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INVITED REVIEW

Society, demography and genetic structure in the spotted hyena

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Abstract

Spotted hyenas (Crocuta crocuta) are large mammalian carnivores, but their societies, called 'clans', resemble those of such cercopithecine primates as baboons and macaques with respect to their size, hierarchical structure, and frequency of social interaction among both kin and unrelated group-mates. However, in contrast to cercopithecine primates, spotted hyenas regularly hunt antelope and compete with group-mates for access to kills, which are extremely rich food sources, but also rare and ephemeral. This unique occurrence of baboon-like sociality among top-level predators has favoured the evolution of many unusual traits in this species. We briefly review the relevant socio-ecology of spotted hyenas, document great demographic variation but little variation in social structure across the species' range, and describe the long-term fitness consequences of rank-related variation in resource access among clan-mates. We then summarize patterns of genetic relatedness within and between clans, including some from a population that had recently gone through a population bottleneck, and consider the roles of sexually dimorphic dispersal and female mate choice in the generation of these patterns. Finally, we apply social network theory under varying regimes of resource availability to analyse the effects of kinship on the stability of social relationships among members of one large hyena clan in Kenya. Although social bonds among both kin and non-kin are weakest when resource competition is most intense, hyenas sustain strong social relationships with kin year-round, despite constraints imposed by resource limitation. Our analyses suggest that selection might act on both individuals and matrilineal kin groups within clans containing multiple matrilines.

Keywords: dispersal, dominance, genetic diversity, kinship, population bottleneck, sex ratio, social network

Introduction

Long-term, individual-based studies of free-living animals offer uniquely rich opportunities for documenting

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the kinship structure of populations, assessing effects of particular phenotypic traits on fitness, and identifying causes of individual variation in reproductive success (Altmann & Altmann 2003; Clutton-Brock & Sheldon 2010). Longitudinal field studies with known pedigrees that span multiple generations have now provided countless insights into important ecological and

evolutionary processes in natural populations (e.g. Clutton-Brock 1988; Schwartz *et al.* 1998; Kruuk *et al.* 2000; Altmann & Altmann 2003; Wroblewski *et al.* 2009). In combination with recent advances in molecular techniques, these enduring research programs continue to shed considerable new light on relationships among sociality, demography and genetic structure in animal populations across multiple ecological time scales.

Long-term field study of the spotted hyena (*Crocuta crocuta*) offers particularly interesting opportunities for elucidating relationships among sociality, demography and genetic structure in an unusually gregarious mammalian carnivore. These large predators live in societies that are far larger and more complex than those of any other mammalian carnivore (Drea & Frank 2003; Holekamp *et al.* 2007). With respect to their size, composition and structure, spotted hyena groups, called 'clans', more closely resemble the social groups of cercopithecine primates than those of other carnivores. Specifically, the size, composition and organizational structure of spotted hyena clans are remarkably like those of troops of baboons, macaques or vervet monkeys (Holekamp *et al.* 2007). As in troops of these primates, priority of access to resources in any particular hyena clan is determined by an individual's social rank. Furthermore, as in a cercopithecine primate troop, a hyena clan may contain several different matrilineal kin groups spanning multiple generations concurrently. Thus hyena clans contain many unrelated individuals as well as close kin, and it is with this genetically diverse group of clan-mates that spotted hyenas must contend in both competitive and cooperative interactions (Van Horn *et al.* 2004a; Smith *et al.* 2010). Like savannah baboons (*Papio cynocephalus*, e.g. Alberts 1999; Buchan *et al.* 2003), spotted hyenas can discriminate both maternal and paternal kin from unrelated clan-mates, and they direct nepotistic behaviour toward both types of kin (Kruuk 1972; Holekamp *et al.* 1997a; Van Horn *et al.* 2004b; Wahaj *et al.* 2004). However, in contrast to baboons or other cercopithecine primates, spotted hyenas are top predators that regularly hunt antelope, and compete with group-mates for access to ungulate carcasses when kills are made.

Fresh carcasses represent extremely rich food sources, but they are also rare and ephemeral, occurring unpredictably in space and time. Therefore, competition at kills is often very intense within clans (Frank 1986; Holekamp *et al.* 1993), even among closely-related animals (Wahaj *et al.* 2004). On the other hand, spotted hyenas routinely form coalitions with their kin to defend carcasses from unrelated conspecifics (e.g. Engh *et al.* 2005; Smith *et al.* 2010), and they also routinely join forces with unrelated clan-mates to advertise and defend their group territories, and to defend their kills

against lions or hyenas from neighbouring clans (Boydston *et al.* 2001; Van Horn *et al.* 2004a; Smith *et al.* 2008). The unique occurrence of baboon-like sociality in well-armed predators occupying the highest trophic positions in African ecosystems has favoured the evolution of many unusual traits in this species, including females that are highly 'masculinized' with respect to both their morphology and their behaviour (e.g. Watts *et al.* 2009). That is, adult females are larger and more aggressive than adult males, they are socially dominant to all adult males born elsewhere, and the female's genitalia are heavily 'masculinized' (Kruuk 1972; Frank 1986; Hamilton *et al.* 1986; Mills 1990; Szykman *et al.* 2003; Van Meter 2009). These unusual traits not only give females top priority of access to food, but they also give females virtually complete control over mating (East *et al.* 1993).

In light of the unusual traits expressed in this species, our goal here is to examine the relationship between social organization and genetic structure within and among hyena social groups. We focus in particular on the role of kinship in hyena societies, and assess how this varies with demographic and ecological conditions. We begin by synthesizing published findings from short- and long-term field studies of spotted hyenas across their geographic range to elucidate variation in demography and sociality. We find that, although clan size and population density vary enormously, clan structure and social organization are remarkably constant throughout the species' range. We then use data from our own 23-year, individual-based study of spotted hyenas in Kenya to summarize the long-term fitness consequences of rank-related variation in resource access among female clan-mates. Here we find that high social rank confers a large fitness advantage after only a few generations, but also that some low-ranking matrilines persist despite their relatively poor access to resources, suggesting that chance plays a role in determining long-term matrilineal representation in hyena populations. Next, based on our own field work, we review patterns of genetic relatedness within and between clans, and consider the roles of sexually dimorphic dispersal and female mate choice in the generation of these patterns.

Finally, we apply social network theory to examine effects of both matriline membership and variation in ecological conditions on social relationships among clan members. In contrast to baboon troops, which are highly cohesive, spotted hyena clans are fission–fusion societies; these are stable social units in which individual group members are often found alone or in small subgroups, and in which subgroup size and composition change frequently over time (Kruuk 1972; Mills 1990; Smith *et al.* 2008). Fission–fusion dynamics permit

spotted hyenas to adjust grouping patterns in response to both short-term and seasonal fluctuations in local prey abundance (Holekamp *et al.* 1997b; Höner *et al.* 2005; Smith *et al.* 2008, 2011). Indeed, feeding competition constrains social relationships in this species, and spotted hyenas adjust their grouping patterns over both short- and long-time scales in response to competition intensity, spending more time with conspecifics during periods of abundant prey, and joining clan-mates at kills in numbers correlated with the energetic value of prey (Holekamp *et al.* 1993; Smith *et al.* 2008). As is the case in most primate species (reviewed by Widdig 2007), individual hyenas are known to associate more closely with kin than with non-kin (Holekamp *et al.* 1997a; Van Horn *et al.* 2004b; Wahaj *et al.* 2004), but it is unclear to what extent matrilineal kinship affects social network structure in the face of varying prey abundance; we address this question here for the first time.

Methods

Study species

Throughout their geographic range, which covers most of sub-Saharan Africa, spotted hyenas form clans whose members all know one another individually, rear their cubs together at a communal den, and who also usually cooperatively advertise and defend a group territory. The stable core of any spotted hyena clan is comprised of one to several matrilineal kin groups (Fig. 1), each containing multiple adult females and their young (Frank 1986; Mills 1990). In addition, each clan also contains one to several adult immigrant males. Because the lifespan of wild spotted hyenas may exceed 18 years (Drea & Frank 2003), but the average age at first reproduction is only 3.5 years (Holekamp *et al.* 1996), individuals from up to five different generations may be present concurrently within the clan. Thus, hyena clans are comprised of a number of different matrilineal kin groups, each containing multiple overlapping generations of long-lived individuals. These group characteristics, in combination with rank-related resource access and cognitive abilities allowing hyenas to remember past social interactions, give rise to a social structure far more complex than that found in any other mammalian carnivore (Holekamp *et al.* 2007).

Like baboon troops, hyena clans are rigidly structured by hierarchical rank relationships that determine priority of access to food (Tilson & Hamilton 1984; Frank 1986; Henschel & Skinner 1987; Smith *et al.* 2011). Among all clan members except young cubs who have not yet learned their status, rank relationships are usually unambiguous, such that there is a clear dominant
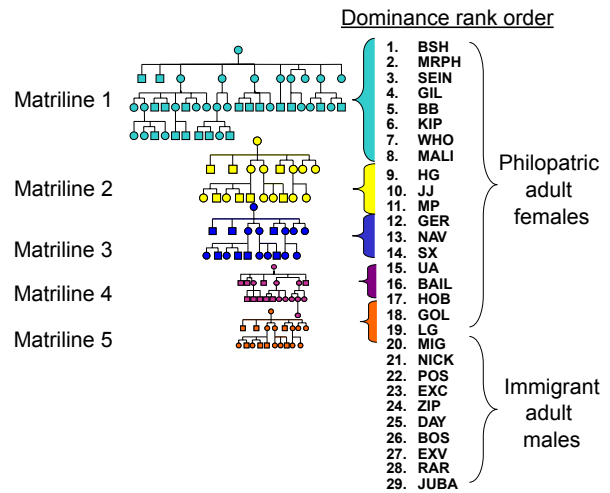

Fig. 1 Dominance rank order of matrilines within one cohort of adults present in a single large clan. The dominance hierarchy of natal animals contains multiple matrilineal kin groups, shown at *left*; each matriline is represented by a *different shade*. *Squares* in genealogies represent males and *circles* represent females. Although only adult females are shown among the natal animals in the vertical listing at *right*, offspring are included in the genealogies shown at *left*; offspring slot into the hierarchy immediately below their mothers. Thus all adult females and their young outrank all immigrant males.

and a clear subordinate within every dyad (Engh *et al.* 2000). Members of a particular matriline usually occupy adjacent rank positions within the clan's dominance hierarchy (Fig. 1). Hyenas of both sexes maintain their maternal ranks as long as they remain in the natal clan; this means females retain their maternal ranks throughout their lives, but males retain them only until they emigrate (Smale *et al.* 1993, 1997).

Whereas female spotted hyenas are strongly philopatric, nearly all males emigrate from their natal clans after they become reproductively mature; natal dispersal usually occurs between 2 and 5 years of age (Smale *et al.* 1997; Boydston *et al.* 2005; Höner *et al.* 2007). Many prospective immigrant males visit neighbouring groups each year on brief 'prospecting' forays, but only a small fraction of these males ever become socially integrated such that they assume positions in new clans as long-term resident males. In addition to resident immigrant males, so called when they are continuously present for at least 6 months, each clan may also contain one or more adult natal males (e.g. those older than 24 months) that have not yet emigrated (Henschel & Skinner 1987; Holekamp & Smale 1998; Höner *et al.* 2005). In habitats where dispersal opportunities are limited, some males may even spend their entire lives in their natal clans (e.g. Höner *et al.* 2007).

All natal hyenas are socially dominant to all immigrants (Kruuk 1972; Frank 1986; Mills 1990; Smale *et al.*

1993). Thus adult females and their offspring can displace adult immigrant males from food; this benefit of rank accrues even to very young cubs. In fact, in 30-min focal animal surveys during which juveniles were feeding on kills when adult immigrant males were also present, only once out of 572 surveys did a juvenile allow an immigrant to feed (Van Horn *et al.* 2004b). The mechanisms by which social rank is acquired differ between immigrant males and natal hyenas. Regardless of their maternal rank in the natal clan, when males emigrate they appease all new hyenas they encounter, so they enter a new clan at the very bottom of its overall dominance hierarchy (Smale *et al.* 1997). Thus, priority of resource access inevitably declines dramatically after dispersal for sons of high- and low-ranking females alike. Nevertheless, virtually all males emigrate from their natal clans voluntarily; they are not driven out by conspecifics, nor do their ranks fall before dispersal (Smale *et al.* 1997). Ranks of immigrants within the male hierarchy are determined by arrival order in the new clan, because males conform to a strict queuing convention (Smale *et al.* 1997; East & Hofer 2001). By contrast, natal hyenas assume positions in the clan's dominance hierarchy immediately below those of their mothers. This occurs during a long, intensive period of social learning early in postnatal development (Holekamp & Smale 1991, 1993; Smale *et al.* 1993; Engh *et al.* 2000).

Although rank relationships among adult clan-mates are generally very stable over long periods of time, changes in rank relationships do sometimes occur, indicating that rank is not genetically determined in this species. For example, an animal's rank can fall substantially within its lifetime due to recruitment of daughters of higher-ranking females, and rank reversals may occur within matrilines, particularly when adult daughters overtake their aging mothers. Furthermore, entire matrilines occasionally reverse their rank order after major fights. That is, revolutionary coalitions sometimes form among members of a low-born matriline to overthrow a smaller but higher-ranking matriline (e.g. Mills 1990; Hofer & East 1996). Collectively these facts suggest that social rank is too labile to be directly determined by behavioural or morphological traits that are strongly heritable; in fact, results from several studies indicate absence of direct genetic influences on offspring rank (Mills 1990; Holekamp *et al.* 1993; Engh *et al.* 2000; East *et al.* 2009).

Spotted hyenas breed year-round throughout their range, although some populations have birth peaks or troughs that are temporally associated with varying prey abundance (Holekamp *et al.* 1999). The mating system of the spotted hyena is polygynandrous. Both males and females mate promiscuously, and no enduring pair bond develops between the sexes (Szykman *et al.* 2001; Engh *et al.* 2002; East *et al.* 2003). Females have been observed to mate with up to three males during a single estrous period, and members of both sexes have been known to copulate with several different mates over the course of several years (Engh *et al.* 2002). Many twin litters are sired by multiple males (Engh *et al.* 2002; East *et al.* 2003). Females usually bear litters of one or two cubs in dens, where cubs are sheltered for the first 9–14 months of their lives. Weaning occurs very late in spotted and other bone-cracking hyenas compared to all other mammalian carnivores of the same or larger body size (Watts *et al.* 2009); hyena cubs are typically weaned when they are 12–18 months old (Holekamp *et al.* 1996). Spotted hyenas of both sexes are physiologically competent to breed by 24 months of age (Glickman *et al.* 1992; Dloniak *et al.* 2006), although most individuals delay reproduction for at least another year after puberty (Holekamp *et al.* 1996).

Methods used in our review of the literature

We reviewed patterns of demography and social organization described in 23 published studies of spotted hyenas, and extracted data documenting population density, clan size, home range size, sex ratio among adult clan members, and percent of each clan comprised of adults. We report home range size in square kilometres, and in most cases home range size is synonymous with the size of the average territory defended by clans in a particular part of Africa. However, in some regions, spotted hyenas do not engage in active territorial defence or boundary marking, and in those cases, home range size is determined based strictly on patterns of space use by clan members. Where spotted hyenas defend territories but also travel well outside the boundaries of their territories to forage, we report mean size of defended territories as home range size. Values for hyena density and mean clan size are as reported in the original field studies.

Observational methods in our long-term field study in Kenya

We focus here most heavily on insights gleaned from our long-term study of one large social group in the Talek region of the Masai Mara National Reserve, Kenya (henceforth, the Mara). We have observed the Talek clan continuously since June 1988, and L. G. Frank (1983, 1986) monitored it before us, from 1979 to 1987. We also assess the generalizability of our findings among clans. We currently work with six Mara clans, and from 2003 to 2005, we also monitored two large clans in Amboseli National Park. We employ the same

observational methods in each clan. That is, we recognize all individual hyenas by their unique spot patterns, and sex them based on the dimorphic morphology of the erect phallus (Frank *et al.* 1990). Assignment of an individual's social rank within its clan is based on its position in a matrix ordered by submissive behaviour displayed during dyadic agonistic encounters (Martin & Bateson 1986; Engh *et al.* 2002; Smith *et al.* 2011). Using field vehicles as mobile blinds, researchers observe hyenas 21–31 days each month, recording which individuals are present, and all occurrences of agonistic interactions. We initiate an observation session each time we encounter one or more hyenas separated from other clan members by at least 200 m; hyenas in different sessions are typically separated by at least 1 km (Smith *et al.* 2008). Upon arrival at each session, and during subsequent scans performed every 15–20 min, we record the identity and activity of every hyena in that focal subgroup. Sessions last from 5 min to several hours, and end when we leave an individual or group. We use these session data below as we apply social network theory to assess the effects of kinship on social relationships among members of the Talek clan as they cope with varying ecological conditions.

Genotyping and assessment of relatedness within and among clans and populations

To evaluate patterns of relatedness within and among clans of spotted hyenas in the Mara and Amboseli, individual hyenas from both populations were genotyped at 8–12 microsatellite loci using DNA extracted from blood, tissue or faeces (Van Horn *et al.* 2004a; Watts *et al.* 2011). Pairwise relatedness values (R) based on both maternal and paternal kinship were estimated for individuals sampled from each population using the program RELATEDNESS 5.0 (Queller & Goodnight 1989). All microsatellite loci were in Hardy–Weinberg equilibrium in both Mara and Amboseli populations. Patterns of R were examined using longitudinal data collected on the Talek clan and cross-sectional data collected on multiple clans in both populations (Mara, $N = 335$ genotyped hyenas; Amboseli, $N = 80$ genotyped hyenas). Population comparisons were based on samples from two clans of hyenas in each park, collected during overlapping 2-year periods. Clans were similar in size in both populations, and covered similar geographic sampling areas (Watts & Holekamp 2008). Finally, to assess the scope of kin-biased dyadic interactions in the clan, we used data from Smith *et al.* (2010) to calculate the number of dyadic pairs present in the clan for a large cohort ($N = 31$) of adult females present concurrently in the Talek clan from January, 1996 to December, 2000. This was a period of social stability occurring between clan fission events. We assigned 222 pairs of adult females present during this period to one of the three following kinship categories based on their maternal and paternal relationships: close kin (coefficient of relatedness (r) = 0.5; mother–daughter or full sisters), distant kin (r = 0.125–0.25; grandmother–granddaughter, maternal or paternal half sisters, aunt–niece) or non-kin ($r \sim 0.00$).

Assessment of reproductive skew

To quantify the degree of reproductive skew among Talek hyenas, we calculated Nonacs binomial skew index B (Nonacs 2000, 2003), using the software SKEW (Nonacs 2003; http://www.eeb.ucla.edu/Faculty/Nonacs/shareware.htm). Nonacs' skew index B ranges from −1 to +2; positive values indicate that skew is greater than expected, and negative values indicate that skew is less than expected such that reproduction is more evenly distributed than expected. $B = 0$ indicates random mating. Because the accrual of a reproductive benefit (i.e. a cub) could only be assessed for males via genetic paternity analysis (Engh *et al.* 2002; Van Horn *et al.* 2004a), this constrained the set of potential benefits, and the set of potential beneficiaries, to hyenas that were genotyped. Because variation in survival, or tenure in a group, can produce reproductive skew aside from an impact of any behavioural interactions (Crespi & Yanega 1995), we calculated tenure within the clan for each potential beneficiary (i.e. immigrant male, or adult natal male or female) within the dates set by the conceptions of the cubs for which paternity was known. We estimated the one-tailed P value associated with the observed B for females, and for males, relative to the random accrual of reproductive benefits, via 10 000 simulations. We also used 10 000 simulations in our power analysis, and we generated the two-tailed 95% C.I. for B.

Methods used to analyse the effects of kinship and prey abundance on social network structure

To evaluate the persistence of maternal kinship effects in structuring social networks within the Talek clan in the face of fluctuating food availability, we documented variation in local prey abundance at biweekly intervals throughout our longitudinal study, as described by Cooper *et al.* (1999). Although paternal kinship may further structure social relationships within clans, we were specifically interested in elucidating the persistence of long-term social network structure, and knowledge of paternity was unavailable for the early years of our long-term study. Therefore, here we considered natal dyads belonging to the same matriline within the

Talek clan (e.g. grandmother–grandchildren, mother–offspring, maternal sister and half-sister pairs) to be maternal kin, and natal hyenas from different matrilines to be non-kin. These relationships were established based on pedigree construction using genetic parentage assignment (Engh *et al.* 2002; Van Horn *et al.* 2004a) and nursing associations between mothers and offspring (Holekamp *et al.* 1993).

We assessed association patterns based on the co-occurrence of dyad members in observation sessions, as done previously for this species (e.g. Holekamp *et al.* 1997b; Szykman *et al.* 2001; Smith *et al.* 2007). Briefly, we calculated the Twice-Weight Association Index (AI) of Cairns & Schwager (1987) for each pair of individuals, hyenas A and B, during the period for which they were concurrently present in the clan. We calculated $AI_{A,B}$ as: $(A+B_{together}) / [(A_{without\ B}) + (B_{without\ A}) + (A+B_{together})]$ where $(A+B_{together})$ is the number of sessions in which A and B are present together, $(A_{without\ B})$ is the number of sessions in which A was present without B, and $(B_{without\ A})$ is the number of sessions in which B was present without A.

We constructed a social network for each consecutive 4-month interval from 1988 through 2003. These intervals correspond to predictable seasonal variations in prey abundance observed throughout our study (Holekamp *et al.* 1997b, 1999; Smith *et al.* 2008): one 4-month period of superabundant prey (June to September) each year, and two periods of relatively low prey density (October to January and February to May). We assigned a life history stage (cub, subadult or adult) to each hyena using detailed demographic and genealogical records, and estimated (to ±7 days) the ages of cubs born in the clan when they were first observed above ground, based on pelage, size, and behaviour (Holekamp & Smale 1998). Hyenas were considered to be cubs while they were residing at dens. We considered hyenas to be den-independent subadults when we found them more than 200 m from the current communal den on at least four consecutive occasions; this usually occurred when youngsters were roughly 9 months old (Boydston *et al.* 2005). Here we considered natal males older than 24 months to be reproductively mature adults (Glickman *et al.* 1992; Curren LJ, Weldele ML, Holekamp KE 2011, unpublished electroejaculation data.), and classified females as adults at 36 months of age or at their first known date of conception, whichever occurred first. If a hyena changed life history stages during a 4-month sampling period, then it was assigned to the life history stage it occupied at the midpoint of the sampling period.

We depict the Talek clan as a social network comprised of 'nodes' representing individual actors connected by associations, called 'ties' (Wasserman & Faust 1994). Each node within the network represents a natal hyena present in at least five observation sessions during a sampling period. For each hyena within each network, we calculated the 'strength' of its social ties with group-mates as the sum of its association indices with all clan-mates in each of three categories (all natal hyenas, maternal kin, and non-kin), and divided each sum by the number of other potential actors (minus the focal hyena) in each network class. Defined this way, 'standardized strength' measures the extent to which each hyena associates with all potential actors in the network (Barthelemy *et al.* 2005). Because even weak associations are potentially important for the maintenance of clan structure, we constructed weighted, unfiltered networks based on all associations (Croft *et al.* 2008; James *et al.* 2009).

All statistical analyses of social networks were conducted using individual hyenas as sampling units. We limited our analysis to those natal hyenas observed to be in a particular life history stage during periods of both low and high prey when both kin and non-kin were available to them as social partners. If a particular focal hyena occupied the same life history stage within multiple networks, then we constructed a single mean value across networks for that hyena. We used non-parametric statistics to analyze network traits because we were unable to transform these non-normally distributed data, and we corrected for multiple testing using sequential Bonferroni adjustments (Rice 1989). Specifically, using STATISTICA 6.1, we compared means between two, or among more than two, independent groups using Mann–Whitney U and Kruskal–Wallis tests, respectively. We compared the means of two dependent groups using Wilcoxon-signed rank tests. Differences between groups were considered significant at alpha ≤0.05.

Results and Discussion

Variation in the demography and social structure of spotted hyenas across their range

Spotted hyenas occupy an extraordinarily diverse array of habitats in sub-Saharan Africa, including savanna, deserts, swamps, woodland and montane forest. Densities of spotted hyenas vary by orders of magnitude among these habitats. In the deserts of southern Africa, hyena densities can be as low as one hyena per hundred square kilometres (Tilson & Henschel 1986; Mills 1990). The highest population densities reported for this species occur on the prey-rich savannah plains of Kenya and Tanzania (e.g. Kruuk 1972; Frank 1986; Höner *et al.* 2005; Watts & Holekamp 2008; Watts & Holekamp 2009), and surprisingly, in the montane forest of Aber-

dare National Park in Kenya (Sillero-Zubiri & Gottelli 1992); in these areas, densities of spotted hyenas often exceed one animal per square kilometer. However, across 23 study populations the mean density was 0.45 hyenas/km^2, ranging from 0.009 to 1.65 hyenas/km^2 (Holekamp & Dloniak 2010).

In association with varying population densities, clans range in size from the tiny groups found in the Kalahari and Namib deserts, which may contain as few as four or five members (Tilson & Henschel 1986; Gasaway et al. 1989; Mills 1990), to the large clans in eastern Africa, which may contain over 90 members (Kruuk 1972; Frank 1986; Hofer & East 1993a; Holekamp et al. 1993). Across 19 study populations in which all individual members were known for one or more clans, mean clan size was 28.8 hyenas, but this ranged from 3 to 67 hyenas (Holekamp & Dloniak 2010), with the largest clans occurring in the populations of highest density (linear regression: $r^2 = 0.717$, $P < 0.0001$, Fig. 2A).

The home ranges occupied by clans of spotted hyenas also vary enormously with population density (Fig. 2B).

Home range size for clans studied throughout sub-Saharan Africa ranges from 13 to 1 065 km^2, with a mean of 169 km^2 (Holekamp & Dloniak 2010). As population density and the number of hyenas per clan increase, home range size decreases, although this relationship is non-linear (Fig. 2B: $r^2 = 0.562$, $P = 0.0001$, following log transformation of both variables). This pattern of decreasing home range size with increasing population density is similar to that found in other mammalian carnivores (e.g. Trewhella et al. 1988). This pattern is also consistent with the hypothesis that habitat carrying capacity for hyenas, as reflected in both clan size and population density, is limited by food availability (Mills 1990). Indeed, in most parts of Africa, clan size increases with local prey density (Trinkel et al. 2006). However, in the Serengeti, large aggregations of migratory herbivores within commuting distance of hyena territories permit a decoupling of clan size from prey availability within the territory per se (Hofer & East 1993a; b). Furthermore, in the island-like habitat on the floor of Ngorongoro Crater, mean size of seven resident clans was more closely related to overall prey availability in the Crater than to that in the territory of any particular clan (Höner et al. 2005).

The small clans inhabiting the deserts of southern Africa usually contain only one or two matrilines (e.g. Mills 1990) and a single immigrant male, whereas the large clans in the prey-rich plains of eastern Africa may contain over 10 matrilines and several immigrant males (e.g. Frank 1986). Among adult clan members, sex ratios are at least slightly female-biased in most well-studied populations (Table 1) and average 1.8 adult females for every adult male. On average, clan membership is
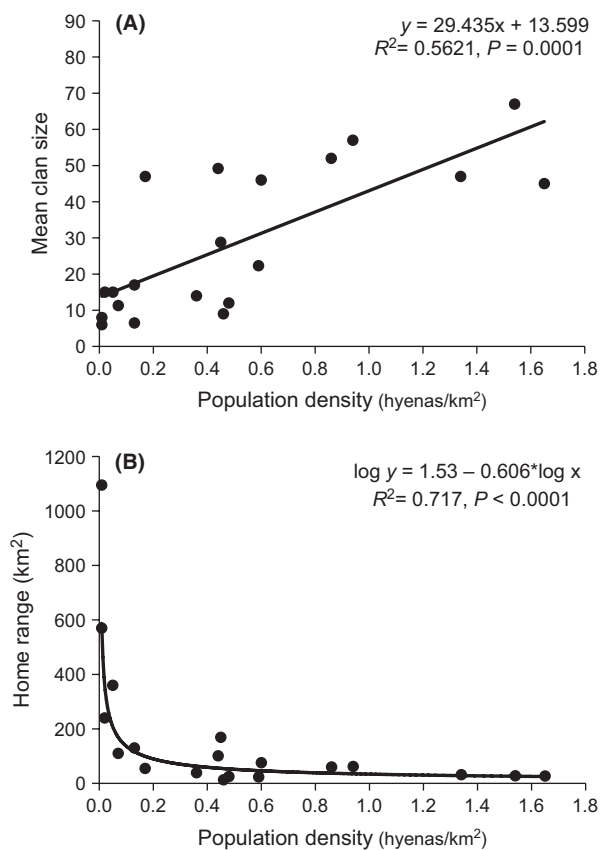

Fig. 2 Relationships between hyena density and (A) clan size and (B) home range size for spotted hyena clans across sub-Saharan Africa. Data drawn from published studies listed by Holekamp & Dloniak (2010) in their Table 3.

Table 1 Sex ratios among adult clan members, and percentage of clan membership comprised of adults, in those populations for which these data are available

| Study area	Adult sex ratio (# of females/ # of males)	% clan membership comprised of adults	Reference
Serengeti	1.2	63	(Hofer & East 1993a)
Ngorongoro	1.2	69	(Höner et al. 2005)
Kalahari	2.5	36	(Mills 1990)
Chobe	3.1	56	(Cooper 1989)
Kruger	2.5	73	(Henschel & Skinner 1987)
Amboseli	1.7	46	(Watts & Holekamp 2008)
Aberdares	1.0	—	(Sillero-Zubiri & Gottelli 1992)
Mara	1.8	47	Current study
Mara	1.5	48	(Frank et al. 1995)
$\bar{x}$	1.8	55	
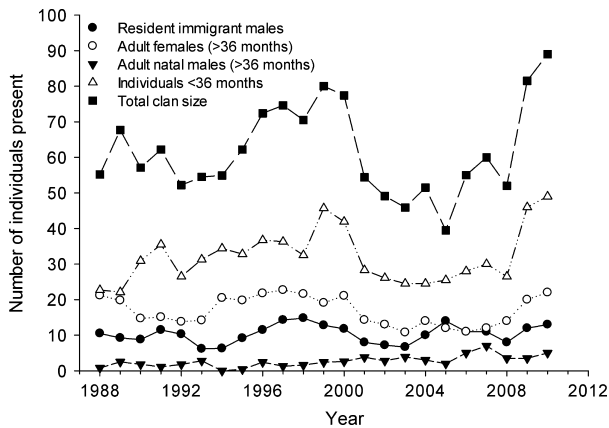
Fig. 3 Long-term variation in the composition of one large clan in Kenya, the Talek clan. Here monthly mean composition of the clan is averaged within year, from 1988 to 2010.

Fig. 4 Schematic diagram showing how social rank mediates reproductive success among adult female spotted hyenas. The *arrows* running from left to right represent rank effects within a generation. The *bottom arrow* indicates the positive feedback of maternal kin joining forces on the maintenance of these rank effects into the next generation. Footnotes indicate published papers containing data that support claims in this diagram: (1) Frank (1986) (2) Hofer & East (1993b); Holekamp *et al.* (1997b); Boydston *et al.* (2003a); Kolowski *et al.* (2007); White (2006); Höner *et al.* (2005); (3) Holekamp *et al.* (1996); Hofer & East (1993c, 1996, 2003); Watts *et al.* (*2009*); Swanson *et al.* (2011); (4) Holekamp *et al.* (*1997a*); Smith *et al.* (2008, 2010).

roughly evenly split between immature and mature individuals (Table 1).

Of all the adult males present in a clan at a particular time, adult natal males generally comprise 25–40%, and the rest are immigrants (Holekamp & Smale 1998; Höner *et al.* 2005, 2007). Figure 3 shows temporal variation over 22 years in the composition of one large clan in Kenya. Relative representation in the clan of each demographic sub-group remains surprisingly stable over time. Clan size reached its apex in 2010, after 2 years of severe drought in Kenya, during which the Talek hyenas had frequent access to dead cattle as well as their normal prey base.

Effects of social rank on female fitness

The nature of the food resources on which spotted hyenas rely creates a competitive environment that shapes hyena social relationships. Individual hyenas experience strong direct and indirect selection to assist their kin in attaining and maintaining social rank and the resources to which their rank entitles them (Smith *et al.* 2010). Because an adult's social status determines its priority of access to food during competitive interactions over kills (Fig. 4), rank has profound effects on hyenas' intake of calories and nutrients (Holekamp & Smale 2000; Hofer & East 2003). Furthermore, high social rank also permits adult female spotted hyenas to reduce energy expenditures demanded by long-distance travel to remote feeding sites (Fig. 4). For example, subordinate females in Kenya are far less likely than dominant females to forage in the central prey-rich areas of the clan's territory (Boydston *et al.* 2003). Where females often hunt migratory antelope outside the boundaries of the clan's territory, as in the Serengeti, low-ranking females need to commute to distant prey much more
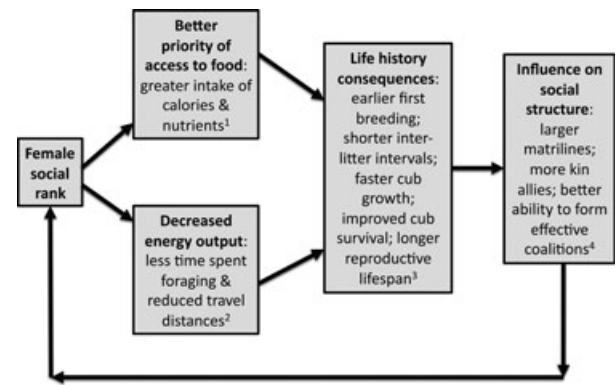
frequently than do high-ranking females (Hofer & East 1993a; b) The relatively high ratio of energy gain to energy loss enjoyed by high-ranking female hyenas has important consequences with respect to reproductive success and life-history traits (Fig. 4).

All adult female clan-members breed, but initiation of breeding efforts depends on immediate energy availability in this species, so females reproduce at rates that increase with social rank (Frank *et al.* 1995; Holekamp *et al.* 1996; Hofer & East 2003). High-ranking females obtain more resources (Frank 1986; Holekamp & Smale 2000), and thus are able to provide better nourishment to their cubs. The rank-related variation in females' ability to access food has striking effects on the growth rates of their cubs, with high-ranking cubs growing much faster than their low-ranking peers (Hofer & East 1996, 2003). Dominant females can also wean their cubs at much younger ages, and much smaller body sizes, than can subordinate females (Frank *et al.* 1995; Holekamp *et al.* 1996; Watts *et al.* 2009).

The age at which females first bear young is strongly correlated with maternal rank, with daughters of the alpha female first giving birth at around 2.5 years of age, and daughters of the lowest-ranking females doing so at 5–6 years of age (Holekamp *et al.* 1996; Hofer & East 2003). Although rank does not affect litter size in hyenas, perhaps because females typically have only two functional nipples, inter-litter intervals are much shorter among dominant than subordinate females, and

dominants are more frequently able to support pregnancy and lactation concurrently. Therefore the annual rate of cub production is substantially higher among dominant than subordinate females (Holekamp *et al.* 1996). Maternal rank affects the likelihood that cubs will survive to reproductive maturity, and it also has a pronounced effect on longevity among adult females; daughters of high-ranking females live longer than do daughters of low-ranking females (Watts *et al.* 2009). Because both birthrates and survivorship are so much greater among high- than low-ranking hyenas (Watts *et al.* 2009), dominant hyenas tend to have many more surviving kin in the population at any given time than do subordinates (Figs. 1, 5), and thus they enjoy a much larger network of potential allies, should the need for those arise (e.g. Van Horn *et al.* 2004a; Smith *et al.* 2010). Because high-ranking females start breeding earlier, live longer, and produce more surviving cubs per unit time, we have observed as much as a fivefold difference in lifetime reproductive success between the highest- and lowest-ranking females in our Kenyan study populations (Holekamp & Smale 2000). Thus a female's social rank has enormously important fitness consequences. These effects, as they have accrued over 30 years, are shown in Fig. 5 for 19 adult females present in the Talek clan in 1979 (Frank 1983).

When L. G. Frank (1986) began working with the Talek clan in 1979, he knew nothing about genealogical relationships among adult females, but he was able to discern their rank relationships based on outcomes of
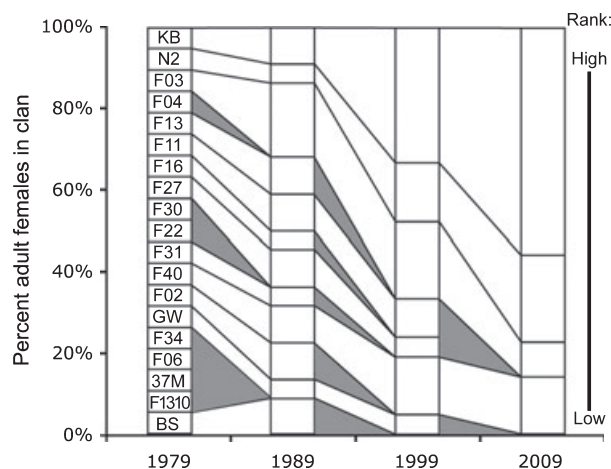

Fig. 5 Rank-related variation in fitness among adult female spotted hyenas. Cells in the 1979 column (from Frank 1983) represent 19 adult females present in the Talek clan that year, shown in descending rank order. Cells in the 1989, 1999, & 2009 columns represent descendants of those original 19 females, and their proportional representation in the clan. *Gray triangles* represent extinction events for entire matrilines. Numbers of adult females present in the clan have ranged from 13 to 25 during this period.

agonistic interactions, as described in 'Methods'. In Fig. 5, each of the 19 adult females present in the clan in 1979 is assigned a different cell in the leftmost column, arranged in descending rank order, and cells in subsequent columns represent this female and her descendants, or her descendants alone. Of 19 adult females originally present in the Talek study clan in 1979 (Frank 1983, 1986), only four had living descendants among the 22 adult females present in the clan in 2009 (Fig. 5). The alpha female in 1979, who then represented only 5% of the adult female population, gave rise to over half the current adult females. Furthermore, the descendants of the 1979 alpha and beta females together now comprise nearly 80% of the adult female population. Although it can be seen here that high-ranking females clearly enjoy a large fitness advantage over subordinates, it is also clear from Fig. 5 that the relatively low-ranking matriline deriving from female F40 persists over many generations despite the energetic handicaps with which its members must cope. This suggests that chance may play an important role in determining which subordinate matrilines persist over extended time periods.

Patterns of relatedness within and among hyena clans and populations

The pattern apparent in Fig. 5 might lead the uninformed reader to expect that hyena clans should be relatively recently derived from a single high-ranking ancestor, and that natal clan-mates might therefore be expected to be closely related to one another. However, our data show clearly that this is not the case. Estimated average R values for the Talek clan fit expectations among dyads of known genealogical relationships (Fig. 6). Average genetic relatedness among natal members of the Talek clan was extremely low ($R = 0.011 \pm 0.002$, Van Horn *et al.* 2004a; Fig. 6), and similar to R values for males immigrating into the Talek clan from myriad neighbouring clans (mean R values among adult immigrant males was 0.009 ± 0.007; Van Horn *et al.* 2004a; Fig. 6). Nevertheless, Van Horn *et al.* (2004a) found that average relatedness is greater within than among matrilines of spotted hyenas, even across successive generations, but also that relatedness is diluted across generations within matrilines. Finally, the decline in mean R values across territorial boundaries separating neighboring hyena clans (Fig. 7) suggests that most successful dispersal by male hyenas occurs to nearby clans. This is consistent with dispersal distances documented for radio-collared males born in our study clans (Smale *et al.* 1997; Boydston *et al.* 2005).

Although the hyena populations in the Masai Mara and Amboseli are currently quite similar with respect
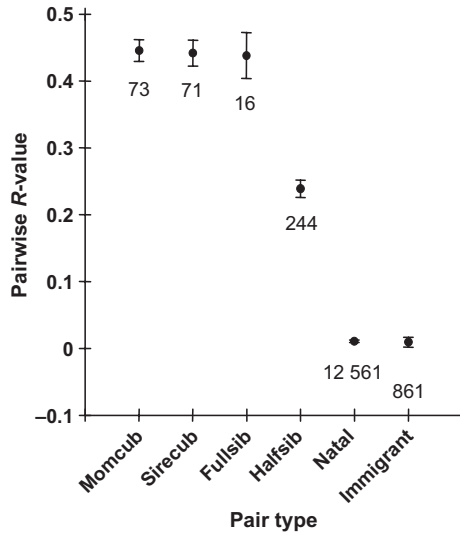
Fig. 6 Pairwise *R* values within the Talek clan of any two natal animals, any two resident immigrants and four types of close kin: mothers and cubs (momcub), sires and cubs (sirecub), full-sibling pairs (fullsib) and half-sibling pairs (halfsib). Sample sizes indicate number of *R* values. Mean values are presented ±SE. Reproduced with permission from Van Horn *et al.* (2004a).
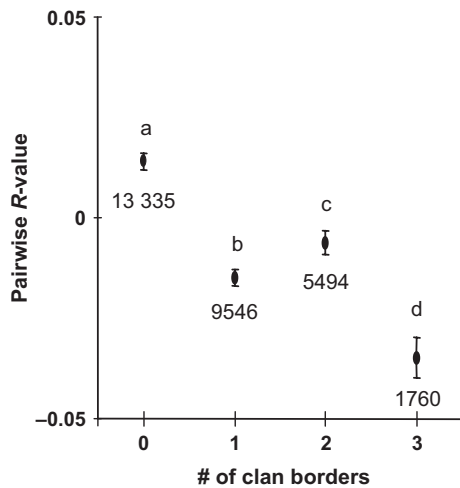

Fig. 7 Pairwise *R* values for natal animals from the Talek clan and six other clans are shown in relation to the number of clan borders separating spotted hyenas; there are no clan borders separating members of the same clan. Sample sizes indicate number of *R* values. Mean values are presented ±SE. Reproduced with permission from Van Horn *et al.* (2004a).

to many demographic characteristics (e.g. Table 1), their recent population histories differ markedly. Whereas our Mara hyena study population has remained consistently large since at least the late 1970s, with a density of at least 0.86 hyenas/km² (Frank 1986), the population in Amboseli National Park experienced

a demographic bottleneck during the 1970s and 1980s, in which a large population was reduced to approximately 50 individuals (C. Moss, personal communication; Faith & Behrensmeyer 2006), representing a population density of only 0.13 hyenas/km². The bottleneck appears to have lasted approximately 25 years; based on an estimated generation time for spotted hyenas of 5.7 years (Watts *et al.* 2011), the bottleneck thus spanned roughly four generations. In the mid-1990's, the Amboseli population exploded in size, likely resulting from changes in the local prey base and extirpation of the local lion population by pastoralists, and reached a population density of 1.65 hyenas/km² by 2003–2005 (Watts & Holekamp 2008). Despite these historical differences between parks, patterns of relatedness among natal animals were remarkably similar between Amboseli and the Mara (Watts *et al.* 2011). As in the Mara, average relatedness was higher among Amboseli clanmates than among hyenas born and living in adjacent clans. Moreover, we found no differences between the populations in measures of genetic diversity (Watts *et al.* 2011). Although the social and genetic make-up of the ancestors of the current Amboseli population are unknown, the relatively low levels of relatedness and high levels of genetic diversity in Amboseli indicate it is unlikely that they are descended from a group of closely related individuals.

The patterns of relatedness apparent in both our Mara and Amboseli populations conform to the theoretical expectation (Lukas *et al.* 2005) that mean relatedness among natal clan members should be similar to that among immigrants. These patterns in spotted hyenas are likely shaped by at least five factors. First, social structuring by matrilines within clans, and by clans within populations, most likely facilitates the maintenance of genetic diversity among natal hyenas (Sugg *et al.* 1996). Second, clan sizes in both our Mara and Amboseli study populations are quite large, and the number of possible dyads per clan increases exponentially with the number of clan members (Lukas *et al.* 2005). High average relatedness among natal individuals is only expected in very small groups (Lukas *et al.* 2005). Third, mean *R* values are affected by the proportion of related dyads present in a clan at any give time, and this is relatively small compared to the total number of dyads present. For example, when we used data from Smith *et al.* (2010) to calculate and classify the number of dyadic pairs present in the clan for a large cohort ($N = 31$) of adult females, we found 222 adult female dyads present concurrently in the Talek clan from 1996 through 2000. Of these, only 11% ($N = 25$ dyads) were close kin ($R = 0.462 \pm 0.028$), and 16% ($N = 36$ dyads) were distant kin ($R = 0.279 \pm 0.040$); thus nearly three quarters of the 222 female dyads

(73%, $N = 161$ dyads) were non-kin ($R = -0.228 \pm 0.006$). Fourth, in both Mara and Amboseli populations, patterns of relatedness are undoubtedly affected by male dispersal behaviour. Specifically, immigration into each clan of males from multiple neighbouring clans contributes to low average relatedness within clans, as well as to the maintenance of genetic variation. Furthermore, male spotted hyenas emigrate at high rates (East & Hofer 2001; Boydston et al. 2005), causing a regular influx of paternal genes via dispersing males. Male spotted hyenas also exhibit great behavioural plasticity (Mills & Hofer 1998; Boydston et al. 2003b; Hayward 2006; Kolowski & Holekamp 2009), which probably facilitates their dispersal across potential barriers, including areas with substantial anthropogenic activity. Consequently, it is highly likely that there was migration into the Amboseli population from surrounding areas, and just a few migrants into a small population can be sufficient to maintain or restore genetic variation (Keller et al. 2001; Vilà et al. 2003; Hogg et al. 2006). Finally, the low mean relatedness among natal animals in our study populations is likely caused in part by relatively low reproductive skew among resident male hyenas (Engh et al. 2002; Holekamp & Engh 2009). We discuss effects of dispersal and skew patterns further below.

Effects of dispersal, mate choice and reproductive skew on patterns of relatedness

Although male spotted hyenas are highly mobile, and physically capable of traveling long distances quite quickly (e.g. Hofer & East 1993a), their ability to join new clans is evidently constrained by the severe aggression directed at potential immigrants by resident immigrant males (Smale et al. 1997; Boydston et al. 2001; Szykman et al. 2003). Most habitats in which spotted hyenas occur appear to be saturated such that clan territories form a mosaic covering the entire landscape (Kruuk 1972; Boydston et al. 2001). Each territorial border is thus a potential barrier to dispersal. Most males successfully engaging in natal dispersal immigrate into clans separated from their natal ranges by only one or two territorial borders (Smale et al. 1997; Boydston et al. 2005; Höner et al. 2010). In contrast to lions and other carnivores in which coalitions of related males often disperse together (e.g. Pusey & Packer 1987; Caro 1994), male spotted hyenas disperse alone, such that resident immigrant males represent a true mélange of clans, and accordingly, relatedness among immigrants is extremely low (Van Horn et al. 2004a; also see Fig. 6).

Although the mating system of the spotted hyena is polygynous, matings are not monopolized by high-ranking males, and aggressive contest competition appears to have little influence on male reproductive success (Engh et al. 2002; East et al. 2003). This is in marked contrast to the situation in most other gregarious mammals (e.g. Hoelzel et al. 1999; Di Fiore 2003; Alberts et al. 2006), where reproductive success is strongly correlated with fighting ability and intra-sexual rank. Instead, the strongest determinants of reproductive success among male spotted hyenas are dispersal status, length of residence as immigrants in new clans after dispersal, the number of young females present in the clan when immigrants first arrive there, and female choice of mates (Engh et al. 2002; East et al. 2003; Höner et al. 2007; Van Horn et al. 2008). Adult natal male hyenas are socially dominant to immigrant males, and most of them show strong sexual interest in clan females (Holekamp & Smale 1998), yet they sire only 3% of cubs in their natal clans. By contrast, immigrants sire 97% of cubs, indicating that females prefer to mate with immigrants over adult natal males (Engh et al. 2002; Van Horn et al. 2008). Among resident immigrant males, social rank is correlated with male reproductive success, but regression analysis showed that tenure in the clan predicts this far better than does male rank (Engh et al. 2002). Immigrants do not typically begin to sire offspring until they have resided in their new clan for 1 or 2 years, during which time they occupy the lowest rank positions in the male queue (Engh et al. 2002; East et al. 2003).

To quantify reproductive skew, paternity was assigned to 71 cubs as in Engh et al. (2002). These cubs were conceived from 14 July 1987 to 7 June 2000; they were the offspring of 29 females and 20 males. All but one cub was the offspring of an immigrant male. An additional 33 adult natal males and 26 immigrant males did not sire any cubs. Although the reproductive benefit per female hyena ranged from 1 to 7 cubs, the skew observed among the 29 females was not significantly different from that expected at random ($B = -0.0067$, $P = 0.991$) or through equal accrual of benefits (i.e. the lower 95% CI $= -0.0131 < 0$), and it is clear that the production of cubs was not monopolized (i.e. the upper 95% CI $= 0.0006 < 0.976$). Presumably the degree of skew observed among Talek females is due largely to variation in lifespan among the adult females (also see Swanson et al. 2011). The range in number of offspring was greater among males than females (1–15 cubs per male), and the reproductive skew among the 79 males was statistically greater than that expected through random accrual of benefits ($B = 0.0544$, $P = 0.0001$), or equal accrual of benefits (i.e. the lower 95% CI $= 0.0323 > -0.0136$), but reproduction was not monopolized by any single male (i.e. the upper 95% CI $= 0.0843 < 0.9835$). Reproductive skew among male spotted hyenas was thus lower than among males of

Table 2 Reproductive skew (B) among polygnous male mammals

Species	B^1	B range[2]	Sample size	Reference
Mountain gorilla, *Gorilla beringei*	0.38	0.34–0.43	4 groups, 22 males	(Bradley *et al.* 2005)
White-faced capuchin, *Cebus capucinus*	0.24	0.13–0.40	8 groups, 58 males	(Muniz *et al.* 2010)
European badger, *Meles meles*	0.18	−0.062–0.63	25 groups	(Dugdale *et al.* 2008)
Rhesus macaque, *Macaca mulatta*	0.08	0.08–0.08	2 groups	(Dubuc *et al.* 2011, Widdig *et al.* 2004)
Spotted hyena, *Crocuta crocuta*	0.05	n/a	1 group, 79 males	Current study
Greater horseshoe bat, *Rhinolophus ferrumequinum*	0.02	n/a	1 group	(Rossiter *et al.* 2006)
Collared peccary, *Pecari tajacu*	0.01	−0.10–0.33	6 groups, 25 males	(Cooper *et al.* 2011)

[1]Mean B values are reported where data from multiple social groups were available.
[2]Minimum and maximum values of B reported where data from multiple social groups were available.

most other polygynous species for which B has been quantified (Table 2), perhaps because role reversed sexual dimorphisms in body size and dominance status are so rare in other mammals (Holekamp & Engh 2009). Interestingly, as in spotted hyenas, collared peccaries are sexually monomorphic, and in greater horseshoe bats, females are larger than males, and in both these species, B values are quite low, as they are in spotted hyenas.

Female choice of mates appears to be the key determinant of patterns of paternity in this species. At least 40% of female spotted hyenas mate with multiple males during any given oestrous period, and 25–40% of twin litters are multiply sired (Engh *et al.* 2002; East *et al.* 2003). Males of all ranks sire offspring, but surprisingly, the alpha male in each immigrant cohort generally sires fewer cubs than do males in lower rank positions (Engh *et al.* 2002). Immigrant male rank is not correlated with age, and immigrants as old as 18 years have high-quality sperm and ejaculates (Curren LJ, Weldele ML, Holekamp KE 2011, unpublished electroejaculation data.), so their fertility does not appear to decline as they age. Thus the fact that alpha males sire relatively few cubs suggests an important role for female choice in determining reproductive success among males. Not only do females clearly prefer immigrant males over adult natal males, but they also frequently choose lower-ranking immigrants over the alpha male in the immigrant queue (Engh *et al.* 2002; Van Horn *et al.* 2008). High-ranking male hyenas cannot monopolize reproduction if females prefer not to mate with them. Absolute female control over mating has thus reduced selection for male fighting ability, and has led to low levels of combat among resident immigrant males, and to the evolution of a male social queue (East & Hofer 2001; East *et al.* 2003).

Given the powerful influence of female mate choice in spotted hyenas, it appears that males have been obliged to develop strategies to maximize their reproductive success that supplement or replace male–male combat. We find much heavier reliance in this species than in most other mammals on alternative modes of sexually selected interactions, such as endurance rivalry (e.g. queuing, East & Hofer 2001), and sperm competition may also play an important role in spotted hyenas (Curren LJ, Weldele ML, Holekamp KE 2011, unpublished electroejaculation data.). Female dominance and male-like genitalia make sexual coercion impossible in this species (East *et al.* 1993; Frank 1997). Instead, each female determines whether or not a single male will monopolize her during a given estrous period, and if so, which male this will be. Females can tolerate or refuse male mating attempts according to their own reproductive interests, and this unusual degree of female control appears to reduce the strength of the relationship between social status and reproductive success among males.

Preliminary data from our long-term study indicate that female spotted hyenas tend to produce paternally unrelated offspring. For example, despite persistent availability of individual males during successive reproductive cycles, females seldom permit a single male to sire more than one of their litters. In all known cases where sires were still present in the clan when a female conceived her next litter after successfully weaning at least one member of her last litter, only 3 of 30 females, bearing 4 of 49 litters and having one to four chances to remate, ever chose to mate again with a sire of one of their earlier litters. One result of this apparent tendency to have new males sire each successive litter is that large clans are characterized by networks of kin comprised mostly of mothers, offspring and maternal half-siblings sired by different males. In the final section of this paper, we assess the dynamics and stability of kin associations within the clan's overall social network, and inquire how these vary with resource availability.

Effects of kinship and prey abundance on social network structure

Social scientists have long-recognized the importance of social network theory in explaining human social

organizations (reviewed by Newman 2003b), but formal social network theory has only recently been applied to explain the structuring of animal societies (Krause *et al.* 2007; Croft *et al.* 2008; Wey *et al.* 2008; Sih *et al.* 2009). Although human social networks are often characterized by homophily, with individuals preferentially associating with others that possess traits similar to their own (e.g. McPherson *et al.* 2001; Newman 2003a), we do not yet know if this is true among kin-biased network structures of wild animals (but see Smith *et al.* 2010; Wey & Blumstein 2010; Wiszniewski *et al.* 2010; Wolf & Trillmich 2008). Within spotted hyena clans, dyadic patterns of association reflect social preferences (e.g. Holekamp *et al.* 1997a; Szykman *et al.* 2001; Smith *et al.* 2007). For example, patterns of association predict the extent to which hyenas engage in affiliative behaviours such as greeting and coalition formation (Smith *et al.* 2010, 2011). Hyenas are also most tolerant of close associates, withholding aggression from these group-mates both at and away from food (Smith *et al.* 2007). However, it remains unclear to what extent dyadic preferences generate subgroup cliques or communities, which in turn might structure the social group as a whole. Understanding such processes is important for identifying the levels of selection acting to maintain sociality in general, and cooperation in particular, among group-living animals (Croft *et al.* 2004; West & Gardner 2007). Moreover, many workers assume that relationships among individual members of vertebrate social groups reflect long-term strategic interests of individual group members (e.g. Silk *et al.* 2006a,b, 2010). Although such relationships should theoretically be resilient in the face of short-term fluctuations in ecological conditions, recent evidence has called this notion into question (Henzi *et al.* 2009). Instead, it is possible that individuals only base social preferences on the immediate value of the commodities offered by potential trading partners (e.g. Noë & Hammerstein 1994; Barrett *et al.* 1999). Furthermore, such effects have never been explored in mammalian carnivores. Here we applied social network theory to assess the dynamics and stability of kin associations among natal animals within our Talek study clan.

We inquired specifically about the extent to which members of distinct matrilines within hyena clans represent differentiated cliques or subgroups comprised of individuals who are more closely connected to one another than to members of other subgroups within the clan. Because maternal kin occupy similar social ranks (Fig. 1) and function as important social allies to one another (Engh *et al.* 2002; Wahaj & Holekamp 2006; Smith *et al.* 2010), we predicted that maternal kin would generally form stronger ties than non-kin within their social networks. Because feeding competition is

intense in this species and promotes the tendency for hyenas to spend time away from group-mates (Kruuk 1972; Tilson & Hamilton 1984; Frank 1986; Smith *et al.* 2008), we also expected that social relationships among hyenas would respond dynamically to changes in resource abundance. That is, hyenas should maintain the strongest ties with clan members when feeding competition is relaxed during periods of abundant prey, as indicated by our biweekly prey censuses.

Overall, our social network analysis revealed that the Talek clan is a dynamic social group comprised of kin-based subgroups, which in turn are comprised of individuals in multiple life-history stages. The strength of each hyena's ties within its social network decreased significantly as it progressed through each successive life history stage; this was particularly striking among natal males (Kruskal–Wallis test: $H_{2,395} = 161.2$, $P < 0.0001$, Fig. 8). On average, den-dependent cubs ($N = 136$) had significantly stronger ties to clan-mates than did den-independent subadults ($N = 151$) or natal adults (Fig. 8; $N = 108$, Mann–Whitney *U*-tests: $Z = -9.27$ and -11.1, respectively, $P < 0.00001$ for both). Moreover, subadults were more strongly connected to clan-mates than were adult hyenas ($Z = -9.27$, $P < 0.00001$). We detected no sex difference in strength of
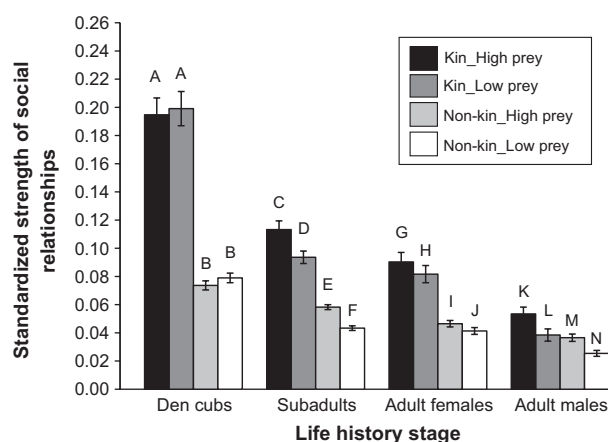

Fig. 8 Mean ± SE standardized strength of social relationships, a measure of the tendency for individual natal hyenas to associate with other natal hyenas. Relationships depicted are limited to those among natal animals that were concurrently alive with maternal kin (based on matriline membership) and non-kin during periods of low (February–May, October–January) and high (June–September) prey abundance as a function of each focal hyena's life history stage. Standardized strength among den cubs ($N = 136$) and subadults ($N = 151$) were statistically similar between the sexes, but adult females ($N = 62$) maintained stronger social ties than did adult natal males ($N = 46$) within their social networks. Immigrant males were excluded from this analysis. *Letters above bars* indicate statistically significant differences for matched comparisons (see text) after correcting for multiple testing at $P < 0.05$.

connections involving den-dwelling cubs (N_M = 70, N_F = 66) or subadults (N_M = 76, N_F = 75) within their social networks (Z = 0.77 and 1.88, P = 0.44 and 0.12, respectively), but adult females (N = 62) were significantly more strongly connected within the clan than were adult natal males (N = 46, Z = 4.34, P = 0.00001). Therefore, we pooled data from males and females for subsequent analysis involving cubs and subadults, but performed separate analyses for adults of each sex. In general, individuals in all three life history stages preferentially maintained social connections with maternal kin over non-kin (Fig. 8). That is, cubs, subadults, and adults were more strongly connected to maternal kin than to non-kin, as indicated by significantly greater standardized strength within, than between, matrilines ($Z \geq 0.49$, and $P \leq 0.000001$ for all cases).

In addition to kinship, prey abundance also influences inter-individual relationships among natal hyenas, as illustrated by the networks within a single ''cohort'' of natal animals from a year-long period (Fig. 9). This cross-sectional analysis extends the longitudinal data in Fig. 5, by showing that even after excluding den cubs, members of the alpha matriline still have far more kin available as social allies than do natal animals from low-ranking matrilines (Fig. 9). Importantly, despite the fission-fusion nature of their society, individual hyenas maintain stable group membership by fostering both direct ties to preferred companions (Fig. 8) and indirect ties to clan-mates with whom they rarely come into direct contact (Fig. 9).

Among both subadults and adults, but not among den-dwelling cubs, network dynamics varied predictably in response to variation in local prey abundance (Fig. 9). Both maternal kin (Z = 0.16) and non-kin (Z = 0.88) maintained strong ties with den-dwelling cubs irrespective of prey abundance (Wilcoxon Sign-Ranks Test: $P \geq 0.379$ for both, Fig. 8). However, both subadults and adults were more strongly socially connected to maternal kin during periods of relative prey abundance than during periods of prey scarcity (Wilcoxon Sign-Ranks Test: $Z \geq 2.58$ and $P \leq 0.01$ for all comparisons), and their connections to non-kin were also stronger during periods of high than low prey ($Z \geq 3.13$ and $P \leq 0.001$ for all). Thus subadults and adults were more strongly connected to clan-mates during times when competition for food was least intense; however, regardless of prey availability, they remained more strongly connected to their relatives than to non-kin.

Our finding that hyenas maintain differentiated relationships with preferred social companions throughout the year differs from that of Henzi *et al.* (2009), whose social network analysis of two cohorts of female chacma baboons (*Papio hamadryas ursinus*) suggested that companionships identified during times of food scarcity
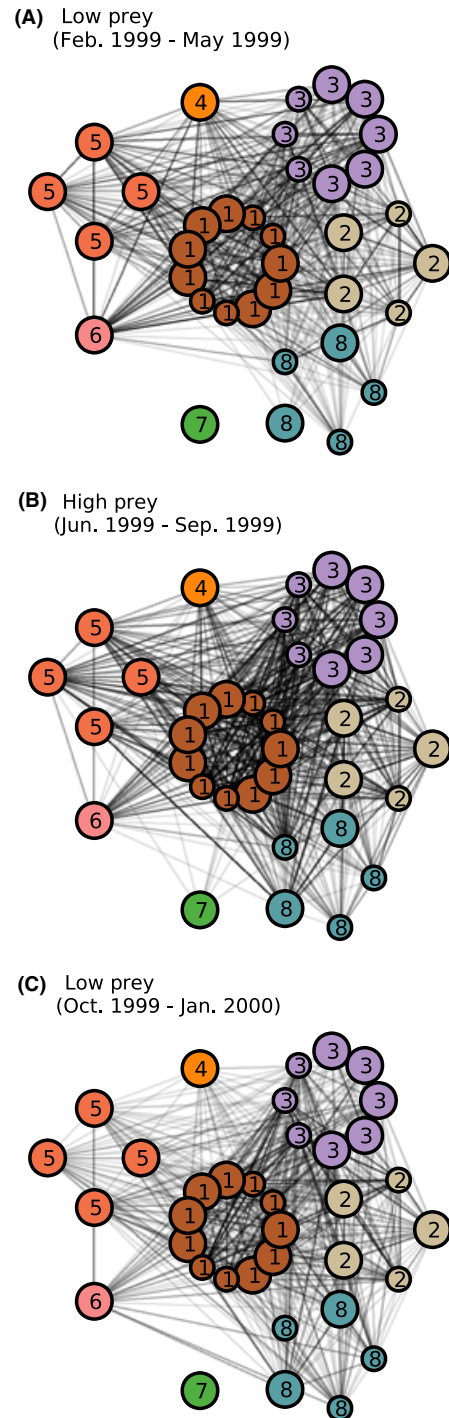

(A) Low prey
(Feb. 1999 - May 1999)

(B) High prey
(Jun. 1999 - Sep. 1999)

(C) Low prey
(Oct. 1999 - Jan. 2000)

Fig. 9 Variation in social networks within the Talek clan during periods of low (A and C) and high (B) prey abundance. Each matriline present in the clan during this 12-month period is assigned a unique number. The highest possible matriline rank is 1. Large nodes represent adults and small nodes represent subadults. *Line darkness* is directly proportional to the strength of the association index (tie) between each connected pair of hyenas. Den-dwelling cubs were not included in these networks because their relationships did not significantly vary between periods of low and high prey abundance (Fig. 8).

were replaced by casual acquaintanceships when food was plentiful, and that the strength of social relationships declined as food abundance increased. In contrast, our data demonstrate that hyenas were most strongly connected to social partners during periods when food was most abundant, indicating that social relationships among hyenas are constrained by feeding competition. Interestingly, in this respect, hyena networks more closely resembles those of honeybees (*Apis mellifera*) and European shore crabs (*Carcinus maenas*) than those of Chacma baboons. Among honeybees, network density increased with food abundance (Naug 2008). Similarly, in the otherwise non-social shore crab, partner number (node degree) and clique size increased when dispersed food was experimentally clumped (Tanner & Jackson 2011). Among spotted hyenas, the positive relationship between network density and prey abundance might be mediated either by improved payoffs from information exchange when food is abundant or by the stronger need to forage solitarily when prey are relatively scarce.

Conclusions and unanswered questions

Spotted hyenas live in large, complex societies structured like those of cercopithecine primates. As in the societies of many mammals, the social ranks of individual females have profoundly important fitness consequences, and rank in fact affects the persistence of entire matrilineal kin groups within hyena clans. Among other mammalian carnivores, in which group size is smaller than in our study groups, average *R* values may vary greatly within social groups, but average relatedness within groups is much higher than in spotted hyenas (e.g. Spong *et al.* 2002; Griffin *et al.* 2003; Baker *et al.* 2004; Dugdale *et al.* 2008). The greater variation in size of spotted hyena clans generates an exponentially greater variation in the number of dyads present per clan, and in the dyadic relatedness among individuals. Large clans are dynamic networks of relationships among individuals who may be very closely, or only very distantly, related to one another. Nepotism is common in hyena societies, and relationships among matrilineal kin are more affiliative, cooperative and stable than are relationships among individuals that are maternally unrelated (East *et al.* 1993; Holekamp & Smale 1993; Smale *et al.* 1993; Engh *et al.* 2000; Van Horn *et al.* 2004b; Wahaj *et al.* 2004; Smith *et al.* 2010). Consistent with this, we found here that maternal kinship is a critical determinant of network structure within hyena clans, and that the importance of maternal kin affiliations was clear even when social relationships were most severely constrained by ecological conditions.

In large hyena clans, mean relatedness among individual members is very low due to ubiquitous male dispersal and strong female preferences for immigrants as mates, as well as for males with which they have not mated previously. Although there are undoubtedly limits to the abilities of male hyenas to move across human-dominated landscapes, male-biased dispersal, low reproductive skew and great behavioural plasticity should help maintain viability of spotted hyena populations even within African national parks that have effectively become islands isolated from one another by dense human settlements and inhospitable agricultural landscapes. Although this needs to be determined empirically, if this hypothesis is correct, then despite their status as top predators, spotted hyenas might be expected to fare better in their struggle against extinction than other large carnivores with more restricted dispersal abilities, greater reproductive skew or less behavioural plasticity. Although the effects of increasing anthropogenic activity on demography, social relationships and genetic structure within clans and populations may be considerable, we have only recently begun to explore them (e.g. Pangle & Holekamp 2010; Holekamp & Dloniak 2010).

Many questions remain unanswered about society, demography and genetic structure in the spotted hyena. Our data suggest an important effect of chance in determining which subordinate matrilines persist over many generations. Although chance has been shown to play an important role in shaping the evolution of experimental laboratory populations (e.g. Travisano *et al.* 1995), we know very little about how chance affects fitness in free-living mammals. In addition to social rank, body size has recently been shown to influence fitness among female spotted hyenas (Swanson *et al.* 2011). However, it is not yet known whether size affects fitness in both sexes, nor how effects of larger body size are mediated to affect fitness in females. Finally, as is true in most mammals due to male-biased dispersal, lifetime data on reproductive success are much more difficult to obtain from male spotted hyenas than from females, so we know little about the contributions made by sons to their mothers' fitness. Although strong rank-related maternal effects are known to influence reproductive success among female spotted hyenas (e.g. Fig. 5), we know much less about maternal rank effects on males over the course of their lifetimes. Höner *et al.* (2010) recently presented data indicating that sons of high-ranking females enjoy greater reproductive success during their early years in their new clans than do their lower-ranking counterparts. However, the mechanisms mediating maternal rank effects on reproductive success among male hyenas are completely unknown.

Little is currently known about the mechanisms mediating variation in relatedness among clans within populations. We cannot assume that observed

movements of male hyenas translate directly into gene flow because several different variables might make observations unreliable indicators of genetic structure. Although a male may move from one clan to another, it is unclear whether he will achieve reproductive success in the new clan. Similarly, immigrants from distant clans may have different reproductive success than immigrants from neighbouring clans. Indeed, without looking at the genetic data it is impossible to know how male dispersal and reproductive success affect relatedness across clans. Roughly 40% of immigrant males are known to engage in secondary dispersal (Van Horn et al. 2003), but the effects of this behaviour on gene flow are unknown, as are the forces prompting established resident immigrants to move to yet another new clan. Although secondary dispersal might be expected among males with which females refuse to copulate, the basis on which females choose their mates also remains poorly understood in this species.

In spite of the low overall levels of relatedness among clan-mates, maternal kinship generates sub-groups of allies who cooperate to win in resource competition within clans. Even ubiquitous male dispersal and paternal gene flow can neither overwhelm the influence of female philopatry nor eliminate the potential indirect fitness benefits of cooperating with kin over unrelated clan-mates (Van Horn et al. 2004a). We do not currently know whether individuals with large networks of kin allies enjoy comparatively large fitness benefits over extended time periods, after controlling for effects of social rank. Nor do we know whether matrilineal kin groups with the strongest social relationships under each particular set of ecological conditions do better on average in the long-term than those whose members associate less closely. However, our data certainly suggest these as possibilities. Extinctions of entire matrilines during a period spanning less than 10 generations (Fig. 5) further suggest that strong selection may be operating on both individuals and kin groups within large clans. If so, then after controlling for family size and social rank, the most cohesive or most cooperative families might be expected to enjoy the greatest fitness, even when losses accrue to some individual family members as a result of their greater social cohesion, for example, due to resource losses or injuries during competition within matrilines over food. Furthermore, we might expect to be able to use network analysis to detect trade-offs between individual and family level adaptations in this and other gregarious species. It would be fascinating to determine, for example, whether matrilines such as the one descended from female F40 in Fig. 5 persist over multiple generations while others die out because social bonds among their members are unusually weak or strong, given its rank within the clan. In any case, there can be no doubt that the most significant and predictable subgroups within spotted hyena clans are matrilineal kin groups.

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Data accessibility

All data supporting the results in the paper are archived with Dryad as doi:10.5061/dryad.tg582.