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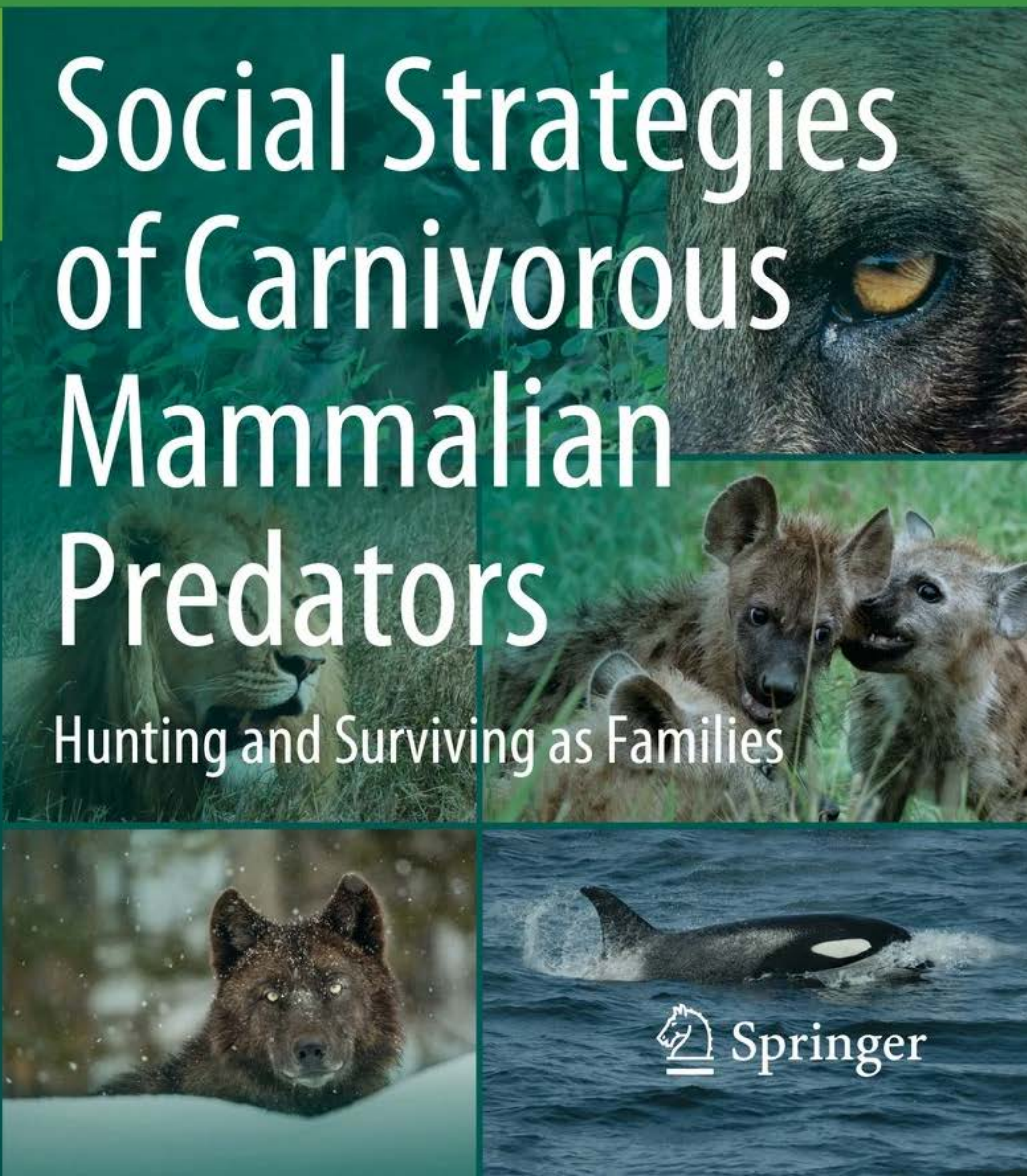
Social Strategies of Carnivorous Mammalian Predators

Hunting and Surviving as Families



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Chapter 5
Hunting Success in the Spotted Hyena: Morphological Adaptations and Behavioral Strategies

Jennifer E. Smith and Kay E. Holekamp

Abstract Once considered mere scavengers, it is now widely recognized that hunting is more important than scavenging in the feeding ecology of spotted hyenas (*Crocuta crocuta*). In this chapter, we outline the extraordinary morphological and behavioral adaptations possessed by these bone-cracking hyenas for efficient hunting and foraging within the context of their complex social organization. These social carnivores live in female-dominated societies structured by fission-fusion dynamics in which individuals hunt alone or in small groups to avoid feeding competition but join forces in large-scale cooperation with kin and non-kin groupmates to defend food from African lions (*Panthera leo*) and members of neighboring groups of hyenas. We discuss how social rank and age influence every aspect of their hunting behavior and consider the inevitable trade-offs faced regarding cooperative hunting of ephemeral prey. Finally, we evaluate what is known about the cognitive demands and conservation implications associated with the behavioral flexibility possessed by these efficient hunters.

Keywords Cooperative hunting · Cursorial hunting · Dominance · Fission-fusion dynamics · Feeding competition · Group hunting · Lion · Ontogeny · Prey · Spotted hyena (10 listed, 5–10 requested)

The original version of this chapter was revised: Fig. 5.17 and Fig. 5.18 have been swapped to correspond to their captions. The correction to this chapter is available at
https://doi.org/10.1007/978-3-031-29803-5_10

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M. Srinivasan, B. Würsig (eds.), *Social Strategies of Carnivorous Mammalian Predators*, Fascinating Life Sciences, https://doi.org/10.1007/978-3-031-29803-5_5

Artistic rendering and illustrations by Britney Danials

My decision to study the social lives of spotted hyenas—rather than those of lions—was largely shaped by what started as a typical morning in Kay Holekamp's hyena camp in Kenya. We woke up before the sun for a quick cup of coffee and then drove into the darkness of the Massai Mara Reserve. At 6:28 am, roughly an hour into our morning observations, the African sunrise had faded, and we came upon a lone, immigrant male spotted hyena, Lebowski. He was running along the horizon and testing a herd of wildebeest. By 6:30 am, much to our surprise, he managed to grab onto the hind leg of one adult female wildebeest and bring it down to the ground. Shortly after that, Lebowski started to bite at its stomach and disembowel it. However, this wildebeest was not going down without a fight. By 6:36 am, she emerged on her feet and pushed Lebowski away with her horns before falling down. She attempted to stand up again at 6:39 am. The struggle continued for several minutes. By 6:42 am, Lebowski attempted to feed again. But, at 6:45 am, the wildebeest stood up again and took one final step before taking its final breath. Lebowski fed first on its liver and spleen before moving onto the other organs. This *was a magnificent triumph, given that Lebowski only weighed roughly 100 pounds (48 kg) and his prey weighed roughly three times that. In the distance, another spotted hyena vocalized (whooped), and a lion roared a minute later, but Lebowski continued to quietly eat. By 7:00 am, his stomach was fully distended, and Lebowski had consumed nearly one-third of his own body mass! As I would soon learn, although this hunt was not particularly graceful, finding a male hunting away from members of his group was common. Male hyenas often hunt and eat quietly on their own because females and their offspring are socially dominant to (and can easily usurp food from) immigrant males. Given all of this, I was left to wonder how anyone could ever have mistaken these socially complex and efficient hunters as mere scavengers. – Jennifer Smith*

5.1 Introduction

Once considered mere scavengers in popular culture, Hans Kruuk's (1966, 1972) seminal research surprised many biologists by demonstrating that hunting is more important than scavenging in the feeding ecology of spotted hyenas (*Crocuta crocuta*, Fig. 5.1). Spotted hyenas are efficient hunters that directly kill 43–95% of the food they eat (Holekamp & Dloniak, 2010), typically scavenging one-third or less of their diets from other large carcass-producing hunters (Kruuk, 1972). Since this groundbreaking revelation, dozens of subsequent studies have further confirmed the central role of hunting behavior in the lives of these efficient predators (Bearder, 1977; Cooper, 1990; Hayward, 2006; Henschel, 1986; Henschel & Skinner, 1990; Henschel & Tilson, 1988; Hofer & East, 1993; Holekamp et al., 1997; Mills, 1990; Smith et al., 2008; Smuts, 1979, Tilson et al., 1980).

Unlike the other species in the family Hyaenidae (e.g., striped [*Hyaena hyaena*] or brown [*Parahyaena brunnea*] hyenas), spotted hyenas regularly hunt medium- and large-sized ungulates on their own or with other members of their social group (Cooper, 1990; Hofer & East, 1993; Kruuk, 1972; Mills, 1990; Smith et al., 2008; Tilson & Hamilton, 1984). Spotted hyenas can even capture large ungulates, such as eland (*Taurotragus oryx*) weighing around 500 kg (Mills, 1990). A comprehensive meta-analysis (Hayward, 2006) confirmed several major findings regarding the hunting behavior of spotted hyenas, including that they are efficient hunters capable of killing at least 30 different prey species. Data from 3478 kills reported across 15 studies collected in six countries, capturing the full geographic distribution of spotted hyenas, suggest that spotted hyenas capture virtually every prey species available to them except for adult African elephants (*Loxodonta africana*, Fig. 5.2, Hayward, 2006), although spotted hyenas do prey upon new-born elephant calves in Zimbabwe (Salnicki et al., 2001). Notably, the Hayward (2006) study lacks information on other potential prey species such as hippo (*Hippopotamus amphibious*),

Fig. 5.1 Spotted hyenas are efficient predators able to capture prey exceeding their own body size such as wildebeest and oryx. Individual spotted hyena hunters capture most ungulate prey items when hunting alone or in pairs, but some prey, such as plains zebra, may only be taken down cooperatively (photos by Jennifer Smith, Gus Mills, and Joey Verge)

rhino (*Rhinoceros* spp.), and sable antelope (*Hippotragus niger*) in Kruger (Henschel & Skinner, 1990) and steenbok (*Raphicerus campestris*), duiker (*Sylvicapra grimmia*), springhare (*Peripatopsis capensis*), and Cape hare (*Lepus capensis*) in the Kalahari (Mills, 1990).

At sites for which the following prey species were available, spotted hyenas successfully hunted impala (*Aepyceros melampus*, 11 studies), Thomson's (*Eudorcas thomsonii*) and Grant's gazelles (*Nanger granti*, six studies), Cape bushbuck (*Tragelaphus sylvaticus*, four studies), springbok (*Antidorcas marsupialis*, three studies), and gemsbok (also called oryx, *Oryx gazella*, three studies, Hayward, 2006). They also commonly hunt Greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (also called gnu, *Connochaetes taurinus*), hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnus*), and Cape buffalo (*Syncerus caffer*, Hayward, 2006).

A single spotted hyena commonly captures prey weighing roughly 100 kg (220 lb.), a mass that far exceeds its own since a typical adult spotted hyena weighs from 45 to 70 kg (90–150 lb., Hayward, 2006). Cooperative hunting permits spotted hyenas to capture even the most difficult prey, such as plains zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), and gemsbok, which may involve 20 or more individuals joining forces to chase prey for up to 4 km and at speeds reaching up

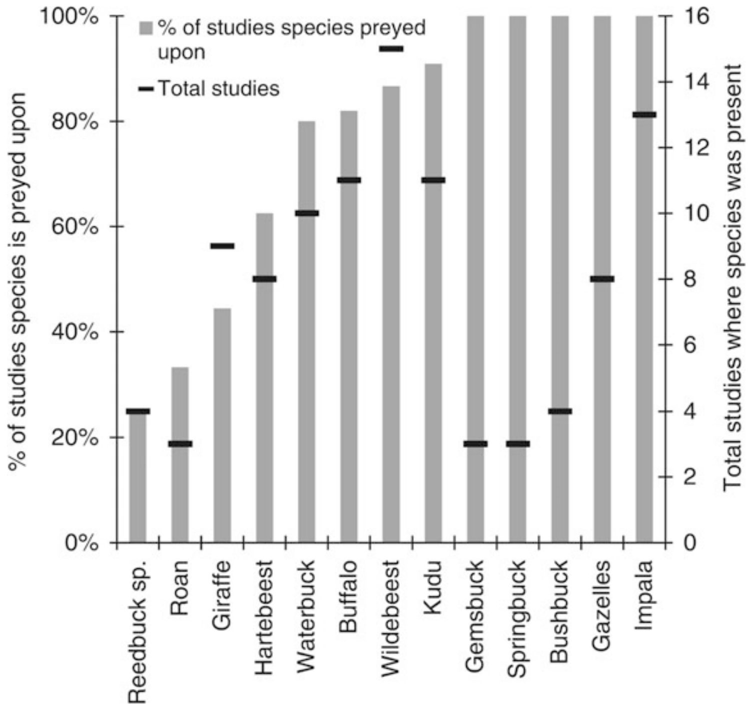

Fig. 5.2 Data from a comprehensive meta-analysis of 15 studies on spotted hyenas observed in six different countries across the full geographic distribution of spotted hyenas demonstrates the common and infrequently killed prey of spotted hyena in relation to prey availability. Reprinted with permission from Hayward (2006) (Figure 1, page 610), Journal of Zoology, 270(4)

to 50–60 km per hour (Kruuk, 1972). As a result, like wolves (*Canis lupus,* see Chap. 4 this book), cheetahs (*Acinonyx jubatus*), and lions (see Chaps. 2 and 3 this book), spotted hyenas are successful in roughly one-third of all hunts (Holekamp et al., 1997), and they regularly capture prey as large as 182 kg (400 lb.) or more (Hayward, 2006).

Spotted hyenas are efficient but socially complex hunters, and in this chapter, we outline the extraordinary morphological and behavioral adaptations possessed by spotted hyenas for efficient hunting within the context of their social organization. We discuss how social rank and age influence every aspect of their hunting behavior and consider the inevitable trade-offs faced regarding cooperative hunting of ephemeral prey that represent short-lived prey patches. Finally, we evaluate what is known about the cognitive demands and conservation implications associated with the behavioral flexibility possessed by these efficient hunters.

5.2 Morphological and Behavioral Adaptations for Efficient Hunting

Spotted hyenas possess myriad morphological and behavioral adaptations, making them more specialized and successful in cursorial hunting than any of the other bone-cracking hyaenids (Mills, 1990; Werdelin & Solounias, 1991). Morphological adaptations of spotted hyenas include their specialized teeth, which permit the capture and consumption of large prey. Rather than relying on stealth for prey capture, as do most felids, spotted hyenas are cursorial hunters that capture prey by running down a selected prey animal and chasing it over long distances (Kruuk, 1972; Mills & Harvey, 2001). Due to their keen eyesight (Calderone et al., 2003), spotted hyenas are capable of successfully capturing prey during the day or at night, and temporal variation in hunting success has not been reported (Kolowski et al., 2007; Kruuk, 1972). A typical hunt involves one or more individuals first rushing at a group of prey animals, standing briefly to observe the prey animals' locomotor behavior, selecting one target individual, and then chasing that individual for 75 m to 4 km before grabbing and disemboweling it (Cooper, 1990; Holekamp et al., 1997; Kruuk, 1972; Mills, 1990; Fig. 5.3). This pursuit hunting is facilitated by the spotted hyena's flexible spine and its specialized limbs/girdles (Andersson & Werdelin, 2003). With hind limbs that are slightly shorter than their forelimbs and tarsal bones that can be greatly overextended (Spoor & Badoux, 1989), spotted hyenas have a distinctive sloping appearance. As a result, these efficient runners exhibit a "rocking-horse gallop" that allows them to cover large distances and lope for hours (Eloff, 1964; Frank, 1986; Hofer & East, 1993; Tilson & Henschel, 1984).

Spotted hyenas use their robust forequarters and thick neck muscles to capture, pull down, drag, and otherwise carry heavy prey. It is the post-cranial skeleton and muscles of spotted hyenas that set them apart as more efficient cursors than any other extant or extinct bone-cracking species of hyena (Werdelin & Solounias, 1991). After being captured, prey can take from 0.5 to 13 min to die (Kruuk, 1972), and feeding competition quickly ensues as additional hyenas recruit to the kill site (Fig. 5.4). When feeding on a freshly killed herbivore, spotted hyenas use their strong canines and incisors to tear into and disembowel prey, often consuming meat from around the loins and anal region of their kill before opening the abdominal cavity to access the soft organs and muscles. After this, individual spotted hyenas often carry off pieces of the carcass, such as a limb or rib cage from an antelope, away from the main kill scene to eat independently elsewhere, away from conspecifics (Fig. 5.5, Kruuk, 1972).

Ungulate carcasses represent ephemeral, defensible, and energy-rich food patches (Engh et al., 2000; Frank, 1986; Smith et al., 2008; Tilson & Hamilton 1984). A single adult spotted hyena is capable of ingesting meat and bone at the rate of 1.3 kg (2.8 lb.) per minute. Moreover, a hungry group of hyenas can devour a large antelope in less than one-half hour, leaving behind only a bloody patch (Kruuk, 1972; Mills, 1990). A single adult spotted hyena can consume 14.5 kg (32 lb.) of meat in a sitting, for example, an adult can consume a gazelle fawn in less than one minute, and a

Fig. 5.3 Spotted hyenas are efficient hunters that directly kill 60–95% of the prey they consume and regularly capture prey nearly three times their own size, such as the wildebeest (above) and a hippo (below). Their powerful jaws permit these bone-cracking hyenas to devour the entire prey item to a pile of bones in a matter of minutes (photos by Heather E. Watts and Kate Yoshida)

group of 35 hyenas can devour an adult zebra (up to 450 kg or 1000 lb.) in as few as 36 min (Kruuk, 1972). As a result, individual spotted hyenas experience competition when feeding on fresh ungulate carcasses, and individuals often gain a competitive

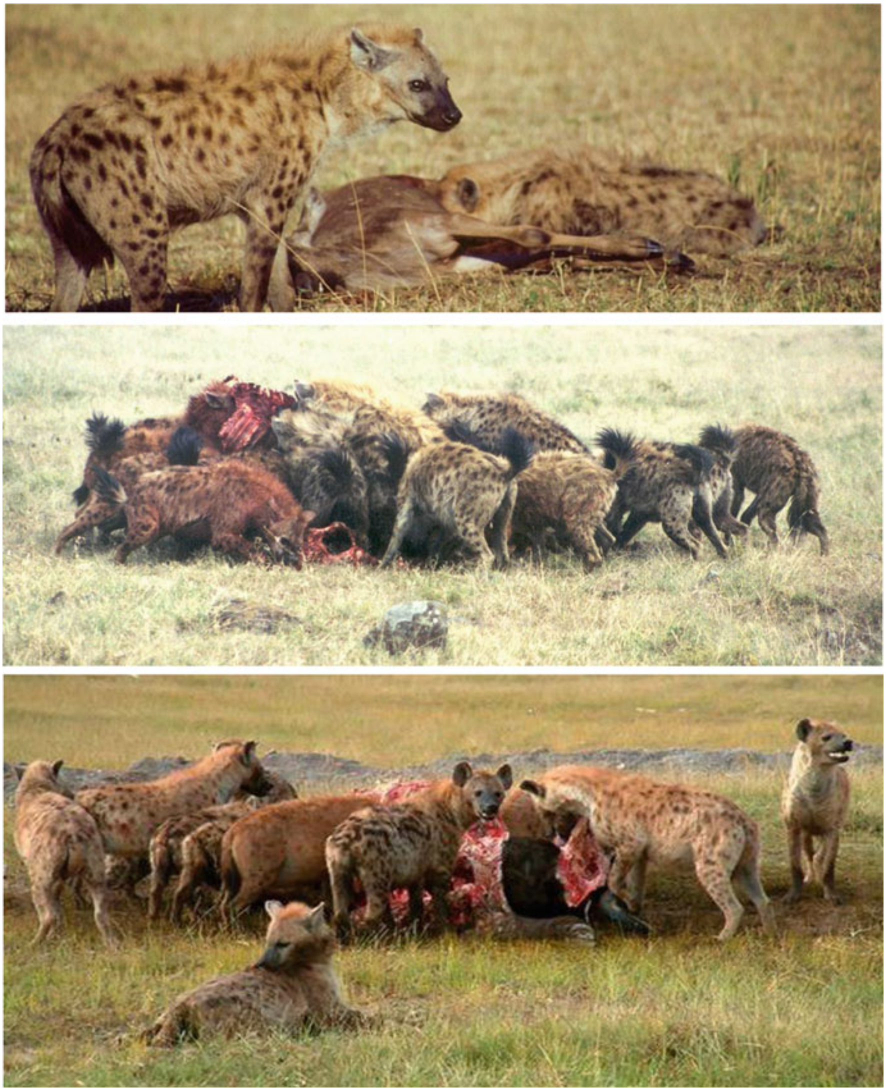

Fig. 5.4 Scramble feeding competition is extremely intense among spotted hyenas. These animals feed on rich, but ephemeral, fresh ungulate carcasses in subgroups containing up to 56 competitors. A hyena's relative rank position in the social dominance hierarchy of the clan determines its priority of access to food at kills. Low-ranking hyenas often must wait on the sidelines and feed only after high-ranking hyenas have had their fill (photos by Joseph Kolowski, Kay E. Holekamp, and Anne L. Engh)

advantage over conspecifics by feeding quickly (Kruuk, 1972). Moreover, dominance relationships determine an individual's priority of access to food (Engh et al., 2000; Frank, 1986; Smith et al., 2008; Tilson & Hamilton 1984).

Fig. 5.5 Spotted hyenas will often carry off parts of the main kill to avoid scramble competition to forage on their own. This hyena in the top photo is walking off with the leg of a kudu, presumably to avoid feeding competition with competitors at the main kill scene (photo by Bernard Dupont). In the bottom photo, one hyena is running away with a topi skull and spine while being chased by a second hyena (photo by Eli M. Swanson)

5.3 Female-Dominated Societies Structured by Fission-Fusion Dynamics

Spotted hyenas are social carnivores that live in permanent complex and female-dominated societies called clans that contain as few as six (Tilson & Henschel, 1984), and more than 120, individuals (Green et al., 2018). Adult females and their offspring are socially dominant to all adult immigrant males (Frank, 1986; Kruuk, 1972). Immigrant males queue for social status within groups and use affiliative behavior to court females (East et al., 2003; East & Hofer, 2001; Szykman et al., 2007). As is the case for many group-living animals (Aureli et al., 2008), spotted hyena societies are characterized by fission-fusion dynamics (Holekamp et al., 2000; Smith et al., 2008). Even though 120 or more individuals may concurrently belong to a single clan of spotted hyenas, all clan members are rarely, if ever, found together in a single location. Instead, individual animals make active decisions to leave (fission) or join (fusion) group-mates belonging to the larger social unit on an hour-to-hour basis (Smith et al., 2008). To avoid costly feeding competition, most social carnivores (Creel & Macdonald, 1995; Smith et al., 2012), including African lions (*Panthera leo leo*) (Packer et al., 1990), live in groups structured by fission-fusion dynamics. Individual spotted hyenas regularly separate from group-mates (fission) to forage on their own when food is scarce and come together (fusion) again when food is abundant or cooperative defense against intruders is beneficial (Smith et al., 2008). Whereas the ability to capture a larger array of prey animals more successfully appears to be a by-product of group-living, the benefits of cooperative defense of shared resources from lions and neighboring conspecifics rather than those associated with group hunting appear to have favored group-living (Smith et al., 2008). The constraints imposed by limited food resources explain the tendency for spotted hyenas to spend much of their time alone, even for individuals residing in large clans and areas of high prey abundance (Smith et al., 2008). These patterns vary with ontogeny, social rank, and reproductive state. Adults spend roughly 20–40% of their time alone (Smith et al., 2008).

The structure, size, and complexity of spotted hyena clans are more similar to those of cercopithecine monkeys than those of other social carnivores, which typically reside in small groups of closely related individuals, at least among members of one sex (Holekamp et al., 2015). Large clans may contain several different matrilineal kin groups and several immigrant males born elsewhere. Mean relatedness is very low between members of different matrilines, due mainly to rapid and constant gene flow via male dispersal among clans (Holekamp et al., 2012; Van Horn et al., 2004). As in many cercopithecine monkeys (e.g., Chapais, 1992; Cheney, 1977; Horrocks & Hunte, 1983; Walters, 1980), coalition formation plays an important role in the acquisition and maintenance of a stable social relationship (Fig. 5.6, Engh et al., 2000; Holekamp & Smale, 1993; Smale et al., 1993, Smith et al., 2010, Strauss et al., 2020; Strauss & Holekamp, 2019; Zabel et al., 1992). Early in ontogeny, each hyena comes to understand its own position in its clan's dominance hierarchy (Holekamp & Smale, 1993; Smale et al., 1993). This

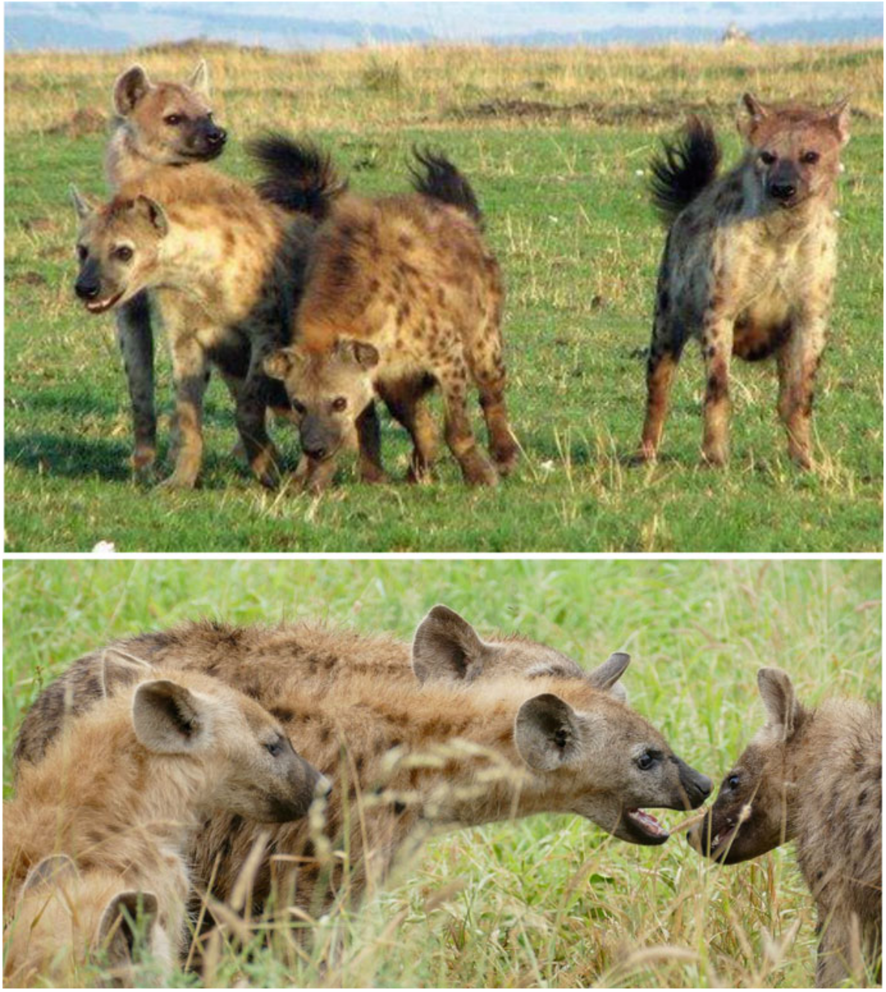

Fig. 5.6 Spotted hyenas inherit their social rank directly below that of their mother based on a period of associative learning over which mothers intervene on behalf of their offspring. An individual's social rank within the female-dominated societies of spotted hyenas determines priority of access to food at kills (photos by Kate Yoshida and Bernard Dupont)

process requires a type of associative learning called "maternal rank inheritance" in which the mediating mechanisms are identical to those observed in cercopithecine primates (Engh et al., 2000; Holekamp & Smale, 1991). As a result, dominance relationships are extremely stable across time and contexts. Because social rank determines a hyena's priority of access to energetically rich but ephemeral kills, dominance rank is particularly important when multiple individuals arrive to feed together on a fresh carcass (Frank, 1986; Smith et al., 2011).

5.4 Effects of Social Rank and Age on Hunting and Feeding Success

Because reproductive success among female spotted hyenas is determined by food consumption (Holekamp et al., 1996), and because social rank determines priority of access to food, social status profoundly affects the reproductive success of spotted hyenas (Frank et al., 1995; Hofer & East, 2003; Holekamp et al., 1996), such that high-ranking offspring grow faster, survive better, and reproduce earlier than their low-ranking counterparts (Frank et al., 1995; Hofer & East, 2003; Holekamp et al., 1996; Watts et al., 2009). Prenatal exposure to maternal hormones evidently differentially prepares offspring for competition at kills (Dloniak et al., 2006; Holekamp et al., 2013; McCormick et al., 2021), high-ranking mothers expose their offspring to higher levels of circulating androgens in utero than do low-ranking mothers.

Beyond the effects of social rank, cubs of both sexes born to mothers with high concentrations of androgens exhibit significantly higher rates of aggression across the lifespan than do individuals born to mothers with low concentrations (Dloniak et al., 2006; Holekamp et al., 2013; McCormick & Holekamp, 2022). Androgen exposure apparently enhances maternal aggression, without which youngsters would rarely be able to feed at kills because young hyenas are unable to tear off and consume pieces of a carcass nearly as quickly as can adults (McCormick et al., 2021). Skull development is not complete until 35 months of age, which is nearly 2 years after weaning, and more than 1 year after reproductive maturity, which occurs at roughly 24 months old (Fig. 5.7, Tanner et al., 2008). Thus, aggressive displacement of clan-mates from kills by their mothers allows young to feed at carcasses, juveniles are otherwise severely handicapped during competitive feeding by the slow and protracted development of their skulls (Watts et al., 2009).

In addition to being severely handicapped while competing with adults to quickly consume ungulate prey once captured, young hyenas are also poor at capturing prey in the first place (Fig. 5.8). Juveniles are relatively slow to arrive at fresh kills (East & Hofer, 1991; Holekamp et al., 1997). Hunting behavior of juvenile hyenas differs from that of adults in multiple respects, each of which is detrimental to their overall feeding success compared to adults (Fig. 5.9). As occurs in most large carnivores as part of the learning process, juvenile spotted hyenas stalk more non-mammalian prey and smaller mammals than do adult spotted hyenas (Holekamp et al., 1997; Mills, 1990).

In some cases, juvenile spotted hyenas hunt passerine birds and invertebrates in their first few months of life, but in general, juveniles are unable to successfully capture even small mammalian prey until roughly 9 months old or later (Holekamp et al., 1997). Juveniles more frequently require assistance in securing prey than do older animals and sometimes employ inappropriate hunting tactics, such as attempting to capture a zebra on their own (Holekamp et al., 1997). When juveniles hunt ungulate prey, they often do so by joining larger hunting groups than adults, and they are less successful at hunting than are adult hyenas (Holekamp et al., 1997). Most juveniles are unable to successfully capture an antelope on their own until

Fig. 5.7 Juvenile spotted hyenas are handicapped because they lack the well-developed feeding apparatus of adult competitors. Unlike juveniles, adult spotted hyenas can easily crack large bones such as this giraffe femur shown here. An ontogenetic series of spotted hyena skulls illustrating changes in size and shape throughout development in frontal view (from left to right) at 3 months, 11 months, 22 months, and 11 years of age. Note that skull development is still far from complete at 22 months. In fact, skull development is not complete in this species until at least a year after puberty, which occurs in both sexes at roughly 24 months of age (photos by Anne L. Engh, Bernard Dupont, and Jeremy Herliczek)

reaching 1.4 years of age, and young hyenas do not achieve adult competency levels at hunting until they are 5–6 years old, long after sexual maturity (Holekamp et al., 1997). Thus, juveniles and young adult hyenas are generally ineffective predators that only reach adult competency levels after years of practice, a behavioral pattern that appears to distinguish spotted hyenas from other large carnivores.

As one of the three species of bone-cracking hyenas, adult spotted hyenas (but not juveniles) can eat and digest nearly all parts of their prey (Wilson & Russell, 2009). This aspect of the spotted hyena's life results in the production of feces that, when dried by the sun on the African savannah, are notably bright white with a powdered bone matrix containing high levels of calcium, this also occurs for feces of striped and brown hyenas (Kruuk, 1972; Mills, 1990). Only adult spotted hyenas can generate enormous bite forces (Tanner et al., 2008), including those large enough

Fig. 5.8 Juvenile spotted hyenas are physically smaller than adults and lack the skills required to efficiently capture ungulate prey on their own, only reaching full competency at 5–6 years of age, long after reaching reproductive maturity at 24–36 months (photos by Bernard Dupont)

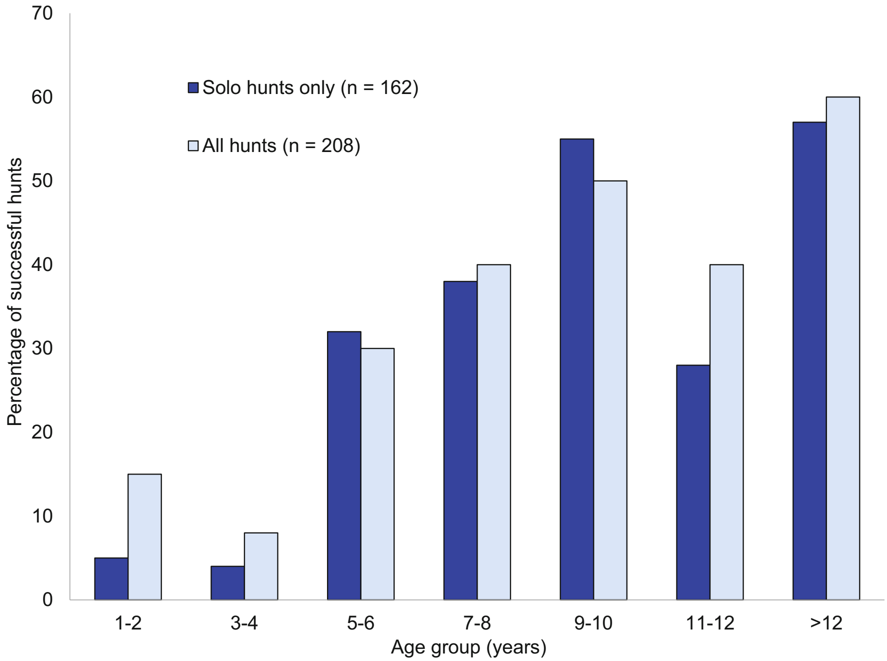

Fig. 5.9 Effects of age on the percentage of successful hunts by spotted hyenas in the Maasai Mara Reserve in Kenya. Redrawn with permission from Holekamp et al. (1997) (Figure 6, p. 12), Journal of Zoology, 242

to break open the leg bone of a giraffe and other large bones to access the nutritious marrow hidden inside (Fig. 5.7, Kruuk, 1972).

The large body size of adult females appears to have an evolutionary advantage, the largest adult female hyenas enjoy the highest lifetime reproductive success (Swanson et al., 2011). Although low-ranking females who survive to adulthood are generally larger than their high-ranking counterparts, and although their larger size may allow them to intimidate males better, body size is not a good predictor at all of rank, and even small subadult females can dominate males (Holekamp & Smale, 1993). Instead, we hypothesize that the larger body size of the low-ranking females may help them by allowing them to bring down animals like wildebeest and topis (*Damaliscus lunatus jimela*) on their own more efficiently than if they were smaller (Holekamp et al., 1997). That is, if a large body size appears to be especially helpful to low-ranking females, then a large body size may enhance the ability of large females to kill, steal, or process food more effectively than smaller females. Further data are required to understand the extent to which selection on large body size in female spotted hyenas is more strongly linked to running speed and hunting ability (e.g., long legs for cursorial hunting) or increased feeding performance at kills. The combined evolutionary history of bone-cracking (an attribute unique to Hyaenids) and its associated morphology, hunting of live prey, and intensive feeding competition in groups, is unique among mammalian carnivores. These combined traits likely led to the evolution of female aggressiveness, females that are slightly stronger and larger than males, and female dominance in spotted hyenas.

5.5 Social Coordination and Cognitive Demands of Hunting

Because group hunting permits individuals to capture prey animals many times larger than can be captured by a lone hunter, researchers have speculated that group hunting in gregarious carnivores from wolves and lions to spotted hyenas likely requires intelligent coordination and division of labor to facilitate coordinated attacks (e.g., Guggisberg, 1962; Peters & Mech, 1975). Comparative studies suggest that the co-evolution of large brains (relative to body size) is an important correlate of cooperation among mammalian carnivores (Creel & Creel, 1991; Finarelli & Flynn, 2009; Smith et al., 2012). Others have suggested that understanding the evolution and mechanisms of cooperation among mammalian carnivores can even provide useful insights into understanding early hominids (Hill, 1982; Kaplan & Hill, 1985; Schaller & Lowther, 1969; Smith et al., 2012).

Spotted hyenas possess the ability to solve the same problem in multiple ways and regularly use a single behavior to solve multiple problems, traits that are often characteristic of intelligent mammals living in complex societies, including monkeys and apes (Holekamp et al., 2007). Thus, it is possible that spotted hyenas could also engage in cognitively demanding problem-solving when attempting to engage in cooperative hunting. However, all current evidence available from spotted hyenas raises the provocative notion that not all coordinated group hunting in large carnivores requires primate-like mental processes or even role specialization (Holekamp et al., 2007). Instead, the most parsimonious explanation is that social facilitation and simple rules of thumb, such as "Take your own best line of approach to the target prey animal, unless another hunter already occupies that position" may explain patterns of cooperative hunting in spotted hyenas (Holekamp et al., 2000).

The lack of evidence for complex mental algorithms for cooperative hunting by spotted hyenas is of particular interest since multiple lines of evidence indicate that the social complexity and social intelligence of spotted hyenas exceeds that of other mammalian carnivores (Figs. 5.10 and 5.11). For example, spotted hyenas regularly form coalitions (Engh et al., 2000; Smith et al., 2010), reconcile after fights (Smith et al., 2011; Wahaj et al., 2001), discriminate among social partners (Smith et al., 2007; Wahaj et al., 2004), innovate to solve problems (Benson-Amram & Holekamp, 2012), and follow leaders to coordinate collective behavior (Smith et al., 2015, 2016). Thus, spotted hyenas make adaptive social decisions, and when asked to solve a foraging problem on their own, spotted hyenas innovate by inventing novel solutions using a diversity of exploratory behaviors (Benson-Amram & Holekamp, 2012; Drea & Carter, 2009). For example, in captivity, pairs quickly learned to tug two ropes in unison to earn a food reward without training and experienced hyenas helped inexperienced partners solve this cooperation task (Drea

Fig. 5.10 Spotted hyenas live in socially complex groups in which they coordinate multiple forms of collective action outside of the hunting domain, such as forming coalitions directed toward intruders and groups mate (photos by Kate Yoshida and David Greene)

& Carter, 2009). In their natural habitat, free-living hyenas with the greatest diversity of exploratory behaviors, a measure similar to creativity in humans, are most likely to solve a puzzle box for a food reward (Benson-Amram & Holekamp, 2012).

Foraging by spotted hyenas is more complex than in other social terrestrial carnivores because hyena hunting and feeding involve interactions among group members of low mean relatedness (Van Horn et al., 2004). For example, hyenas hunt

Fig. 5.11 Spotted hyenas offer new insights into animal minds based on their interactions with an experimental box containing a food reward during a test trial in the natural habitat in Kenya (photo by Sarah Benson-Amram)

cooperatively with group-mates that include kin and non-kin (Holekamp et al., 1997), and similar to mammal hunting killer whales (*Orcinus orca*, Reisinger et al., 2017), preferentially tolerate some non-kin over others in feeding contexts (Smith et al., 2007), suggesting a degree of meat sharing (feeding tolerance) among unrelated spotted hyenas. This is in contrast to patterns for other carnivores, such as lions and African wild dogs (*Lycaon pictus*, Creel & Creel, 1995; Packer et al., 2001), that only hunt cooperatively and share meat within family units (reviewed by Clutton-Brock, 2009). Interestingly, male coalitions of cheetahs (*Acinonyx jubatus*) also sometimes share food with non-relatives (Mills & Mills, 2017). Field experiments aimed at revealing the cognitive processes involved in joining kin and non-kin in group hunting should further elucidate the rules governing this form of cooperation.

Given their social complexity and their ability to innovate to accomplish foraging tasks, one might also expect spotted hyenas to engage in socially complex foraging strategies when hunting. In several species of socially complex mammals, there is evidence that members of different populations hunt using different tactics. For example, only some populations of Indo-Pacific bottlenose dolphins (*Tursiops sp.*) engage in sponging behaviors, the carrying of sea sponges to protect their rostrums from sharp rocks when hunting (Krützen et al., 2005) and cooperative tendencies, as well as prey selection, varies among chimpanzee (*Pan troglodytes*) populations (Newton-Fisher, 2007). Although we currently lack evidence of among clan differences in social hunting strategies, there are clear differences in ways hyenas in different regions track migratory prey.

In the Serengeti of Tanzania spotted hyenas commute to capture migratory prey for 46–62% of the year, with a mean commuting distance of 40 km and each trip spanning from 3 to 10 days (Hofer & East, 1993) whereas those of the Maasai Mara of Kenya usually only hunt within their home territories (Holekamp et al., 1997). Future work should investigate potential interpopulation differences in social hunting strategies and prey selection across multiple clans, both of which are likely driven by local ecology.

Although spotted hyenas may use one or more communicative behaviors to coordinate grouping behavior prior to setting off to hunt, we currently lack definitive evidence of advanced planning of hunting behavior per se in spotted hyenas. However, Kruuk (1972) speculated that individual spotted hyenas may use long-distance calls to recruit additional hunting partners prior to starting a hunt and there is some evidence that hyena hunters produce rallying vocalizations, called "whoops," to gather scattered group members where their assistance is needed to acquire or defend resources (East & Hofer, 1991; Gersick et al., 2015). We also know that spotted hyena greetings, which occur when two hyenas stand parallel to one another, lift their legs, and each sniffs the other's anogenital region (East et al., 1993; Kruuk, 1972), serve multiple social functions. Greetings promote social cohesion, reduce conflicts at reunions, and promote coalition formation (Smith et al., 2011, 2015; Wahaj et al., 2001). Although the role of greetings in promoting cooperative hunting remains to be studied for spotted hyenas, African wild dogs (Creel, 1997; Creel & Creel, 2002) and gray wolves in North America (Mech, 1970) regularly engage in greetings and other social "rallies" prior to setting off on a group hunt. Thus, the role of whoops and greetings in rallying hunting parties also warrants further study in the spotted hyena.

Role specialization during hunting has been documented for a few animals such as dolphins (Gazda et al., 2005), African lions (Heinsohn & Packer, 1995; Stander, 1992), and Taï chimpanzees, *Pan troglodytes verus* (Boesch, 2002). In these species, particular individuals within the social group repeatedly assume the same specific role when hunting. However, there is little evidence for role specialization as a cooperative hunting strategy among spotted hyenas. Instead, spotted hyenas appear to follow simple rules of thumb such as "Move wherever you must during a chase to keep the selected prey animal between you and another hunter" (Holekamp et al., 2000). However, some categories of individuals (rather than specific individual animals) are significantly more likely to initiate or participate in hunting than others. Low-ranking females hunt at significantly higher rates and in smaller hunting parties than do high-ranking individuals (Holekamp et al., 1997, Fig. 5.12). This finding is particularly interesting given that in many other circumstances adult females, particularly high-ranking ones, most often assume leadership roles to promote collective behaviors (Smith et al., 2020; Smith & van Vugt, 2020). For example, high-ranking adult females are most likely to initiate group travel (Holekamp et al., 2000; Smith et al., 2015), coalition formation (Engh et al., 2000; Smith et al., 2010), and between-group conflicts ("clan wars," Boydston et al., 2001).

Because adult male hyenas are physically smaller and weaker than their adult female or large juvenile followers, why do they initiate hunts most often (Holekamp

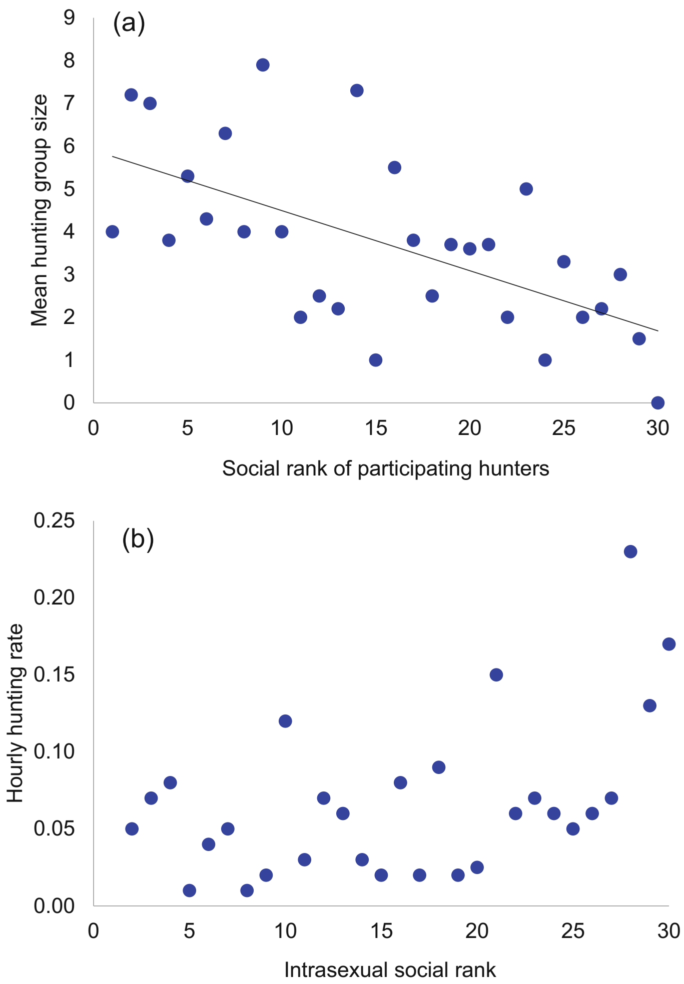

Fig. 5.12 Effects of adult female social rank on (**a**) mean hunting group size and (**b**) hourly rates in spotted hyenas. Redrawn with permission from Holekamp et al. (1997) (Figures 3 and 5, pp. 8 and 10), Journal of Zoology, 242

et al., 1997)? This is likely because immigrant males in each clan have the lowest priority of access to food (Frank, 1986; Kruuk, 1972; Tilson & Hamilton, 1984). Low-ranking individuals must therefore initiate hunts more often than high-ranking individuals because they are most likely to be displaced from carcasses by socially-dominant animals once kills are acquired through displacements of low-ranking males by high-ranking ones. Thus, "cooperative aiding" in hunts by dominant followers may be more akin to free-riding than social support per se, and high-ranking individuals often also benefit from cooperative defense of kills from lions, which are their main interspecific competitors.

A review of 13 studies documents that spotted hyenas lose many kills to lions (70%, versus only 35% lost by lions to hyenas, Périquet et al., 2015). Because even the largest spotted hyena is much smaller than a lion, multiple spotted hyenas must join forces to defend kills from kleptoparasitism by lions (Fig. 5.13). It is in this context that cooperative strategies appear most complex, group defense involves many more hyenas cooperating when spotted hyenas join forces against lions or during clan wars than is typical for either hunting itself or most other forms of cooperative behavior (Smith et al., 2008, Fig. 5.14).

5.6 Cooperative Hunting Improves Hunting Success

Cooperative hunting generally improves hunting success in spotted hyenas, and members may only capture certain prey species (e.g., adult zebra, buffalo, giraffe) when hunting cooperatively with group-mates (Holekamp et al., 1997). Hunting group size is defined based on the number of hyenas participating at the end of a chase. That is, a solo hunt was one conducted from start to finish by a single hyena whereas a group hunt ended with 2 or more participating hyenas (Holekamp et al., 1997). Overall, two or more adults are about 25–35% more successful in capturing targeted ungulate prey than are solo hunters (Cooper, 1990; Gasaway et al., 1991; Holekamp et al., 1997; Kruuk, 1972; Mills, 1990), but quantitative measures of this advantage vary across study areas and with the prey species hyenas are targeting.

In the Serengeti of Tanzania, cooperative hunting increased capture success by 33% and 34%, respectively, when targeting gazelle and wildebeest (Kruuk, 1972). For example, lone hunters only captured wildebeest calves in 15% of attempts but captures increased to 23% for pairs and to 31% for hunting parties of three or more (Kruuk, 1972). In the Kalahari Desert, the increased benefit of cooperative hunting was reported as 31% for gemsbok, 39% for wildebeest, and 50% for young eland (Mills, 1990). In the Maasai Mara of Kenya, Holekamp et al. (1997) demonstrated the importance of cooperation for hunting success by demonstrating that the probability of an individual hyena successfully capturing a prey animal increases by approximately 20% with the presence of a second hunter, but that the addition of subsequent hunters does not significantly increase hunting success. These data were further supported by Smith et al. (2008) who demonstrated the extraordinary costs of ensuing feeding competition incurred by pairs of hunters compared to solo hunters. Taken together, these findings suggest that while spotted hyenas are more likely to capture prey when hunting cooperatively rather than on their own, there are diminishing returns for increasing hunting party size beyond that necessary for the effective capture of a particular prey species. We discuss these trade-offs in more detail in the next section.

Fig. 5.13 Spotted hyenas routinely engage in complex forms of cooperation when joining forces with clan members to direct coalitionary aggression toward lions (which are three to five times larger than a single hyena). Multiple spotted hyenas are therefore required to cooperatively defend kills produced by spotted hyenas hunting from kleptoparasitism by lions (photos by Stephanie Dloniak and David Greene)

5.7 Feeding Competition Limits Social Cohesion

Despite the obvious benefits of enhanced prey capture from group hunting, roughly three-quarters of hunts are made by lone hyenas and this has puzzled many researchers (Cooper, 1990; Holekamp et al., 1997; Kruuk, 1972). In the Maasai Mara of Kenya, most species of prey were pursued by lone hunters, and the mean hunting group size for these spotted hyenas is only 1.7 hyenas (Smith et al., 2008, Fig. 5.14), varying with the size of the prey hunted with mean ± S.E. hunting group sizes for 1.2 ± 0.1 for topi, 1.7 ± 0.3 for impala, 2.1 ± 0.1 for Thompson's gazelles, 2.9 ± 0.3 for wildebeest, and 9.1 ± 0.5 for zebra (Holekamp et al., 1997). Detailed

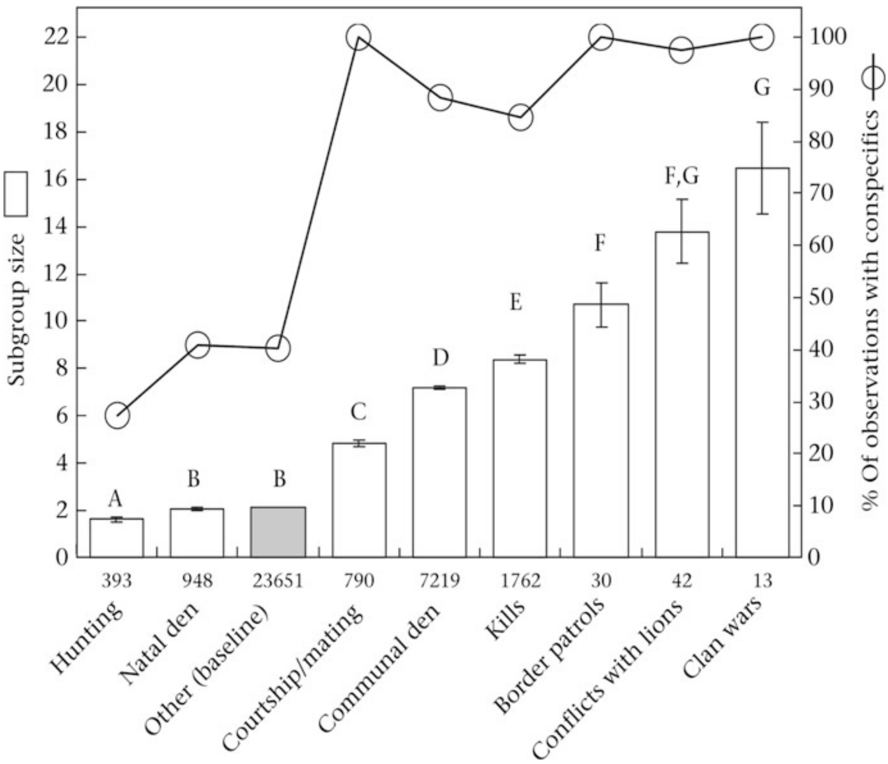

Fig. 5.14 Mean ± SE subgroup size and proportion of observations in which spotted hyenas were found in subgroups containing more than one individual as functions of the context in which groups formed. Sample sizes, shown below each bar, represent numbers of observation sessions assigned to each context. Different letters indicate statistically significant differences between contexts after correcting for multiple testing. The shaded bar represents the baseline value of subgroup size occurring in "other" sessions, against which other groups were compared. Reprinted with permission from Smith et al. (2008) (Figure 4, p. 627), Animal Behaviour, 76(3)

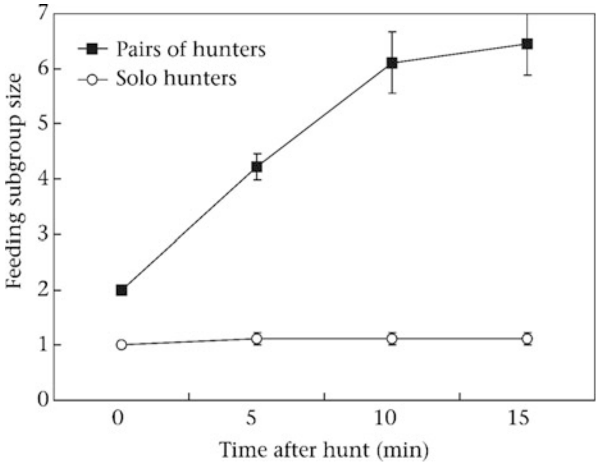

Fig. 5.15 Feeding subgroup size during the first 15 min after solo hunters or pairs of hunters killed ungulates of similar size ($N = 9$ matched pairs of hunts). Feeding competition is more intense when spotted hyenas hunt cooperatively than when they hunt alone. Reprinted with permission from Smith et al. (2008) (Figure 7, P. 630) from Animal Behaviour, 76(3)

observations of grouping patterns before and after hunting offer definitive insights into why cooperative hunting is so rare.

One long-term study in the Maasai Mara compared the numbers of new arrivals and total competitors present 5, 10, and 15 min after either solo hunters or pairs of hunters successfully captured wildebeest or topi (Smith et al., 2008, Fig. 5.15). They found that the total numbers of competitors present at kills only increased significantly over these 15 min when multiple hyenas cooperatively captured prey. In the first five minutes, an average of two more competitors arrived at kills made by pairs than at kills made by solo hunters. Furthermore, ten minutes after prey capture, more than six competitors were present at kills made by two hunters, whereas lone hunters almost always continued to feed alone and very few new conspecifics arrived at any of the kills sampled more than 10 min after prey capture. These investigators also found that, although the most common hunting group size is one hyena, the average feeding group size was eight, and feeding groups contained as many as 56 hyenas all competing to feed on the same kills (Fig. 5.14). These data suggest that, by hunting alone, an individual may feed for up to 15 min without competitors, consuming up to 20 kg of flesh, a mass that greatly exceeds its daily energy requirement. Thus, solo hunting generally increases an individual's net energy gain (Fig. 5.16). The costs of competition are particularly high for low-ranking individuals because although the amount of food, on average, that any individual consumes declines as foraging group sizes increase, dominance rank determines priority of access to food during these competitive feeding situations. Moreover, once the food is obtained directly from hunting, or in fewer cases scavenged from the landscape, the number of spotted hyenas that gather to feed at a carcass roughly match the relative mass of the carcass (Fig. 5.17, Smith et al., 2008).

Prey abundance influences prey selection, the tendency for hyenas to spend time with conspecifics (rather than alone), the density of spotted hyenas in an area, and the average sizes of spotted hyena clans, hunting parties, and foraging groups

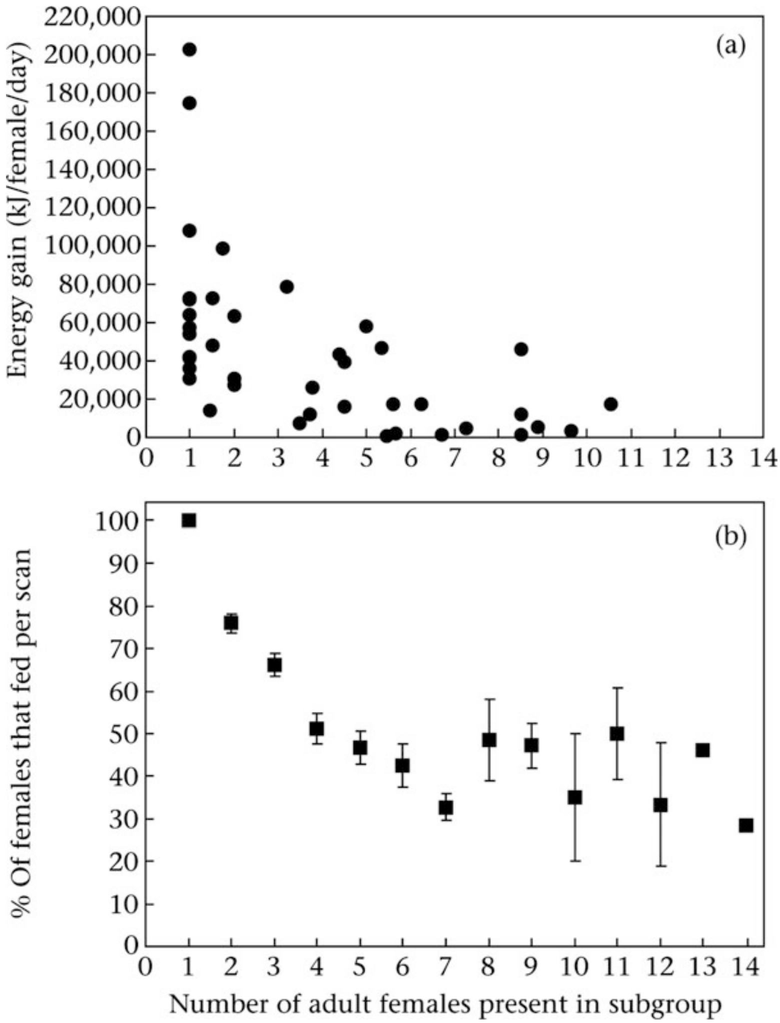

Fig. 5.16 (**a**) Per capita daily energy gain as a function of the number of adult females present at fresh ungulate kills ($N = 41$) and (**b**) mean ± SE percentage of adult females observed feeding per scan as a function of the number of adult females present within each subgroup at kills ($N = 426$ sessions). Reprinted with permission from Smith et al. (2008) (Figure 8, page 630), Animal Behaviour, 76(3)

(Figs. 5.14, 5.17, and 5.18). Spotted hyenas also generally allocate hunting efforts to prey species that are most locally abundant (Cooper, 1990, Holekamp et al., 1997, Kruuk, 1972). Moreover, during times of the year when resident ungulates are joined by migratory wildebeest and zebra, hunting success for spotted hyenas also generally increases (Holekamp et al., 1997). Although adult buffalo are particularly difficult

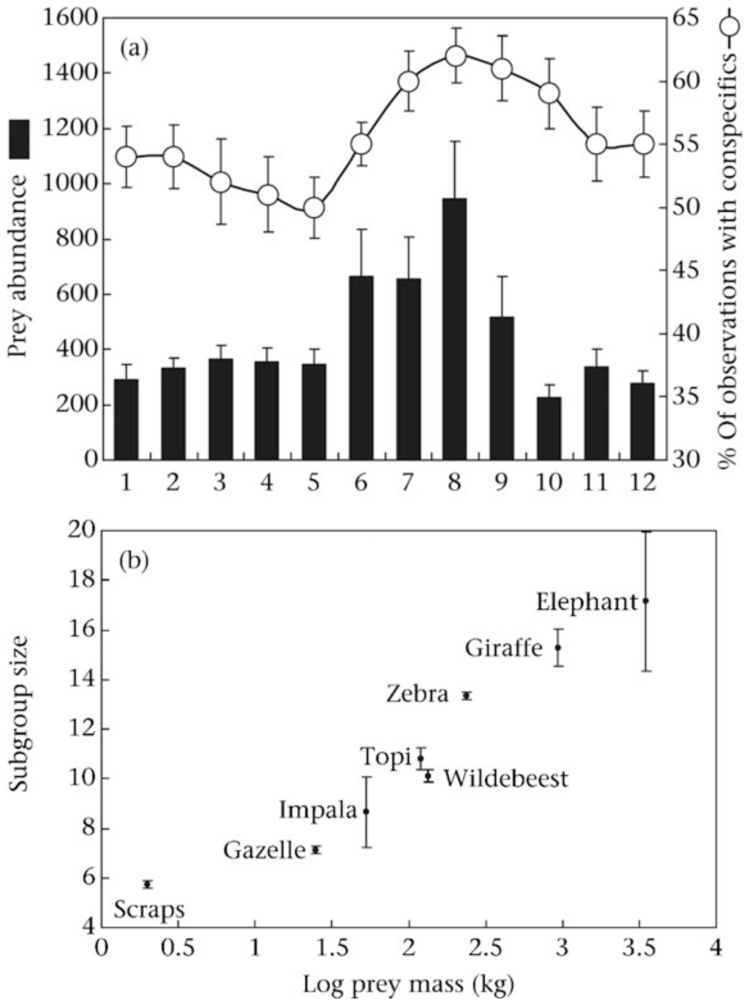

Fig. 5.17 Monthly mean ± SE (**a**) numbers of prey animals counted each month during biweekly ungulate censuses and percentage of observation sessions in which spotted hyenas were found in subgroups containing more than one individual and (**b**) subgroup sizes as a function of prey mass from observations at sessions with scraps ($N = 1315$) or fresh kills of Thomson's gazelle ($N = 382$), impala ($N = 53$), wildebeest ($N = 706$), topi ($N = 108$), zebra ($N = 193$), giraffe ($N = 29$), and elephant ($N = 13$). Reprinted with permission from Smith et al. (2008), Figure 6 (page 629), Animal Behaviour, 76(3)

for spotted hyenas to capture even when hunting in groups, spotted hyenas allocate more hunts toward capturing buffalo prey when buffalo are relatively abundant in the area (Höner et al., 2002). Spotted hyenas hunt some of the most energetically valuable of the ungulates (e.g., buffalo, giraffe, and plains zebra) at lower rates than they hunt most smaller ungulates (Hayward, 2006). This is likely because medium-

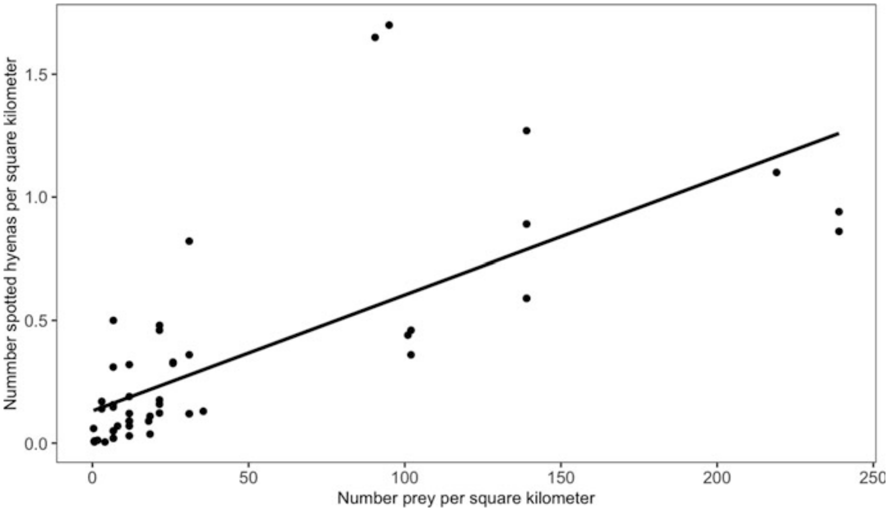

Fig. 5.18 The positive relationship between the densities of prey and spotted hyenas per square kilometers from a total of 51 published from 29 unique sites across sub-Saharan Africa ($R^2 = 0.53$, $F_{1,50} = 55.6$, $P < 0.00001$, regression line: $y = 0.005x + 0.131$). Data drawn from published studies listed by Holekamp and Dloniak (2010) in their Table 3 and new information from Bauer (2007), Bauer et al. (2015), Bohm (2012), Cozzi et al. (2013), Creel and Creel (2002), Crosmary et al. (2018), Davis (1964), Gasaway et al. (1991), Graf et al. (2009), Henschel et al. (2014), Kirsten et al. (2017), Loveridge et al. (2016), Mills (2006), M'soka et al. (2016), Purchase (2004), Smuts (1976), Tilson and Hamilton (1984), Trinkel (2003)

sized gazelles and wildebeest are easily captured by lone hunters, but some prey, such as zebras, are only effectively captured by large groups (e.g., 9–11 spotted hyenas, Holekamp et al., 1997; Kruuk, 1972; Mills, 1990). Hunting group size consistently increases with size of the selected prey (Cooper, 1990; Kruuk, 1972). Future studies are needed to understand the precise effects of prey size and hunting group size on hunting efficiency (per capita consumption).

5.8 Conservation Implications of Behavioral Flexibility While Foraging

Despite their striking abilities to capture large prey under challenging circumstances, most terrestrial species in the mammalian order Carnivora have experienced substantial population declines and range contractions over the past two centuries (Ripple et al., 2014). With human populations rapidly changing landscapes across the globe, many carnivores with their large home ranges, high energetic demands, and conflicts with humans are vulnerable to habitat fragmentation, overhunting, and poisoning (Woodroffe & Ginsberg, 1998). Compared to other species of large mammalian carnivores, however, spotted hyenas are coping with anthropogenic threats relatively well. They are ecologically and numerically dominant to other carnivores in sub-Saharan Africa (Holekamp & Dloniak, 2010). This is partly due to the extraordinary behavioral, physiological, and morphological flexibility of spotted hyenas. They occupy a diverse range of habitats across Africa, including savanna, desert, swamps, woodland, and montane forest up to 4000 m of elevation and, like most carnivores, rarely require direct access to water (Holekamp & Dloniak, 2010). They even co-exist in areas with high human densities, such as in urban centers in northern Ethiopia (Abay et al., 2011; Yirga et al., 2013, 2017).

The apparent success of this species is in part attributed to their combined powerful bone-cracking morphology, their ability to chase down and kill antelope, and their behavioral flexibility, which permits them to forage on foods ranging from termites to elephants and to hunt the broad range of ungulate prey discussed earlier in this chapter, depending upon the relative abundance and species of prey locally available. Thus, unlike lions, adult spotted hyenas are efficient extractive foragers endowed with bone-cracking jaws capable of meeting their energetic demands through scavenging. Because lions and spotted hyenas actively compete for access to the same prey items (Hayward, 2006), the human killing of lions can even act to indirectly benefit spotted hyenas in highly disturbed areas (Green et al., 2018; M'soka et al., 2016). For example, anthropogenic disturbances acting to decrease lion numbers are associated with an increase in juvenile survival by spotted hyenas in Masai Mara National Reserve, Kenya (Green et al., 2018). Nevertheless, despite its large overlap in its foraging niche with lions, the spotted hyena's flexible foraging habits likely permit its success across its geographic range (Hayward, 2006; Yirga et al., 2012). Moreover, the immune systems of spotted hyenas appear to cope far better with bacteria and diseases acquired while foraging than those of sympatric carnivores without an evolutionary history of foraging on carrion (Flies et al., 2016).

Further insights about how anthropogenic activity shapes varied aspects of a spotted hyena's behavioral repertoire relevant to hunting decisions can be gleaned from comparing the behavioral responses of individuals adjacent to human settlements and those at a relatively undisturbed part of the same national park. For example, spotted hyenas born in disturbed areas are more likely to interact with novel objects and are more exploratory than juveniles residing at less disturbed sites (Greenberg & Holekamp, 2017; Turner et al., 2020). In contrast to the results of studies on birds and small mammals, juveniles living in disturbed areas are more—not less—risk averse than those born in less disturbed ones (Greenberg & Holekamp, 2017; Turner et al., 2020). Moreover, although highly social hyenas live the longest, there is stabilizing selection on boldness suggesting trade-offs between the costs and benefits associated with risk-taking in the presence of lions (Yoshida et al., 2016). Bold or shy females had shorter lifespans than those in the middle of the shy-bold continuum (Yoshida et al., 2016).

Despite this, the extraordinary plasticity of spotted hyenas appears to permit them to modify their diets more easily than is possible for other sympatric carnivore species (Holekamp et al., 2012). Their flexible dietary niche has some consequences for their social structure. First, individuals spend significantly more time away from conspecifics when ungulate prey are relatively scarce (e.g., fewer ungulates, Smith et al., 2008) and social networks are generally sparser during these periods of time (Holekamp et al., 2012). However, spotted hyenas still preferentially associate with kin over non-kin during times of prey scarcity (Holekamp et al., 2012) and are significantly more likely to engage in elaborate greetings with kin at reunions during times of prey scarcity to reinforce social bonds (Smith et al., 2011).

Despite being a conservation success story compared to other large carnivorous mammals, and despite retaining the status of the most abundant carnivore in Africa today, populations of spotted hyenas are declining outside of protected areas. Humans represent a major mortality source (Watts & Holekamp, 2009), and humans often directly kill hyenas in response to (or in fear of) livestock depredation (Kissui, 2008; Kolowski & Holekamp, 2006). Unfortunately, domesticated livestock are easy prey for spotted hyenas living in human-altered landscapes (Fig. 5.19, Hoffmann & Montgomery, 2022; Kolowski & Holekamp, 2006; Mukeka et al., 2019). Intentional poisoning by humans can influence social and demographic patterns of spotted hyenas (Holekamp et al., 1993), and patterns of human activity can also influence their hunting behavior, thereby restricting access to prey (Mills & Harris, 2020). Thus, spotted hyenas are being negatively affected by humans. For example, anthropogenic disturbance by pastoralist activity is also a stressor in their lives (Van Meter et al., 2009), influencing activity patterns (Kolowski et al., 2007). Although not yet empirically studied, we suspect that the disruption of social units by humans negatively influences the fitness of individuals and reduces group efficiency. This has important consequences for the loss of African grasslands which are of great ecological, cultural, and economic importance.

Because spotted hyenas are relatively easy to monitor over long periods and more ecologically resilient to human perturbations than are other large African carnivores, long-term studies on spotted hyenas offer a useful indicator of how and the extent to which large carnivores can cope with and respond to human-induced rapid environmental change (Smith et al., 2017; Green et al., 2019). Many questions remain regarding the potential for anthropogenic factors to affect the hunting and feeding habits of these top predators, including effects on their patterns of cooperation and competition, ranging from social cohesion to group-level phenomena such as group defense, in this socially complex and highly intelligent mammalian carnivore.

Fig. 5.19 Like many large carnivores, spotted hyenas are in conflict with humans over resources, and they sometimes kill livestock such as the sheep (above) and cow (below) as shown here. Spotted hyenas are commonly killed in response to livestock depredation, even within protected areas (photos by Wilson Kilong and Joseph M. Kolowski)

Acknowledgments We thank the Kenya Wildlife Service, the Narok County Government, and the Kenyan National Committee on Science, Technology and Innovation, the Naboisho Conservancy, the Mara Conservancy, the Wildlife Research and Training Institute, and Brian Heath for permissions to study spotted hyenas in Kenya. Thanks to many current and former members of the Mara Hyena Project for detailed data collection. We extend our gratitude to the editors, Mridula Srinivasan and Bernd Wursig, for the invitation to contribute to this book and for their useful edits at every stage of the writing process. We would also like to extend special thanks to Todd K. Fuller, Gus Mills, and Julie C. Jarvey for offering useful comments that helped to improve an earlier version of this chapter. This work was supported by NSF grants OISE1853934, IOS1755089 and IOS1949911 to KEH.

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