Early life relationships matter: Social position during early life predicts fitness among female spotted hyenas

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Summary

1. How social development in early life affects fitness remains poorly understood.
2. Though there is growing evidence that early-life relationships can affect fitness, little research has investigated how social positions develop or whether there are particularly important periods for social position development in an animal's life history. In long-lived species in particular, understanding the lasting consequences of early-life social environments requires detailed, long-term datasets.
3. Here we used a 25-year dataset to test whether social positions held during early development predicted adult fitness. Specifically, we quantified social position using

three social network metrics: degree, strength, and betweenness. We determined the social position of each individual in three types of networks during each of three stages of ontogeny to test whether they predict annual reproductive success (ARS) or longevity among adult female spotted hyenas (*Crocuta crocuta*).

4. The social positions occupied by juvenile hyenas did predict their fitness, but the effects of social position on fitness measures differed between stages of early development. Network metrics when individuals were young adults better predicted ARS, but network metrics for younger animals, particularly when youngsters were confined to the communal den, better predicted longevity than did metrics assessed during other stages of development.
5. Our study shows how multiple types of social bonds formed during multiple stages of social development predict lifetime fitness outcomes. We suggest that social bonds formed during specific phases of development may be more important than others when considering fitness outcomes.

Keywords: Longevity, Ontogeny, Reproductive success, Social development, Social networks, *Crocuta crocuta*

Introduction

The early social environments of both human and non-human animals affect later-life phenotypes and fitness outcomes (e.g. Belsky, Steinberg & Draper 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 environments reduce it (e.g. Lee *et al.* 2013; Douhard *et al.* 2014; Leris & Reader

2016). However, despite a growing understanding of the relationship between early social relationships and adult traits (e.g. Silk 2003; Lee *et al.* 2013; Kurvers *et al.* 2020), the long-term fitness consequences of an individual's early social network, and its position within that network, have seldom been explored. Data from the few studies in which these social metrics have been investigated suggest that early-life social networks can have important fitness consequences. For instance, early and adult social environments of Alpine marmots (*Marmota marmota*) both independently and additively affect the longevity and reproductive success of dominant females (Berger *et al.* 2015). Juvenile social positions in various bird species directly and indirectly influence adult reproductive success (McDonald 2007; Royle *et al.* 2012; Szipl *et al.* 2019). The early social environment of individuals has also been linked to learning propensity across fish (Taborsky *et al.* 2012; Leris & Reader 2016), birds (White, Gersick & Snyder-Mackler 2012; Langley *et al.* 2020), and mammals (Chiyo, Moss & Alberts 2012). Furthermore, dispersal tendencies often depend on how embedded individuals are in their networks across taxa (Blumstein, Wey & Tang 2009; Nicolaus *et al.* 2012; Godfrey *et al.* 2014). Despite what is known regarding social networks and fitness, the link between early-life social position and lifetime fitness remains poorly understood.

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. However, some stages of development may be more important than others with respect to their influence on adult traits (Bateson 1979). As an extreme example, experimental studies have shown that there are sensitive periods during early life for social development (Harlow & Harlow 1962; Bateson & Hinde 1987; Bateson & Gluckman 2011). Rhesus macaques (*Macaca mulatta*) that fail to develop secure attachments during infancy experience negative long-term health consequences for which later normal socialization cannot compensate (Conti *et al.* 2012). Even among free-ranging adult mammals, variation in social capital, which includes an individual's real or perceived social resources, is increasingly linked to differential fitness outcomes; although, these depend on the stage of adulthood under consideration (Almeling *et al.* 2016; Brent, Ruiz-Lambides & Platt 2017; Ellis *et al.* 2017). The transition from juvenile to adult is an important stage of development 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 those cited above focus on a single stage of development during infancy or adolescence, or on multiple stages during adulthood, we know of no prior research assessing multiple stages of social development from infancy through adulthood and their respective influences on adult traits among free-living animals. The dearth of such studies may be due in part 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 free-living spotted hyenas (*Crocuta crocuta*) to test how social position, indicated by network metrics describing an individual's relationships with its group-mates, during each of three life stages predict their fitness. Spotted hyenas offer a particularly good model system in which to use SNA to explore social development and its influence on fitness. They live in complex fission-fusion societies, called clans, in which individuals are often found alone or with small subgroups of clan-mates (Smith *et al.* 2008), so their tendency to associate with particular group-mates can be measured directly, as can their tendency to spend time alone. In contrast to most other mammals living in complex societies, spotted hyenas also advance through life-history stages that are clearly bounded by unambiguous milestones, such as cessation of dependence on dens for shelter

(Holekamp & Smale 1998). The discrete developmental stages in the life histories of spotted hyenas allow us to document network features separately in each stage of life and assess their effects on fitness.

Each clan of spotted hyenas is structured by a linear dominance hierarchy in which adult females and their offspring dominate breeding males (Frank 1986a; Holekamp *et al.* 2012). Hyena dominance rank determines priority of access to food, so rank has profound effects on fitness measures, including both longevity and reproductive success (e.g. Holekamp, Smale & Szykman 1996; Höner *et al.* 2010; Swanson, Dworkin & Holekamp 2011). Young hyenas of both sexes acquire dominance ranks in their natal clan immediately below those of their mothers by a protracted learning process during the first two years of life; an individuals' dominance rank is not fully learned until it is around 18 months old (Holekamp & Smale 1991; Smale, Frank & Holekamp 1999), which suggests that social interactions may be less strongly influenced by dominance rank during early life than during later life stages (Turner, Bills & Holekamp 2018). Most male spotted hyenas disperse from their natal clans after puberty, whereas females are philopatric (Smale, Nunes & Holekamp 1997; Höner *et al.* 2010).

Our 25-year dataset enabled us to inquire whether early-life social position has long-term fitness consequences for female hyenas. Furthermore, we inquired whether social network metrics assessed during one stage of development have more important fitness consequences than those assessed during other developmental stages. We know that dominance rank and maternal effects can have lasting consequences for cub survival and for dispersal success of males in this species (Holekamp *et al.* 1996; Watts *et al.* 2009; Höner *et al.* 2010), so we controlled for rank in all our analyses and predicted that dominance rank would be positively related to both reproductive success and longevity. We have also documented dramatic changes in the social networks of individuals over the course of ontogeny that are largely independent of dominance rank in this species (Turner *et al.* 2018). Therefore, we hypothesized that social position measured during different stages of development would differentially predict fitness among adult female spotted hyenas. Specifically, we predicted that being more central and having stronger relationships would positively influence adult reproductive success and longevity; these metrics indicate that the individual has more social capital or support, which has been linked to adult fitness outcomes in hyenas and other species (Silk *et al.* 2010; Brent *et al.* 2011; Vullioud *et al.* 2018). Furthermore, because den-dwelling hyena cubs have no control over which group-mates visit the den, and thus with which group-mates they can associate, we anticipated that network metrics measured during this stage of development would be less effective predictors of fitness than those measured in later life stages when hyenas are independent of the den and can choose their own associates. Finally, we inquired whether social network metrics measured during early life stages better predict fitness measures than do network metrics measured in early adulthood, after hyenas have fully learned their dominance ranks.

Materials and 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 of roughly 83 km^2 in the Talek region. We only explored fitness outcomes for females, as we could follow them throughout their lives to obtain fitness measures, whereas many males disperse to unstudied clans. Data were collected via daily monitoring, roughly 6 hrs/day, from June 1988 through December 2013. We identified individual hyenas by their unique spots, determined their sex based on phallic morphology (Frank, Glickman & Licht 1991), and determined their birthdates to ±7 days based on their appearance when first observed (Holekamp *et al.* 1996).

To explore the social development of our subjects, we partitioned ontogeny into three stages (Fig. 1). The Communal Den (CD) stage was separated from the Den Independent (DI) stage by the distinct milestone of becoming independent of the communal den. Both CD and DI stages occurred before achievement of reproductive maturity, which occurs at 24 months of age in this species. Our third stage, the adult stage, represented a period of early adulthood after reaching reproductive maturity. 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 the CD 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 each cub was first seen, 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 (Boydston *et al.* 2005). Den-independent hyenas continue to visit the communal den, but they no longer rely on it for shelter (Holekamp & Smale 1998).

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 *et al.* 1996). Although offspring are weaned 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 jaw musculature remain far from fully developed (Tanner et al. 2009; Watts et al. 2009; Swanson et al. 2013). During this second stage of development, juveniles learn their ranks in relation to any remaining clan members with whom they failed to interact at the communal den. Here the DI stage started when a cub became den-independent, and it was equal in length to the length of its CD stage. Because hyenas reach puberty at 24 months of age, here all natal animals under 24 months were considered juveniles. We defined the adult stage of development as starting on the day an individual reached 24 months of age, and extending from that date for a period equal in length to that of its CD stage. For each individual, all stages of development were of the same length so we could fairly compare network metrics among stages, and each individual subject was observed during all three stages of development. Mean (±SE) stage length was 7.17±0.13 months.

Spotted hyena clans are composed of multiple matrilines of adult females, their young, and adult breeding males, most of which are immigrant males born elsewhere. Adult females and their young tend to be core figures in hyena societies, whereas adult males occupy more peripheral positions (Kruuk 1972; Holekamp *et al.* 1997; Szykman *et al.* 2001). Rank relationships among adult females are quite stable over long periods (Holekamp *et al.* 2012; Vullioud *et al.* 2018). High-ranking females enjoy markedly greater reproductive success than do low-ranking females (Holekamp *et al.* 1996; Swanson *et al.* 2011). Females' ranks were based on their wins and losses in dyadic agonistic interactions using informed MatReorder (Strauss & Holekamp 2019b). Females in the two juvenile stages analyzed here (CD and DI) were assigned the dominance ranks of their mothers, but as young adults they were assigned their own ranks; at reproductive maturity, each female enters the adult hierarchy in a position immediately below that of her mother.

Behavioral data collection

Throughout the 25-year study period, daily behavioral observations were conducted year-round from vehicles, which we used as mobile blinds. Observations were made each day between 0530 and 0900 h and between 1700 and 2000 h. Each observation session (henceforth called ‘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 (Smith *et al.* 2008); this occurred when either all hyenas were out of sight or they were all resting. In the absence of vocal communication, hyenas appear to be unaware of one another when separated by more than 200 m. We ended sessions with only one hyena present after five minutes unless it started hunting and/or joined other hyenas. Session lengths ranged from 5 to 638 minutes (mean 11±0.06 minutes). 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 hyena subgroups. Each subgroup sighted or found via telemetry was then visited to determine its composition. Female hyenas in this study were observed, on average, in 88.8±5.0 sessions during the CD stage, 88.5±4.6 sessions during the DI stage, and 75.2±4.4 sessions during the adult stage (Table S1). On average, they were seen in 0.43±0.02 sessions per day during the CD stage, 0.40±0.02 sessions per day during the DI stage and 0.35±0.02 session per day during the adult stage.

To maximize independence of observations, we used only the first session in which an individual was seen during morning or evening observation periods. From session data, we determined association patterns using the simple ratio association index (AI) (Cairns & Schwager 1987), see Appendix S1 for this calculation). At the beginning of each observation session, and subsequently at 15-20 minute intervals, we performed scans in which we recorded the identities of all individuals present (Altmann 1974).

We used all-occurrence sampling (Altmann 1974) to record all agonistic and affiliative interactions occurring within each observation session. Detailed descriptions of the aggressive behaviors we recorded can be found in Szykman et al. (2003). Regarding affiliative behavior, we focused on greetings, in which hyenas stand head to tail, lift their hind legs, and sniff one another's ano-genital region; greetings have been found to promote social bonds (Smith *et al.* 2011). Table S1 shows mean numbers of interactions of each type for each individual in each stage of development.

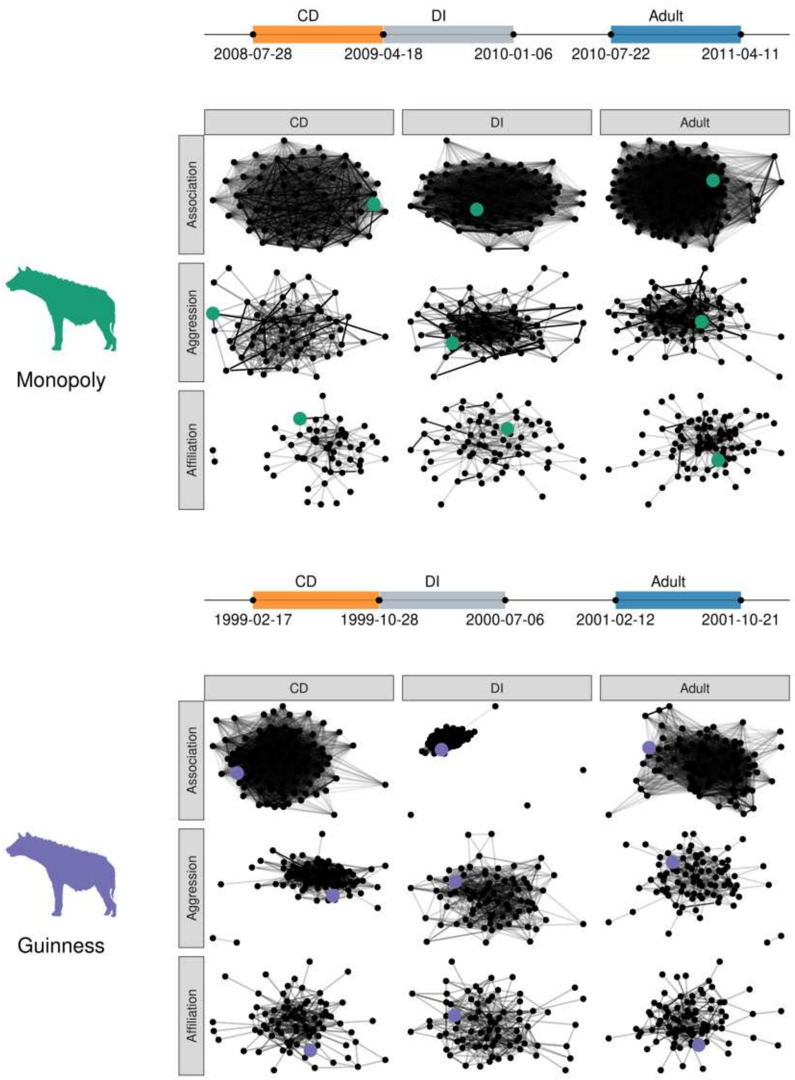

Figure 1. An example for two of our focal females, Monopoly and Guinness, of their association, aggression, and affiliation networks that were built for each of their developmental stages: communal den (CD), den-indpependent (DI), and early adult (Adult). Each stage was of equal length. The green dot indicates Monopoly and the purple dot indicates Guinness in each of their networks. Monopoly was high-ranking whereas Guinness was low-ranking. From each of these networks we calculated their (out-/in-) degree, (out-/in-) strength, and betweenness. Whole networks were made for each of 79 focal females during each of their three stages of development, yielding 9 networks per female. Thus, we made a total of 711 observed networks.

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. Using methods developed earlier (Turner *et al.* 2018), we built three types of whole networks. Networks could include all individuals of both sexes in the clan for each focal female during each stage of development: we built association, aggression, and affiliation networks. Here networks based on associations were undirected, as they merely indicated co-occurrence, but both aggression and affiliation networks were directed. Depending on the network type, each network tie was weighted such that it reflected either purely the association index within the dyad (the AI) or behavioral interaction indices that controlled for variation in opportunity to emit the behavioral acts (see below for more detail, Fig. 1).

Using the 'igraph' package (version 1.2.4) (Csardi & Nepusz 2006) in R (version 3.5.1) (R Core Team 2019), we built three social networks per subject per network type, with each network based on data collected during the CD, DI, or adult 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. These criteria produce robust social networks during all three stages of social development in spotted hyenas (see Appendix S2, (Turner *et al.* 2018). To assess the robustness of our results here, we also ran our analyses with minima of 25 and 50 sightings per focal individual per stage, respectively (see Appendix S2, Tables S2 and S3), but these denser networks did not differ appreciably from those built using a minimum of 10 sightings per developmental stage, so our analyses below use an inclusion criterion of 10 sightings to maximize our sample sizes. Seventy-nine females met the criteria for being included as focal individuals. Simple ratio AIs (Cairns & Schwager 1989) were used to build association networks for focal animals, as these AIs are known to be robust indicators of social bond strength (Hoppitt & Farine 2018). In interaction networks, we calculated behavioral indices of aggression and affiliation to represent the strength of relationships between dyads. These were calculated as the residuals of the regression of AIs predicting the interaction rate (Godde *et al.* 2013 for more detail see Appendix S1; Whitehead & James 2015). This was done to account for opportunity to interact and individual variation in gregariousness among individuals. Rates in aggression networks were calculated as the number of aggressive acts an individual initiated or received within each dyad over the relevant developmental stage, weighted by the intensity of said aggression (1 to 3 indicating lowest to highest, as described in (Szykman *et al.* 2003). Similarly, the rate in each affiliation network was weighted based on numbers of greetings between the focal individual and each of its group-mates divided by the length (in days) of the specified developmental stage. In both aggression and affiliation networks, we used only interactions in which we were certain of the identities of both the initiator and the receiver.

Network metrics

For each focal individual, during each stage of development (CD, DI, and early adulthood), in each network type (association, aggression, or affiliation networks), we calculated several measures of social network position. First, to supplement network metrics, we calculated the proportion of observation sessions during each stage of development in which each female was found alone ("alone rate"), when she clearly could not be interacting with other animals, as the number of sessions in which she was found alone divided by the total number of sessions in which that female 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. In association networks, strength is roughly proportional to group size, whereas in interaction networks it indicates the quality of interactions by accounting for how often or how intensely dyads interact (Farine & Whitehead 2015). Network strength has long-lasting social and fitness consequences in other gregarious species (e.g. dolphins and rodents,(Stanton & Mann 2012; Wey *et al.* 2013). Lastly, we calculated "betweenness" centrality, 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 2009). Indirect ties, like betweenness, are frequently hypothesized to help maintain cohesion in complex societies (Lehmann & Dunbar 2009), like those of spotted hyenas. Because 'igraph' calculatates betweenness prioritizing weak links rather than strong links, as we do in behavioral ecology, we inverted the edge weight in the calculation (1/edge weight).

We focused on these three social network metrics (degree, strength, and betweenness) in particular because they are some of the few that have been linked to individual or group success multiple times in other species (e.g. Stanton & Mann 2012; Nunez, Adelman & Rubenstein 2015; Brent *et al.* 2017; Blumstein *et al.* 2018).

Fitness measures

We explored two different fitness outcomes to test how well they were predicted by metrics describing juvenile social position. Specifically, we focused on annual reproductive success (ARS) and longevity, two measures known to be robust fitness measures in spotted hyenas (Swanson *et al.* 2011). ARS was calculated as the number of cubs borne by the focal female over her 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 (at least 2 years) 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 to ensure that all individuals would have a complete Adult stage before dying. Ultimately, 66 females met our criteria for which we also had ARS data, and we had longevity measures for 65 females who met our inclusion criteria. The mean ARS for the females observed in this study was 1.4±0.05 (range: 0.71-2.9) cubs per year, and mean longevity was 7.6±0.46 (range: 3.2-19) years.

Models and statistical analyses

We employed generalized linear mixed models (GLMM) to predict how alone rate and specific social position metrics predicted 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 networks), we explored both the out- and in-degree centrality and out- and in-strength. All predictor variables were scaled alike for easier comparisons. We also included the dominance rank of each individual as a fixed effect in all models to control for any rank effects. Additionally, we log-transformed our fitness outcomes to normalize their distributions. We fit these models using the 'lme4' package in R (version 1.1.21, (Bates *et al.* 2015).

We ran separate models for CD, DI, and adult stages to determine whether the social position of an individual in each stage, represented by the network metrics calculated for that individual during that stage, predicted 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 to account for effects of group size on network metrics. 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 an offset for the number of sessions in which the focal individual was observed during each developmental stage to control for opportunity for interactions to be observed. Both of these values were log-transformed to make their scales more closely comparable to those of our response measures. We 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 can "inherit" their mothers' social networks (Ilany & Akcay 2016). We then used Akaike information criteria (AIC) for model selection to determine which network metrics during each stage best predicted the fitness outcomes. Henceforth, we present the top model(s) identified by AIC for each fitness measure in each developmental stage (dAIC < 2).

To account for the inherent lack of independence in social network data, we took a null model hypothesis approach, as is commonly done with social network data (Farine 2017). In this approach, we compare the parameters of our observed models with parameters of random models (as opposed to comparing parameters to zero, as done in most frequentist statistics) to determine whether the value of a variable differs significantly from what might occur at random. We employed data-stream permutations on data collected daily to generate randomized networks for our null models to help account for individuals having variable numbers of observations (Farine & Whitehead 2015; Farine 2017). As with our observed models, raw interaction data of each type (association, aggression, and affiliation) were randomized for each focal individual in each developmental period, and we then re-generated networks based on randomized interaction data. One caveat here is that aggression and affiliation networks are dependent on association networks because an individual can only directly interact with an individual with whom it associates. To account for that fact in our randomizations, we first permuted our association networks then permuted the aggression and affiliation networks within the new association networks. We performed 1000 randomizations for each female in each stage of development, and the metrics of the focal females in these randomized networks were then used to build null GLMMs to compare parameter estimates with the parameter estimates of our observed GLMMs (Farine 2017). A parameter was considered a strong predictor of the fitness outcome if the observed model estimate fell outside the 95% distribution of the randomized null model parameter estimates for all three thresholds of 10, 25, and 50 observations per life stage (Tables S2 and S3). If the observed estimate fell outside the 95% distribution for the 10 observation threshold, but within one or more of the larger thresholds, we considered the metric to have have a weaker, less certain relationship with the fitness outcome than the metrics that were significant at all three threshold values (Wasserstein, Schirm & Lazar 2019). Because our random distributions were not centered around 0 (Farine 2017), we calculated a corrected effect size by taking the difference between the observed coefficient value and the median of the distribution of the coefficient values based on the randomized networks. Furthermore, 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, and VIFs of 5 are still moderately collinear (O'brien 2007); the VIF values in all our models were between 1.0 and 3.6 (correlations between metrics in this study are shown in Table S4).

Results

Mean values (±SE) for all network metrics during each stage of development appear in Table S5.

The best CD model for ARS was a better fit than the best DI model (dAIC > 7.5, Table S6), but the adult model was better than either the CD (dAIC > 10, Table S6) or DI model (dAIC > 19, Table S6). In models predicting longevity, during all three developmental stages, two models were statistically indistinguishable from one another (dAIC < 2, Table S7). The CD and DI models were also indistinguishable from one another (dAIC < 2, Table S7). Although the CD model was a better fit than the adult model (dAIC > 2, Table S7), the DI model for longevity was indistinguishable from the adult model (dAIC < 2, Table S7).

Effect of social network positions across ontogeny on fitness

a) ARS

We found that network metrics assessed during early ontogeny did in fact predict the later-life fitness of female hyenas. The best model for all stages of development predicting ARS included only degree in association networks, and out- and in-degree in aggression and affiliation networks; this model did not include alone rate, strength, or betweenness metrics. Association degree positively related to adult ARS and affiliation out-degree showed a negative trend (Table 1). When female hyenas were in the DI stage, those that associated with more individuals also had greater adult ARS (Table 1). During the adult stage, female hyenas enjoyed greater ARS who associated with more individuals, aggressed on fewer individuals, and tended to affiliate with fewer individuals (aggression and affiliation out-degree), and who also had more affiliations directed towards them (affilition in-degree); of these, association degree had the greatest effect (Table 1).

Table 1. Observed model estimates, 95% randomization ranges, two-tailed p-values (P_{rand}), and corrected effect size for each of the model variables explaining ARS among 66 adult females based on social network positions during communal den (CD), den independent (DI), and adult stages. P_{rand} is calculated by comparing the observed model estimates with the distribution of the model estimates from the 1000 randomizations of the network data. Bolded values indicate that the observed estimates fall outside of the 95% distribution at all observation threshold values, and italicized values indicate that the observed estimates did not fall outside of the 95% distribution at all observation number thresholds. Strength and betweenness did not appear in any of the best models, so they are not included here. The random effect is the standard deviation (sd) of the different intercepts for the random effect of mother.

network type	term	CD effect size	estimate	range	P_{rand}
	dominance rank	-0.064	-0.062	-0.048 to 0.058	*0.021*
association	degree	0.098	-0.335	-0.487 to -0.371	**0.005**
aggression	out-degree	0.025	-0.116	-0.223 to -0.068	0.304
	in-degree	-0.054	-0.077	-0.087 to 0.037	0.07
affiliation	out-degree	-0.114	-0.125	-0.124 to 0.108	*0.048*
	in-degree	0.097	0.084	-0.129 to 0.107	0.087
	mother (random effect sd)		0.458		
network type	**term**	**DI effect size**	**estimate**	**range**	**P_{rand}**
	dominance rank	-0.016	-0.125	-0.157 to -0.061	0.288
association	degree	0.08	-0.423	-0.535 to -0.472	**0.001**
aggression	out-degree	0.027	-0.029	-0.109 to -0.003	0.207
	in-degree	-0.001	-0.024	-0.075 to 0.029	0.479
affiliation	out-degree	-0.072	-0.124	-0.161 to 0.081	0.137
	in-degree	0.03	-0.016	-0.165 to 0.07	0.327
	mother (random effect sd)		0.403		
network type	**term**	**Adult effect size**	**estimate**	**range**	**P_{rand}**

	dominance rank	-0.034	-0.198	-0.219 to -0.105	0.15
association	degree	0.197	-0.086	-0.326 to -0.237	**<0.001**
aggression	out-degree	-0.102	-0.223	-0.191 to -0.054	**0.008**
	in-degree	-0.005	-0.087	-0.173 to 0.011	0.464
affiliation	out-degree	-0.172	-0.219	-0.168 to 0.083	*0.012*
	in-degree	0.146	0.047	-0.208 to 0.03	*0.03*
	mother (random effect sd)		0.213		

CD

network type	term	corEffect	estimate	randRange	Prand
	dominance rank	-0.064	-0.062	-0.048 to 0.058	*0.021*
association	degree	0.098	-0.335	-0.487 to -0.371	**0.005**
aggression	out-degree	0.025	-0.116	-0.223 to -0.068	0.304
	in-degree	-0.054	-0.077	-0.087 to 0.037	0.07
affiliation	out-degree	-0.114	-0.125	-0.124 to 0.108	*0.048*
	in-degree	0.097	0.084	-0.129 to 0.107	0.087
	mother (random effect sd)		0.458		

DI

network type	term	corEffect	estimate	randRange	Prand
	dominance rank	-0.016	-0.125	-0.157 to -0.061	0.288
association	degree	0.08	-0.423	-0.535 to -0.472	**0.001**
aggression	out-degree	0.027	-0.029	-0.109 to -0.003	0.207
	in-degree	-0.001	-0.024	-0.075 to 0.029	0.479
affiliation	out-degree	-0.072	-0.124	-0.161 to 0.081	0.137
	in-degree	0.03	-0.016	-0.165 to 0.07	0.327
	mother (random effect sd)		0.403		

Adult

network type	term	corEffect	estimate	randRange	Prand
	dominance rank	-0.034	-0.198	-0.219 to -0.105	0.15
association	degree	0.197	-0.086	-0.326 to -0.237	**<0.001**
aggression	out-degree	-0.102	-0.223	-0.191 to -0.054	**0.008**
	in-degree	-0.005	-0.087	-0.173 to 0.011	0.464
affiliation	out-degree	-0.172	-0.219	-0.168 to 0.083	*0.012*
	in-degree	0.146	0.047	-0.208 to 0.03	*0.03*
	mother (random effect sd)		0.213		

b) Longevity

The best models for the CD stage predicting longevity, like those predicting ARS, included degree in association networks and both out-degree and in-degree in aggression and affiliation networks, and the second best model included strength in association networks and both out-strength and in-stength in aggression and affiliation networks; neither included alone rate or betweenness metrics. Those individuals lived longer who associated with more individuals and initiated fewer affiliations, but also received more affiliations (Fig. 2, Table 2). Furthermore, those who were higher ranked and received aggression from fewer individuals tended to live longer (Table 2). In the strength model, hyenas lived longer who had lower association strength, lower affilition out-strength, and higher affiliton in-strength. Affiliation metrics during the CD period had the strongest effects in both models (Table 2). The longevity of female hyenas was best predicted by betweenness in all networks followed by degree in association networks and both out-degree and in-degree in aggression and affiliation networks during the DI; alone rate and strength did not appear in the best models. In the betweenness model, females lived longer who were lower ranked, and had lower association betweenness but higher affiliation betweenness. In the degree model, those females lived longer who were higher ranked and associated with more individuals (Table 2). Association metrics had the strongest effects. During the adult stage, the best models were the same as the DI stage, but the degree model was top ranked followed by the betweenness model. In the degree model, females lived longer who associated with more individuals, and in the betweenness model, affilition betweenness had a weak, negative relationship with longevity (Table 2).

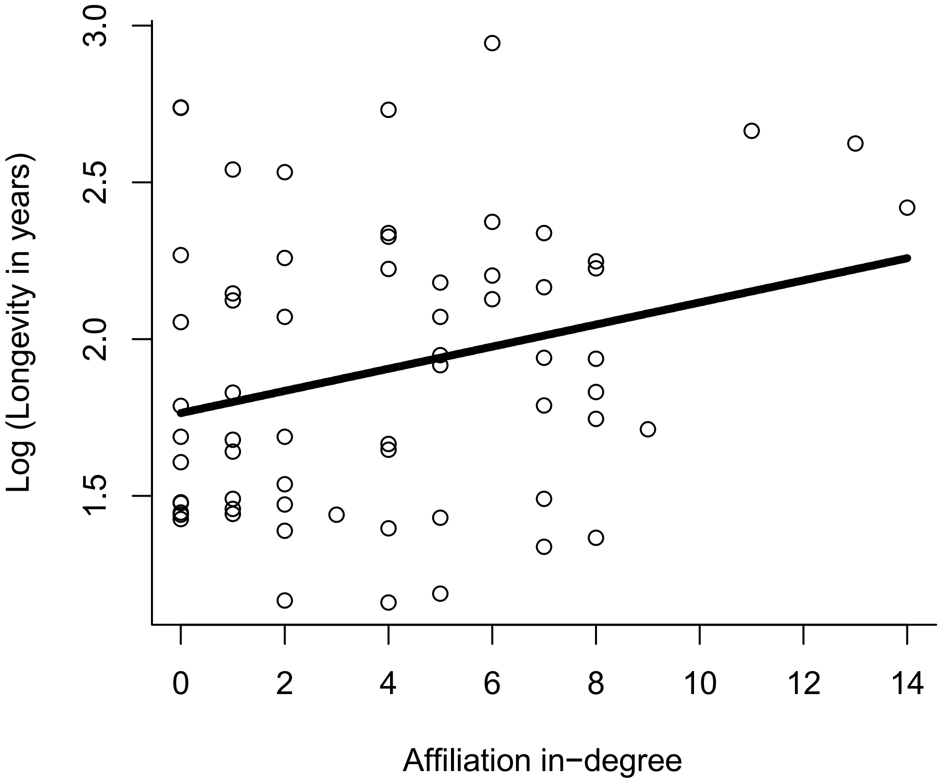

Figure 2. The relationship between longevity and the number of individuals that directed greetings towards the 65 focal females during the CD stage. Longevity was log transformed. The dark line indicates the relationship between the social network metric and longevity estimated as a linear regression.

Table 2. Observed model estimates, 95% randomization ranges, two-tailed p-values (P_{rand}), and corrected effect size for each of the model variables explaining longevity among 65 adult females based on social network positions during communal den (CD), den independent (DI), and adult stages. When two models during a developmental stage had dAIC<2, both were included, and the first shown was the better of the two. P_{rand} was calculated by comparing the observed model estimates with the distribution of the model estimates from 1000 randomizations of the network data. Bolded values indicate significance in that the observed estimates fall outside of the 95% distribution at all observation threshold values. Italicized values indicate that the observed estimates fell within the 95% distribution of one or two observation number thresholds, and dashes indicate that the metric did not appear in the best model. The random effect is the standard deviation (sd) of the different intercepts for the random effect of mother.

		CD							
		degree				strength			
network type	term	effect size	estimate	range	P_{rand}	effect size	estimate	range	P_{rand}
	dominance rank	0.091	0.302	0.146 to 0.245	*0.003*	0.049	0.239	0.129 to 0.252	0.092
association	degree	0.124	-0.292	-0.453 to -0.378	**<0.001**	--	--	--	--
	strength	--	--	--	--	-0.089	-0.401	-0.358 to -0.267	**0.002**
aggression	out-degree	-0.069	-0.2	-0.227 to -0.04	0.121	--	--	--	--
	in-degree	-0.117	-0.056	-0.02 to 0.146	*0.01*	--	--	--	--
	out-strength	--	--	--	--	0.012	-0.108	-0.189 to -0.045	0.385
	in-strength	--	--	--	--	-0.061	0.049	0.038 to 0.174	0.081
affiliation	out-degree	-0.405	-0.409	-0.152 to 0.146	**<0.001**	--	--	--	--
	in-degree	0.383	0.37	-0.167 to 0.127	**<0.001**	--	--	--	--
	out-strength	--	--	--	--	-0.327	-0.342	-0.138 to 0.109	**<0.001**

	in-strength	--	--	--	--	0.279	0.247	-0.159 to 0.094	**<0.001**
	mother (random effect sd)		0.543				0.544		

DI

			betweenness				degree		
network type	term	effect size	estimate	range	P_{rand}	effect size	estimate	range	P_{rand}
	dominance rank	-0.121	-0.154	-0.1 to 0.045	**0.004**	0.121	0.143	-0.027 to 0.071	**<0.001**
association	degree	--	--	--	--	0.083	-0.365	-0.477 to -0.414	**<0.001**
	betweenness	-0.395	-0.469	-0.205 to 0.071	**<0.001**	--	--	--	--
aggression	out-degree	--	--	--	--	-0.012	-0.043	-0.093 to 0.038	0.361
	in-degree	--	--	--	--	-0.003	0.021	-0.032 to 0.078	0.465
	betweenness	0.045	-0.062	-0.467 to 0.053	0.32	--	--	--	--
affiliation	out-degree	--	--	--	--	0.072	0.037	-0.172 to 0.109	0.191
	in-degree	--	--	--	--	-0.115	-0.159	-0.171 to 0.099	0.077
	betweenness	0.194	0.074	-0.236 to 0.004	**0.004**	--	--	--	--
	mother (random effect sd)		0.601				0.556		

Adult

			degree				betweenness		
network type	term	effect size	estimate	range	P_{rand}	effect size	estimate	range	P_{rand}
	dominance rank	-0.009	-0.031	-0.075 to 0.037	0.391	0.077	0.002	-0.206 to 0.058	0.189
association	degree	0.203	-0.196	-0.426 to -0.369	**<0.001**	--	--	--	--
	betweenness	--	--	--	--	-0.061	-0.188	-0.27 to 0.045	0.243
aggression	out-degree	-0.017	-0.106	-0.171 to -0.006	0.335	--	--	--	--
	in-degree	-0.006	-0.112	-0.205 to -0.009	0.462	--	--	--	--
	betweenness	--	--	--	--	0.132	-0.016	-0.54 to 0.042	0.148
affiliation	out-degree	-0.069	-0.082	-0.175 to 0.142	0.248	--	--	--	--

in-degree	-0.126	-0.17	-0.195 to 0.119	0.088	--	--	--	--
betweenness	--	--	--	--	-0.163	-0.32	-0.292 to -0.021	*0.019*
mother (random effect sd)		0.56				0.613		

Discussion

Social position during ontogeny predicts fitness

Annual reproductive success (ARS) and longevity were both predicted by specific juvenile social network metrics, supporting the hypothesis that social position measured during different stages of development would differentially predict fitness among adult female spotted hyenas. Degree, or the number of individuals with which a female interacts early in life, appeared in at least one of the best models for all three developmental stages. This suggests that the number of relationships experienced during early life has lasting impacts throughout the lifetime of the individual. Specifically, associating with many individuals was positively related to both ARS and longevity in all three developmental stages. Overall, the early-life direct network metric of degree had a stronger influence on reproductive success than did the indirect network connectivity measure, betweenness, which played a role in predicting longevity. Out-degree in aggression networks negatively predicted ARS during the young adult stage of life. By contrast, aggression network metrics did not strongly influence longevity. Affiliation network metrics did not predict ARS but strongly related to longevity, first positively then negatively, over ontogeny. Finally, model selection indicated that the adult stage best predicted the ARS data, but the CD and DI stages best predicted female longevity. Thus, we found that the social environments females experienced as juveniles had lasting influences into adulthood, as has been seen in many other species.

Contrary to our expectations, an individual's dominance rank position during the studied stages of postnatal development did not consistently predict either its ARS or its longevity. Although it has been well-documented that maternal rank affects juvenile survivorship in this species (Watts *et al.* 2009), of those hyenas who survived past three years of age in our study, their ranks early in life did not always predict their fitness in adulthood. However, regardless of the rank an individual held early in life, its early social position within its network strongly influenced its ARS and longevity. Young hyenas start learning their ranks at the communal den, and do not fully solidify their rank relationships with all adults in the clan until they are approximately 18 months old after which they remain relatively stable (Smale *et al.* 1999; Strauss & Holekamp 2019a), so perhaps it should not surprise us that the social bonds they developed as juveniles were as good or better at predicting their eventual fitness than their juvenile ranks. Dominance rank can be a source of stress while concurrently providing an individual with resource benefits (Gesquiere *et al.* 2011). If a female hyena survives to 3 years of age, she may develop other strategies to counteract any negative effects of low dominance rank on fitness such as having fewer indirect associative connections (Vandeleest *et al.* 2016), as we saw here. We rarely saw an effect of early rank in our analyses, but we consistently saw effects of other social metrics on female fitness, particularly the number of individuals with whom females associated.

Our study is one of only a few inquiring how juvenile sociality predicts multiple measures of fitness regardless of the adult social environment. Graylag geese who are more closely connected as juveniles enjoy greater reproductive success years later (Szipl *et al.* 2019). The adult social environment of Alpine marmots was a strong driver of reproductive success whereas the number of helpers present in early life was a strong driver of longevity (Berger *et al.* 2015). Similarly, in spotted hyenas we found that ARS was much better predicted by the adult model, but models of juvenile stages better predicted longevity. Social network metrics assessed in spotted hyenas can change dramatically over ontogeny (Turner *et al.* 2018), but they become more consistent and stable as hyenas mature (Smith, Memenis & Holekamp 2007; Smith *et al.*

2011; Yoshida, Van Meter & Holekamp 2016); thus it is noteworthy that social network metrics measured during both the CD and DI stages predicted longevity better than did those measured during the adult stage. The adolescent period is known to be a sensitive period in other species (Sachser *et al.* 2013), as it may be for female hyenas with respect to their longevity in particular. The stages of development in this study represent periods of intense social learning for female hyenas. We propose that the choices females make during juvenile stages regarding with whom and how they interact help prepare them for long-term success in hyena society.

Linking early social position and fitness

By assessing multiple phases of hyena development, we are one step closer to demonstrating causality in the relationship between early sociality and adult fitness outcomes (Hill 1965), though several factors may mediate this relationship. Our data demonstrate that female hyenas who had more associates during all stages of development, and who initiated fewer direct interactions, tended to enjoy greater ARS and lived longer; this suggests that gregariousness is costly to females. Unfortunately, our data cannot indicate whether or not individuals are actively avoiding one another. However, our results do suggest that successful individuals experience less competition for resources with others in the clan. In species with strict linear hierarchies, like cercopithecine primates and spotted hyenas, higher ranks guarantee better access to resources, and this improves their reproductive success (Holekamp *et al.* 1996; Johnson 2003; Liu *et al.* 2018). However, our current dataset indicates that lower ranking females may adopt alternative strategies to improve their reproductive success. Rank for these females does not predict ARS, but females who interact with fewer individuals have fewer competitors for resources. Competition for resources goes hand-in-hand with aggression in hyenas (Frank 1986b). Thus, minimizing competition is likely the best explanation for the link between early social network metrics and ARS: females who directed attacks at fewer individuals during the young adult stage had greater ARS than others, regardless of their rank. By contrast, aggression metrics did not predict longevity.

Our results also suggest that social capital, or social support, relates to survivorship in hyenas starting at an early age. Social capital is often linked to other traits that may be mediating the fitness outcomes we observed here (Silk, Seyfarth & Cheney 2018). For instance, more focused social networks may represent a form of social buffering, where social bonds are known to augment fitness and reduce stress. On the other hand, some species have higher concentrations of stress hormones when they are in more connected social positions (Ponzi *et al.* 2016; Szipl *et al.* 2019). Rhesus macaques with smaller association networks but more connected grooming networks had lower glucocorticoid levels, suggesting that the quality of the relationship matters (Crockford *et al.* 2008; Brent *et al.* 2011). Furthermore, studies of many primate species show that strong affiliative networks, frequently characterized by high rates of grooming, reduce stress responses and improve longevity (Wittig *et al.* 2008; Silk *et al.* 2010; Brent *et al.* 2017). Though we did not measure stress hormones here, female hyenas in our study lived longer when they had focused association networks and when they were better integrated into their broader affiliation network, as is also seen among primates. Although most studies focus strictly on adults, our findings highlight the need to explore the relationship between social support and adult stress phenotypes at earlier developmental stages to determine how it relates to adult fitness and what mediates this relationship.

Studies of effects of early adversity in other species increasingly demonstrate that both the social environment and stress experienced during early life can affect adult fitness via epigenetic mediation (Hunter & McEwen 2013; Tung *et al.* 2016). Juvenile hyenas with higher association degrees have higher global genome methylation (Laubach 2019), which suggests that epigenetic effects may be mediating the relationship between early social relationships and adult fitness. We see this as a fascinating avenue for further study to better understand which mechanistic variables affect fitness, and how these effects are mediated, as fitness in hyenas is clearly not determined exclusively by either rank or genetic inheritance.

Conclusion

Our study enhances our understanding of how early social development relates to adult fitness. The importance of social network positions emerging very early in life has rarely been reported before for other species. Most studies, whether exploring the influences of social position during early ontogeny or during adulthood, measure fitness in terms of reproductive success, but studies that address how social network positions predict longevity are considerably more rare. Of the studies linking social position to longevity in non-human animals, only two (Stanton & Mann 2012; Nunez *et al.* 2015) consider juvenile social development. Although this research area is growing, there are still critical gaps in our understanding of early social development, especially with respect to the factors mediating the relationship between early social position and fitness.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Association and interaction indices

Appendix S2. Assessing network robustness.

Table S1. Mean±SE of observation "sessions" and number of behaviors.

Table S2. Model output predicting ARS for assessing network robustness.

Table S3. Model output predicting longevity for assessing network robustness.

Table S4. Pearson correlations between dominance rank, alone rate, and all network metrics.

Table S5. Mean±SE of all network metrics during each stage of development.

Table S6. Model comparisons using AIC for the best models predicting ARS.

Table S7. Model comparisons using AIC for the best models predicting longevity.

Fig. S1. The relationship between longevity and association degree during the DI stage.

Fig. S2. Patterns in degree centrality and betweenness to assess network robustness

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Ethics: All procedures performed in studies involving animals 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.

Data accessibility: Data are available as files for reviewers and editors but will be made available on Dryad once accepted for publication.

Authors' contributions: JWT conceived the idea and designed analyses with the help of PSB and KEH. KEH provided the archival data. PSB transformed the archival data for analysis with the help of JWT and ALR. ALR and JWT developed the R code to perform the analyses, and JWT analyzed and interpreted the data. JWT & KEH wrote the manuscript. All authors gave final approval for publication.

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