Abstract

      Social networks are effective tools for analyzing relationships within populations. Higher connectivity between actors in the network can lead to individual benefits, such as information exchange, higher social rank, and access to resources. Spotted hyenas (*Crocuta crocuta*) live in large clans and maintain a complex social structure, making them an ideal study population when analyzing social networks. They have well-defined social ranks determined by maternal kinship. Cubs inherit social rank from their mothers, resulting in subgroups of female descendants with the same social rank, called matrilines. We examined the Talek clan in Kenya's Maasai Mara National Reserve using observational data collected over a 22 year study. Our study focuses on adult female hyenas because of their dominant role in the social hierarchy. Modeling the hyena population as a social network allows us to show relationships between the connectivity, social rank, and reproductive fitness of matrilines. Previous studies indicate that social rank influences fitness, but chance also plays a significant role in the success of low-ranking matrilines. Our results indicate that a model including social interactions between matrilines and within matrilines predict fitness more accurately than a model involving rank alone. Future studies might test such a model on similarly structured species.

Introduction

      Patterns of associations among individuals, social structure, which are constantly changing (Sih *et al.* 2009). Aspects within social structure such as individual experiences, importance of individuals among associations, and indirect connections can have significant effects on social dynamics (Sih *et al.* 2009). Social networks are used to examine the effects that these aspects within social structure have on social dynamics by analyzing connections between individuals within a population (Lewis *et al.* 2012). For example, individuals differ in their importance within the network which causes these individuals to have a larger effect on the group social dynamics (Sih *et al.* 2009). Social network analysis is used to quantify the connections and interactions between individuals in the network (Hobson *et al.* 2013). These connections are constructed by characteristics such as affiliative and agonistic behaviors (Hobson *et al.* 2013). In social network analysis, individuals are represented by nodes, and the connections between individuals are represented by edges, or lines (Wey *et al.* 2007). These edges can be weighted, representing the strength of connections between individuals (Opashi *et al.* 2010). An increase in connections between individuals in the network, results in increased benefits, such as access to resources (Holekamp *et al.* 2012).

      Spotted Hyenas live in large clans and have a complex social structure, which makes them an ideal species for analyzing social networks (Holekamp *et al.* 2012). In Sub-Saharan Africa, spotted hyenas (*Crocuta crocuta*) live in clans consisting of 10-100 individuals (Holekamp *et al.* 2012). Within these clans, females are more aggressive and dominant, both

behaviorally and morphologically, than male spotted hyenas (Holekamp *et al*. 2012). Because females are dominant to males, they control access to resources and mating (Watts *et al.* 2009). Spotted hyenas mate with multiple partners, and females typically have liters of one to two cubs (Watts *et al.* 2009). The cubs are raised and protected in dens for the first 9-14 months, and at 24 months, cubs are considered young adults and are able to breed (Holekamp *et al*. 2012). In the spotted hyena population, clans have a hierarchal structure where rank is determined by maternal kin (Engh *et al.* 2000; East *et al.* 2009; Holekamp *et al*. 2012). Cubs inherit their rank from their mothers, leading to subgroups of descendants of female kin called matrilines (Engh *et al.* 2009; Holekamp *et al.* 2012).

Within the spotted hyena population, individual and matrilineal ranks typically remain constant. All females outrank all males in the clan (Holekamp *et al.* 2012). Cubs of higher-ranking mothers immediately outrank all females of lower rank (Holekamp *et al*. 2012). Once male cubs have reached puberty, 24 months, they voluntarily emigrate to other clans from their birth clan, obtaining the lowest rank as an immigrant male to their new clan (Holekamp & Smale 1998). Although rare, matrilineal ranks can change due to revolutionary coalitions, members of lower ranks forming coalitions to overtake members of higher ranks (Smith *et al.* 2010). Individual ranks change more frequently. For example, if the adult daughter of a higher ranking female overtakes her aging mother (Holekamp *et al.* 2012).

Our study analyzes collected data specific to the female spotted hyena from the Talek Clan in the Masai Mara National Reserve. We focus on adult female spotted hyenas because of their dominant role, and on matrilines because they are considered the most predictable subgroups in hyena clan social structure (Holekamp *et al*., 2012). Data from previous studies of the Talek Clan, suggest that an increase in fitness characterized by reproductive successes is due to matrilineal rank (Holekamp *et al*. 2012). However, rank is clearly not the sole factor influencing fitness, as some low-ranking matrilines persist longer than higher ranked ones (Holekamp *et al.*, 2012). Holekamp *et al.* (2012) suggests this persistence and success may be attributed to chance, or could be affected by particular connectivity traits in the matriline. Using observational data, we quantified matrilineal rank, reproductive fitness, and connectivity among female individuals and among matrilines to show the relationships in the network. We hypothesized that we could predict a matriline's fitness with its social rank and connectivity, and the interaction of these factors, better than social rank or connectivity predicting fitness alone.

Methods
Data Processing
_____We processed interactive, agonistic, and hyena profile data into forms suitable for analysis. To account for and observe the change in the social network over time, we divided the data into annual segments between January 1st and December 31st for the years 1989 - 2009. We

isolated relevant individuals, defined as female residents of the Talek clan who were present in the observations. We included only females because of their dominant role in the spotted hyenas' social structure. Data on males are difficult to process because males remain in the clans for a shorter period of time, matrilineal kinship is impossible to determine for most alien males, and their ranks are less definite and subordinate to the female dominance structure.

In both agonistic and social interactions, only adults were considered. Hyena cubs and young adults do not yet understand their social standing in the clan (Holekamp *et al.* 2012). Therefore they do not behave in a representative way of their social rank in either aggression or friendly interaction. Also, cub interactions are often confined to the den, and do not represent social trends (Holekamp *et al.* 2012). Since the data was separated into years, most hyenas were not adults at all times, and were often observed before they could be considered adults. To resolve this, we assigned every hyena a date indicating when they became an adult, which was the earlier of the date of that hyena's first cub and the hyena's third birthday (Holekamp *et al.* 2012). Aggressive and social interactions were only considered if both members of the observed dyad were adults by the date of the observation.

We defined matrilines with the tabulated profile data that included the name of nearly every hyena's mother. Multi-generational maternal connections were established by checking for individuals whose mother was the mother or daughter of another hyena. Using a function of igraph, an R package, a depth first search was used to find the equivalence relation for the matrix, which found the connected components of the corresponding graph.

Variable Calculations

We calculated social rank yearly from a table of over 45,000 dyadic aggressive interactions, which we treated as dominance displays of superior social rank. A hyena's social rank is shared and expressed by every individual in its matriline, so we treated every matriline as an individual, ignoring agonistic interactions between individuals in the same matriline. We assumed every instance of aggression was the aggressor displaying her matriline's rank to be superior to the recipient's. We found the proportion $P_{i,j}$ of aggressive interactions between matrilines i and j in which matriline i was the aggressor, divided by the total number of aggressive interactions between the two matrilines. From these values, we calculated the David's score of every matriline for every year to determine the rank (David 1987).

We calculated the connectivity between dyads of individuals from nearly 80,000 observations of individuals or groups of individuals over the 21 year span. If two individuals were observed in a group, we counted the interaction in a square matrix of all possible hyena pairs. The diagonal values of this matrix counted the observations of hyenas alone or with hyenas omitted from analysis. The Twice-Weight Association Index for every pair of hyenas was then calculated from these sums and organized into a square matrix of associations for every year (Cairns & Schwager 1987). (twice equation)

Twice-Weight Association Indices were then used to calculate values for each matriline's overall degree of connectivity to the rest of the clan. For every matriline, we added all Twice-Weighted Association Indices for all possible connections that year between individuals in the matriline and individuals outside of the matriline, divided by the total number of possible connections between the individuals in the matriline and individuals in the rest of the clan (external). Similarly, we generated internal connectivity summary values for every matriline in every year, defined for each matriline as the total of all Twice-Weight Association Indices between members in the matriline, divided by the number of possible connections between members in the matriline (internal).

To examine the effects of the social ranks of each of a matriline's connections, we generated an inter-matrilineal connectivity matrix, quantifying the degree of connectivity between each possible pair of matrilines. We defined the social connectedness between two matrilines as the sum of the Twice-Weighted Association Indices between all pairs of observed individuals that year in each matriline divided by the total number of possible connections between all observed individuals that year. These values were organized into a square matrix of inter-matrilineal associations, with diagonal values representing the internal connectivity of each matriline. The square matrix was in turn multiplied by the corresponding vector of matriline ranks, to return a vector whose values represented the sums of a matriline's connections, each weighted by the rank of that connection. (intermatrilineal connectivity)

We calculated yearly matrilineal fitness as the matriline's per capita births (number of births by individuals divided by the number of reproductively viable adults) relative to the clan's overall per capita birth rate that year, to facilitate comparison between matrilines of different sizes and between years with different environmental conditions that may affect birth rate.

Model

To test the hypothesis that fitness can be predicted with rank and social connectedness, we used the lm() function in the R stats package to evaluate a series of linear models for fitness involving the four predictor variables we processed: rank, external connectivity, internal connectivity, and rank-weighted connectivity. Each matriline had a different value for every year, so to evaluate the model overall, we redefined the values over all years, omitting years that we deemed inaccurate. Our matriline determination only considered maternal connections extending as far back as mid-1988, so to guarantee that matrilines were large enough to be substantially more related to one another than they were to individuals whose maternal connections extended earlier than mid-1988, we focused on data after approximately one generation, beginning in 1992. Outside of our analysis, Holekamp & Dloniak (2010) reported a clan split beginning in 2000, so to fairly determine connectivity, we only considered data before that year. We redefined rank over the entire interval 1992-1999, counting all aggressive interactions together to find David's Score rank values for the entire interval. We also summed all yearly connectivity values

(internal and external, respectively) over the interval, and divided by the number of years that the matriline was present (ignoring years in which the matriline was unobserved and thus not representative of its connectivity). For the inter-matrilineal connectivity matrix used to weight rank, we divided the sum over the interval by the number of year that the matriline pair was present. Fitness was averaged over all years.

We first tested linear models of previously reported correlations as null hypotheses. Social rank is known to positively influence fitness in spotted hyenas, and social network theory has repeatedly demonstrated a benefit conferred by increased connectedness to different groups (Holekamp, 2012).To establish the validity of these respective hypotheses, we evaluated how well rank predicted fitness and how well degree of external connectivity predicted fitness. The success of these models, measured by R-squared value, significance of predicted coefficients, and the Aikake information criterion (AIC), was then used for comparison alongside more complicated fitness models involving the summation and interactions of rank, external connectivity, internal connectivity, and rank-weighted connectivity.

Results

Our model was the sum of three terms that related connectivity to rank. These connectivity terms were different and independent. The interaction of external connectivity to rank simply measured the total connectivity of a matriline multiplied by its rank, and the interaction of internal connectivity to rank was evaluated similarly. The connectivity matrix that weighted rank represented a different effect. By multiplying the social rank of a connected matriline by the degree of that connection, and adding these values for every connection that the focal matriline has, we can evaluate the connectivity-weighted effect of *other* matrilines' social ranks on the focal matriline.

Plot 1
Figure #1 represents a linear regression model that attempts to predict matriline fitness from matriline rank. As previously stated, social rank has been shown to play a significant role in determining fitness. The regression model returned a significant coefficient for rank. However, with an R-squared value of 0.58, our model suggests that other factors also contribute to fitness.
Plot 2
Figure #2 represents a linear regression model that attempts to predict matriline fitness from the rank-weighted connectivity matrix, rank-weighted internal connectivity and rank-weighted external connectivity. The positive coefficient for the rank-weighted connectivity matrix, 0.022, indicates that higher connectivity to higher ranks confers a benefit, while higher connectivity to lower ranks decreases fitness. Lower connectivity to either low or high ranks affects fitness to a lesser degree.

While related, the rank-weighted internal and external connectivity parameters provide different information than the rank-weighted connectivity matrix, although the non-matrix parameters are less significant. The positive coefficient for rank-weighted internal connectivity indicates that higher, positive ranking matrilines confer a fitness benefit from having a high internal connectivity. By having a higher internal connectivity, high-ranking matrilines have a stronger defense from revolutionary coalitions of lower ranking matrilines. Also, higher internal connectivity among high-ranking matrilines allows them to control kills and other resources.

Conversely, the negative coefficient of the rank-weighted external connectivity indicates that lower ranking matrilines, specifically those with a rank less than zero, confer greater fitness benefit from a high external connectivity. Because of their low social rank, these matrilines may benefit from increased information exchange, especially because lower ranked individuals are known to hunt farther from the center of the clan territory. Also, as mentioned before, lower ranking matrilines may form multiple-matriline coalitions to challenge higher-ranked matrilines.

The R-squared for this model, 0.834, indicates that rank and connectivity more accurately predicts fitness than rank alone.

Plot 3

Figure #3 represents a linear regression model that attempts to predict matriline fitness from the same parameters as Figure #2, with the addition of rank as a parameter. Although this model has a higher R-squared value, 0.875, and AIC, 0.25, the actual model may not present any additional information. Like Figure #2, the coefficients for the rank-weighted connectivity matrix and rank-weighted internal connectivity are positive, while the rank-weighted external connectivity coefficient is negative. However, the coefficient for rank alone is negative and not significant. Also, this contradicts the results of Figure #1, which positively correlates fitness with rank. Perhaps this regression attributes a negative coefficient to rank in order to balance the fitness benefits from connectivity for the lower ranks.

Discussion

Based on our social network plots, we noticed the clan appeared to be separating in 2003 (figure). After further investigation using dendrograms and clustering plots, it was clear that the split began in 2000 (figure). The split divided individuals within the same matriline. Internal connectivity decreased as certain members of the same matriline stopped associating with one another. In 2004, the connectivity between matrilines increased, but one year later there were distinct groups seen in the network plots. The break in the clan divided individuals into Talek East and Talek West. In the later years only Talek West was observed. The clustering plots and dendrograms support the observations of the Talek clan gradually separating between 1998 and 2001 (Holekamp & Dloniak 2010). However, the social network plots showed the fission at a later date. The continued interactions between Talek East and Talek West in 2003 and 2004 may

have been weather or prey related.

The average temperatures in 2003 were higher than those of previous years. Average precipitation of the two week intervals decreased about an inch from the previous year. The increase in temperature along with the decrease in rainfall may be possible explanations for the low prey count seen in 2004. The total prey count for the year 2004 was half of what was reported in 2003. This prey decrease could explain the interaction of the two clans. Our social network plots only show what individual hyenas were seen together and it is possible that members of different clans were seen together to compete over the available resources. Previous clan splits within the Talek clan were seen to occur when prey availability was very low (Holekamp *et al.* 1993). Holecamp *et al.* (1993) observed the clan split in 1989 not to separate matriline members, but rather complete matrilines would emigrate together. This clan split was caused by human influence as in 1998 part of the clan was poisoned by contaminated food resources (Holekamp & Dloniak, 2010). The individuals who consumed the poisoned food were in the same matriline which could explain why complete matrilines disappeared or moved. After a portion of the clan died, portions of territory were left undefended allowing lower-ranked matrilines to move (Holekamp & Dloniak, 2010). The hyenas that emigrated would have periods of absenteeism from the clan before the final emigration (Holekamp *et al.* 1993). Our results would not allow us to see the absenteeism of certain individuals because we divided the observations into years instead of months. It is quite possible that we do not notice the clan fission in 2000 with just our social network plots because we included the observations of the entire year. If we used monthly intervals, certain individuals may have shown to be leaving the clan in the gradual manner that was observed by Holekamp & Dloniak (2010).

The clan fission observed in the late 1990s was also due to human influence which may explain the unusual division of matrilines. During this time cattle was herded directly through the territory of the Talek clan (Holekamp & Dloniak 2010). Hyenas began to move to territories furthest away from the cattle transit route. Previous to the cattle transit route, communal dens were always located in the same area. In the beginning of 1998 two communal dens were located, one of the east and the west side of the Talek territory (Boydston *et al.* 2003). These two clusters, East and West, began to socialize less and less between 1998 and 2000, by 2001 clan wars were observed (Holekamp & Dloniak 2010). Our social network plots for the early 2000s show connections between the East and West Talek clans which might be from observations documenting clan wars.

Another possible cause of the fission was to reduce the potential of severe aggression within the clan. Spotted hyenas may decide to separate into separate clans to separate themselves from opponents that exert potentially lethal aggression (Smith *et al.* 2008). It would be interesting to have a further investigation done on the rare fission and fusion of clans. Years including and after 2000 were affected by this clan split, rendering our methods of rank,

matriline, and connectivity calculations inaccurate.

The way we calculated rank took into consideration all agonistic behaviors observed. Certain aggressive behaviors may be unrelated to the difference in rank. We are unsure if aggression that was recorded as unprovoked has a greater impact on rank than maternal intervention. Eliminating the aggression between individuals in the same matriline might have also skewed ranks because the aggression may have indicated a matriline separating. A problem we encountered with matrilines that had no adults present were they were given no rank. This may have occurred because the only observed adults in that matriline disappeared and the females that remained in that matriline have not reached adulthood. A matriline consisting of a single cub may still out rank a matriline with older individuals because of the maternal rank inheritance.

Initially, we evaluated rank for all individuals with the Clutton-Brock Index (Clutton-Brock, 1979). This score seemed appropriate because the Clutton-Brock Index treats an instance of aggression as present or absent, as opposed to measuring its proportion of incidence, and hyena ranks are strongly linear, with aggression unlikely to be ever reciprocated by a lower rank. However, hyena ranks are also shared between all members of a matriline, and our calculated ranks varied within each matriline. To reconcile this, we set the highest individual rank in the matriline as the representative rank for the entire matriline. Upon review, this method created a number of inconsistencies, and essentially ignored the aggressive interactions involving the majority of hyenas. We decided to instead calculate David's Score directly for matrilines, by treating every agonistic interaction as a representation of dominant rank by the aggressor's matriline over the recipient's matriline. We found that some matriline ranks remained constant, while others changed, and the new David's Score ranks were more consistent over time, and better correlated with fitness, which seemed to confirm the superiority of our latter method.

Furthermore, the scale of David's Score may be more biologically accurate than Clutton-Brock Index. The Clutton-Brock Index divides instances of aggression by instances of receiving aggression, and therefore varies exponentially between 0 (exclusive) and infinity. David's Score treats wins and losses additively, and therefore varies linearly across negative and positive numbers. In linear models, this attributes opposite but absolutely similar effects to high and low rank, while the Clutton-Brock attributes exponentially large effects for high ranks and very small effects of the same sign for low ranks.

Adolescents initially show aggressive behavior towards individuals of higher and lower ranks equally (Smale *et al.* 1993; Engh *et al.* 2000). However, this interaction will switch where the individuals of higher rank are aggressive to individuals of lower rank. This change between cub and young adult behavior is considered irrelevant in our model. Our model determines the adult age for every hyena because the adult age is determined by when a female first has cubs or reaches 36 months (Holekamp *et al.* 1997; Holekamp *et al.* 2012). Hyenas may have their adult

rank by the age of 24 months (Engh *et al.* 2000). Therefore, it is possible that a hyena who was still considered a young adult outranked another adult hyena but was not shown in our model.

The exclusion of male hyenas should not have skewed our model. Male hyenas are very difficult to work with as most males leave their natal clans (Holekamp *et al.* 1997). The immigrant males would be nearly impossible to count for the maternal data. Immigrant and emigrant males are outranked by all female hyenas (Holekamp *et al.* 2012). The males interacting with the female hyenas should not interfere with ranks being overturned between female hyenas. It would also be difficult to monitor fitness of the males because hyenas are polygynandrous (Szykman *et al.* 2001; Engh *et al.* 2002). Therefore using the number of cubs an individual has to determine fitness would be virtually impossible with males unless genetic testing was used.

A possible bias with using the Twice-Weight Association Index is the lack of distinction between positive and negative interactions. If two hyenas are seen together only a few times in the course of the year, they would have a small Twice-Weight Association. Our model only takes in consideration that the value is small not that the interactions between the hyenas was detrimental to one and positive for another. However, this bias would be very small because observations recorded hyenas together for more than a few minutes and the chances of an interaction being negative the entire time is very rare. In the future, it might be valuable to categorize interactions into positive and negative.

The first few years of data do not include enough maternal data to determine accurate matrilines. We calculated 20 different matrilines, but it is likely that some individuals are related. These matrilines are constant for all years we observed. There is a possibility that a matriline splits after a certain number of generations. Relatedness between individuals in a matriline decreases after three generations, but there is no connection to matriline rank decreasing (Van Horn *et al.* 2004). We assume that the multiple generations in a matriline do not influence rank. Another possibility is that the matrilines should have been divided based on the clan split in 2000. For individuals that were previously in the same matriline but in different clans they would now be considered different matrilines. The previous fission in 1989 showing matrilines emigrating as a group makes it difficult to determine if the matrilines should be divided into two distinct matrilines (Holekamp *et al.* 1993).

Future research

Our data examined change over yearly intervals.
Our model might be biased by certain conditions
Generational cap for matrilines
Use seasonal data intervals instead of yearly intervals?
Can trends in connectivity or aggression predict a clan split years down the line? Or are these

splits too unpredictable? Related to climate/prey?

Appendix / Figures / Descriptions
Social network plots were created using the tkplot function within the igraph package in R (Csardi & Nepusz, 2006). The nodes represent every individual, and change in area proportionally to the rank of that individual's matriline; i.e., the highest rank, 1, has the largest area. Node color was arbitrarily chosen by the rainbow color palette function for each matriline. Edge thickness between nodes was determined by squaring the Twice-Weight Association Index between the individuals represented by the nodes. Multiple edges between individuals were summed, and nodes with no edges were removed. Individuals in the same matriline were grouped together in the same position throughout all years, until the clan noticeably split in 2003.

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