

Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure

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Abstract

In group living animals, the structure of social interactions among group members can have important consequences for individual fitness. Changes in resource abundance can influence social interactions with an expected weakening of social ties during times of resource scarcity. Although human infrastructure and activity often impose a disturbance to animal populations, it can also be a source of reliable resources that are relatively easy to access. We evaluated if the social networks differed among four spotted hyaena clans experiencing contrasting levels of human activity and infrastructure in the Kruger National Park, South Africa. The clan living in an area of high human activity and infrastructure had a less dense social network than the other clans, and the clan living in an area with limited human activity and infrastructure had shorter path lengths than the other clans, suggesting that it had more closely associated individuals. Our results did not support substantial differences among clans in the relative social network positions of animals from different age and rank classes. Contrary to our expectations, we suggest that anthropogenic resources may have weakened the social cohesiveness within spotted hyaena clans. We also argue that our study supports previous suggestions that there may be individual variation within broader classes of rank, age and sex in the position of individual animals in social networks.

Key words: social interactions, social network, graph theory, large carnivore, Carnivora, anthropogenic, sociality

Introduction

In carnivores, group living entails both costs and benefits to individuals, and the evolution of group living is predominantly associated with a need to defend a territory and associated resources, as well as the ability to cooperatively hunt larger prey (Creel & Macdonald, 1995; Gittleman, 1989; Macdonald, 1983; but see Dalerum, 2007 for an alternative view). Many group living carnivores rely on complex social interactions among group members to maintain the cohesiveness of the social group. Social interactions among group members can therefore be critically important for the survival and fitness of many group living species, including carnivores (Alexander, 1974). Social network analysis provides a powerful tool for quantifying social interactions (reviewed by Croft, James & Krause, 2007). The analyses of interaction networks have for instance been used to identify key individuals in social groups (Lusseau, 2003), the resilience of social groups to external perturbations (Flack, Krakauer & de Waal, 2005), and the effects of social interactions on disease transmission (Weber et al., 2013.).

Resource abundance can influence several aspects of sociality in mammals. For instance, patchy resources combined with individual variation in movement patterns associated to such resources can influence both the density of social networks and the bond strength within them (Spiegel, Leu, Bull & Sih 2017), the availability of food resources can influence social group sizes (Newsome, Ballard, Dickman, Fleming, van de Ven et al., 2013), and limitations in critical resources can affect intra-group competition and subsequent aggressive encounters (Banks, Piggott, Stow & Taylor, 2007). Strong social bonds can, however, lead to increased tolerance for group members at patchy resources, although social bonds may not always be strong enough to overcome competition (Marshall, Carter, Ashford, Rowcliffe & Cowlshaw, 2015). Consequently, social ties have been observed to be weakened both during periods of low (Holekamp, Smith, Strelhoff, Van Horn & Watts, 2012) and high resource abundance (Henzi, Lusseau, Weingrill, van Schaik & Barrett, 2009). Hence, despite a clear importance of resource abundance and distribution on the structure of social interactions within animal groups (e.g., Ansmann, Parra, Chilvers & Lanyon 2016; Firth & Sheldon 2015), the direction of such effects may not be uniform.

While human population growth is classically associated with carnivore population declines (Woodroffe, 2000), some carnivore species successfully utilise anthropogenic resources. Such utilisation has been associated with changes in diet, demography, life history traits, space use and social behaviour (e.g., Beckmann & Berger, 2003a,b; Belton, Cameron & Dalerum, 2016; Contesse, Heggin, Gloor, Bontadina & Deplazes Contesse, 2004; Prange, Gehrt & Wiggers, 2003). Many species that frequently seem to utilise anthropogenic resources live in social groups (e.g., banded mongoose *Mungos mungo*: Flint, Hawley & Alexander, 2016; coyotes: Fedriani, Fuller & Sauvajot, 2001; spotted hyaenas: Kolowski & Holekamp, 2008). Anthropogenic resources alter both resource distribution and abundance within a landscape. However, the extent to which anthropogenic resources can influence the social interactions of group living species remains relatively poorly understood (however see Firth & Sheldon 2015 for an experimental approach), and studies of wild carnivores have so far have been limited to interactions linked to localized anthropogenic resources such as food associated with garbage dumps (Flint et al., 2016).

The spotted hyaena (*Crocuta crocuta*) is a large hyaenid that live in social groups known as clans (Kruuk, 1972). The clan is dominated by a female matriarch and a strict linear rank hierarchy is followed by other females in the clan and their sub-adult offspring (Frank, 1986). Young adult males disperse between the ages of two and six (Holekamp & Dloniak, 2010). Immigrant males follow a linear rank hierarchy which typically is based on tenure. This hierarchy is below all females and their offspring (East & Hofer, 2001). The spotted hyaena has often been reported to exploit anthropogenic food sources (Kolowski & Holekamp, 2008; Yirga et al., 2015). However, although both diet (Yirga et al., 2012) and space use (Kolowski & Holekamp, 2008; Belton et al., 2016) have been associated with access to anthropogenic resources, the influence of anthropogenic

resources on social interactions within hyaena clans has so far received limited attention. This is unfortunate, since the pattern of social interactions is a central component of spotted hyaena biology, and previous studies have shown that patterns of social interactions can be influenced by both external factors such as resource abundance (Holekamp et al., 2012) as well as the structures of social interactions themselves (Ilany, Booms & Holekamp 2015).

In this study we quantified the social networks of four spotted hyaena clans with contrasting levels of human activity and infrastructure inside the Kruger National Park in South Africa, and quantified the relative roles of individuals of different sex, age and rank classes within these social networks. We expected that contrasts in human activity and infrastructure would lead to a variation in resource distribution and abundance, either directly through anthropogenic food (e.g., garbage, Flint et al. 2016) but also indirectly in the form of modified habitat that could be favourable for hunting (Belton et al., 2016). While we appreciate that human activity can influence animal behaviour both by altering resource abundance and by acting as a disturbance, activity patterns of visitors and staff within the KNP are strictly controlled and there is no legal persecution. We therefore argue that the level of disturbance is minimal, and that most effects of humans likely are caused by altering resource abundance, at least for a large carnivore such as the spotted hyaena.

Holekamp et al. (2012) suggested that increased competition during periods of low resource abundance may have weakened the social bonds within a spotted hyaena clan in Kenya. Anthropogenic resources are often easily accessible and can supplement native prey, and there is limited variation in the amount of native prey among the clans in our study (Belton, 2017). We therefore expected a positive association between human activity and infrastructure and resource abundance for the respective clans. We subsequently predicted that hyaena clans in areas with more dense infrastructure and more human activity would show more group cohesiveness caused by a decreased level of resource competition. We expected this effect on group cohesiveness to be manifested in more dense and complex social networks, with stronger associations among individuals. In addition, the ability to procure food is highly dependent on sex, age and rank in spotted hyaenas (Frank, 1986). Hence, we also expected that the effect of human activity and infrastructure would differ among animals with different sex, age and rank. We expected stronger effects of human activity and infrastructure for males, young animals and animals of low social rank, since young animals have previously been observed to be the predominant users of anthropogenic resources in the Kruger National Park (Belton, 2017), and sex, age and rank are all directly related to access to- or the ability to procure food (e.g., Frank, 1986; Tanner, Zelditch, Lundrigan, B.L. & Holekamp 2010).

Methods

Study area

This study took place in a 5000 km² southern portion of KNP (Fig. 1). Vegetation in the study area is characterised by woodland with basalt soils dominated by *Clerocarya caffra* and *Acacia nigrescens*, with *Combretum* species on granite soils (Ogutu & Owen-Smith, 2003). Rainfall is seasonal with the majority falling between October and March, with a peak in January and February (Venter, Scholes & Eckhardt, 2003). Average annual rainfall is approximately 650 mm for the Southern section (Venter & Gertenbach, 1986). For this study we defined the months October – March as wet season and April – September as dry season. Mean monthly temperatures range from 7 to 32°C (Venter & Gertenbach, 1986). KNP hosts a diverse array of herbivorous and carnivorous mammals. Prey available for hyaenas in the Southern section of the park include, along with small mammals; impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*), imbabala bushbuck (*Tragelaphus sylvaticus*), nyala (*Nyala angasii*), common reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and Cape buffalo (*Syncerus caffer*). Other megaherbivores

such as African elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and giraffe (*Giraffa camelopardalis*) are also available, but are presumably only used by hyaenas as carrion. Impala in particular constitutes a large part of the hyaena diet in KNP (Henschel & Skinner, 1990; Belton, 2017). Four large carnivores live in sympatry with hyaenas in KNP; African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*).

Study population

We collected data between May 2007 and December 2009 on the four clans, during which time each experienced different levels of human activity (Table 1). Part of the data collection was done concurrently among clans (see below). The clans were distributed within the south western section of the KNP, and had non-overlapping home ranges (Fig. 1a). Clans were frequently visited for behavioural observations (at least weekly), and also opportunistically encountered at other times (see below). We did not use radio collars to re-locate the hyaenas. All individuals in each clan were individually recognisable by their unique coat spot patterns, and each time a clan was observed we counted all present clan members. Based on these records, we calculated monthly values for clan size as well as sex, age and rank ratios. If an animal was not seen during a month but was subsequently observed in later months it was added retrospectively to the tally. Mean clan sizes (mean \pm sd) were 10 (\pm 1.67) for Doispans (DP), 18.67 (\pm 1.37) for Afsaal (AF), 24.56 (\pm 4.10) for Kruger Gate (KG) and for Skukuza (SK) 25.1 (\pm 1.10), Sex ratios (Male:Female, DP = 1 : 1.22, AF = 1 : 1.29, KG = 1 : 0.87, SK = 1 : 1.16) and age ratios (Adult : Young adult : SA, DP = 1 : 0.20 : 0.8, AF = 1 : 0.70 : 1.70, KG = 1 : 0.48 : 1.16, SK = 1 : 1.39 : 1.49) for the clans were similar.

The Doispans clan denned in a remote area. The shortest route between the den areas and the closest camp site was 27.5 km away on dirt roads and the main gate was 14.5 km away. Phabeni gate, a smaller gate with limited use was situated 18.8 km from the clan. The Doispans clan therefore experienced substantially less human disturbance than the other clans. The Afsaal clan frequently denned by the side of the road within (500m) of the Afsaal picnic site. The Afsaal picnic site consists of a shop, a cafeteria and a picnic area, all of which are unfenced, with an adjoining fenced residence typically housing four to five staff. There was also associated fenced living quarters for staff. We observed tourist deliberately feed this clan. The Kruger Gate clan resided in an area that received high levels of activity during daylight hours but with a lower amount of infrastructure such as roads, houses and tourist installations compared to the Skukuza clan. The clan denned by the main road midway between Skukuza camp site and Paul Kruger Gate, a main entrance to the park that is situated 12 km from the Skukuza. The home range of the Skukuza clan encompassed the Skukuza camp site and associated staff village (Belton et al., 2016). Skukuza is the largest camp site in KNP and hosts up to 300 visitors. It is also the administrative hub for the whole of KNP with a large staff village. Hyaenas in the Skukuza clan had free access to the unfenced staff village consisting of 250 houses, an enclosed staff compound, a golf course, a shop, communal areas, and administrative buildings beside an enclosed area with tourist accommodation. The staff area combined with the camp site covers 4.3km² and houses approximately 2300 staff (Foxcroft, Richardson & Wilson, 2008). The combined area of these two structures creates the largest area of human modified habitat in the park. Vegetation is homogeneous throughout this southern section of the Kruger National Park (Rutherford et al., 2006), as are prey densities (Seydack et al., 2012). Therefore, one of the main differences between the areas where these clans resided are likely related to the variation in human activity and infrastructure (Belton et al., 2016).

In addition to our prior knowledge regarding the facilities associated with the home ranges of each clan, we used two other types of quantified data to provide a robust ranking among clans in terms of the amount of human activity they experienced, and the amount of infrastructure their home ranges possessed. We used the amount of roadside litter as a proxy for the relative amount of human

activity in the areas surrounding each clan, and road density as an index of human infrastructure. We argue that human activity and infrastructure likely influence several dimensions of spotted hyaena resource distribution and availability, and that these influences may be both direct and indirect (e.g., Belton et al., 2016). However, a robust ranking among clans would still facilitate interpretations of our results. We recorded litter and road density in circular areas of two sizes, one of 30km² and one of 50km², surrounding the spatial centroid of all sites that were used for observations of each clan (Fig 1b). These sizes approximate the annual home ranges observed for two of these clans during the study period (33.7 km² for the Skukuza clan and 50.5 km² for the Doispane clan, Belton et al., 2016). We recorded roadside litter during the 2010 wet season, when we counted all litter within one metre of the edges of the road while driving sections of the roads to look for spotted hyaena scats (Belton, 2017). Road densities were calculated from official park maps, and roadside litter were calculated as part of a concurrent study. We stress that this information was used to enable an informed ranking of the different clans in terms of their human exposure. This ranking was used to interpret the results from our social network analyses. However, we have not directly included these data as predictors in our analyses since it would necessitate strong and in our mind unsupported assumptions behind the mechanistic effects of how humans may have altered the social structure within and among the observed spotted hyaena clans.

Behavioural observations

Interaction data were collected during visits to den sites, at known carcass locations and during opportunistic encounters with clan members (Fig 1b). Although we appreciate that these observation locations may have provided contrasting social contexts, nearly 90% of the observations were made at den sites (100% in the Doispane clan, 89% in the Afsaal clan, 83% in the Kruger Gate clan and 94% in the Skukuza clan), and social relationships can carry over across different contexts (Firth & Sheldon, 2016). To maximize the number of pairwise interactions, we therefore utilized observations from all our locations. While animals may spend different amounts of time at the dens, any biases will have been similar across clans and hence will not have influenced our comparisons in relation to human activity. The frequency of den site visits varied over the course of the study. Newly identified clans were visited nightly, but visits of individual clans could be as little as weekly depending on other demands of the project. We typically recorded behavioural observations at dawn and dusk. At dusk, animals would often stay for a few hours, before leaving to utilise their home range. In the morning adults would congregate at the den site for a few hours and then leave to go and rest elsewhere. Subadults were often out of the den even when adult animals were not present. For logistic reasons we only conducted behavioural observations when the clans were utilising a den by a road. Monitoring of active den sites was focussed around dawn and dusk. To attempt to capture data on the arrival and departure of each individual, observations began 2 hours before sunrise or sunset. Observations ended when all adults had left the den. Observation hours varied depending on the presence of animals at the den site. Sessions lasted between one and 4 hours (Doispane: 01:15 ± 00:54; Afsaal: 02:31 ± 01:21; Kruger Gate: 01:16 ± 00:45; Skukuza: 01:50 ± 01:27). The clans were observed over the following periods; Doispane clan (31 visits): 09/04/2008 – 26/07/2008, Kruger Gate clan (17 visits): 18/03/2008 – 23/12/2008, Afsaal clan (32 visits): 17/07/2009 – 29/11/2009, Skukuza clan (41 visits): 06/04/2009 – 06/10/2009. We recorded behaviour for a total of 38 hours at the Doispane clan, for 40 hours at the Afsaal clan, for 40 hours at the Kruger gate clan and for 73 hours at the Skukuza clan.

We recorded all pair-wise interactions between clan members during each observation period (Altmann, 1974; Holekamp & Smale, 1991). In each interaction the initiator and receiver of the interaction were recorded, if possible, although we have only used this information for assessment of social rank. Interactions included approaches, genital greeting, muzzle greeting and play. We used aggressive and subordinate behaviour to determine dominance between individuals, in combination with genital greetings (Kruuk, 1972; Mills, 1990; East, Hofer & Wickler, 1993; Smith et al., 2011). Aggressive interactions included chasing, lunging, biting or snapping and were further

confirmed by submissive and defensive behaviours such as carpal crawl, moving away, giggling and bared teeth from the receiver. A genital greeting consists of two animals standing side to side, nose to tail, and asymmetries in this greeting point to a dominant and subordinate relationship between the animals (Kruuk, 1972). Each animal sniffs at the other's genitals and leg lifting can occur. Although Smith et al. (2011) found weaker relationships between the direction of genital greetings and rank than earlier studies, we have included it in our general assessment of rank since it appear to be a consistent indicator of rank in most cases (Glickman et al., 1997). A muzzle greeting was defined as two animals coming together and sniffing each others muzzle area. This behaviour was often observed when a female that was lying down and nursing was approached by another adult.

Age and sex classification

Each individual was sexed based on the shape of the phallic glans (Frank, Glickman & Powch, 1990), and categorised into one of three age classes; sub-adults (0-24 months), young adult (25-48 months) and adult (> 48 months). We based age class determinations on pelage and size for animals with unknown birth dates at the start of the study, the definition of spots on the coat, and length of coat. Age classification was confirmed retrospectively by frequently taking photos of all young animals and comparing them to animals of known age. If an animal switched between two age classes within a season, we used the age class it inhabited for the majority of time within that season. Adult males needed to be observed at a den site at least once during the study period to be considered as part of the clan. Males that did not meet this criterion were regarded as transient and excluded from analysis.

Determination of dominance hierarchies

Individuals within spotted hyaena clans live in distinct social dominance hierarchies. We used the outcomes of pair-wise interactions to assign the social rank of each individual. Since there is no clear dominance asymmetry in a muzzle greeting, we did not use this behaviour to determine rank relations. Similarly, we excluded all play behaviour from rank calculations. In this study we used a broad classification of social rank relations and classed each animal as 'alpha', 'high', 'low', or 'immigrant'. Following Kolowski and Holekamp (2008) females and natal males were classed as high or low ranked. However, because of the central position of the alpha female in hyaena social structure (Frank, 1986), we added a separate dominance class for alpha females as well. We assigned all adult males to a separate immigrant class which we regarded to be subordinate to females. We used information from previous studies to assist with assigning ranks due to sparse data for some individuals. Since a female's cubs hold the rank below their mother with all previous offspring following sequentially behind the most recent (Holekamp & Smale, 1991), we could assign some ranks based on the rank of the mother. Conversely, following Frank (1986), we used interactions between offspring to infer maternal dominance in cases when data between mothers were missing. Individuals with unknown maternity were included in the hierarchy following the results of interactions with other group members. Immigrants were defined as adult and young adult males that were frequently subordinate to subadult and adult group members. Because the hierarchy among immigrant males is based on tenure (East & Hofer, 2001), new immigrant males that joined the clans during the study were added consecutively to the bottom of the hierarchy. We defined all individuals in the lower 50% of relative rank orders of nonimmigrant individuals as low ranked, and all other nonimmigrant individuals except the alpha females as high ranked. The exception was Kruger Gate clan, where a number of young adult males of unknown maternity were dominant over the immigrant males and were assigned to the lower rank.

Quantification of interaction structures

We used social networks to quantify properties of the social networks of the four spotted hyaena clans, since they offer a powerful framework for testing the structure of social organisation and social interactions between animals (Krause, Lusseau & James, 2009). A mathematical graph

consists of nodes (or vertices) which are connected by links (edges). In animal social networks, the nodes usually represent individual animals and links some form of social association among these animals. Networks are built from interaction matrices, which can either be symmetric, in cases when the directions of the social interactions are not known or not of interest, or asymmetric, in which case the directions of the interactions are known.

Based on our observations of social interactions described above, we created one weighted symmetric interaction matrix for each clan to represent the network of social interactions (Newman, Watts & Strogatz, 2002). We based these matrices on the total number of interactions within each pair of group members. We have visualized the interaction matrices using mathematical graphs. Due to overly sparse matrices we could not create networks for each season. There are many metrics and indices available to quantify the structure of interactions in such social networks (e.g. Wey et al., 2008). In this study, we used four weighted indices to quantify the properties of the social networks of each clan; density, bond strength, path length and clustering coefficient. Except for density (see below), we used a modified version of the simple ratio index (*SRI'*) as weights for each cell within the interaction matrices (Cairns & Swager 1987). We calculated the index as $SRI' = X / (Y_A + Y_B - X)$, where X is all the interactions between individuals A and B , Y_A is all interactions observed for individual A and Y_B is all interactions observed for individual B . Hence, in this form the *SRI'* gives the probability that A and B has interacted with each other given that we observed an interaction including either A or B . Density quantifies the ratio of the number of observed edges to the number of theoretically possible edges. High density scores indicate that a large number of the possible interactions are realised (Wasserman & Faust, 1994), and subsequently that many of the individuals in the group are interacting with each other. Conversely a low density score suggests fewer individuals interact within a social group (e.g., Madden, Drewe, Pearce & Clutton-Brock, 2009). We used a weighted density index calculated as the sum of all observed interactions divided by the total number of possible links (Darst, Reichman, Ronhovde & Nussinov, 2013). Hence, this interaction density is not directly informed by the network structure, but rather from the frequency of interactions. Since the strength of social bonds may be influential for social dynamics (Granovetter, 1973), we also used the average *SRI'* value per link as a measure of bond strength. Path length quantifies average length between all pairs of individuals in the group, quantified as number of social partners that are necessary to connect the two focal individuals, and hence describes the level of separation among individuals within a social group (Wey et al., 2008). High path length scores indicate that some group members only interact very indirectly with others, and it is therefore a measure of group cohesiveness. For instance, a high path length score in a hyaena clan could be caused by a limited amount of interactions between immigrant males and lower ranking females and dominant animals (Frank, 1986). We used a weighted path length that included the *SRI'* values of each dyad as edge weights. The global clustering coefficient of a network describes the tendency of nodes within a network to cluster together (Wasserman & Faust 1994). It is based on the propensity of a network to form triads, and quantifies the probability that the adjacent nodes of a node are connected (Luce & Perry, 1949). In a social context, the clustering coefficient provides an evaluation of how a group of individuals divide themselves into sub-groups. Here, we used the weighted global clustering coefficient suggested by Opsahl & Panzarasa (2009) to quantify the clustering coefficient for the social network of each hyaena clan.

We used ego-based equivalents of our four indices to relate the position and importance of each individual in the four social networks to its sex, age and rank. Node degree quantifies the number of incoming and outgoing interactions for each node. In a social context, the node degree represents the number of interactions that an animal has been involved in. High node degree scores suggest that a certain individual may be driving the network structure. We used node strength as a measure of node degree, in which we summarized the *SRI'* values for all links to a given node (Barrat,

Barthelemy, Pastor-Satorras & Vespignani Barrat, 2004), and average bond strength (i.e. the average *SRI*' value per link) to quantify the relative strength in the social bonds among individuals. Path length describes the shortest paths between any given sets of nodes within a network, and therefore explains the social distance of a given animal to its group members. We used the weighted average path length calculated using Dijkstra's algorithm (Dijkstra, 1959). The local clustering coefficient of an individual node quantifies the probability that it is connected to its adjacent nodes, and is calculated as the ratio of the triangles connected to a node and the triples that are centered on this node. High local clustering scores indicate a high amount of cliquiness, i.e. that the interaction partners of an animal are also interacting more frequently among themselves than with others. We used the weighted local clustering coefficient proposed by Barrat et al. (2004) to quantify the clustering around each specific node.

Statistical analyses

Network size can influence several network metrics (e.g., Albert and Barabási 2002). Since our observed clan sizes were correlated with the relative rank of human activity and infrastructure, we compared if the social network of each clan differed from expectations based on randomly generated networks of the same size as each observed clan. Following Manly (2006), we also used deviations from these random expectations, e.g., *D*-values, to compare global network metrics across clans (see below). We created 1000 permuted matrices for each clan, in which we kept the network size (i.e. clan size) and both the total number of links (i.e. degree distribution) and the link weights) as in the respective original matrix, but we randomly shuffled links and among pairs of group members and weights among the new links (Erdős and Rényi, 1959, see Bejder, Flechter & Brager, 1998 for implementations in animal social networks). We selected this null model since it provides an intuitive framework to evaluate topology against, while avoid making unnecessarily speculative assumptions regarding link distributions. For each of these 1000 permutations we calculated both the path length and the global clustering coefficient, and compared the observed values to the expected ones based on the permuted matrices using *z* score transformations. We did not conduct evaluations against random expectations for density and bond strength because our chosen null model would have been identical to our observed matrix. We similarly compared the values of individual metrics to those of the random expectations. For these individual comparisons, neither node strength nor bond strength is trivial, since the values may have shifted within the matrix).

We expected that human activity and infrastructure would lead to increased resource availability and hence lower intra group resource competition, and subsequently more dense and complex social networks (e.g., Holekamp et al., 2012). This would be manifested in a positive association between human activity and infrastructure and all of our global metrics except path length, i.e. we would expect clans in areas of high levels of human activity and infrastructure to have higher density, bond strength and clustering values, but lower path lengths. As a heuristic way of comparing the four observed networks in terms of bond strength, path length and the global clustering coefficient while controlling for network size, we calculated *D*-values as the deviations between the observed values and each of the 1000 values from the permuted matrices (Manly, 2006). We used these *D*-values as the response variable in one-way permutation based ANOVAs to evaluate the effect of clan on the deviation in observed path lengths from random expectations. We used pair-wise permutation tests to compare the *D*-values among clans. In these pair-wise comparisons, we adjusted the *p*-values for multiple hypotheses testing using the false discovery method (Benjamini & Hochberg, 1995). We used permutation based techniques since the sample size of our data was determined by the number of randomized matrices we created, and our analyses violates assumptions of independence associated with more commonly used statistical methods (e.g., linear models, Croft et al. 2011).

We also expected that the effect of human activity and infrastructure on node based social metrics would differ among animals with different sex, age and rank, due to differences in the ability to procure food. We expected a higher increase in node strength, bond strength and local clustering coefficients, but a lower increase in local path length among clans for males, young animals and animals of low social rank. To evaluate these expected differences we similarly created D-values for each individual for all four metrics by extracting its observed values from each of the 1000 random permutations. We evaluated if the clans differed in the relative differences among age and rank classes using a distance based permutation based manova (Anderson 2001), with the D-values as response variables and clan, age, sex and the two way interactions between clan and age and clan and sex as predictors. We evaluated these effects separately for females and males, and constructed one model for each metric and sex. Three animals in the Kruger Gate clan shifted age class from subadult to young adult during the observation period. For each of these animals, we used the age class at the median point of the observation period as the age class in the analyses. No other animal shifted age group and no animal shifted rank class during the observations. We did not include higher-order interactions since the social structure of spotted hyaena clans do not allow for fully resolved high-order interactions among our classes of sex, age and rank. For instance, there are per definition no immigrant females, nor are there any adult males of high or low rank. We note that our quantification of social rank was based on a subset of the interactions included in the social interaction matrices. However, although this may have caused a certain level of inter-dependence, we have included rank in the analyses since it is an important characteristic of individuals within spotted hyaena clans (Frank, 1986).

Statistical analyses were carried out using the software environment R version 3.3.0 for Linux (<http://www.r-project.org>). Network quantification and randomizations were conducted using functions in the user contributed packages *igraph* (Csárdi & Nepusz, 2006) and *tnet* (Opsahl, 2009). Permutation based tests were carried out using functions in the package *lmPerm* (Wheeler, 2010) and *Vegan* (Oksanen et al., 2013).

Ethical note

This study was observational and did not require any manipulation or handling of animals. Care was taken to not disturb the animals when being observed. We have, however, included observations on two spotted hyaenas that were fitted with radio collars for a concurrent study (Belton et al., 2016). The captures required to fit and remove these collars were conducted by South African National Parks Board's wildlife veterinarians, and the use of these radio collars for research purposes was approved by the University of Pretoria Animal Use and Care Committee (protocol number EC010-07) and the Kruger National Park Animal Use and Care Committee. All research was carried out under a research permit from the South African National Parks Board for the project "Impact of human habitation on population dynamics of spotted hyaenas".

RESULTS

The Skukuza clan resided in the area with the highest amount of recorded litter and with the highest road density, the Kruger Gate clan resided in an area of high amount of litter but lower road density, and both Afsaal and Doispane clans resided in areas of low road densities and with limited amounts of recorded litter (Table 1, Fig. 1b). These broad indices of infrastructure and activities coincide with our observations of other types of human activity and infrastructure within the park.

All of the four social networks were sparse (Fig. 2). We observed the highest interaction densities in the Doispane and Afsaal clans and the lowest in the Skukuza clan, and the Doispane clan also had higher bond strength than the other clans (Table 1). There were significant differences among the clans in terms of the deviation from random expectations in path length ($F_{3,3996} = 17640$, $p < 0.01$), with the Afsaal, Kruger gate and Skukuza clans having longer path lengths than random

expectations (Table 1). Similarly, there were significant differences among the clans in terms of deviations from random expectations in cluster coefficients ($F_{3,3996} = 2244$, $p < 0.01$), with all clans having higher clustering coefficients than random expectations (Table 1). The deviation between the observed and expected path length was lower for Doispane than all other clans (Afsaal, $Z = -43.17$, $p_{\text{adj}} < 0.01$; Kruger Gate, $Z = -42.59$; Skukuza, $Z = -43.06$, $p_{\text{adj}} < 0.01$) and higher for the Skukuza clan than all the other clans (Afsaal, $Z = 11.09$, $p_{\text{adj}} < 0.01$; Kruger gate, $Z = 41.92$, $p_{\text{adj}} < 0.01$). The Afsaal clan had higher deviation between the observed and expected path length than the Kruger gate clan ($Z = 42.59$, $p_{\text{adj}} < 0.01$). The deviation between the observed and expected clustering coefficient was higher for Afsaal than for all other clans (Doispane, $Z = 33.68$, $p_{\text{adj}} < 0.01$; Kruger Gate, $Z = 40.59$; Skukuza, $Z = 23.83$, $p_{\text{adj}} < 0.01$;) and lower for the Kruger gate clan than all the other clans (Doispane, $Z = -7.31$, $p_{\text{adj}} < 0.01$; Skukuza, $Z = -37.38$, $p_{\text{adj}} < 0.01$). The Skukuza clan had higher deviation between the observed and expected path length than the Doispane clan ($Z = 25.92$, $p_{\text{adj}} < 0.01$).

There were no significant interaction effects of clan and deviations from random expectations of any of the individual metrics for females (Table S1), although there were a trend for an interaction effect of clan and rank on female node strength ($F_{6,28} = 1.56$, $p = 0.08$, Fig 2a). There was a significant interaction effect of clan and age for the deviation in node strength for males ($F_{6,24} = 1.72$, $p = 0.03$, Fig 2e), and a trend for a significant interaction effect of clan and rank on male bond strength ($F_{6,24} = 1.72$, $p = 0.03$, Fig. 2f) There were no main effects of clan, age, or rank for any of the metrics for either females or males (Table S1). Instead, there were large individual variation in the deviation from random expectations in all observed metrics (Tables S2-S5). The alpha female in the Afsaal clan had higher bond strength, and a higher clustering coefficient than random expectations, but longer path length, and the alpha females in both the kruger Gate and the Skukuza clans similarly had higher deviation bond strength than random expectations (Tables S2-S5, Fig 3b-d).

DISCUSSION

The four clans differed in their overall network properties, and all clans generally differed in cohesiveness compared to randomly generated networks. While it is expected that the interaction patterns among individuals of a highly social species will differ from random interaction structures (Wey et al., 2008), we suggest that at least parts of the differences among clans could have been caused by the experienced differences in human activity and its associated resources. The clans that experienced the highest human activity had less dense social networks than the other clans, indicating that animals in this clan were interacting less with group members. Conversely, we observed the opposite for path length where the clan with the least amount of human activity and infrastructure had shorter path lengths. Although our observations with regards to node strength could have been caused by sample bias or group size effects, we suggest that these combined results imply that anthropogenic activity, and possibly associated resources, may have weakened the social bonds within the observed spotted hyaena clans. We note that such an interpretation would contradict previous observations of spotted hyaenas that suggest stronger social bonds when food supply is high (Holekamp et al., 2012), but agree with suggestions that chacma baboons (*Papio hamadryas ursinus*) experience a weakening of social bonds in periods of high food abundance (Henzi et al., 2009).

We found limited differences among clans in respect to the relative roles of individuals of different age, rank and sex. These observations suggests that while human activity may have influenced the overall cohesiveness of the observed clans, it did not influence the relative strength of interactions among group members of different sex, age and rank categories. Social interactions have been related to a broad array of factors, such as relatedness to interaction partner (Wiszniewski et al., 2010; Chiyo et al., 2011; Carter, Seddon, Frère, Carter & Goldizen, 2013, although relatedness may

not always determine social interactions, see Arnberg, Shizuka, Chaine & Lyon, 2015), similarity of interaction partner in terms of age, sex and rank (i.e. homophily, McPherson, Smith-Lovin & Cook, 2001), and familiarity with interaction partner (Kurvers et al., 2013). Previous observations suggest that both kinship and age are strong determinants of interaction strength within spotted hyaena clans, and that kinship related effects on social bonds are robust against fluctuations in resource abundance (Holekamp et al., 2012). Our observations support these findings, and further highlight that the relative association patterns among group members within hyaena clans may be resilient to external perturbations.

Our observations suggest that there were not necessarily stronger differences among clans in the effects of rank and age for females than for males on their roles in the social networks. Across all clans, we also found relatively limited consistent differences among sex, age and classes, and we did not find that the alpha females had more central and connected roles in the respective networks of all the groups. While our observations agree with those made by Holekamp et al. (2012) in that alpha females are not necessarily the most connected individuals, our study contradicts their findings in that we found no consistent effects of sex or age. This is somewhat surprising, since both sex, age and rank are important factors in the spotted hyaena social structure. For instance, males show much lower levels of aggression than females (Frank, 1986), and younger animals tend to have stronger social ties compared to old animals (Holekamp et al., 2012). Instead, our data may support a strong individual variation in social connectivity (e.g., Blumstein, Petelle & Wey, 2013). However, we acknowledge that the rank based observations at least partly could have been a methodological artefact, since we estimated social rank from a sub-set of the same behavioural observations that were included in the social interaction matrices.

We recognise some methodological shortcomings of our study. First, it is based on a very low sample size, with only four clans included in the analyses. Hence, it stands as largely descriptive and our data may not be suitable for strong biological inferences. However, many studies on social networks within animal societies rely on observations of single groups (e.g., spider monkeys *Ateles geoffroyi*: Ramos-Fernandés, Boyer, Aureli & Vick, 2009, chacma baboons: Henzi et al., 2009, spotted hyaenas: Holekamp et al., 2012, but see Royle, Pike, Heeb, Richner & Kölliker, 2012 for an exception). Therefore, we have very limited information of variation among social groups in the network properties even in the most well studied species. Second, seasonality plays an important role in resource availability in African savannas (Pereira, Owen-Smith & Moleón, 2013), and can influence the social networks of spotted hyaenas (Holekamp et al., 2012). Although our data were pooled across both seasons it did not contain any bias in terms of seasonality in the observations among the four groups. We therefore argue that than any seasonal influences on social interactions likely did not strongly affect our group comparisons. Such an argument is further supported by observations on birds, which have shown that dyadic interactions may be stable across seasons (Shizuka et al., 2014; Firth & Sheldon, 2016). Finally, we collected most of our interaction data at or close to active den sites. Social associations may be strongly context dependent (Kurvers et al., 2013), and there may also have been a bias in terms of the amount of time different classes of animals were present at the dens. However, although we can not rule out that other interaction structures may be observed at other locations, both observational (Firth & Sheldon, 2016) and experimental data (Firth & Sheldon, 2015) suggest that social interactions may carry over across different contexts. In addition, any bias in the attendance of different classes of animals likely was similar among clans. Hence, by maintaining a consistent sampling protocol among the different clans, we argue that any potential biases caused by sampling at den sites, both in terms of context dependence and attendance, likely were consistent among clans and hence did not substantially influence our comparisons.

To conclude, our observations suggested that the spotted hyaena clan in an area of high amounts of human activity and infrastructure had a less dense social network than clans with less human

activity and infrastructure, and that the spotted hyaena clan in an area with the least amount of human activity and infrastructure had the most closely associated individuals. However, we did not find strong differences among clans in the relative roles of individuals of contrasting sex, age and rank classes. We stress that these results were obtained using only four clans, and hence that our observations may not be suited for drawing strong biological inferences. We argue that further research is required to evaluate the influences of human activity and anthropogenic resources on the social dynamics of animal societies, both inside and outside protected areas. Such influences could have important ramifications for both effective environmental resource management as well as an improved understanding of how external factors influence animal social interactions.

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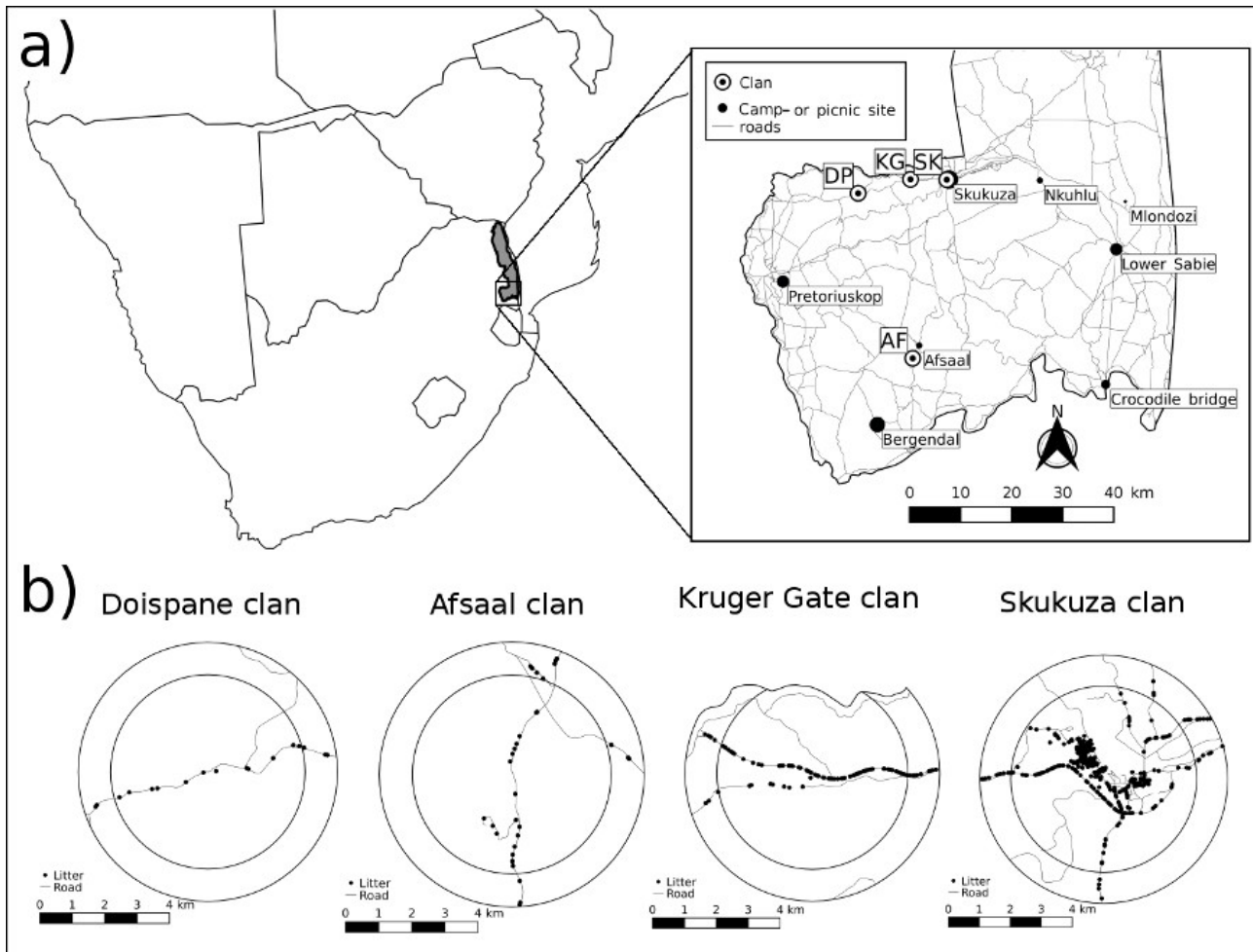


Figure 1: Location of of the Kruger National Park in Southern Africa and the locations of four spotted hyaena clans living in areas with contrasting amount of human activity and infrastructure (a), as well as 30km² and 50km² circular areas around the observation points of each clan including roads and observed pieces of litter (b). The Doispane clan (DP) lived in an area with very limited human influence, the Afsaal (AF) and Kruger gate (KG) clans lived in areas of intermediate amounts of human infrastructure and activity, and the Skukuza (SK) clan lived close to the largest village complex within the Kruger National Park, Skukuza. The camp- and picnic sites are coded by their relative size.

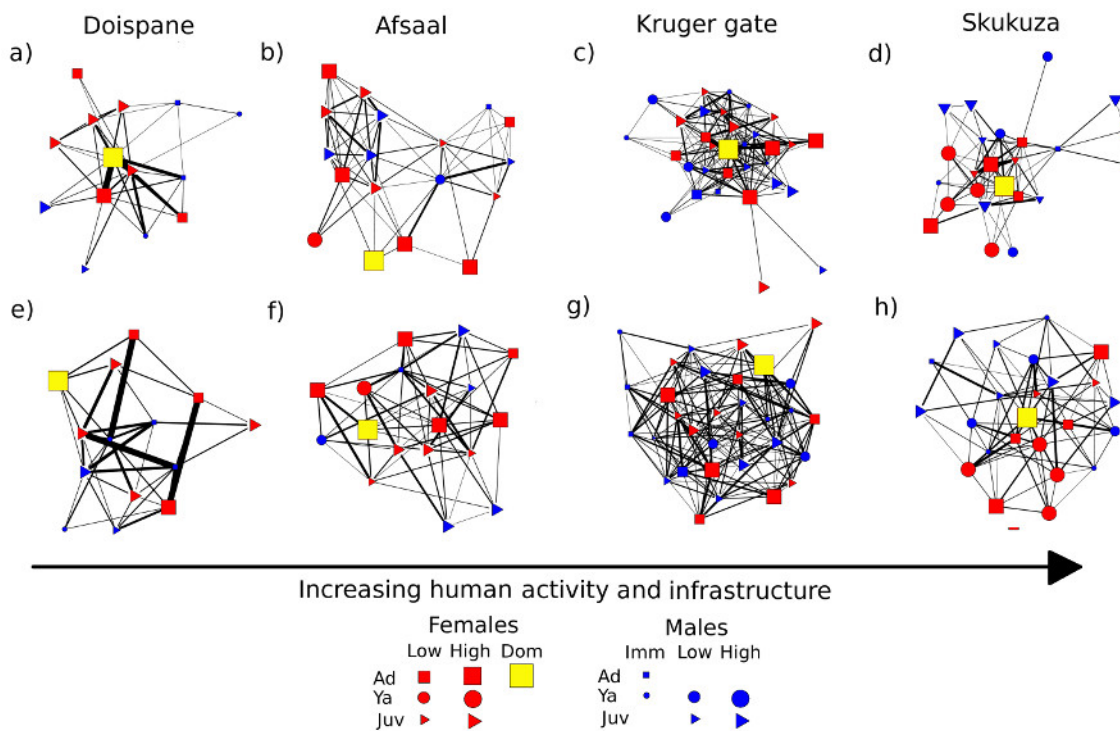


Figure 2. Observed (a-d) and random (e-h) social networks of four spotted hyaena clans living in areas with contrasting amount of human activity and infrastructure in the Kruger National Park. The Doispane clan lived in an area with very limited human influence, the Afsaal and Kruger gate clans lived in areas of intermediate amounts of human activity and infrastructure, and the Skukuza clan lived close to the largest village complex within the Kruger National Park. Edges are weighted by the simple ratio index, i.e., the ratio of the number of interactions between two animals to the total the total number of times the two animals were observed in any interactions.

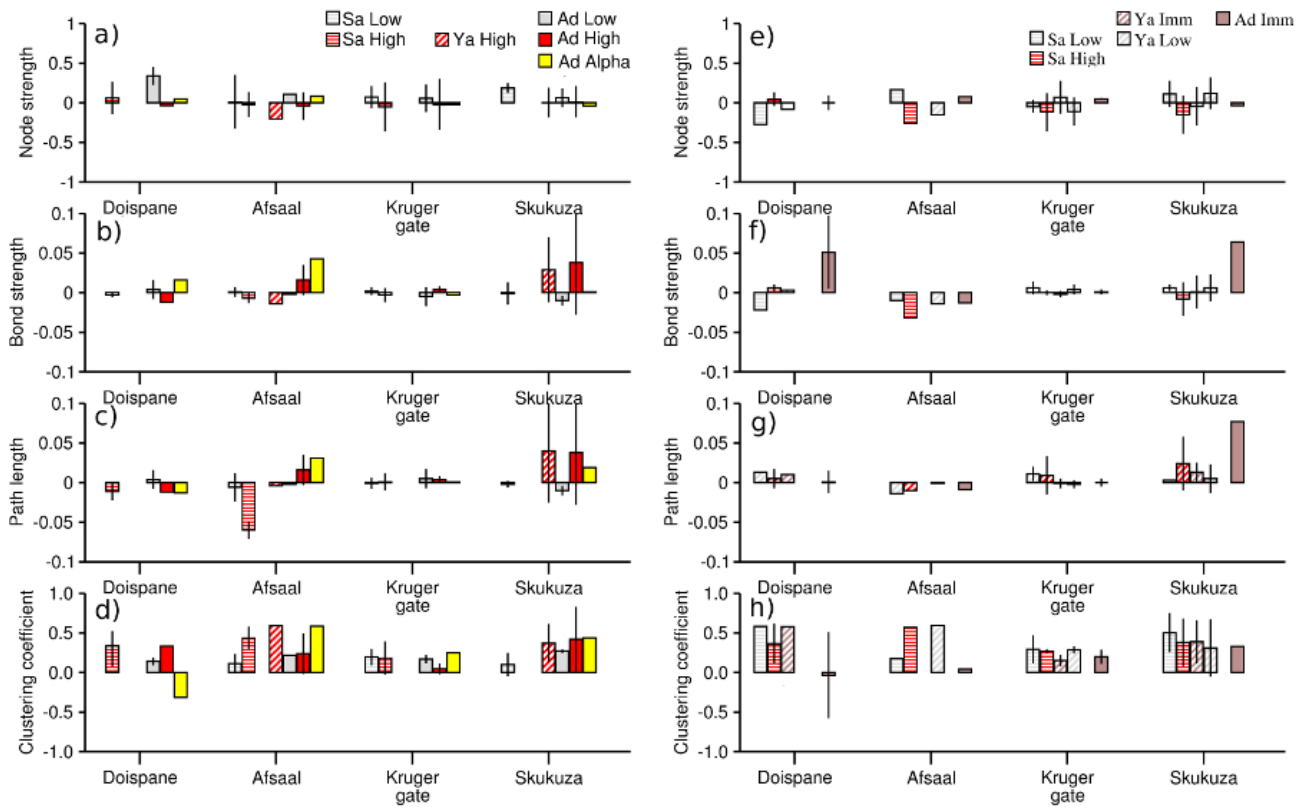


Figure 3. Average (\pm sd) deviations (D-values) from the observed value of each individual and 1000 random permutations of links and link weights for node strength (i.e. weighted node degree) (a,e), bond strength (b,f), average path length (c,g) and clustering coefficient (d,h) for female (a-d) and male (g-h) spotted hyaenas of different age (Sa – subadult, Ya – young adult, Ad – adult) and rank (Imm – immigrant, Low, and High) classes in four clans living in areas with contrasting amount of human infrastructure and activity in the Kruger National Park. The Doispaine clan lived in an area with very limited human influence, the Kruger Gate and Afsaal clans lived in areas of intermediate amounts of human infrastructure and activity, and the Skukuza clan lived close to the largest village complex within the Kruger National Park. The indices were based interaction matrices built from behavioural observations.

Table 1: Estimated and measured levels of human activity and infrastructure (i.e., roads, buildings and tourist installations) of four hyaena clans in the Kruger National Park, as well as observed interaction density and bond strength, and the deviation (D-values) in path length and the global clustering coefficient from random expectations for the social networks of these clans. Road and litter density were estimated within circular areas of 30km² and 50km² surrounding the spatial coordinate of the observation locations. The sizes of these areas approximately correspond to the annual home ranges recorded for two of the clans (Doispane 50.5km²; Skukuza 33.7 km²).

Clan	Human activity and infrastructure						Interaction density	Bond strength	Path length			Clustering coefficient		
	Human activity		Road density ¹		Litter density ²				D-value ³	Z	P	D-value ³	Z	P
			30km ²	50km ²	30km ²	50km ²								
Doispane	Low	Low	0.31	0.29	1.85	2.07	0.43	0.07 ± 0.06	-0.04 ± 0.03 (-0.09 – 0) ⁴	-1.31	0.10	0.16 ± 0.06 (0.04 – 0.39)	2.96	<0.01
Afsaal	Low	Intermediate	0.41	0.36	1.67	1.86	0.41	0.07 ± 0.04	0.13 ± 0.02 (0.10 – 0.17) ⁴	8.23	<0.01	0.27 ± 0.04 (0.18 – 0.39)	7.75	<0.01
Kruger Gate	High	Intermediate	0.68	0.66	8.53	7.66	0.34	0.04 ± 0.03	0.05 ± 0.01 (0.04 – 0.06) ⁴	8.09	<0.01	0.15 ± 0.02 (0.10 – 0.23)	8.58	<0.01
Skukuza	High	High	1.90	1.35	9.51	9.17	0.29	0.06 ± 0.04	0.14 ± 0.02 (0.10 – 0.18) ⁴	6.49	<0.01	0.23 ± 0.03 (0.17 – 0.37)	7.24	<0.01

¹ Km of road / km²

² Number of pieces of litter / km of road

³ Mean ± sd

⁴ 95% range

Supplementary material 1

Table S1

Results from permutation based ANOVAs evaluating the differences among clans in the effects of age and rank class among female and male spotted hyaenas on node strength, bond strength, path length and clustering coefficient.

Term	Node strength			Bond strength			Path length			Clustering coefficient		
	F	df	p	F	df	p	F	df	p	F	df	p
<u>Females</u>												
Clan	0.96	3,28	0.443	0.75	3,28	0.759	1.35	3,28	0.211	1.23	3,27	0.267
Age	2.16	2,28	0.059	1.19	2,28	0.237	1.43	2,28	0.208	1.46	2,27	0.209
Rank	1.39	2,28	0.192	1.24	2,28	0.233	0.73	2,28	0.558	1.11	2,27	0.333
Clan x age	1.19	4,28	0.264	1.01	4,28	0.414	1.02	4,28	0.421	0.44	4,27	0.933
Clan x rank	1.56	6,28	0.083	1.10	6,28	0.317	0.73	6,28	0.736	0.90	6,27	0.563
<u>Males</u>												
Clan	1.11	3,24	0.343	1.62	3,24	0.151	4.12	3,24	0.022	1.37	3,22	0.264
Age	1.36	2,24	0.220	1.03	2,24	0.363	0.67	2,24	0.550	1.14	2,22	0.320
Rank	0.70	2,24	0.628	1.63	2,24	0.185	0.57	2,24	0.620	0.37	2,22	0.795
Clan x age	1.72	4,24	0.036	1.13	4,24	0.353	0.58	4,24	0.652	1.52	4,22	0.199
Clan x rank	0.64	6,24	0.859	2.13	6,24	0.073	1.21	6,24	0.289	0.97	6,22	0.449

Table S2

Observed values of node strength, bond strength, path length and clustering coefficients, as well as mean \pm sd of the deviation from 1000 randomly permuted interaction matrices (d-values) and associated z tests for each animal in the Afsaal spotted hyaena clan.

Age	Rank	Sex	Node strength					Bond strength					Path length					Clustering coefficient				
			obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p
ad	alpha	f	0.554	0.083	0.165	0.506	0.613	0.111	0.043	0.016	2.665	0.008	0.102	0.031	0.013	2.397	0.017	1.000	0.586	0.134	4.361	0.000
ad	hi	f	0.606	0.130	0.163	0.799	0.424	0.055	-0.013	0.015	-0.819	0.413	0.053	-0.017	0.013	-1.325	0.185	0.555	0.141	0.131	1.077	0.281
ad	hi	f	0.282	-0.189	0.170	-1.109	0.268	0.094	0.026	0.017	1.548	0.122	0.105	0.034	0.013	2.654	0.008	0.407	-0.011	0.137	-0.079	0.937
ad	hi	f	0.563	0.087	0.166	0.524	0.600	0.094	0.027	0.015	1.722	0.085	0.102	0.031	0.013	2.466	0.014	0.650	0.234	0.125	1.871	0.061
ad	hi	f	0.270	-0.197	0.169	-1.163	0.245	0.090	0.023	0.017	1.368	0.171	0.111	0.040	0.013	3.015	0.003	1.000	0.595	0.135	4.420	0.000
ad	low	f	0.577	0.107	0.171	0.629	0.529	0.064	-0.002	0.016	-0.148	0.882	0.059	-0.011	0.013	-0.855	0.393	0.630	0.217	0.137	1.587	0.112
sa	hi	f	0.266	-0.205	0.165	-1.241	0.215	0.053	-0.014	0.017	-0.839	0.401	0.066	-0.005	0.013	-0.358	0.720	1.000	0.595	0.131	4.545	0.000
sa	hi	f	0.555	0.084	0.173	0.488	0.626	0.062	-0.005	0.017	-0.322	0.747	0.053	-0.017	0.014	-1.233	0.218	0.801	0.399	0.131	3.040	0.002
sa	hi	f	0.524	0.053	0.174	0.304	0.761	0.065	-0.002	0.017	-0.139	0.889	0.075	0.004	0.013	0.272	0.786	0.734	0.315	0.137	2.289	0.022
sa	low	f	0.728	0.253	0.168	1.504	0.133	0.073	0.005	0.016	0.325	0.745	0.051	-0.019	0.012	-1.560	0.119	0.436	0.025	0.123	0.200	0.841
sa	low	f	0.257	-0.227	0.167	-1.359	0.174	0.064	-0.004	0.017	-0.254	0.800	0.078	0.007	0.013	0.564	0.573	0.608	0.196	0.133	1.473	0.141
ya	hi	f	0.266	-0.204	0.164	-1.240	0.215	0.053	-0.014	0.016	-0.883	0.377	0.066	-0.004	0.013	-0.345	0.730	1.000	0.593	0.132	4.505	0.000
ad	imm	m	0.556	0.075	0.172	0.433	0.665	0.056	-0.013	0.017	-0.769	0.442	0.063	-0.009	0.013	-0.646	0.518	0.451	0.043	0.131	0.332	0.740
sa	hi	m	0.428	-0.053	0.168	-0.317	0.751	0.071	0.003	0.017	0.151	0.880	0.068	-0.003	0.013	-0.245	0.806	0.486	0.082	0.126	0.650	0.516
sa	hi	m	0.545	0.076	0.172	0.440	0.660	0.078	0.010	0.016	0.626	0.531	0.089	0.018	0.013	1.402	0.161	0.968	0.550	0.139	3.951	0.000
sa	hi	m	0.586	0.113	0.168	0.672	0.501	0.073	0.006	0.016	0.404	0.687	0.069	-0.001	0.013	-0.085	0.932	0.874	0.463	0.138	3.364	0.001
sa	low	m	0.639	0.165	0.168	0.978	0.328	0.058	-0.010	0.017	-0.597	0.551	0.057	-0.014	0.013	-1.080	0.280	0.585	0.177	0.137	1.289	0.197
ya	low	m	0.319	-0.151	0.173	-0.874	0.382	0.053	-0.014	0.017	-0.850	0.395	0.069	-0.001	0.013	-0.099	0.921	1.000	0.594	0.128	4.645	0.000

Table S3

Observed values of node strength, bond strength, path length and clustering coefficients, as well as mean \pm sd of the deviation from 1000 randomly permuted interaction matrices (d-values) and associated z tests for each animal in the Doispans spotted hyaena clan.

Age	Rank	Sex	Node strength					Bond strength					Path length					Clustering coefficient				
			obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p
ad	alpha	f	0.413	0.048	0.170	0.283	0.777	0.083	0.016	0.025	0.634	0.526	0.050	-0.013	0.017	-0.797	0.425	0.106	-0.314	0.190	-1.649	0.099
ad	hi	f	0.336	-0.037	0.166	-0.226	0.821	0.056	-0.012	0.024	-0.516	0.606	0.050	-0.013	0.016	-0.861	0.389	0.753	0.333	0.196	1.700	0.089
ad	low	f	0.786	0.421	0.166	2.539	0.011	0.079	0.012	0.024	0.479	0.632	0.047	-0.016	0.014	-1.146	0.252	0.601	0.176	0.183	0.965	0.335
ad	low	f	0.623	0.259	0.169	1.537	0.124	0.062	-0.005	0.025	-0.200	0.841	0.057	-0.007	0.017	-0.409	0.683	0.533	0.107	0.186	0.574	0.566
sa	hi	f	0.397	0.030	0.161	0.188	0.851	0.066	-0.001	0.024	-0.061	0.951	0.057	-0.006	0.016	-0.416	0.677	0.763	0.342	0.183	1.865	0.062
sa	hi	f	0.264	-0.097	0.165	-0.587	0.557	0.066	-0.001	0.026	-0.047	0.963	0.066	0.001	0.018	0.080	0.936	1.000	0.580	0.188	3.092	0.002
sa	hi	f	0.331	-0.044	0.169	-0.259	0.796	0.066	-0.001	0.023	-0.057	0.954	0.046	-0.016	0.014	-1.163	0.245	0.876	0.453	0.179	2.538	0.011
sa	hi	f	0.718	0.357	0.168	2.133	0.033	0.060	-0.007	0.025	-0.293	0.770	0.041	-0.023	0.015	-1.473	0.141	0.399	-0.024	0.191	-0.125	0.900
ad	imm	m	0.424	0.066	0.158	0.418	0.676	0.085	0.018	0.024	0.757	0.449	0.075	0.011	0.015	0.782	0.434	0.764	0.350	0.181	1.934	0.053
ad	imm	m	0.301	-0.066	0.167	-0.396	0.692	0.150	0.083	0.024	3.410	0.001	0.055	-0.009	0.015	-0.566	0.571	0.000	-0.420	0.188	-2.236	0.025
sa	hi	m	0.103	-0.261	0.166	-1.573	0.116	0.034	-0.032	0.024	-1.348	0.178	0.053	-0.010	0.016	-0.631	0.528	1.000	0.570	0.188	3.030	0.002
sa	low	m	0.095	-0.275	0.168	-1.639	0.101	0.047	-0.022	0.026	-0.830	0.407	0.078	0.013	0.020	0.663	0.507	1.000	0.584	0.191	3.057	0.002
ya	imm	m	0.278	-0.083	0.163	-0.509	0.611	0.070	0.003	0.023	0.132	0.895	0.074	0.010	0.014	0.725	0.468	1.000	0.578	0.185	3.127	0.002

Table S4

Observed values of node strength, bond strength, path length and clustering coefficients, as well as mean \pm sd of the deviation from 1000 randomly permuted interaction matrices (d-values) and associated z tests for each animal in the Kruger Gate spotted hyaena clan.

Age	Rank	Sex	Node strength					Bond strength					Path length					Clustering coefficient				
			obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p
ad	alpha	f	0.409	-0.020	0.134	-0.152	0.880	0.037	-0.003	0.008	-0.362	0.718	0.040	0.001	0.005	0.230	0.818	0.587	0.248	0.074	3.348	0.001
ad	hi	f	0.043	-0.388	0.132	-2.946	0.003	0.043	0.003	0.008	0.346	0.729	0.075	0.036	0.006	6.459	0.000					
ad	hi	f	0.653	0.223	0.131	1.698	0.090	0.041	0.000	0.008	0.061	0.951	0.033	-0.005	0.005	-1.017	0.309	0.348	0.001	0.080	0.019	0.985
ad	hi	f	0.526	0.096	0.135	0.711	0.477	0.048	0.008	0.008	0.917	0.359	0.040	0.002	0.005	0.354	0.723	0.436	0.094	0.082	1.155	0.248
ad	low	f	0.628	0.203	0.131	1.554	0.120	0.035	-0.005	0.008	-0.658	0.511	0.031	-0.008	0.005	-1.510	0.131	0.458	0.117	0.079	1.495	0.135
ad	low	f	0.295	-0.133	0.133	-0.994	0.320	0.042	0.002	0.008	0.307	0.759	0.039	0.001	0.005	0.139	0.890	0.518	0.172	0.078	2.196	0.028
ad	low	f	0.528	0.101	0.131	0.767	0.443	0.059	0.019	0.008	2.232	0.026	0.044	0.005	0.006	0.937	0.349	0.563	0.220	0.082	2.672	0.008
sa	hi	f	0.233	-0.205	0.133	-1.538	0.124	0.047	0.006	0.008	0.800	0.424	0.051	0.012	0.005	2.376	0.018	0.438	0.094	0.079	1.186	0.236
sa	hi	f	0.184	-0.251	0.129	-1.952	0.051	0.037	-0.004	0.008	-0.467	0.641	0.040	0.001	0.005	0.230	0.818	0.767	0.423	0.076	5.571	0.000
sa	hi	f	0.742	0.304	0.133	2.281	0.023	0.029	-0.012	0.008	-1.463	0.144	0.028	-0.010	0.005	-1.900	0.057	0.376	0.034	0.077	0.437	0.662
sa	low	f	0.574	0.151	0.128	1.177	0.239	0.048	0.008	0.008	0.934	0.350	0.040	0.001	0.006	0.152	0.879	0.534	0.188	0.075	2.520	0.012
sa	low	f	0.269	-0.158	0.133	-1.184	0.236	0.045	0.005	0.008	0.593	0.553	0.049	0.011	0.005	2.063	0.039	0.644	0.298	0.084	3.566	0.000
sa	low	f	0.470	0.036	0.133	0.268	0.789	0.043	0.003	0.008	0.314	0.753	0.036	-0.003	0.005	-0.479	0.632	0.633	0.288	0.078	3.706	0.000
sa	low	f	0.593	0.165	0.134	1.229	0.219	0.035	-0.005	0.008	-0.677	0.499	0.032	-0.007	0.005	-1.361	0.174	0.386	0.046	0.077	0.589	0.556
sa	low	f	0.602	0.168	0.136	1.238	0.216	0.040	0.000	0.008	0.010	0.992	0.033	-0.005	0.005	-1.054	0.292	0.501	0.155	0.079	1.967	0.049
ad	imm	m	0.466	0.034	0.131	0.259	0.795	0.039	-0.002	0.008	-0.188	0.851	0.031	-0.007	0.005	-1.433	0.152	0.449	0.103	0.078	1.331	0.183
ad	imm	m	0.486	0.053	0.138	0.381	0.703	0.044	0.004	0.008	0.458	0.647	0.040	0.001	0.005	0.243	0.808	0.619	0.277	0.074	3.750	<0.001
ad	imm	m	0.482	0.055	0.136	0.402	0.688	0.040	0.000	0.008	-0.020	0.984	0.032	-0.007	0.005	-1.260	0.208	0.562	0.218	0.076	2.863	0.004
sa	hi	m	0.403	-0.025	0.134	-0.186	0.852	0.040	0.000	0.008	0.030	0.976	0.035	-0.003	0.006	-0.576	0.565	0.629	0.287	0.076	3.786	<0.001
sa	hi	m	0.043	-0.390	0.133	-2.926	0.003	0.043	0.003	0.008	0.328	0.743	0.075	0.037	0.005	6.973	0.000					
sa	hi	m	0.485	0.056	0.140	0.400	0.689	0.037	-0.003	0.008	-0.360	0.719	0.033	-0.006	0.005	-1.145	0.252	0.599	0.252	0.079	3.168	0.002
sa	low	m	0.341	-0.088	0.133	-0.661	0.508	0.034	-0.006	0.008	-0.712	0.477	0.041	0.003	0.005	0.553	0.581	0.553	0.211	0.075	2.803	0.005
sa	low	m	0.407	-0.028	0.134	-0.206	0.837	0.051	0.011	0.008	1.326	0.185	0.047	0.008	0.005	1.688	0.091	0.581	0.237	0.072	3.286	0.001
sa	low	m	0.295	-0.129	0.134	-0.964	0.335	0.049	0.009	0.008	1.145	0.252	0.062	0.023	0.006	4.114	0.000	0.897	0.551	0.084	6.593	<0.001
sa	low	m	0.482	0.054	0.129	0.415	0.678	0.048	0.008	0.008	0.922	0.357	0.049	0.010	0.005	1.891	0.059	0.518	0.172	0.078	2.203	0.028
ya	imm	m	0.205	-0.223	0.130	-1.713	0.087	0.041	0.001	0.008	0.062	0.950	0.047	0.008	0.006	1.391	0.164	0.489	0.148	0.078	1.888	0.059
ya	imm	m	0.497	0.074	0.138	0.539	0.590	0.033	-0.006	0.008	-0.795	0.426	0.035	-0.004	0.005	-0.753	0.452	0.546	0.197	0.078	2.519	0.012
ya	imm	m	0.665	0.239	0.134	1.782	0.075	0.035	-0.005	0.008	-0.633	0.527	0.035	-0.004	0.005	-0.709	0.478	0.403	0.056	0.082	0.682	0.496
ya	imm	m	0.607	0.186	0.132	1.409	0.159	0.043	0.003	0.008	0.427	0.669	0.034	-0.004	0.005	-0.840	0.401	0.551	0.207	0.080	2.598	0.009
ya	low	m	0.440	0.014	0.134	0.102	0.919	0.040	0.000	0.008	0.004	0.997	0.034	-0.005	0.005	-0.968	0.333	0.598	0.255	0.079	3.227	0.001
ya	low	m	0.194	-0.238	0.127	-1.879	0.060	0.048	0.008	0.008	1.010	0.313	0.041	0.002	0.005	0.432	0.665	0.667	0.320	0.077	4.149	<0.001

Table S5

Observed values of node strength, bond strength, path length and clustering coefficients, as well as mean \pm sd of the deviation from 1000 randomly permuted interaction matrices (d-values) and associated z tests for each animal in the Skukuza spotted hyaena clan.

Age	Rank	Sex	Node strength					Bond strength					Path length					Clustering coefficient				
			obs	d.mean	d.sd	z	p	obs	d.mean	d.sd	z	p	obs	n	d.sd	z	p	obs	d.mean	d.sd	z	p
ad	alpha	f	0.381	-0.041	0.178	-0.230	0.818	0.063	0.001	0.017	0.066	0.947	0.090	0.019	0.013	1.506	0.132	0.732	0.437	0.134	3.250	0.001
ad	hi	f	0.293	-0.128	0.177	-0.727	0.467	0.146	0.084	0.017	4.887	0.000	0.205	0.134	0.012	10.740	0.000	1.000	0.708	0.139	5.107	<0.001
ad	hi	f	0.582	0.153	0.170	0.898	0.369	0.053	-0.009	0.016	-0.570	0.569	0.064	-0.006	0.012	-0.500	0.617	0.422	0.133	0.129	1.034	0.301
ad	low	f	0.395	-0.019	0.168	-0.113	0.910	0.056	-0.006	0.018	-0.320	0.749	0.069	-0.002	0.014	-0.172	0.863	0.580	0.286	0.142	2.016	0.044
ad	low	f	0.572	0.149	0.167	0.892	0.372	0.048	-0.014	0.016	-0.888	0.375	0.060	-0.010	0.012	-0.804	0.421	0.547	0.255	0.143	1.778	0.075
sa	low	f	0.648	0.227	0.174	1.303	0.193	0.072	0.009	0.018	0.508	0.611	0.066	-0.005	0.015	-0.317	0.751	0.287	-0.002	0.137	-0.015	0.988
sa	low	f	0.564	0.142	0.171	0.830	0.406	0.051	-0.011	0.017	-0.643	0.520	0.071	0.001	0.013	0.096	0.923	0.497	0.205	0.136	1.507	0.132
ya	hi	f	0.341	-0.072	0.170	-0.421	0.674	0.085	0.024	0.017	1.367	0.172	0.079	0.009	0.013	0.647	0.518	0.589	0.293	0.144	2.028	0.043
ya	hi	f	0.293	-0.124	0.170	-0.729	0.466	0.146	0.084	0.017	4.966	0.000	0.205	0.134	0.013	9.911	0.000	1.000	0.712	0.137	5.206	<0.001
ya	hi	f	0.702	0.280	0.171	1.642	0.101	0.047	-0.015	0.017	-0.880	0.379	0.059	-0.011	0.013	-0.807	0.420	0.442	0.149	0.131	1.140	0.254
ya	hi	f	0.338	-0.080	0.171	-0.466	0.641	0.085	0.022	0.018	1.275	0.202	0.097	0.026	0.015	1.747	0.081	0.618	0.330	0.145	2.280	0.023
ad	imm	m	0.381	-0.037	0.167	-0.221	0.825	0.127	0.064	0.018	3.653	0.000	0.148	0.077	0.014	5.720	0.000	0.625	0.329	0.142	2.310	0.021
sa	hi	m	0.077	-0.342	0.175	-1.956	0.051	0.077	0.015	0.017	0.864	0.388	0.145	0.075	0.014	5.384	0.000					
sa	hi	m	0.515	0.088	0.172	0.513	0.608	0.051	-0.011	0.017	-0.634	0.526	0.077	0.006	0.013	0.493	0.622	0.625	0.329	0.136	2.414	0.016
sa	hi	m	0.437	0.017	0.168	0.103	0.918	0.062	0.000	0.017	-0.011	0.991	0.080	0.009	0.013	0.665	0.506	0.405	0.109	0.141	0.770	0.441
sa	hi	m	0.056	-0.368	0.173	-2.131	0.033	0.028	-0.035	0.017	-2.035	0.042	0.078	0.007	0.013	0.558	0.577	1.000	0.705	0.140	5.028	<0.001
sa	low	m	0.419	-0.005	0.168	-0.032	0.974	0.070	0.008	0.017	0.470	0.638	0.073	0.003	0.012	0.236	0.814	0.970	0.678	0.130	5.221	<0.001
sa	low	m	0.645	0.228	0.171	1.335	0.182	0.065	0.003	0.016	0.181	0.857	0.072	0.002	0.013	0.159	0.873	0.621	0.329	0.136	2.413	0.016
ya	imm	m	0.155	-0.270	0.169	-1.596	0.111	0.052	-0.012	0.018	-0.659	0.510	0.089	0.018	0.013	1.413	0.158	1.000	0.703	0.143	4.912	<0.001
ya	imm	m	0.351	-0.075	0.166	-0.452	0.651	0.088	0.025	0.016	1.537	0.124	0.092	0.021	0.013	1.646	0.100	0.521	0.210	0.138	1.523	0.128
ya	imm	m	0.631	0.211	0.170	1.237	0.216	0.053	-0.011	0.017	-0.610	0.542	0.070	-0.001	0.015	-0.059	0.953	0.543	0.254	0.136	1.864	0.062
ya	low	m	0.408	-0.021	0.174	-0.119	0.905	0.082	0.018	0.017	1.036	0.300	0.089	0.017	0.013	1.296	0.195	0.856	0.562	0.136	4.134	<0.001
ya	low	m	0.684	0.260	0.170	1.529	0.126	0.057	-0.006	0.018	-0.340	0.734	0.063	-0.008	0.014	-0.583	0.560	0.353	0.055	0.140	0.391	0.696