp, 2017), but we did not observe such a trend among denindependent subadults or adults. This difference may be because, as hyenas age, their risk-taking behaviors become more flexible. For example, Yoshida et al. (2016) found that adult males showed more plasticity than females in their risk-taking behaviors around lions by not being as consistent over time as were the females.

Boldness affects survival

As has been previously found in regards to other boldness measures (Greenberg & Holekamp, 2017; K. Yoshida et al., 2016), aspects of risk-taking behavior in response to our mock intruder significantly predicted survival for females. Our results indicate that those females that are too bold have greater survivorship because those that spent a greater proportion of time in close proximity to the mock intruder had reduced survival. Thus, it appears to pay to not spend much time in risky situations. These results support previous research indicating that dendwelling juveniles that were less likely to survive to puberty when they were more bold (Greenberg & Holekamp, 2017). These results, however, contrast with previous studies in adults that demonstrated that being intermediately bold in interactions with lions improved longevity.

Thus, different pressures may affect the survival implications of boldness in different contexts (A. M. Bell & Stamps, 2004; Guenther, Finkemeier, & Trillmich, 2014; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Sinn, Gosling, & Moltschaniwskyj, 2008; Stamps & Groothuis, 2010).

In this study we were unable to determine how boldness affected fitness traits other than longevity. For instance, although there is much research supporting the notion that bolder individuals have shorter lifespans, there is sometimes a trade-off in which bolder individuals have higher reproductive success (B. R. Smith & Blumstein, 2008). Many subjects in our study were males, which we could usually not follow after dispersal to assess their fitness, and many others were females that only became reproductively mature a few years ago. Therefore, we were unable to get accurate estimates of reproductive success in these subjects. However, this would be an interesting question to address in the future.

Consistency in boldness measures

We found evidence that risk-taking behaviors by spotted hyenas were consistent across contexts and across life-stages. Greenberg and Holekamp (2017) found consistency between responses to novel objects and responses to a baited box among juveniles. Here we found that consistency extends to an entirely different context involving responses to a mock intruder during later life-history stages. Furthermore, with the exception of absolute minimum distance to lions or our mock intruder, experimentally manipulated risk-taking responses were consistent with natural risks taken in the presence of lions; previously, it was unknown how experimentally manipulated and naturally occurring behaviors would relate to each other in the wild (Watanabe et al., 2012; K. Yoshida et al., 2016). Here it appears that experimentally manipulated boldness

was consistent with naturally-occurring boldness responses. These results also indicate that risktaking behaviors are consistent regardless of whether or not individuals are influenced by conspecifics, as the two previous studies measured risk-taking behaviors of individuals in social groups whereas the current study only tested individuals when they were alone.

Our study is unique in that it compares multiple ways of measuring boldness in a wild animal. Previously, Watanabe et al. (2012) found that correlations between different methods of assessing boldness in captive hermit crabs (*Coenobita clypeatus*) were not necessarily better than chance. Here, we found that most measures of boldness were significantly consistent.

Our findings add to the growing literature indicating that risk-taking behaviors can be consistent within individuals across vastly different contexts. Our data also show that risk-taking by carnivores is affected differently by human disturbance than is risk-taking by birds and small mammals. This difference may be due to the fact the carnivores are at greater risk from humans than small mammals and birds (Fernández-Gil et al., 2016; Miller, Jhala, & Schmitz, 2016). Large predators such as lions and hyenas actively avoid areas of high risk due to anthropogenic disturbance (Boydston et al., 2003; Green et al., 2017; Loveridge, Valeix, Elliot, & Macdonald, 2016). Our data suggest that, in addition to space use patterns and circadian timing of activity changing in response to anthropogenic activity, the temperament traits of hyenas are changing as well. The fact that anthropogenic disturbance can influence temperament traits may also have useful implications for carnivore conservation (Anthony & Blumstein, 2000; Greggor et al., 2016; Miranda et al., 2013).

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CHAPTER 5

HUMAN DISTURBANCE NEGATIVELY AFFECTS SOCIAL STRUCTURE AND SOCIAL DEVELOPMENT IN WILD SPOTTED HYENAS

ABSTRACT

Anthropogenic disturbance can radically change the social behavior of group-living animals. Here, we test how anthropogenic disturbance affects the social structure and social development of a highly gregarious carnivore in the wild. Specifically, we compare the social networks of spotted hyenas (*Crocuta crocuta*) occupying areas of the Masai Mara National Reserve, Kenya that are under different management schemes such that one has a high level of human disturbance and the other area is far more "pristine." Further, we explore how the development of juveniles' social position differs between these two areas and test how the differences in social development affect their survival. We found that groups that experienced lower levels of anthropogenic disturbance were more cohesive than in the high-disturbance area. Furthermore, juveniles in areas of high-disturbance interacted with more individuals but less strongly and were between fewer individuals in the group than were juveniles in areas of lowdisturbance, which affected their survival. The negative effects of disturbance on social development could have important implications for conservation, and these should also be explored in other species that are more endangered and less flexible than spotted hyenas.

INTRODUCTION

Rapid environmental change, particularly that due to anthropogenic disturbance, can dramatically alter the behavior of animals (reviewed in Miranda et al., 2013; Monaghan, 2008). Anthropogenic disturbance has radically changed the social structures of group-living species ranging from bottlenose dolphins (*Tursiops* sp.) to wolves (*Canis lupus*) (Chilvers & Corkeron,

2001; López & Shirai, 2008; Rutledge et al., 2010). Dolphins that experience greater human disturbance in the form of fishing practices and tour groups have more disconnected groups and less cooperation within groups (Ansmann, Parra, Chilvers, & Lanyon, 2012; Chilvers & Corkeron, 2001; López & Shirai, 2008). In wolves, disturbance changes the demography of wolves such that pack members are less related than is the case under less disturbed conditions (Rutledge et al., 2010).

Changes or disturbances to social structures can be highly problematic in species with complex societies because the social positions of individuals can have important fitness consequences affecting both their longevity and reproductive success (Berger et al., 2015; Brent et al., 2017; McDonald, 2007; Silk, 2003; Silk et al., 2010; Stanton & Mann, 2012; Thompson & Cords, 2018). Specifically, early social development can be very important to adult fitness and can be highly sensitive to disturbance. For instance, studies in humans have shown that early socialization and environmental stressors can have dramatic effects on future success (Belsky et al., 2007). When the social development of infant rhesus macaques (Macaca mulatta) does not allow formation of secure attachments, they grow into dysfunctional adults (Anderson & Mason, 1978; H. F. Harlow & Harlow, 1962). Zebra finch (Taeniopygia guttata) chicks exposed to higher concentrations of stress hormones develop weaker association with their parents but are less choosy about the other groupmates with which they associate, making them hold more central positions in the group, than do chicks exposed to lower concentrations of stress hormone (Boogert, Farine, & Spencer, 2014). Early socialization and social position have important adult fitness consequences (Berger et al., 2015; Stanton & Mann, 2012), so it is possible that anthropogenic disturbance might affect social development in harmful ways.

Spotted hyenas (*Crocuta crocuta*) are a good model system in which to test how anthropogenic disturbance affects social development. They have been observed to respond to anthropogenic disturbance in several different ways. For instance, hyenas excrete higher concentrations of stress hormones in areas of higher human activity, specifically more intensive livestock grazing by local pastoralists, than in areas characterized by little or no human disturbance (Van Meter et al., 2009). In an area of high anthropogenic disturbance, we have observed a clan containing 141 individuals, which is the largest clan ever recorded anywhere; the average is 47 individuals in savanna habitats, and 28 throughout the species' range (Holekamp & Dloniak, 2010). Although earlier studies have not specifically inquired how anthropogenic disturbance is affecting the social structure experienced by hyenas in early developmental stages, there are some indications of potentially significant effects. In areas of high-disturbance, mothers decrease their attendance at the communal den (Kolowski & Holekamp, 2009). Because hyenas "inherit" their social networks from their mothers (Ilany & Akcay, 2016), this decrease in maternal presence in disturbed areas may affect social development differently than in cubs in less disturbed areas, where mothers are present with them at dens more often. Also, human disturbance leads to dramatic changes in hyenas' space use, which may result in clan fission (Boydston et al., 2003). In the clan fission described by Boydston et al. (2003), social relationships appeared to weaken within the clan before the split. In South Africa, clans that experienced more human disturbance were found to be less cohesive than those experiencing less disturbance (Belton, Cameron, & Dalerum, 2018).

In this paper, we inquire how human disturbance influences the overall structure of hyena society, the positions individuals hold within their social groups, and the social development of young spotted hyenas using social network analysis (SNA). Spotted hyenas offer a particularly

good model system in which to use SNA for two reasons. First, in contrast to primates, dolphins, and most other mammals living in complex societies, spotted hyenas advance through lifehistory stages that are clearly demarcated by unambiguous milestones such as cessation of dependence on dens for shelter (Holekamp & Smale, 1998a). These milestones allow us to partition early development into clear stages. Second, spotted hyenas live in societies, called clans, that are as complex as troops of baboons or macaques (Holekamp et al., 2015). Furthermore, as in these primates, dispersal behavior in hyenas is strongly sexually dimorphic; most males emigrate to new groups shortly after puberty, whereas females remain in their natal groups for life (Smale et al., 1997). As in the societies of some cercopithecine primates, hyena social rank determines priority of access to key resources, which has profound effects on fitness (e.g., Holekamp et al., 1996; Swanson et al., 2011)). However, in contrast to cercopithecine primates, spotted hyenas live in fission-fusion societies in which individuals are often found alone or with small subgroups of clan-mates (Kruuk, 1972). The fission-fusion nature of hyena sociality allows us to complement social network metrics with measures of time spent alone and relationship strength among clan-mates as reflected in association indices.

First, we explore how the social structure of the entire clan is affected by human disturbance. We then inquire whether anthropogenic disturbance alters the development of social networks and individuals' positions within these networks. We focus specifically on the social networks of individual hyenas during two early stages of development, the first when cubs live at dens, and the second after cubs become independent of dens. If human encroachment is affecting the development of social roles in the spotted hyena, we would expect to see differences in the social network metrics of individuals during early ontogeny between areas of high- and low-disturbance. For instance, cubs that develop in an area of high human disturbance may develop

fewer, weaker ties in a more disconnected network structure than cubs in a less disturbed area. Lastly, we test whether or not the effects of human disturbance and early social position influence survivorship to examine how potential modifications to social development affect one measure of fitness in this species.

METHODS

Study site and subject animals

This study took place in the Masai Mara National Reserve, Kenya. Study subjects were spotted hyenas inhabiting two different regions within the Masai Mara National Reserve (henceforth, the Reserve), in southwestern Kenya. The Mara Conservancy (TMC), which is a relatively pristine area in the western portion of the Reserve managed by a private nonprofit organization that strictly prohibits cattle grazing and human presence except in tour vehicles. We will therefore refer to TMC as our 'low-disturbance' area. We have monitored three clans in this region continuously since 2008: Happy Zebra, Serena North, and Serena South. These clans had on average 37 ± 2 (range: 32-42), 53 ± 3 (range: 46-60), and 48 ± 3 (range: 42-55) hyenas respectively. The other region, which is much more heavily disturbed than TMC, has been monitored continuously since 1988. This area is just inside the northeastern border of the Reserve near the burgeoning town of Talek. We refer to this as our 'high-disturbance' area because, since the late 1990s, there has been exponential human population growth along the border of the reserve and unrestricted development of tourism infrastructure (Boydston et al., 2003; Green, 2015; Kolowski & Holekamp, 2009; Van Meter et al., 2009; Watts & Holekamp, 2009). Pastoralists are active with their livestock both day and night inside the Reserve here, and direct conflict between hyenas and livestock is common both inside and outside the Reserve in

this area (Kolowski & Holekamp, 2006). Since 2005, humans have been responsible for the majority of hyena deaths in the Talek area (through spearing, snaring and poisoning) for which mortality sources can be determined (Holekamp & Dloniak, 2010).

Through historical analyses and comparative studies with populations living in more pristine areas, numerous behavioral effects of increased human activity have been documented in the Talek population, including increased nocturnality, greater daily distances travelled, lower rates of den attendance by mothers, active avoidance of livestock and herders, and a preference for areas with dense vegetative cover (Boydston et al., 2003; Kolowski et al., 2007; Kolowski & Holekamp, 2009). We followed one large clan during the period of this study from the high-disturbance area, named after the local town, Talek. The Talek clan contained 114±12 (range: 76-141) hyenas on average during the study period.

Detailed behavioral and demographic data (described in detail below) used in this study were collected via daily, year-round monitoring from January 2009 through December 2013. Thus, we have five overlapping years of data where the only major environmental difference between TMC and Talek was the level of anthropogenic disturbance. We identified individual hyenas by their unique spots, determined the sex of each animal based on its phallic morphology (Frank et al., 1991), and determined its birthdate to ± 7 days based on its appearance when first observed (Holekamp et al., 1996).

Spotted hyenas live in mixed-sex, matrilineal societies organized by linear dominance hierarchies (Frank, 1986; Holekamp et al., 2012), and they acquire their social ranks via a learning process typical of old-world monkeys called "maternal rank inheritance" (Holekamp & Smale, 1991; 1993). Young hyenas of both sexes acquire social ranks immediately below those of their mothers during the first two years of life. Clans contain multiple matrilines of adult natal
females and their young, but most breeding males are immigrants born elsewhere. Females are socially dominant to males among adults because males enter the hierarchy of their new clan at the bottom when they immigrate into a new social group (East & Hofer, 2001). Adult females and their young tend to be core figures in hyena societies; adult males are more peripheral (Holekamp et al., 1997a; Kruuk, 1972; Szykman et al., 2001). Rank relationships among adult females are quite stable over long periods (Holekamp et al., 2012). High-ranking females enjoy significantly greater reproductive success than do low-ranking hyenas (Hofer & East, 2003; Holekamp et al., 1996; Swanson et al., 2011); low-ranking hyenas are also more strongly affected by fluctuations in prey abundance than are high-ranking hyenas (Holekamp et al., 1996). Here we assigned each adult a social rank based on its wins and losses in dyadic agonistic interactions. Cubs were assigned the social ranks of their mothers.

To explore the social development of our subjects, as in previous studies (Turner, Bills, Sociobiology, 2018, 2018), we partitioned ontogenetic development into two pre-pubertal stages, the Communal Den (CD) stage and the Den Independent (DI) stage, based on the distinct life history milestone of becoming independent of the communal den. Young hyenas in our study area live at a communal den with other members of their cohort until they are 9-10 months old. During this stage, social interactions are more limited than during later stages because cubs' choices of social partners are restricted to members of their cohorts and whichever denindependent hyenas choose to visit the den. Thus, the first stage of development on which we focus in this paper was the CD stage, lasting from the date on which each cub was first seen until its date of den independence. All subjects were first seen within the first three months of life and were restricted to animals with known dates at which they became independent of the communal

den. We determined that a juvenile was independent of the den when it was found away from the den on at least three consecutive occasions.

During the DI stage of development, juveniles are independent of the den, and potentially able to interact with all their clan-mates, but they remain dependent on their mothers for food until they wean, on average, at 14 months of age (Holekamp & Smale, 1998a). During this second stage of development, juveniles learn their ranks in relation to clan members with whom they did not interact at the communal den. The DI stage of development here was defined for each individual to start when the cub became den-independent, and to be equal in length to the length of its CD stage for SNA. Although juveniles could be weaned at any time during the DI stage, and although this transition might conceivably influence network metrics during this stage, youngsters continue to rely heavily on their mothers for assistance in feeding throughout the DI stage because their skulls and skull musculature are far from fully developed (Swanson et al., 2013; Tanner et al., 2009; Watts et al., 2009). Thus, it seemed unlikely that DI metrics would be strongly affected by variable weaning ages among juveniles.

Within individuals, the two stages of development were of the same length for consistent comparisons, and each individual subject was observed during each stage of development, so sample sizes were the same across all developmental stages. Mean stage length was 8.15 ± 0.73 months for Happy Zebra hyenas (n=12), 7.97 ± 0.68 months for Serena North hyenas (n=15), 9.43 ± 0.45 months for Serena South hyenas (n=20), and 6.81 ± 0.26 months for Talek hyenas (n=45). Periods are shortest in the Talek clan because disturbance is causing Talek cubs to become independent at younger ages (t=-2.497, df=305.7, p=0.0131).

Behavioral data collection

Behavioral observations were conducted year-round over the 5-year study period, from our vehicles, which we used as mobile blinds. Observations were made daily between 0530 and 0900 h, and again between 1700 and 2000 h. Each observation session was initiated when we found one or more hyenas separated from others by at least 200 m and terminated when we left that individual or group. In the absence of vocal communication, hyenas appear to be completely unaware of one another when separated by more than 200 m (J. E. Smith et al., 2008). Although no focal hyenas were radio-collared for this particular study, subgroups of hyenas were located either via use of radio telemetry or while observers drove daily circuits in which all highpoints within the study clans' home range were visited. By making 360-degree visual scans with binoculars from each highpoint, we were able to sample all parts of the clan's territory every day for presence of subgroups of hyenas. Each subgroup sighted or found via telemetry was then visited to determine its composition.

To maximize independence of observations, we used only the first session in which an individual was seen during morning or evening observation periods. At the beginning of each observation session and subsequently at 15-20 minute intervals, we performed scan samples in which we recorded all individuals present (Altmann, 1974). From our session data, we determined association patterns based on the twice-weight index of association (Cairns & Schwager, 1987), as used previously (Holekamp et al., 1997a; 2012; Szykman et al., 2001). Because some subgroups were easier to find than others, given their size or the presence of one or more individuals fitted with radio collars, the twice-weight index was the association index most appropriate for our sampling methods (Cairns & Schwager, 1987); dyadic twice-weight

association indices are robust and accurate indicators of social bond strength in spotted hyenas (Holekamp et al. 1997, 2012; Smith et al 2007).

Network construction

Social networks consist of groups of more than two individual animals (nodes) connected by behavioral interactions or co-occurrences in space (ties or links) and portrayed as graphs or matrices. Ties can be directed if the behavior has an initiator and a receiver, or undirected when there is no clear direction in the relationship. Here networks based on associations were undirected, as they indicated co-occurrence.

We used the R package, 'network' version 1.13.0 (Butts, 2008; 2015) to build social networks. To address how entire social networks differ between clans inhabiting areas of high and low-disturbance, we built association networks that included every animal in each clan on a yearly basis from 2009-2013. Each tie in each association network was calculated as a twice-weight association index (AI), which represented the number of times individuals A and B were seen together divided by the total number of times A and B were seen together plus the total number of times A was seen without B plus the total number of times B was seen without A (Cairns & Schwager, 1987). AIs have been shown to be robust and accurate indicators of social bond strength in spotted hyenas (Holekamp et al., 1997a; 2012; J. E. Smith et al., 2007). We did not include the Happy Zebra clan in these analyses because a larger percentage of its observations took place at dens (32% compared to 25% or less for all other clans), artificially making its networks appear more connected and stronger than those in the other two low-disturbance clans, which had more varied types of sessions. As these networks are built based on observations over the entire year, all members of each clan were represented in the networks.

Next, to test how the development of social network positions is affected by anthropogenic disturbance, two social networks were built per subject (high-disturbance = 45 individuals, low disturbance = 47 individuals) that met our criteria for inclusion per network type, each based on data collected during one of the two stages of ontogenetic development. The focal individual had to be seen at least ten times during each developmental stage for its network to be calculated, and each of its social partners also had to be seen at least ten times during a particular stage to be included in the network. This led to $83\pm0.6\%$ of the clan to be represented in the networks of the high-disturbance area and $83\pm2\%$ of the clan to be represented in the low-disturbance area networks.

Network metrics

We calculated several social network metrics. First, we calculated degree centrality, here called "degree," which is the number of other individuals to which the focal individual is connected. Degree is an important metric in social networks, as having a higher degree can indicate that an individual is more of a social hub, which in turn can affect that individual's fitness and its exposure to both information and pathogens (e.g., Barocas et al., 2011; Hamede et al., 2009; Royle et al., 2012). We also calculated network strength as the sum of the weights of all connections to the focal individual. Strength indicates the quality of interactions by accounting for how often or intensely dyads interact, which can have long-lasting social and fitness consequences (Stanton & Mann, 2012; Wey et al., 2013). Lastly, we calculated between members of any dyad in the network that run through the focal individual. Thus, individuals with higher betweenness, often referred to as "brokers," link more individuals that are otherwise

unconnected (Lehmann & Dunbar, 2009a). Indirect ties, like those measured by betweenness, are frequently hypothesized to help maintain the cohesion of complex societies (Lehmann & Dunbar, 2009a). Social network metrics were calculated using the 'statnet' package (v.2016.9) in R (Handcock et al., 2008)

For each focal individual, we calculated these same network metrics in each developmental period. We also calculated the proportion of observation sessions in which it was found alone, when it clearly could not be interacting with other animals, as the number of sessions in which the individual was seen alone divided by the total number of sessions in which the individual was observed during that developmental stage.

Models and statistical analyses

We employed generalized linear mixed models (GLMM) to predict how anthropogenic disturbance affected specific social network metrics. We fit these models using Markov chain Monte Carlo (MCMC) routines, to account for violation of assumptions of independence among relational data, using the 'MCMCglmm' package in R (Hadfield, 2010). We used uninformative priors for 1000 iterations with a thinning interval of 10. All reported p-values are pseudo p-values calculated in the 'MCMCglmm' package, and differences between groups were considered significant when these p-values were ≤ 0.05 . All effective sample sizes were greater than 862.

We ran separate models for the baseline whole network comparisons as well as for the CD and DI stages to determine whether disturbance affected social network positions. Specifically, we predicted how association degree, strength, and betweenness were affected by the level of anthropogenic disturbance. For the models predicting degree, we used a Poisson

distribution, and we used an exponential distribution for the other metrics. Furthermore, hyenas are known to be more gregarious during periods of high than low prey availability throughout the year (Holekamp et al., 2012), so we included prey density per year per clan in the models. However, prey density did not significantly improve any of the models (dDIC>4). Thus, we only show models here that did not include prey density. Because of the wide range and variation in clan sizes, we included an offset for clan size during the stage in question for each individual; this value was log-transformed to make the scale more closely comparable to those of our response measures. Group size is known to affect network metrics because it limits the number of individuals with which a focal animal can interact. To control for differences in observability and effort among the different clans, we also included a log-transformed offset for the number of observations that occurred in each clan's territory during the period. We also added a random effect of year to control for any other yearly variations.

In the models predicting social position during different stages of development, we made models for the same three network metrics in addition to alone rate during each period of development. We also included the individual's maternal rank during each period as a fixed effect. Additionally, we added a random effect for the identity of the mother of the focal individual. Mothers may have specific parenting styles that affect their offspring, and cubs "inherit" their mothers' social networks as they mature (Ilany & Akcay, 2016). We did not include year, as we did for the whole network models; prey density was also excluded because it did not improve the models, likely because the CD and DI stages included both high and low prey seasons.

Lastly, to inquire disturbance and social development affected survival, we employed a cox proportional hazards model for right-censored data, using the 'survival' package (v. 2.38) in

R (Therneau, 2015; Therneau & Grambsch, 2013). Because we usually cannot follow males after they disperse, we only included females in the survival analysis. This left 25 females in the highdisturbance area and 16 females in the low-disturbance area that met our criteria for inclusion; we monitored the survival of these females up to the end of 2015. We predicted survivorship for each period in separate models with all network metrics and alone rate with an interaction with disturbance level. We also controlled for maternal rank and clan size in the model with a frailty term for the mother's identity.

RESULTS

Mean network metrics as well as number of observation sessions per clan can be found in

Tables 5.1 and 5.2.

Table 5.1 Mean±SE metrics describing the overall association networks of clans in high- and low-disturbance areas of the Masai Mara National Reserve, Kenya

disturbance	clan	sessions	degree	strength	betweenness
low	s north	1117±19	42.5±0.7	7.4±0.2	31.1±3.4
low	s south	651±11	35.3±0.8	5.6±0.2	23.1±2.0
high	talek	2925±19	90.3±1.2	8.7±0.2	70.2±5.3

Table 5.2 Mean±SE metrics describing the association networks of focal individuals from high-(45 hyenas) and low-disturbance areas (47 hyenas) in the Masai Mara National Reserve, Kenya

disturbance	clan	stage	sessions	alone	Degree	strength	betweenness
low	happy zebra	CD	52.3±4.5	0.0078 ± 0.004	23.6±1.7	4.5±0.2	0.98±0.2
low	happy zebra	DI	16.3±2.0	0.12±0.04	16.4±3.2	1.7±0.3	0.68±0.2
low	s north	CD	69.2±6.3	0.0063 ± 0.002	40.7±3.2	6.5±0.3	3.1±0.6
low	s north	DI	23.7±6.0	0.057 ± 0.03	17.8±4.9	1.9±0.7	0.85±0.3
low	s south	CD	61.2±3.8	0.0083 ± 0.003	36.5±1.6	5.5±0.2	2.0±0.3
low	s south	DI	25.3±2.3	0.075 ± 0.01	38.0±2.2	2.8±0.2	2.5±0.3
high	talek	CD	55.5±4.2	0.0077 ± 0.003	73.2±2.9	7.7±0.4	5.5±0.7
high	talek	DI	47.2±3.0	0.068 ± 0.008	77.8±2.8	4.9±0.3	5.8±0.6

Overall network differences between clans in high- and low-disturbance areas

Figure 5.1 shows a representative example of the social network structure of clans from high- and low-disturbance areas over the five years of study. Hyenas in areas of low-disturbance associated with significantly fewer individuals than did hyenas in high-disturbance areas (Table 5.3). However, hyenas in low-disturbance areas associated more frequently with those fewer individuals and were in positions of greater betweenness compared to hyenas in the high-disturbance area (Table 5.3). Thus, hyenas in low-disturbance areas were indirectly connected to more individuals than were those in areas of high-disturbance.



Figure 5.1 Representational whole networks in one year (2011) of the clans from high- (Talek) and low-disturbance (S North and S South) areas in the Masai Mara National Reserve, Kenya. For better visibility of the strong relationships, only ties greater than the mean AI (0.06) for this year are shown. Note how many unconnected individuals there are in the Talek clan.

Table 5.3 Posterior means (95% credible intervals) of models testing how human disturbance affects the social positions of all individuals in a clan. Bolded values are statistically significant (p < 0.05)

	degree	strength	betweenness
disturbance: low	-0.823 (-0.868, -0.779)	0.217 (0.161, 0.250)	57.1 (27.5, 90.7)

Effects of disturbance on social development

During the CD stage, cubs in areas of low-disturbance associated with fewer individuals more strongly, and were in positions of greater betweenness, than were cubs in high-disturbance areas (Table 5.4). Anthropogenic disturbance did not affect other social network metrics or how often focal cubs were found alone at dens (Table 5.4). Rank and sex only affected the association strength of den-dwelling hyenas where cubs of higher rank were in positions of greater strength than lower-ranked cubs, and where females had stronger network positions than did males.

	CD			DI		
	disturbance	rank	sex	disturbance	rank	sex
						50
	-98 (-227,	80 (-44,	118 (-18,	172 (43,	26	(-86,
alone	56)	188)	266)	31)	(-79, 131)	184)
			-0.045		0.18	-0.04
	-0.66 (-0.87,	0.02 (-0.15,	(-0.15,	-1.6 (-2.4,	(-0.38,	(-0.25,
degree	-0.44)	0.21)	0.095)	-0.92)	0.74)	0.18)
			-0.18		-0.57	-0.6
	0.19 (0.15,	0.25 (0.2,	(-0.25,	1.1 (1.0,	(-0.58,	(-0.61,
strength	0.23)	0.3)	-0.12)	1.1)	-0.57)	-0.59)
		0.056	-0.21		-0.058	-0.015
	1.2 (0.64,	(-0.23,	(-0.59,	1.4 (1.0,	(-0.39,	(-0.34,
betweenness	1.42)	0.31)	0.08)	1.8)	0.31)	0.36)

Table 5.4 Posterior means (95% credible intervals) of models testing how human disturbance affects social positions during the communal den (CD) and den-independent (DI) stages of development. Bolded values are statistically significant (p<0.05)

During the DI stage, disturbance affected all the social network metrics we examined. Individuals during the DI stage in areas of low-disturbance were found alone more often than those in areas of high-disturbance and, as in the CD stage, they associated with fewer individuals more strongly and were more indirectly connected to others in the clan than were juveniles from the high-disturbance area (Table 5.4). Rank and sex also only significantly affected the association strength of individuals; higher-ranking animals associated less strongly than did lowranking hyenas, and females occupied positions of greater strength than did males (Table 5.4).

Effect of disturbance and social development on survival

Forty-one females met our criteria to be included in the survival analyses, twenty-five of which died by the end of the study. Disturbance and social network positions during the CD stage significantly affected survival (χ^{2}_{11} =29.32, p=0.00203). Females in areas of low-disturbance had higher mortality (β =15.0, p=0.031) as did being in larger clans (β =0.1193, p=0.042). Furthermore, anthropogenic disturbance interacted significantly with association degree (β =-0.3544, p=0.044) to affect survival. Hyenas in areas of low-disturbance that had less strong associations with more individuals enjoyed better survival. In contrast, individuals in areas of high-disturbance that associated with fewer individuals more strongly had greater survival. Alone rate, strength, betweenness, and rank during the CD stage did not affect the survival of cubs in our analyses.



Figure 5.2 Proportion of females surviving in areas of high- and low-disturbance.

During the DI stage, both positions and disturbance significantly affected survival $(\chi^{2}_{11}=41.81, p<0.0001)$. Females in both populations who had more associates survived shorter periods ($\beta=0.1528$, p=0.044). As in the CD stage juvenile females in areas of low-disturbance had lower survival rates than did those from the high-disturbance clan (Fig. 5.2, $\beta=65.2$, p=0.017). Disturbance also interacted significantly with alone rate ($\beta=41.9$, p=0.0095), association degree (Fig. 5.3, $\beta=-0.7534$, p=0.0013) and betweenness ($\beta=5.55$, p=0.00076) to affect survival. Females in low-disturbance areas who were alone less often, interacted with more group-mates, and who were in positions of lower betweenness, enjoyed better survival than did those in similar positions from the high-disturbance area. Associating more strongly with others, rank, and clan size did not affect survival.



Figure 5.3 Association degree shown in relation to age (in years) at death or disappearance for females from areas of high- (25 females; represented by the solid predicted trend line) and low-disturbance (16 females; represented by the dashed predicted trend line) during the DI stage.

DISCUSSION

Disturbance affects hyena social networks

Comparing entire networks of clans between areas of high and low anthropogenic disturbance over five years, we found that there were in fact differences in social network structure. While controlling for the fact that clans in areas of low-disturbance had fewer members than did our high-disturbance clan, we found that hyenas in clans experiencing less anthropogenic disturbance associated with fewer clan-mates but that these associations were stronger than those in the high-disturbance area. Individuals in low-disturbance areas were also in positions of greater betweenness than individuals in high-disturbance areas, indicating that more individuals in low-disturbance areas were in positions that indirectly linked more clanmates. As betweenness is hypothesized to help maintain complex societies via indirect relationships (Kudo & Dunbar, 2001; Lehmann & Dunbar, 2009b), this finding indicates that disturbance may reduce brokerage, or linking otherwise unconnected groups. In fact, starting by the end of 2014, our high-disturbance clan started to show evidence of permanently fissioning into three groups; this clan fission appeared to be complete by May of 2017 (unpublished data). These results are consistent with those from spotted hyenas in South Africa, where clans that experienced less human disturbance were more cohesive than less disturbed clans (Belton et al., 2018).

The fact that the large, highly disturbed clan took so long to split (about 7 years once clan size exceeded 100 clan members, which happened in 2010) might be due to a combination of anthropogenic disturbance factors and large clan size. The Talek clan may have grown so large due to a release of mortality pressure from lions, which were apparently killed or driven out of the area by herders, thus permitting enhanced juvenile survival (Green et al., 2017). It also appeared that the large numbers of hyenas in the Talek clan allowed them to expand the size of their territory by usurping space previously defended by neighboring clans. However, here, we found evidence that the highly disturbed clan was less socially cohesive than the undisturbed clans, so it is surprising that large clan size was maintained for such a long time, as territorial social groups usually need to be cohesive enough to know all their group-mates in order to cooperatively maintain their common territory (Campbell et al., 2011). It may have been possible for the Talek hyenas to maintain an unusually large but less cohesive clan than found elsewhere due to kin tolerance (reviewed in Banks, Piggott, Stow, & Taylor, 2007). Spotted hyenas preferentially associate with kin, and since our study began in 1988, the majority of the clan has

come to consist of descendants of the female who was the alpha animal in 1988 (Holekamp et al., 2012). Thus, greater relatedness may be what held the clan together while the social structure was otherwise becoming unstable. When groups are made up of fewer kin, group or population size is reported to decline in many species (Averbeck, Plath, Wronski, & Apio, 2012; Banks et al., 2007; Bejder et al., 2006). Thus, although human disturbance is negatively affecting social structure in the long-term, there appears to be a level of resilience, which may be related to kinship, that should be further explored in future work (Folke, 2006).

Disturbance affects hyena social development

Just as human disturbance affected the social structure of the entire clan, the social development of individuals was also influenced by anthropogenic disturbance. During both the CD and DI stages, high-disturbance positively affected degree centrality and negatively influenced positions of both strength and betweenness. Juveniles from the low-disturbance areas were also found alone more often than those from the high-disturbance area. Previously, we found that individuals having fewer but stronger relationships during their DI stage live significantly longer lives than their peers (Turner, Bills, & Holekamp, under review); the weakening of ties in areas of high-disturbance could thus potentially have profound fitness consequences. However, Turner et al. also found that being alone more often reduced longevity. Thus, hyenas in areas of high-disturbance may benefit from being alone less often.

Other aspects of ontogeny in hyenas are affected by human disturbance. For instance, cubs from areas of low-disturbance are more neophobic, less exploratory, and bolder than those that grew up exposed to high-disturbance (Greenberg & Holekamp, 2017), indicating that disturbance is affecting personality development. Furthermore, human disturbance affects stress

levels and telomere length in the spotted hyena (Lewin, Treidel, Holekamp, Place, & Haussmann, 2015; Van Meter et al., 2009). In zebra finches, chicks that were exposed to higher stress levels (CORT), had weaker associations but associated with more individuals (Boogert et al., 2014), just as did our hyenas in the high-disturbance area. Stress may be part of what is mediating juvenile social positions in this species. However, future studies will be required to identify the mechanisms by which perturbations to development affect the development of social position, particularly in free-living animals.

Disturbance affects fitness consequences of juvenile social position

The selection pressures affecting juvenile hyena survivorship appear to interact with social positions differently between clans in high- and low-disturbance areas. During the CD stage, associating with fewer individuals benefits the survivorship of hyenas in areas of high-disturbance, whereas associating with more individuals improves survivorship of juvenile females in low-disturbance areas. During the DI stage, associating with fewer individuals improves survivorship for hyenas in the high-disturbance clan, whereas associating with more individuals and being alone less often than those in high-disturbance areas appears to improve survivorship in areas that experienced less anthropogenic disturbance (Fig. 4.3). High levels of betweenness within the network improved survivorship for juveniles from the high-disturbance clan, but not from the low-disturbance clans. Previous research demonstrated that hyenas in our high-disturbance clan have greater survival to maturity than those from areas of low-disturbance, perhaps from reduced mortality from lions in high-disturbance areas, where lion numbers have significantly decreased (Green et al., 2017). Differential mortality threats from lions in the two areas may be what is causing social positions to be differentially related to survivorship. It may

benefit juveniles in low-disturbance areas to associate with more individuals and be alone less often to defend themselves from lions. Without that predation pressure, as in more disturbed areas, it may benefit young hyenas to associate with fewer individuals to avoid such costs of sociality as feeding competition with groupmates, exposure to disease, and stress (e.g., Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011; Dávid-Barrett & Dunbar, 2013; Marescot et al., 2018; Markham & Gesquiere, 2017).

However, the positions that most individuals are holding in the area of high-disturbance do not match the positions that lead to improved survivorship. Hyenas in the high-disturbance area had greater survivorship when they had fewer relationships during the CD stage and fewer direct relationships but more indirect relationships during the DI stage; however, juveniles from the high-disturbance area overall had more, more direct relationships between fewer individuals than cubs from low-disturbance areas, even when controlling for different clan sizes. This discrepancy indicates that human disturbance is negatively affecting social development and could potentially be problematic for overall survival of individuals in areas of high-disturbance beyond the time-frame of this study. We know of no other animal studies conducted in the natural habitat that examine the long-term effects of human disturbance on social development. However, in humans themselves, early stress and socioecological adversity are known to affect children's long-term success in terms of education, jobs, and health (e.g., Belsky et al., 1991; G. W. Evans, 2016; Moffitt et al., 1992; Shalev et al., 2012). Patterns in hyenas similarly indicate that disturbance is having negative effects on development and long-term fitness outcomes.

We found that juveniles living in areas of low-disturbance had higher overall mortality rates than did those from the high-disturbance area. However, Figure 5.2 indicates that after roughly three years of age, that pattern may switch. Hyenas in different stages of life may be

experiencing the disturbance in different ways and to greater or lesser degrees. This finding highlights the need for more longer-term research on the effects of human disturbance on animals in different life stages. Here, we can only explore survivorship up to six years of age due to the shorter study period in our areas of low-disturbance. Juvenile hyenas are highly vulnerable to lions, especially once they are independent of the den but before they reach their full size and maturity. Adults, however, may be more vulnerable to the direct effects of human disturbance as they wander into town or encounter more livestock and herders while hunting than do juveniles, which are not yet as skilled at hunting than adults (Holekamp, Smale, Berg, & Cooper, 1997b). Humans have now surpassed lions as the primary cause of mortality for hyenas in our disturbed study area (Pangle & Holekamp, 2010), which would support this hypothesis.

This study is the first to our knowledge that explores how human disturbance affects both the whole clan social structure as well as the social development of the youngest group members. It highlights that this disturbance is indeed affecting social structure and social development in ways that can have lasting fitness consequences. It is crucial to explore how disturbance is affecting other socially complex species, especially those that are more threatened that spotted hyenas, to determine whether they are also experiencing perturbations in their social development that are reducing their survival.

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