SYMPOSIUM

Reproduction Within a Hierarchical Society from a Female's Perspective

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Synopsis The reproductive biology of many female mammals is affected by their social environment and their interactions with conspecifics. In mammalian societies structured by linear dominance hierarchies, such as that of the spotted hyena (*Crocuta crocuta*), a female's social rank can have profound effects on both her reproductive success and her longevity. In this species, social rank determines priority of access to food, which is the resource limiting reproduction. Due largely to rank-related variation in access to food, reproduction from the perspective of a female spotted hyena can only be understood in the context of her position in the social hierarchy. In this review, we examine the effects of rank on the various phases of reproduction, from mating to weaning. Summed over many individual reproductive lifespans, the effect of rank at these different reproductive phases leads to dramatic rank-related variation in fitness among females and their lineages. Finally, we ask why females reproduce socially despite these apparent costs of group living to low-ranking females. Gregariousness enhances the fitness of females regardless of their positions in the social hierarchy, and females attempting to survive and reproduce without clanmates lose all their offspring. The positive effects of gregariousness appear to result from having female allies, both kin and non-kin, who cooperate to advertise and defend a shared territory, acquire, and defend food resources, maintain the status quo, and occasionally also to rise in social rank.

Because social inequality is a common feature of mammalian societies, the costs and benefits of group-living are not borne equally by all group members (Clutton-Brock 2016). In particular, the reproductive biology of many female mammals is strongly affected by the social milieu in which reproduction takes place. In mammalian societies structured by linear dominance hierarchies, such as those of many primates and carnivores, a female's social rank can have profound effects on both her reproductive success and her longevity (e.g., Creel et al. 1997; Pusey et al. 1997). Whereas most other mammals live alone or with small numbers of kin, spotted hyenas (*Crocuta crocuta*) and cercopithecine primates, such as baboons, macaques, and vervet monkeys, live in large hierarchical social groups composed of both kin and non-kin, and these animals participate in many different types of relationships with their group-mates (Bergman and Beehner 2015). Alloparental care is minimal in these species, but all adult females breed; this requires females to navigate a complex social landscape in order to minimize the costs of group-living while also maximizing reproductive success. Females in these societies must make daily decisions regarding when and how to compete for key resources, as well as when and with which group-mates to cooperate to acquire or defend those same resources. Here we assess the causes and consequences of these decisions for female spotted hyenas.

Spotted hyenas are gregarious carnivores that live in stable fission-fusion groups, called "clans," containing up to 130 individuals (Kruuk 1972; Green et al. 2019). Each clan is structured by hierarchical

rank relationships (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986), and an individual's position in the clan's hierarchy determines its priority of access to resources. A hyena's social rank is not determined by its size or fighting ability (Engh et al. 2000); instead, rank is learned early in life in a fashion virtually identical to the associative learning process in primates that has been dubbed "maternal rank inheritance" (Frank 1986; Holekamp and Smale 1991, 1993; Smale et al. 1993; East et al. 2009; Maestripieri 2009). Aid from group-mates, especially the mother and other kin, is fundamental to the acquisition and maintenance of social rank (Engh et al. 2000; Smith et al. 2010; Strauss and Holekamp 2019; Vullioud et al. 2019). Individuals of both sexes maintain their maternal ranks as long as they remain in the natal clan. Because most males disperse whereas females are philopatric (Herischel and Skinner 1987; Smale et al. 1997; Van Horn et al. 2003), maternal rank effects endure at least until dispersal in males, and throughout the life span in females. All adult female spotted hyenas breed, and all are socially dominant to adult males not born in the clan (Kruuk 1972; Smale et al. 1993). However, females vary greatly in their reproductive success, with high-ranking females contributing far more progeny to future generations than their low-ranking counterparts.

Here we examine reproduction from the perspective of female spotted hyenas during different phases of reproduction, from mating to weaning and social independence. Crucially, all phases of reproduction are influenced by position in the social hierarchy and rank-related variation in feeding ecology, so we start by reviewing rank-related variation in access to food. Low-ranking female hyenas are severely handicapped by their low priority of access to food, and they therefore fare much worse than high-ranking females in the struggle to rear offspring. Disadvantages of low rank at all phases of reproduction accumulate to generate dramatic differences in the long-term reproductive success of females and their lineages. Finally, we inquire why low-ranking females do not simply choose to reproduce on their own, but instead settle for "making the best of a bad job" at the bottom of the female hierarchy. This review, which is the first to explore this question in spotted hyenas, suggests that despite the apparent costs of gregariousness to low-ranking females, it nonetheless has positive effects on their ability to reproduce successfully.

Access to food

Contrary to popular belief, spotted hyenas are efficient predators that consume mainly medium- and large-bodied antelope they kill themselves (Kruuk 1972). None of the other extant hyaenids routinely hunt large mammalian prey, so the spotted hyena is unique in this regard. Although spotted hyenas descended from carrion-feeding ancestors (Werdelin and Solounias 1991; Lewis and Werdelin 2000), the extant animals are excellent hunters who successfully hunt and kill up to 95% of the prey they consume (Holekamp and Dloniak 2010). An adult spotted hyena can single-handedly bring down an antelope weighing three to four times its own body mass. Several hyenas usually join forces to hunt difficult prey like zebra, giraffe, or buffalo, but more common prey like gazelle and wildebeest are typically hunted by one or two individuals (Holekamp et al. 1997b; Smith et al. 2008).

Spotted hyenas typically spend far more time looking for food than consuming it. On average, hyenas in our study population in Kenya feed for only 9.2 min during each 24 h period, whereas they spend roughly 4.8 h traveling around the clan territory in search of food (Kolowski et al. 2007). Prey animals are hard to catch, but represent large, ephemeral packets of energy-rich food occurring unpredictably in space and time. After one or more hyenas kill an antelope, many other hyenas typically converge on the carcass, compete aggressively for the food available there, and feed extremely rapidly. A group of hungry hyenas can make a large antelope disappear entirely in as little as 13 min (K.E. Holekamp, personal observation). With several individuals attempting to ingest as much food as possible while anything remains of the carcass, feeding competition among hyenas at kills is very intense (Kruuk 1972; Frank 1986). Access to each carcass is determined by social rank, with high-ranking individuals using aggression to displace lower-ranking hyenas (Fig. 1), so status has profound effects on hyenas' intake of calories and nutrients at ungulate kills (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986; Mills 1990; Höner et al. 2002; Smith et al. 2008). To avoid direct competition with their higher-ranking clan-mates, subordinate females are far less likely than their dominant counterparts to forage in the central prey-rich areas of the clan's territory; instead, they forage further afield, sometimes far outside their clan's defended territory (Boydston et al. 2003; Green and Holekamp 2019). As a result, time and energy budgets differ markedly between high- and low-ranking females (Kolowski et al. 2007). In hyena populations where females often hunt migratory antelope far 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 and East 1993a, 1993b).
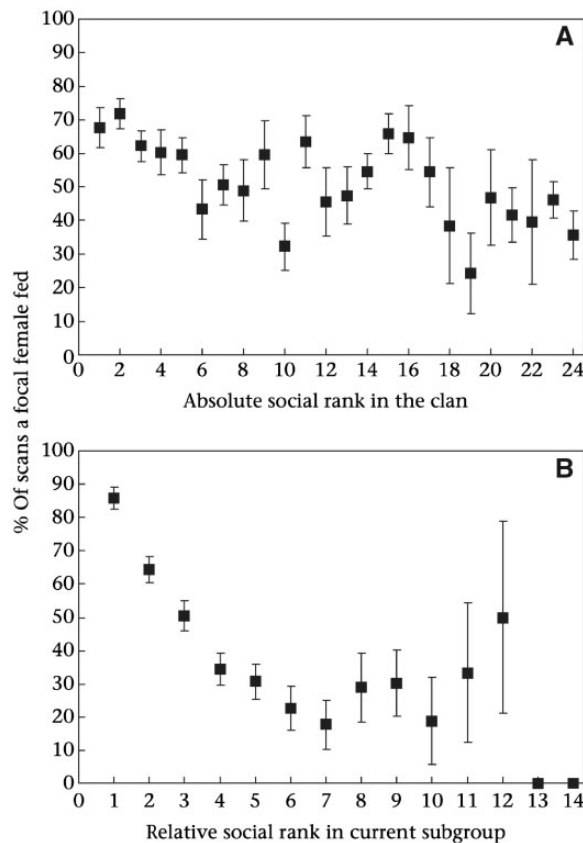
Fig. 1 Rank-related variation in feeding behavior at kills: (**A**) the relationship between food intake and a female's absolute rank in the clan, whereas (**B**) the relationship between food intake and a female's rank relative to other females feeding with her at kills. Reproduced with permission from Smith et al. (2008).

Reproductive sociobiology of female spotted hyenas

Virtually every aspect of reproduction among female spotted hyenas is affected by both food availability, indicated by local prey abundance, and social rank. We have monitored both prey abundance and hyena reproduction for over three decades in Kenya, so here we review food and rank effects on mating, parturition, lactation, weaning, and the transition of offspring to social independence.

Mating

Mating occurs most frequently when prey are abundant (Holekamp et al. 1999). High-ranking females are much more attractive to males as prospective mates than are lower-ranking females (Szykman et al. 2001). The males who associate with a particular female are likely to sire her offspring, and the offspring of dominant females are much more likely to live longer than offspring of low-ranking females (Watts et al. 2009). This suggests that the preferences expressed by breeding males for high-ranking

females are adaptive, although we do not currently understand how males recognize the relative ranks of adult females. Furthermore, sons of higher-ranking females may find it easier to integrate themselves into new clans after dispersal, they may enjoy greater success at securing mating opportunities (Boydston et al. 2005; Höner et al. 2010), and they may even perform elements of the act of mating itself more effectively (e.g., mounting or intromission: Drea et al. 2002; Dloniak et al. 2006) than do sons of low-ranking females. After all, spotted hyenas are the only female mammals lacking an external vaginal opening, so the mating act is unusually demanding for males.

The clitoris of the female spotted hyena is enormously elongated such that it closely resembles the male's phallus; it is a fully erectile structure through which the female urinates, copulates, and gives birth (Glickman et al. 2006). In contrast to most other male carnivores, the male spotted hyena lacks a penile bone so he can cope with the female's odd genitalia by inserting his penis into the downward and forward-facing genital meatus of the female's flaccid clitoris. The absence of a baculum is the ancestral condition among the Hyaenidae; it is absent in all living species and in the fossil record of the Hyaena family (Werdelin and Solounias 1991). The unusual genitalia of the female spotted hyena are unique; even females of other Hyaenid species have unremarkable genitalia. Although mating occurs through the female spotted hyena's enlarged clitoris, it is nevertheless very difficult for males, particularly inexperienced ones, to achieve intromission. The female's unusual genitalia give her complete control over mating, such that coercive sex is impossible in this species (East and Hofer 1997).

Parturition

Although spotted hyenas bear young throughout the year, they exhibit a moderate degree of seasonality in births that reflects responses to seasonal variation in energy availability (Holekamp et al. 1999). Females usually give birth in secluded natal den holes to litters of one or two offspring 110 days after fertilization (Kruuk 1972). Giving birth to a 1 kg cub through the elongated clitoris involves its tearing, and some cubs suffocate during this process (Frank et al. 1991). Visible scar tissue on a young adult female's clitoris indicates that she has borne her first litter.

The age at which females first bear young is strongly correlated with maternal rank, with daughters of the alpha female experiencing their first
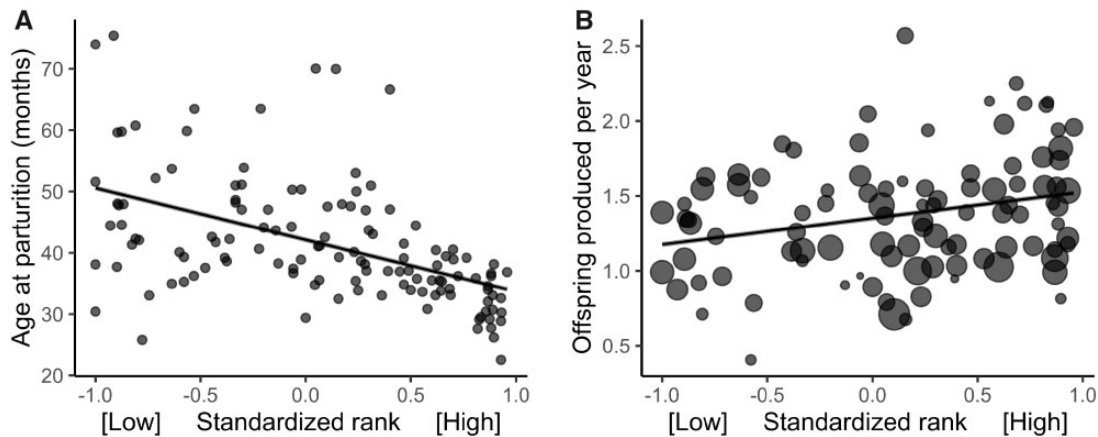
Fig. 2 Rank-related variation in (**A**) age at which first parturition occurs and (**B**) number of offspring produced per year. Size of points in (**B**) corresponds to the duration of reproduction for each hyena depicted here. Some individuals are still alive, so these do not all represent full reproductive lifespans. Twenty five years' worth of new data appear here that were not included in similar figures in Holekamp et al. (1996).

parturition at around 2–3 years of age, and daughters of the lowest-ranking females at 5–6 years of age (Fig. 2A; Holekamp et al. 1996; Hofer and East 2003). Although social rank does not affect litter size in hyenas, inter-litter intervals are much shorter in dominant than in subordinate females, and dominants are more frequently able to support both pregnancy and lactation concurrently, so annual rates of cub production are highest among high-ranking females (Fig. 2B; Holekamp et al. 1996).

The mother keeps her cubs at the natal den for the first 2–3 weeks before moving them to the communal den. Natal dens used by subordinate females tend to be located substantially further from the clan's communal den than do those of dominant females (White 2005; Boydston et al. 2006); because some cubs are lost during maternal transport between natal and communal dens, the greater distances lower-ranking females must carry their cubs increases exposure of their cubs to danger.

Lactation

For ~6 months spotted hyena cubs depend entirely on highly nutritious milk containing concentrated fat and protein (Hofer and East 1995). On average, cubs are weaned at ~13 months of age (range: 8–24 months, Hofer and East 1995; Holekamp et al. 1996). Each clan's territory contains at least one active communal den site, where females rear their offspring together (Kruuk 1972; East et al. 1989; Boydston et al. 2006). Because they need to nurse their cubs frequently, female spotted hyenas shift at parturition from being free-ranging to central-place

foragers, using the den as the central place to which they must frequently return.

The energetic cost of lactation is rank-dependent in spotted hyenas. Because low-ranking females have lower priority of access to food than dominant females, they often expend considerably more time and energy traveling longer distances to forage (Hofer and East 1993a; Green and Holekamp 2019). Subordinate adults are also obliged to hunt at higher hourly rates than are dominants, and subordinates tend to hunt in smaller groups, presumably to minimize feeding competition if a prey animal is killed (Holekamp et al. 1997b). Low-ranking hyenas also spend more time being vigilant at kills than do dominant individuals, and less time feeding (Frank 1986; Pangle and Holekamp 2010).

As a result of rank-related variation in access to food and costs of foraging, subordinate females are less able to attend and nurse their cubs than dominant females (Hofer and East 1993a; Greenberg 2019). This is particularly so in populations that experience large fluctuations in local prey abundance (Hofer et al. 2016), where long-distance commuting is especially costly to lactating females (Goymann et al. 2001). When their mothers commute to feed, dependent cubs may fast for up to 9 days (Hofer and East 1993c). Maternal social status, local prey abundance, and maternal absences while foraging interact to determine the occurrence and intensity of rivalry between members of twin litters for access to maternal teats (Golla et al. 1999; Benhaiem et al. 2012). When they do attend the den, low-ranking females are sometimes denied access to the den hole by their higher-ranking groupmates (White 2007). This rank-related variation in nursing affects the dynamics of

milk transfer from mothers to their young (Hofer et al. 2016). Females increase milk gross energy density and nursing bout duration as nursing frequency declines (Hofer et al. 2016). In addition to the obvious direct effects of low rates of den attendance and poor access to resources on cub growth and survival, these factors may indirectly influence other aspects of cub development. For example, personality development and stress-reactivity in adulthood are both affected by rank-related variation in maternal behavior (e.g., Greenberg and Holekamp 2017; Laubach 2019).

Weaning and social independence

With help from their mothers, high-ranking cubs have access to a larger quantity and higher quality of solid food at weaning than do their low-ranking peers. While cubs are dependent on the den for shelter, the rates at which females return to dens from kills carrying leftover food items for their cubs increases with maternal rank, and the highest-ranking females are also most successful at ensuring their cubs have access to provisioned foods at dens (Holekamp and Smale 1990). After cubs leave the den, dominant mothers are more successful than subordinate females at helping their cubs gain access to ungulate carcasses (Holekamp and Smale 1990). The rank-related variation in cubs' ability to access food has striking effects on cub growth rates (Hofer and East 1996, 2003), with high-ranking cubs growing much faster than their low-ranking peers (Fig. 3). Dominant females can also wean their cubs at much younger ages than can subordinate females (Frank et al. 1995; Holekamp et al. 1996).

Offspring of high-ranking females grow up in a very different social environment than do cubs of low-ranking females, and this environment effectively creates opportunities for expression of behavior in high-ranking juveniles that are unavailable to lower-ranking peers. Dominant cubs associate much more closely with their mothers and other kin than do subordinate cubs, and females from high-ranking matrilines associate more closely with one another than do females of low rank (Holekamp et al. 1997a). Dominant females tend to be more gregarious in general, and they are more attractive social companions, than are subordinate females (Smith et al. 2007), so they occur with their cubs in subgroups of larger mean size than do low-ranking females. Because survivorship is better among dominant than subordinate hyenas (Watts et al. 2009; Strauss et al. 2020), high-ranking females tend to have many more surviving kin in

Fig. 3 Female cubs of adult female hyenas ranking 1st and 19th of 19 adult females present in the clan at that time. The daughter of the alpha female is considerably larger than the other cub, even though they were born only 4 days apart in July 1989. This photograph was taken when both cubs were 6 months old, and clearly shows a dramatic difference in growth rate between the two cubs. Photo by Laura Smale.

the population at any given time than do lower-ranking females, and they thus enjoy much larger networks of potential allies, should the need for those arise (Van Horn et al. 2004; Smith et al. 2010; Ilany et al. 2015; Ilany and Akçay 2016; Turner et al. 2018). Social rank has stronger effects on the development of social network positions in female than male hyenas (Turner et al. 2018). Females and males have different trajectories of social development that appear to prepare them for their respective futures of integrating into their natal clan or dispersing to a new one.

Fitness consequences of rank related variation in reproduction

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 study population (Holekamp and Smale 2000). Long-term monitoring of one clan in the Talek region of Kenya over a period of 40 years reveals that rank-related variation among female hyenas in reproductive success and survival has profound fitness consequences (Fig. 4), with most of 19 matrilines present in 1979 becoming extinct within 20 years, and all but four becoming extinct in only 30 years. In 2019, over 60% of the adult females present in the Talek clan
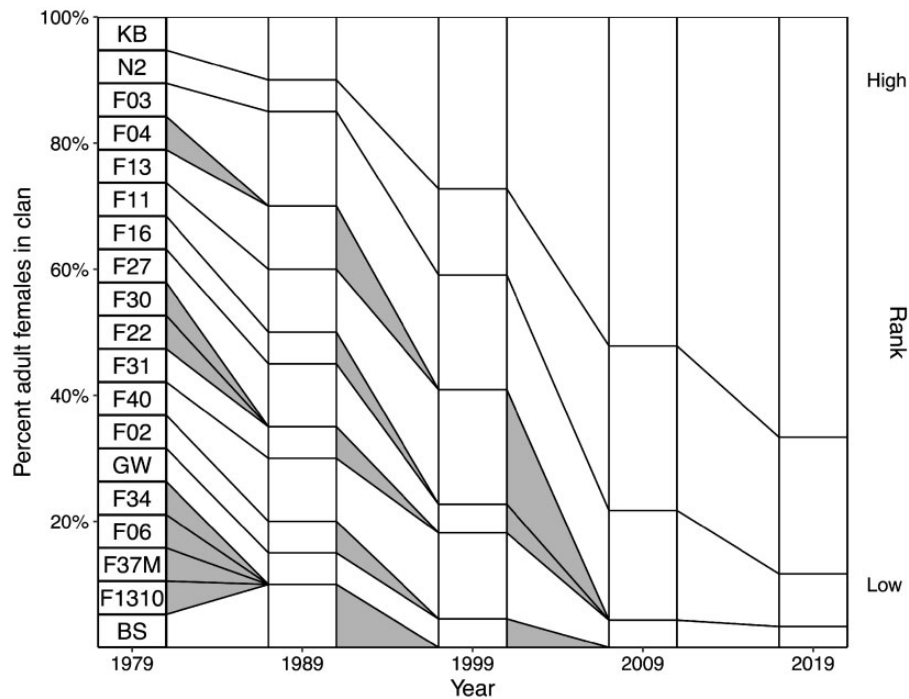
Fig. 4 Fitness consequences of social rank among female spotted hyenas over four decades. Representation among the adult female member of the Talek clan by descendants of the original 19 adult females present in the Talek clan in 1979, when L. G. Frank began his doctoral research with them. Note that, of the 19 females present in 1979, only 4 have surviving female descendants in the clan 40 years later. The gray triangles represent the extinction of entire matrilines. A fourth decade of data appear here that were not included in a similar figure in Holekamp et al. (2012). The data for 1979 were compiled from Frank (1983).

were direct descendants of the female who held the alpha position 40 years earlier (Fig. 4).

Why don't low-ranking females leave the group to reproduce on their own?

Although female dispersal is rare in spotted hyenas, subordinate females do occasionally disperse in groups during permanent clan fission events, when a single parent clan splits into two or more daughter clans (Holekamp et al. 1993; Höner et al. 2005). We have observed four permanent clan fission events, in 1989, 2002, 2016, and 2019, and many low-ranking females improved their social status when they engaged in these mass-emigration events. However, all cubs died that were born to those few low-ranking females who tried to survive with their cubs either by becoming nomadic with them or spending most of their time in the no-man's land between clan territories. Without clan-mates, the reproductive success of female spotted hyenas is invariably extremely low, and in fact gregariousness enhances the survival of female spotted hyenas of all social ranks (Fig. 5; Yoshida et al. 2016). Indeed there are several different aspects of a hyena's life in which it often needs help from clan-mates to succeed, such

that maintenance of the social bonds between females, in particular, can become a matter of life and death.

Even low-ranking females get by with a little help from their friends

What, then, are the benefits gained by females from maintaining social bonds with their clanmates? These benefits accrue in the domains of cooperative hunting of difficult prey, defense of the clan's territory, defense of carcasses, acquisition of carcasses from both intra- and inter-specific competitors, and formation of coalitions, which usually facilitate maintenance of the status quo, but which occasionally result in rank reversals and thus improve social status.

Cooperative hunting of difficult prey

As with lions, it has been hypothesized (e.g., Kruuk 1972; Tilson and Hamilton 1984) that spotted hyenas live in groups because cooperative hunting allows these animals to capture larger prey animals or enhance their hunting success, as occurs in pack-hunting canids (e.g., Creel and Creel 1995). However, although cooperative hunting does
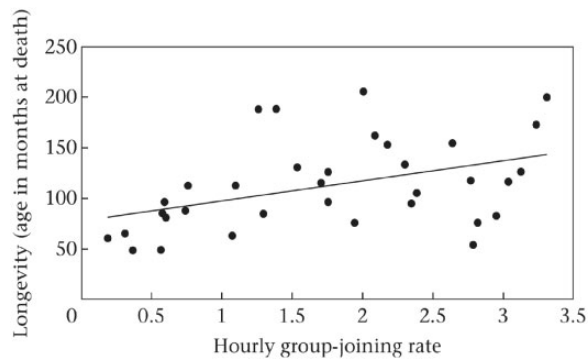
Fig. 5 After controlling for rank, gregariousness enhances fitness in female spotted hyenas. Here, gregariousness is represented by the tendency of individual females to join groups of other females when given a choice of whether or not to do so. Generalized linear model: $t_{31} = 2.695$, $P = 0.011$. Reproduced with permission from Yoshida et al. (2016).

increase the probability of success and allows spotted hyenas to capture larger prey animals, 75% of successful hunts are conducted by lone hyenas (Holekamp et al. 1997b), and only the largest and most challenging of prey species require more than one hyena for a successful hunt (Kruuk 1972; Holekamp et al. 1997b). Difficult prey for spotted hyenas include large-bodied herbivores such as buffalo, hippo, and giraffe, as well as zebra, which are challenging targets for hyenas because of the behavior with which each zebra stallion defends his harem of mares (Kruuk 1972). Consequently, mean hunting group sizes for zebra are 9–11 (Kruuk 1972; Holekamp et al. 1997b). Addition of a second hunter increases the probability of hunting success for any prey by 19% (Holekamp et al. 1997b); nevertheless, average subgroup size during hunting is significantly smaller than the mean subgroup size documented in any other context (Smith et al. 2008). The ancestral bone-cracking hyenas were strict carrion-feeders (Werdelin and Solounias 1991), and carrion simply cannot support large social groups of carnivores (e.g., Jones et al. 2015). Thus, as during the evolution of pride-dwelling lions from solitary felid ancestors (Packer et al. 1990; Mosser and Packer 2009), cooperative hunting was probably not paramount in the evolution of gregariousness in spotted hyenas, although assistance during hunts clearly represents a beneficial side-effect of group living. Instead, the need to defend spatial and food resources from competitors most likely favored the evolution of gregariousness among female hyenas. Most importantly, as in many other gregarious carnivores (e.g., lions, Packer et al. 1990; coatis, Gompper 1996; European badgers, Kruuk and Parish 1977), per

capita rates of food intake generally increase when individual hyenas separate from clan-mates to feed alone (Smith et al. 2008).

Territory defense

Each clan of spotted hyenas occupies a territory over which move herds of their prey, and the herbivores killed by spotted hyenas represent abundant and readily renewable food resources that allow these hyenas to reach high population densities. In parts of Africa where hyena population density is moderate or high, spotted hyenas advertise and defend group territories against encroachment by neighboring conspecifics (Henschel and Skinner 1991). Territories of neighboring clans in these areas generally overlap little or not at all, and group members often scent-mark to advertise territory boundaries. Advertisement is typically undertaken via "border patrols" and deposition of feces in "latrines" along territory boundaries. Aggressive territory defense occurs during "wars" with neighboring clans (Kruuk 1972). Some of the largest groups formed in the fission-fusion society of spotted hyenas are found during border patrols and clan wars (Smith et al. 2008). Most cooperative territorial behaviors are initiated and led by adult female clan members (Smith et al. 2015), and females engage in considerably more scent-marking behavior on border patrols than do males (Boydston et al. 2001).

Because female hyenas are philopatric and require exclusive access to the food available within the territory, they stand to lose more than males from alien intrusions into their territory (e.g., Henschel and Skinner 1991; Heinsohn and Packer 1995). Females attempting to make it on their own or with their current litters away from their natal territories are quickly chased out of other areas by resident hyenas, and females that are absent for long periods receive extreme aggression from their clanmates upon return (Holekamp et al. 1993). Because the outcome of clan wars is determined by the number of participants from each warring clan, territory defense by lone females is impossible. Effective maintenance of group territories also requires that unrelated individuals from multiple matrilines join forces during cooperative defense against neighboring hyena clans (Van Horn et al. 2004). Loss of a clan war can result in substantial reduction in the area of a clan's territory, and repeated losses can further result in overall loss of the territory to a neighboring clan.

Defense and acquisition of carcasses

Spotted hyenas often live and hunt in open habitat where competitors can easily detect kills, which are

typically ephemeral and usurpable food sources that are too large to be monopolized by a single individual. These conditions appear to have favored group-living by females to protect individual prey carcasses. Fresh kills are often contested by intra- and interspecific competitors such as lions or members of neighboring hyena clans (Kruuk 1972; Henschel and Skinner 1991; Lehmann et al. 2017), and hyenas participating in these contests risk injury to themselves and their young. Defense of any but the smallest of carcasses by lone hyenas is impossible in the presence of two or more challengers. As with clan wars, outcomes of contests over specific carcasses are usually determined by the number of participants on each side of the contest.

In addition to being their direct competitors, lions also represent a leading mortality source for spotted hyenas (Kruuk 1972; Mills 1990; Watts and Holekamp 2009). Spotted hyenas can usually only defend food successfully from lions when the ratio of hyenas to lions is high (Kruuk 1972; Cooper 1991). Because lions are three to five times larger than hyenas, the resource holding power of a single lion exceeds that of a single hyena (Kruuk 1972; Cooper 1991; Höner et al. 2002). To counteract this asymmetry in size, spotted hyenas frequently cooperate to mob lions, approaching the lions as a tightknit group while vocalizing loudly in an attempt to overwhelm them and drive them away. Lions and hyenas interact most often at fresh kills, especially as prey size and the number of hyenas present increase (Lehmann et al. 2017). Possession of food at the beginning of an interaction positively affects retention of that food by each predator species. The presence of male lions increases the probability of an interspecific interaction but decreases the likelihood of hyenas obtaining or retaining possession of the food. The occurrence of mobbing is predicted by increasing numbers of hyenas present. Whether or not mobbing results in acquisition of food from lions is predicted by more mobs formed by the hyenas present with the lions, suggesting that this form of cooperation among low and high-ranking hyenas enhances their fitness (Lehmann et al. 2017).

Both high- and low-ranking hyenas benefit from cooperative partnerships with clanmates (Kruuk 1972; Cooper 1991; Boydston et al. 2001). Subordinate females who associate more often with dominant females receive relatively low hourly rates of aggression both away from food and at kills, and they also gain relatively good access to food (Smith et al. 2007). High-ranking females can provide effective coalitionary support to subordinates during within-group contests over food (Frank 1986;

Smale et al. 1995; Engh et al. 2005). These findings suggest that females minimize the costs of group living by initiating social interactions with conspecifics that outrank them, and by forming relationships likely to offer them return benefits in a variety of ways. In exchange for food access made available by dominant females, subordinates join dominants in defense of resources from conspecifics and lions.

Defense or improvement of social status

Coalition formation, also called agonistic aiding, occurs when group members join forces to attack other members of their own social group. Agonistic aiding is beneficial to the recipient, as it increases the recipient's likelihood of winning the fight. Because the outcomes of coalitionary interactions can affect the social ranks of individual group members, and because rank determines priority of access to food, coalition formation can have profound fitness consequences for all participants (Seyfarth 1977; Wrangham 1980; Sterck et al. 1997; Isbell and Young 2002). Females benefit directly by providing support when doing so reinforces their rank positions in the dominance hierarchy (Smith et al. 2010). Over 93% of coalitionary interactions in which two adult females attack a third are directed down the hierarchy (Strauss and Holekamp 2019), so maintenance of the status quo is clearly an important function of coalitionary aggression (Smith et al. 2010). The 7% of coalitionary attacks among triads of adult females directed up the hierarchy are typically associated with active rank changes, where females reverse previously held rank relationships (crossing lines in Fig. 6; Strauss and Holekamp 2019). A female overtaking a clan-mate is likely, not only to increase her lifetime reproductive success, but also to increase the average rank and fitness of her future offspring, who will inherit her new status through the typical process. Females, including low-ranking ones, who are strongly allied with their group-mates are more likely to improve their status than are females with weaker social bonds (Strauss and Holekamp 2019).

Conclusion

Although group-living has many costs for low-ranking female spotted hyenas, primarily associated with their inferior ability to feed competitively at kills, gregariousness nevertheless permits them to succeed at rearing young, albeit at a slower rate than high-ranking females. In contrast, all females inevitably fail who attempt to raise cubs outside their natal territory on their own. Of several females who
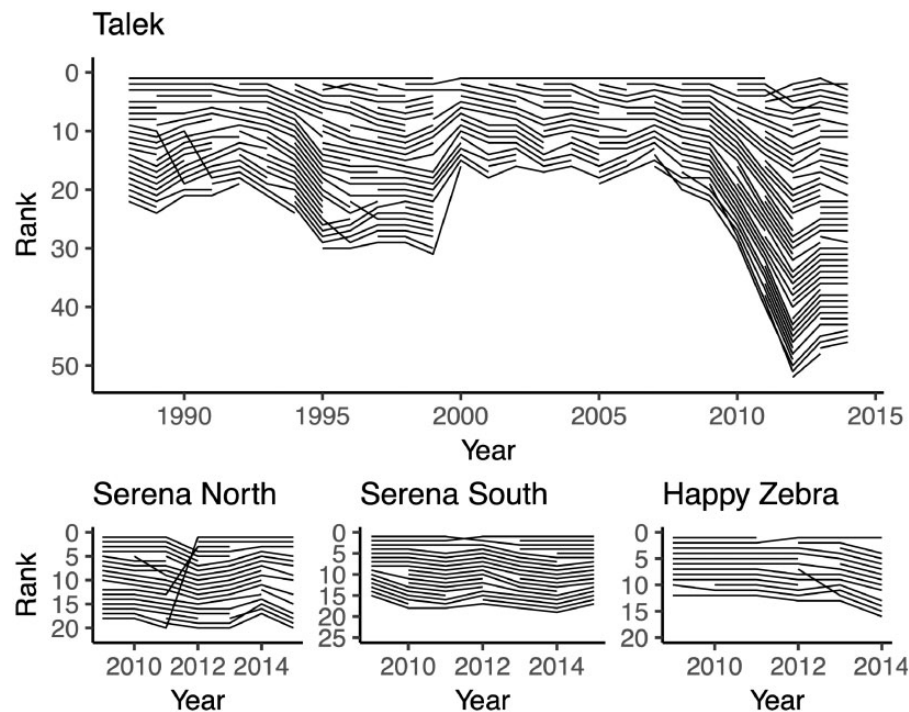
Fig. 6 Yearly ranks of each female in each of four study clans in Kenya. Variation in the number of lines per diagram reflects temporal variation in clan size. Crossing lines indicate rank reversals. By convention, lower numbers indicate higher ranks, where the highest rank is one, and lower ranks have higher numbers. The Talek clan was observed here from 1988 to 2015, but the other three clans were only observed from 2008 to 2015. Note that the Talek clan grew to enormous size starting in 2008. Reproduced with permission from Strauss and Holekamp (2019).

have tried this over the past 40 years in our study population, none have succeeded. Furthermore, benefits of bonding with clanmates accrue to females from cooperative hunting, resource defense, acquisition of carcasses from intra- and inter-specific competitors, and formation of coalitions. These benefits evidently have positive effects on the fitness of females of all social ranks, causing most females to accept the status quo and make the best of a bad job in their natal territory.

Data availability

The new data and code underling this article are available at github.com/MaraHyenaProject doi:10.5281/zenodo.3877278.

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