Spotted Hyenas☆

Jennifer E Smith, Mills College, Oakland, CA, United States
Kay E Holekamp, Michigan State University, East Lansing, MI, United States

Abstract

Extensive study of the spotted hyena (*Crocuta crocuta*) has revealed numerous traits that set this species apart from other mammals. These animals are sex-role reversed in both their anatomy and behavior, and their societies are more complex than those of any other mammalian carnivore. Long-term study of these bizarre animals has led to fascinating discoveries in the domains of ontogeny, behavioral endocrinology, ecology, and evolution. Here, we highlight some key findings and explain how study of this unique model organism has improved our understanding of the fundamental rules governing animal behavior.

Keywords

Behavioral plasticity; Brain evolution; Communication; Conservation; Cooperative hunting; Dominance; Ecological constraints; Fission–Fusion society; Group living; Intelligence; Long-term study; Mate choice; Maternal effects; Resource competition; Sex differences; Siblicide; Social complexity; Social development; Sociality

Background

Overview

Spotted hyenas (*Crocuta crocuta*) exhibit many peculiar traits that set them apart from other mammals, making them a fascinating model organism for the study of animal behavior. Because they appear to violate many of the rules governing mammalian biology, spotted hyenas allow us to gain greater insight into what the rules actually are, and thus to better understand the broad principles governing mammalian behavior. Long-term study of these animals (Smith *et al.*, 2017) provides scientists with rich data to address questions at all four of Tinbergen's levels of analysis (Tinbergen, 1963). Insights include understanding the development of social behavior, endocrine mediation of aggressive behavior, the functional significance of communication signals, and the evolution of sociality and intelligence. The spotted hyena has already taught us many important lessons in these domains, and will undoubtedly teach us many more in future.

Systematic Placement of Hyaenidae Among Mammalian Carnivores

The family Hyaenidae belongs to the order Carnivora (whose members are called "carnivorans" or "carnivores") and the suborder Feliformia, which also contains cats, mongooses, civets, and allies (Wilson and Russell, 2009). Thus, despite their dog-like appearance, these animals are more closely related to cats and other Feliform taxa than to Caniform carnivores such as dogs or bears. Molecular data suggest that the sister group to the hyena family is a Feliform clade containing the mongooses (family Herpestidae) and the fossa (genus *Cryptoprocta*), a Malagasy carnivore that is closely related to mongooses. Fossil data suggest that the Hyaenidae last shared a common ancestor with their Feliform sister taxon in the Oligocene, 25–29 Ma.

The family Hyaenidae contains only four living species, and it is therefore one of the smallest carnivore families. The aardwolf (*Proteles cristata*) is the only surviving member of the subfamily Protelinae; this is part of the once-large clade of 'dog-like hyenas,' called this because they occupied ecological niches now occupied by canids and because they lacked morphological specializations for bone-cracking. The brown hyena (*Parahyaena brunnea*), the striped hyena (*Hyaena hyaena*), and the spotted hyena all belong to the subfamily Hyaeninae, which includes all of the extinct and extant bone-cracking hyenas.

Members of Hyaenidae and Their Ecological Niches

The four extant hyena species occupy three different feeding niches (Wilson and Russell, 2009). Aardwolves are strict insectivores, striped and brown hyenas feed mainly on carrion, and spotted hyenas are efficient predators that feed mainly on medium- and large-sized antelope they kill themselves. Although all four species may spend considerable time with conspecifics each day, all are strictly solitary foragers except for spotted hyenas, which may hunt alone or in large groups (Kruuk, 1972; Mills, 1990;

☆*Change History*: November 2017. Jennifer E. Smith and Kay E. Holekamp updated Addresses, Abstract, keywords, the overview, the Systematic Placement of Hyaenidae Among Mammalian Carnivores section, Key Facts about Spotted Hyenas Sex-Role Reversals section, Life History section, Communication section, Social Complexity and Brain Evolution section, Fission-Fusion Society section, Behavioral Plasticity and Conservation section, reference section, updated Figs. 3, 4, 7, 10 and 13, added Figs. 6, 11, 16, 21, and 22, updated Relevant Websites, and added new YouTube video links to the Relevant Websites section.
This is an update of J.E. Smith and K.E. Holekamp, Spotted Hyenas, In Encyclopedia of Animal Behavior, edited by Michael D. Breed and Janice Moore, Academic Press, Oxford, 2010, Pages 335-349.

 https://doi.org/10.1016/B978-0-12-809633-8.20749-8

Encyclopedia of Animal Behavior, Second Edition, 2019, 190–208

Holekamp *et al.*, 1997). The spotted hyena is still widely regarded as a scavenger that picks up leftovers at the kills of other sympatric carnivores (e.g., cheetah, leopard, or lion) or feeds on carrion. However, this is incorrect. Although spotted hyenas do scavenge opportunistically, they are efficient hunters, and directly kill 60%–95% of the food they eat (Holekamp and Dloniak, 2010) (**Fig. 1**). Spotted hyenas are impressively versatile in their choice of prey and use a number of different hunting techniques (Kruuk, 1972; Mills, 1990; Holekamp *et al.*, 1997).

All three species of bone-cracking hyenas are capable of eating and digesting all parts of their prey except hair, hooves, and the keratin sheath on antelope horns (Wilson and Russell, 2009). Bones are digested so completely that only the inorganic components are excreted in the hyena's fecal material. In fact, the feces of the spotted hyena are usually bright white with powdered bone matrix when they dry (Kruuk, 1972; Mills, 1990). Bone-cracking hyenas, particularly the spotted hyena, can generate enormous bite forces (Tanner *et al.*, 2008). In fact, wild spotted hyenas can even break open the leg bones of giraffe (Kruuk, 1972).

Key Facts About Spotted Hyenas

Sex-Role Reversals

Many normal mammalian sex roles are reversed in spotted hyenas. In contrast to most mammals, adult female spotted hyenas are roughly 10% larger than adult males (Swanson *et al.*, 2013) (**Fig. 2**), they are substantially more aggressive than adult males (Boydston *et al.*, 2001), and they are socially dominant to all adult immigrant males (Frank, 1986) (**Fig. 3**). Female dominance is very rare among mammals, but it does occur in some species of lemurs and mole rats. Dominance relations among spotted hyenas affect virtually every aspect of daily life, including priority of access to key resources such as food and space (Frank, 1986; Smith *et al.*, 2008) (**Fig. 4**). Social rank strongly influences female reproductive performance (Holekamp *et al.*, 1996). High-ranking females enjoy longer reproductive lifespans, experience shorter intervals between litters, and produce more surviving offspring than do lower-ranking females (Holekamp *et al.*, 1996).

Perhaps the most unusual role-reversed trait in this species is the external genital morphology of the female spotted hyena (Glickman *et al.*, 2006). The female's clitoris is virtually indistinguishable from the male's penis. In fact, the external genitalia of female spotted hyenas are so similar to those of male hyenas that people believed for centuries that these animals were hermaphrodites. The female's clitoris is greatly elongated to form a fully erectile pseudopenis traversed by a single urogenital canal through which the female urinates, copulates, and gives birth (**Fig. 5**). There is no external vaginal opening, as the outer labia are fused to form a structure that resembles the scrotal sac of the male. However, the testes of the adult male give the scrotal sac a larger size and more distinctly rounded bulges, and the male's penile glans is pointed, whereas that of the female is blunt, as in **Fig. 6**.

Many of the mysteries associated with sex-role reversed traits among extant spotted hyenas can only be unraveled in light of the historical origins of this species. Spotted hyenas are recently descended from carrion-feeding ancestors, and their physical appearance is very similar to that of extant striped and brown hyenas, both of which make their living primarily by scavenging (Kruuk, 1972; Mills, 1990). In stark contrast to any other hyaenid, however, spotted hyenas experience intense competition associated with feeding on fresh ungulate carcasses (**Fig. 7**). Although the mean hunting group size is 1.5 hyenas, the mean feeding group size is 8, and feeding groups can include as many as 56 hyenas (Smith *et al.*, 2008).

An adult spotted hyena can ingest meat and bone at a rate of 1.3 kg min^{-1} (2.8 lbs min^{-1}), and a group of hungry hyenas can reduce a large antelope to a few scattered bones in less than half an h (Kruuk, 1972; Mills, 1990). Thus, ungulate carcasses represent

Fig. 1 Unlike their carrion-feeding ancestors, spotted hyenas are efficient hunters that directly kill 60%–95% of the prey they consume. These specialized hunters are capable of successfully capturing prey nearly three times their own size, by themselves, including this adult wildebeest (Photo by Heather E. Watts).

Fig. 2 Adult female spotted hyenas (left) are surprisingly masculine in their appearance and are roughly 10% larger than adult males (right) (Photo by Anne L. Engh).

Loser of fights

Winner of fights

	MRPH	SEIN	WHO	MP	NAV	BAIL	MIG	BP	BOS
MRPH	--	24	14	13	28	11	14	21	4
SEIN		--	24	13	17	15	18	11	9
WHO			--	20	31	10	15	17	11
MP		1		--	36	27	12	15	14
NAV			2		--	19	29	13	17
BAIL						--	17	21	12
MIG							--	9	5
BP								--	3
BOS									--

Breeding females (MRPH–BAIL) | Immigrant males (MIG–BOS)

Note: Cubs slot into the hierarchy immediately below their mothers

Fig. 3 A simplified dominance hierarchy constructed from a subset of reproductive adults belonging to one large clan of spotted hyena in Kenya. Breeding females are shown in yellow and immigrant males are in green. The numbers in the matrix indicate the outcomes of agonistic interactions observed within pairs of reproductive adults. Unlike most male mammals, adult immigrant male hyenas appear at the very bottom of the clan's hierarchy. If we were also to include immature natal hyenas in this matrix, then each one would appear immediately below its mother, and would dominate older maternal siblings and immigrant males.

extremely rich but ephemeral food resources. In these intensely competitive feeding situations, juvenile spotted hyenas are severely handicapped because their relatively poorly developed feeding apparatus keeps their feeding speed low compared to that of their adult competitors (Watts *et al.*, 2009) (**Fig. 8**). The available evidence suggests that it was the special combination, apparently unique among living carnivores, of intensive feeding competition coupled with protracted development of a skull adapted for bone-cracking (**Fig. 9**) that favored the evolution of large, aggressive 'role-reversed' females capable of allowing their handicapped cubs access to food (Watts *et al.*, 2009). Thus, the adaptive significance of female dominance and aggressiveness among spotted hyenas appears to be strongly linked to an evolutionary history of bone-cracking.

We suspect that the evolution of predation on live ungulates, group-living, and the ensuing intensive feeding competition led to female aggressiveness and dominance, but that the elongated phallus of the female spotted hyena evolved later as a sexually selected trait. Once females were socially dominant to males, then combat-based forms of male–male competition for mates would most likely have given way to alternative male reproductive strategies based on endurance rivalry and sperm competition (Engh *et al.*, 2000b; East *et al.*2003; Curren *et al.*, 2003). Why females with such heavily 'masculinized' genitalia evolved in spotted hyenas remains one of the most fascinating unanswered questions posed by this species (**Figs. 5 and 6**). We are unlikely ever to know

Fig. 4 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 (Photo by Kay E. Holekamp).

Fig. 5 The reproductive anatomy of an adult female spotted hyena, including the fully erectile pseudopenis. A female must urinate, copulate, and give birth through the single urogenital canal that transverses the enlarged clitoris (Drawing by Christine M. Drea).

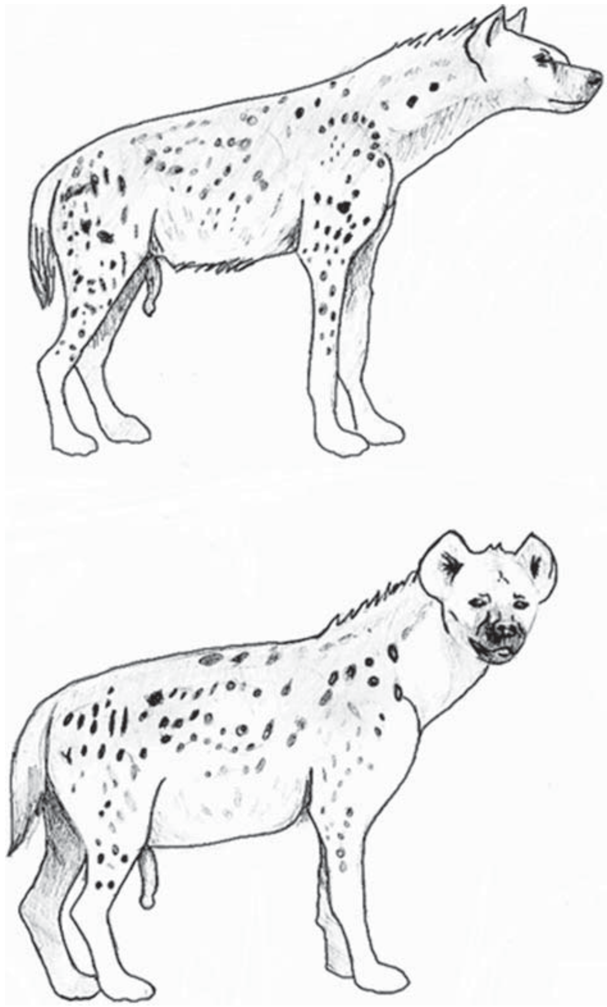

Fig. 6 The female hyena's clitoris (bottom image) is elongated, and distinguishable from the male's penis based on the shape of the penile glans (top image). The glans of the female shown here is blunt, whereas that of the male is pointed, as in the upper animal shown here. The general body outline also differs between the sexes in adulthood, as the male's belly swoops up posteriorly toward his hind legs whereas the female's does not (Drawing by Lily Johnson-Ulrich).

Fig. 7 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 (Photo by Anne L. Engh).

Fig. 8 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 (Photo by Anne L. Engh).

Fig. 9 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 (Photo by Jeremy Herliczek).

for certain why the female's pseudopenis evolved in this species. Nonetheless, the only adaptive hypothesis consistent with the existing data suggests that the elongated and anterior-opening female phallus evolved as part of a bizarre reproductive tract that gives female spotted hyenas more complete control over which sperm fertilize their eggs. The female's unusual anatomy may thus permit postcopulatory cryptic mate choice.

Females in the wild often mate with multiple males when they are in estrus, and the sperm from these competing males must therefore often occur together in the female's reproductive tract (Curren *et al.*, 2003). The ovaries of the female spotted hyena are composed mainly of stromal cells, and they contain very little follicular tissue, so sperm competition in this species may be unusually intense. In addition to being rather long and convoluted, the female's reproductive tract contains vaginal lumina that are full of blind alleys and dead ends, so perhaps only the highest-quality sperm manage to travel all the way up this strange obstacle course to reach the ova. Giving birth through a penis-like clitoris has high costs; some cubs inevitably suffocate during the birth process, and it seems highly unlikely that the female's phallus could be adaptively neutral in the light of this potential cost. Indeed, the benefits of having an elongated clitoris should outweigh its costs, so this odd structure must confer some adaptive advantage. Even if the female's pseudopenis does not function directly to enhance female control over fertilization, it certainly at least gives females the upper hand in the evolutionary arms race between males and females in determining which sex controls reproduction in this species.

Social Organization

Spotted hyenas live in permanent complex, female-dominated societies, called clans, containing 6–130 individuals (Kruuk, 1972; Frank, 1986; Holekamp *et al.*, 2015). The mean clan size across Africa is around 29 hyenas, but abundance of local prey animals determines clan size (Holekamp and Dloniak, 2010). Where ungulates are plentiful year-round, as on some prey-rich plains of eastern Africa, clans are typically large. However, in desert areas of southern Africa, where prey are sparse, clans are very small. Suitable habitat is generally saturated with a mosaic of hyena territories. Border clashes with neighboring clans, called clan wars, are most commonly observed in habitats containing high densities of hyenas, where intrusion pressure is most intense (Kruuk, 1972; Boydston *et al.*, 2001).

Clans are fission–fusion societies in which all members know one another individually, rear their cubs together at a communal den, and defend a common territory (**Fig. 10**), yet clan members spend much of their time alone or in small subgroups (Smith *et al.*, 2008). Each clan is structured by a linear dominance hierarchy, and an individual's position in this hierarchy determines its priority of access to food (**Figs. 3 and 4**). Although small clans may contain only a single matriline and a single breeding male, large clans may contain several different matrilines comprising related females and their offspring, as well as a number of adult immigrant males that are generally unrelated to one another (Holekamp *et al.*, 2012) (**Fig. 11**). Members of the same matriline occupy adjacent rank positions in the clan's dominance hierarchy. Most clans contain individuals from three or four overlapping generations. Relatedness is high within matrilines, but on average, clan members are only very distantly related because of high levels of male-mediated gene flow among clans (Van Horn *et al.*, 2004). In most respects, clans of spotted hyenas bear little resemblance to canid or mongoose packs, lion prides, or groups of any other social carnivores. Instead, they are remarkably similar in their structure, size, and complexity to the female-bonded societies of cercopithecine primates (Holekamp *et al.*, 2015).

Life History

The life histories of spotted hyenas exhibit many notable similarities to those of cercopithecine primates. Like monkeys, spotted hyenas have slow life histories. Hyenas live up to 26 years in the wild. An individual's life history is largely shaped by it's social rank within the clan (Holekamp *et al.*, 1996). Beyond the effects of rank, hormone exposure among juveniles can also have profound effects on the timing of life history milestones (Lewin *et al.*, 2017). Specifically, individuals exposed to high concentrations of IGF-1 early in life tend to be heavier and reproduce at earlier ages than those exposed to low IGF-1 concentrations, suggesting that early exposure to this hormone importantly mediates the timing of development, growth and reproduction in these animals (Lewin *et al.*, 2017). Spotted hyenas are initially born at isolated natal dens (**Fig. 12**); female hyenas bear litters containing one, two, or very rarely three cubs (Kruuk, 1972). After 3 or 4 weeks, the mother moves her newborn cubs to the clan's communal den, where all cubs reside that are less than 9–12 months of age. A communal den may provide shelter for over 20 cubs at once (Mills, 1990). Here cubs are first introduced to the other members of the clan and learn their places in the clan's dominance hierarchy (Engh *et al.*, 2000a). Cubs become independent of the communal den when they are 9–12 months old; when they graduate from the den depends on the harshness of the local environment, with cubs staying longer at dens in harsher habitats (Holekamp and Dloniak, 2010). When they leave the communal den, cubs start traveling around the clan's territory with their mother. On average, weaning

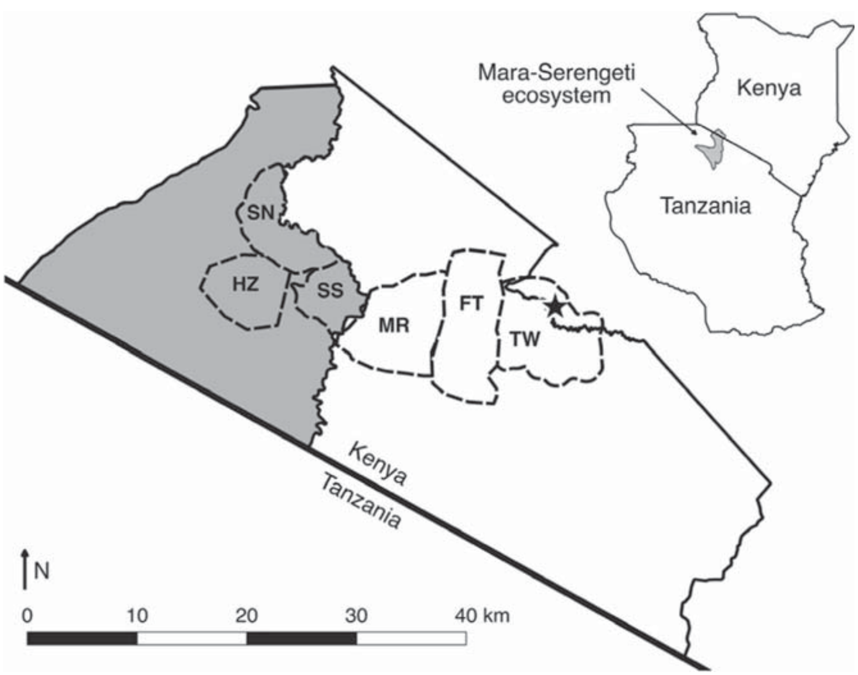

Fig. 10 Dashed lines indicate the territorial boundaries of six clans of spotted hyenas in the Masai Mara National Reserve, Kenya (Image by David S. Green). Reproduced from Green, D.S., Johnson-Ulrich, L., Couraud, H.E., Holekamp, K.E., 2018. Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. Biodiversity and Conservation 27, 1–19. Figure printed with permission by Springer Nature.

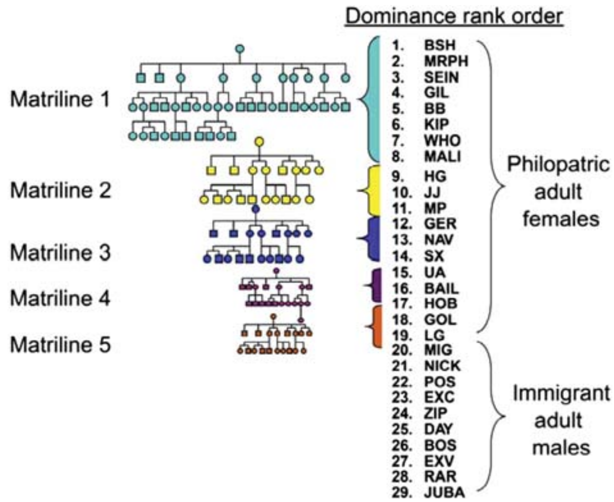

Fig. 11 Dominance rank order of matrilines within one cohort of adults present in a single large clan. The dominance hierarchy of natal animals contains multiple matrilineal kin groups, shown at left; each matriline is represented by a different shade. Squares in genealogies represent males and circles represent females. Although only adult females are shown among the natal animals in the vertical listing at right, offspring are included in the genealogies shown at left; offspring slot into the hierarchy immediately below their mothers. Reproduced from Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., Watts, H.E., 2012. Society, demography and genetic structure in the spotted hyena. Molecular Ecology 21, 613–632.
Figure printed with permission by John Wiley & Sons Ltd.

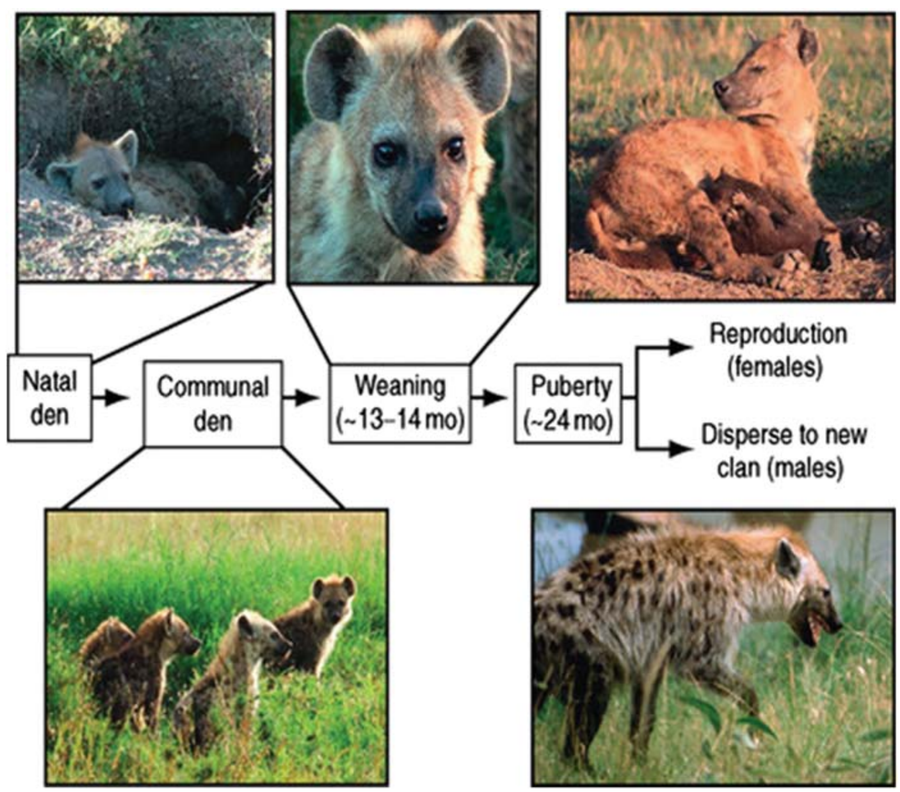

Fig. 12 Spotted hyenas experience several discrete life history stages during their ontogeny. They are born at natal dens, and then are transferred to the communal den where they reside until they are 9–12 months of age. Subadults continue to nurse until 13.5 months of age, on average, and then undergo puberty around 24 months of age. After puberty, males disperse to join a new clan whereas females begin to reproduce in their natal clan (Photos by Jennifer Smith and Heather Watts).

occurs at around 14 months of age, but mothers may continue to nurse their cubs for up to 24 months (Holekamp *et al.*, 1996). Mothers also help their offspring gain access to food at ungulate kills long after weaning, and even after puberty (Watts *et al.*, 2009). Thus, the young of spotted hyenas, like those of many primates, require unusually long periods of maternal support and social learning.

Spotted hyenas of both sexes reach reproductive maturity at around 24 months of age, and most females start bearing young in their third or fourth year (Holekamp *et al.*, 1996). Male hyenas disperse voluntarily from their natal groups 1–76 months after puberty, whereas females are usually philopatric and spend their lives in their natal clans (Höner *et al.*, 2007). As long as natal males remain in the natal clan, they can dominate adult females ranked lower than their own mothers. However, when males disperse, they behave submissively to all new hyenas encountered outside the natal area. This is the phase of ontogenetic development during which females come to dominate males (Smale *et al.*, 1993). When a male joins a new clan, he assumes the lowest rank in that clan's dominance hierarchy (**Figs. 3 and 11**). In this respect, spotted hyenas differ from most primates. Rather than engaging in physical combat to establish dominance relationships with one another, immigrant male hyenas form a queue based on their arrival order (East and Hofer, 2001). The highest-ranking males are those that arrived first in the clan, and the lowest-ranking immigrants, those that arrived most recently (Engh *et al.*, 2002). Males rise in rank only when higher-ranking immigrants die or engage in secondary dispersal (Engh *et al.*, 2002). Due to the female's male-like genitalia, coercive sex is impossible (Holekamp *et al.*, 2015). Among spotted hyenas, females strongly prefer to mate with immigrant males, which sire nearly all the offspring in every clan (Engh *et al.*, 2002). Thus, mate choice by females apparently drives natal dispersal by males (Höner *et al.*, 2007). Roughly 40% of immigrants disperse again, but the benefits of secondary dispersal are unknown.

Communication

Spotted hyenas have an elaborate communication repertoire involving multiple sensory modalities. Group members recognize one another individually on the basis of distinctive vocalizations, visual cues, and odors. Spotted hyenas emit a large array of distinctive sounds: they emit deep groans to call their cubs out of dens, high-pitched squitters to beg for food or milk, and cattle-like lowing sounds to bring group-mates to a common state of high arousal (East and Hofer, 1991). Spotted hyenas are often referred to as laughing hyenas because their 'giggle' vocalizations sound much like high-pitched, hysterical human laughter. The long-distance vocalizations of spotted hyenas, called 'whoops,' are the sounds heard most commonly at night in the African bush (East and Hofer, 1991). Whoops function as rallying calls to gather scattered clan members together to defend the territory boundaries, food resources, the communal den, or clan-mates in danger (East and Hofer, 1991). Spotted hyenas also sometimes whoop to recruit hunting partners, or to reunite mothers and offspring (Kruuk, 1972). Finally, whoops are also used as a form of individual display, particularly by adult immigrant males of high rank (East and Hofer, 1991).

Olfactory communication plays an important role in advertising territorial borders (Boydston *et al.*, 2001) (**Fig. 10**), but also functions to signal intrasexual social status among immigrant males (Theis *et al.*, 2012), and to maintain social cohesion among adult females (Smith *et al.*, 2011). Multiple clan members maintain territory boundaries during border patrols by depositing scent, in the form of paste. Paste is a strong-smelling, yellowish buttery secretion deposited from subcaudal glands onto grass stalks (**Fig. 13**). Individuals also paste deep within their territories. Bacterial communities inhabiting hyena subcaudal glands vary among clans, and bacteria appear to be largely responsible for generating clan-specific odors (Theis *et al.*, 2012). In addition to signaling clan membership, paste also transmits information about an individual's sex, reproductive state, and identity (Theis *et al.*, 2012). Young hyenas engage in pasting behavior long before they produce any paste in their anal sacs, suggesting that cubs paste to acquire group odors from sites where clan-mates pasted earlier.

Spotted hyenas regularly engage in ritualized greeting ceremonies during which two clan members stand parallel to one another and face in opposite directions to sniff the other's anogenital region (East *et al.*, 1993; Smith *et al.*, 2011) (**Fig. 14**). Greetings are most common when clan members reunite after being separated (Smith *et al.*, 2011). The unique aspect of greetings among spotted

Fig. 13 Pasting behavior is the deposition of a strong-smelling, yellowish buttery secretion from the anal gland onto a grass stalk (Photo by Kay E. Holekamp).

Fig. 14 Ritualized greetings reinforce social bonds among groups mates and occur when two spotted hyenas stand parallel to one another with phallic erections and face in opposite directions to sniff the other's anogenital region (Photo by Heather E. Watts).

hyenas is the prominent role of the erect phallus in animals of both sexes. Greetings occur between hyenas of all ages. Cubs can erect their penis or clitoris and engage in greeting ceremonies as early as 4 weeks after birth (East *et al.*, 1993). Greetings most often represent affiliative gestures that reacquaint clan mates and strengthen social bonds (Smith *et al.*, 2011). Directly following fights, greetings may also serve a conciliatory function by reducing rates of subsequent aggression between former opponents (Wahaj *et al.*, 2001) or reduce tensions at subgroup reunions (Smith *et al.*, 2015). Hyenas typically initiate greetings with higher-ranking social partners, and they do so with their phallus erect. Given this, the display of the erect phallus during greetings was originally deemed to be a 'flag of submission' (East *et al.*, 1993), but a multivariate approach based on long-term data later ruled out this hypothesis (Smith *et al.*, 2011). Instead, rank-related patterning of greetings among adult females simply reflects preference for high-ranking social allies; greetings importantly reinforce social bonds at reunions and promote coalition formation, especially among kin and close associates (Smith *et al.*, 2011).

Important Findings

Hormones and Sex Differences

It was long believed that, instead of having an adaptive function, the odd genitalia of the female spotted hyena were probably mere side-effects of selection for other male-like traits in females such as enhanced aggressiveness, and that androgenic hormones must mediate this phenomenon during development (Gould, 1981). However, even when pregnant female spotted hyenas are treated throughout pregnancy with drugs that block the action of androgenic hormones on the fetus, each female offspring of these treated females nevertheless develops a full-sized pseudopenis (Glickman *et al.*, 2006). In fact, development of this strange organ is androgen-independent except for some finishing touches to the final shape of the penile glans (**Fig. 6**). Furthermore, there is no evidence that activational effects of androgens or other steroid hormones mediate aggressive behavior emitted by female hyenas. However, there is support for the idea that organizational effects of androgens mediate female aggressiveness in this species, both in infancy and adulthood (Dloniak *et al.*, 2006; Holekamp *et al.*, 2013b).

Maternal effects mediated by prenatal hormone exposure appear to be important for the nongenetic inheritance of traits related to social rank among wild spotted hyenas (Dloniak *et al.*, 2006; Holekamp *et al.*, 2013a). Dominant females have higher concentrations of androgens during late pregnancy than do subordinate females (**Fig. 15**). However, independent of social rank, cubs of both sexes born to mothers with high concentrations of androgens exhibit higher rates of aggression and mounting behavior as infants than do cubs born to mothers with low concentrations (Dloniak *et al.*, 2006). Interestingly, even in adulthood, females exposed in utero to high androgen concentrations emit aggressive acts toward males at higher rates than do females exposed to relatively low androgen concentrations in the womb (**Fig. 16**) (Holekamp *et al.*, 2013a). Enhanced aggressiveness may help females dominate males and compete for food at kills. Thus, prenatal androgen exposure appears to adaptively influence offspring phenotype.

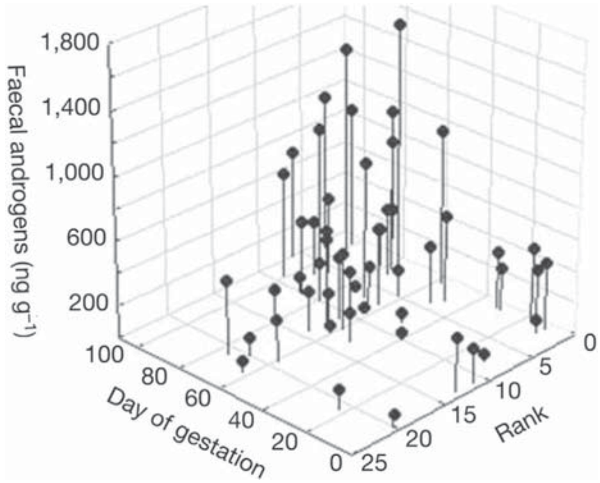

Fig. 15 The relationships among social rank, day of gestation, and fecal androgen metabolite concentration in pregnant wild spotted hyenas. The highest social rank possible is 1. Reproduced from Dloniak, S.M., French, J.A., Holekamp, K.E., 2006. Rank-related maternal effects of androgens on behavior in wild spotted hyaenas. Nature 440, 1190–1193. Figure printed with permission by Macmillan Publishers Ltd: Nature Publishing Group.

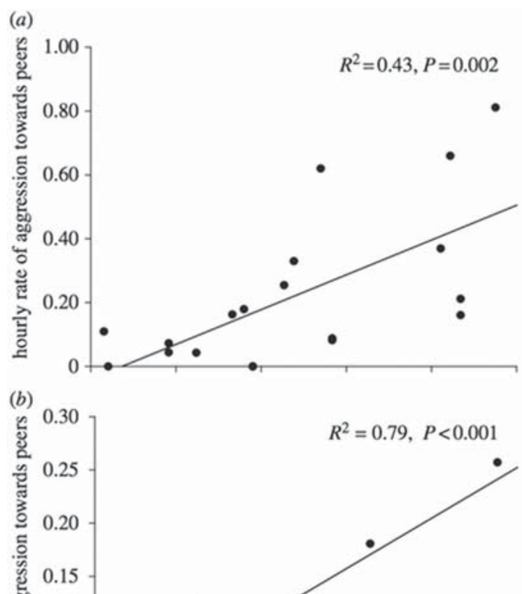

Fig. 16 Relationship between maternal fecal androgen (fA) concentrations during gestation and rates of aggression emitted by the female offspring produced from those pregnancies when offspring were (a) two to four months old (n=19) towards their peers at dens and (b) adults (older than 24 months) towards their adult peers (n=14). Aggressive behavior here occurred in the context of competition over access to solid food as well as in other contexts. Reproduced from Holekamp, K.E., Swanson, E.M., Van Meter, P.E., 2013a. Developmental constraints on behavioral flexibility. Philosophical Transactions of the Royal Society 368 (1618), 20120350. With permission by The Royal Society Publishing.

Social Development

Spotted hyenas are sometimes referred to as the Cain and Abel of the animal world, on the basis of the belief that neonates routinely kill their siblings shortly after birth. Although littermates do engage in aggressive interactions within minutes of birth, and although this can result in obvious scarring of the subordinate littermate, these aggressive interactions seldom result in the death of one

Fig. 17 Black hyena cubs are born with their eyes open and teeth fully erupted, characteristics that are rare amongst carnivores (top). Littermates engage in aggressive interactions within minutes after birth (bottom), which quickly leads to the establishment of a dominance hierarchy between littermates. Reproduced from Frank, L.G., Glickman, S.E., Licht, P., 1991. Fatal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. Science 252, 702–704.

sibling (Wahaj *et al.*, 2007) (**Fig. 17**). Specifically, ultrasonographic data indicate that, both *in utero* and after birth, wild litters do not differ in size from litters born in captivity where siblicide cannot occur (Wahaj *et al.*, 2007) (**Figs. 18 and 19**). The outcomes of early fights between siblings quickly establish dominance relationships among littermates in twin or triplet litters, and the dominant cub subsequently has priority of access to the mother's milk (Wahaj *et al.*, 2007). Siblicide in the spotted hyena is facultative in that it occurs only in some twin litters. Rather than functioning to routinely kill one's sibling, the purpose of the early fighting observed between hyena littermates is to establish an unambiguous dominance relationship within the litter (Wahaj *et al.*, 2007). It appears that the relative costs and benefits of killing one's sibling vary with current socio-ecological conditions. However, cubs born to twin litters often enjoy better survivorship when their siblings also survive the early stages of life than when their siblings die young. Thus, the available data strongly suggest that habitual siblicide would be maladaptive in these animals. Although a cub that manages to kill its sibling will benefit if its mother becomes unable to support multiple cubs, killing a littermate also deprives the killer of a valuable ally and reduces its inclusive fitness.

After establishing dominance relationships within their litter, cubs must also learn their places in the clan's dominance hierarchy. As in many Cercopithecine primates, the social status of a young hyena is not determined by its size or fighting ability, but rather by its mother's social rank (Engh *et al.*, 2000a) (**Fig. 11**). Dominance relations among adult female spotted hyenas are extremely stable across a variety of contexts and over periods of many years (Frank, 1986; Smith *et al.*, 2011). Early in life, young spotted hyenas of both sexes assume the social rank directly below that of their mother (Engh *et al.*, 2000a). The acquisition of social rank in hyenas occurs in a pattern identical to that seen in many monkeys during a process primatologists call 'maternal rank inheritance'. Social status is not genetically inherited, but is acquired instead via a process of social learning that occurs during an extended juvenile period (Engh *et al.*, 2000a). Initially, young hyenas indiscriminately direct aggression toward higher- and lower-ranking peers, but this changes rapidly during the first year of life. Mothers generally intervene only on behalf of their offspring in disputes with lower-ranking individuals, and interventions by high-ranking mothers are more frequent and more effective than those by

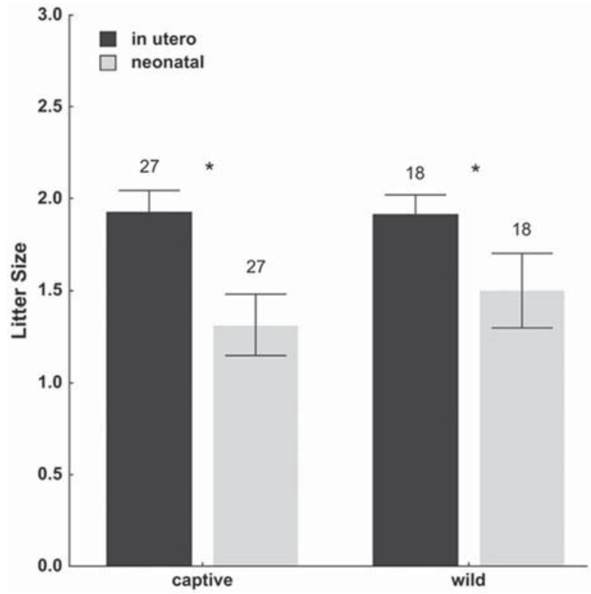

Fig. 18 A comparison of litter sizes within pregnancies before and after birth in captive and wild hyena populations. Significant differences are indicated with asterisks. Numbers above bars represent numbers of pregnant females examined via ultrasonography. Reproduced from Wahaj, S.A., Place, N.J., Weldele, M.L., Glickman, S.E., Holekamp, K.E. 2007. Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive individuals. Behavioral Ecology 18, 974–984.

low-ranking mothers. Over time, cubs learn to direct aggression only toward animals lower-ranking than their own mother. In addition to maternal interventions, other clan members also join hyena cubs during fights to form coalitions (Wahaj *et al.*, 2004; Engh *et al.*2005; Smith *et al.*, 2010). Thus, the mechanisms by which young spotted hyenas acquire their social ranks are virtually identical to those operating in old-world monkeys.

Social Complexity and Brain Evolution

Spotted hyenas have proven to be a useful model for studying the evolution of brains and intelligence (Holekamp *et al.*, 2015). Two competing hypotheses might explain why primates, including humans, have large brains and great intelligence despite the high metabolic costs associated with large brains. The first suggests that intelligence has been favored to enable individuals to cope with challenges imposed by their physical environment. The second is the social complexity, or social brain, hypothesis, which posits that the need to anticipate, respond to, and manipulate the social behavior of other group members was the primary force shaping the evolution of the brain. The frontal cortex of the brain mediates much social decision-making in mammals, and the demands of complex sociality may have favored the evolution of the large frontal cortex in humans and other primates. If selection pressures associated with life in complex societies favor the evolution of cognitive abilities and nervous systems in primates, then convergent attributes of brains and cognition should also occur in nonprimates living in large, elaborate societies in which social dexterity enhances individual fitness. Because spotted hyenas live in large, complex societies, and because they last shared a common ancestor with primates 90–100 MYA, they offer an excellent nonprimate model in which to test predictions of the social complexity hypothesis (Holekamp *et al.*, 2015) (**Fig. 20**).

Many workers agree that the most challenging societies are those in which animals live in stable multigenerational units, group members recognize one another individually, individuals form cooperative coalitions and compete for access to resources with both kin and non-kin, and juveniles engage in a substantial amount of social learning during development. Spotted hyenas face all these challenges (Holekamp *et al.*, 2015). In fact, in addition to the size and structure of spotted hyena clans resembling those of primate troops, patterns of competition and cooperation within clans are also similar to those in primate troops (Engh *et al.*, 2000a). As in cercopithecine primates, spotted hyenas use multiple sensory modalities to recognize their maternal and paternal kin, and other conspecifics, as individuals (Wahaj *et al.*, 2004). Like monkeys, spotted hyenas discriminate among social partners on the basis of their relative value; they recognize third-party kin and rank relationships among members of their clan (Engh *et al.*, 2005). Naturalistic observations of these animals indicate that they track changes in the composition of their current subgroup; and they implement this knowledge to make adaptive social decisions (Smith *et al.*, 2007, 2010). Hyenas also form coalitions with group members to acquire and reinforce their dominance status (Smith *et al.*, 2010).

Spotted hyenas also demonstrate the ability to innovate, defined as the ability to invent a novel solution to a problem or use a familiar behavior to solve a novel problem. Spotted hyenas, for example, possess the ability to innovate when presented with a puzzle box in their natural habitat (**Fig. 21**) (Benson-Amram and Holekamp, 2012). Those individuals who exhibit the greatest

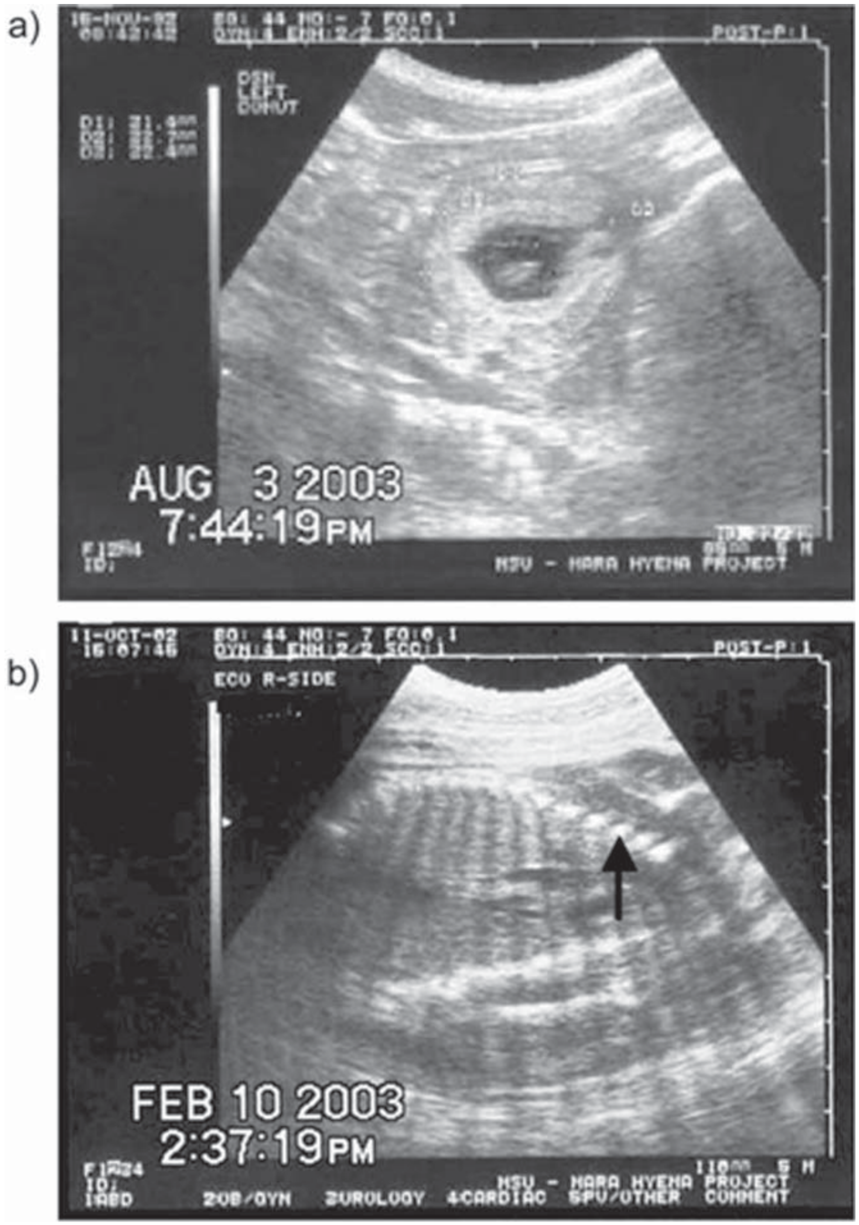

Fig. 19 Sonographic images of (a) early pregnancy (gestational age here was 43 days) indicated by the presence of a gestational sac and thickened endometrial cavity. The gray donut-shaped outer circle is the endometrial wall of the uterine horn and the dark hypoechoic center represents the amniotic fluid and the developing fetus, (b) late pregnancy (gestational age here was 97 days) indicated by skeletal development. The white bands across the screen indicate the vertebrae (arrow) and ribs of the fetus. Reproduced from Wahaj, S.A., Place, N.J., Weldele, M.L., Glickman, S.E., Holekamp, K.E., 2007. Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive individuals. Behavioral Ecology 18, 974–984.

diversity of exploratory behaviors, resembling some measures of human creativity, are the most successful problem-solvers (Benson-Amram and Holekamp, 2012). In contrast, the other species in the family Hyaenidae all live in far less complex societies than those of the spotted hyena, predicting that the frontal cortex in spotted hyenas should be the largest in the family. As predicted by the social complexity hypothesis, the spotted hyenas indeed have the largest brains and the largest frontal cortex of all the extant species of hyenas, even after correcting for its relatively large body size (Arsznov *et al.*, 2010). Thus, the available data strongly suggest convergent evolution of brains and social intelligence between spotted hyenas and primates. However, although the social complexity hypothesis appears able to account for differential neurological measures among extant hyaenids and for the social cognitive abilities of spotted hyenas, it cannot explain the evolution of general intelligence in spotted hyenas or other animals. Thus general intelligence must be favored by selection pressures outside the social domain.

Fig. 20 Spotted hyenas offer an excellent model in which to test the social complexity hypothesis because they live in large, complex societies remarkably similar in size and composition to those of many species of cercopithecine primates (Photo by Laura Smale).

Fig. 21 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).

Fission – Fusion Sociality

Like chimpanzees, spider monkeys, elephants, lions, many canids and dolphins, spotted hyenas live in fluid, fission–fusion societies (Smith *et al.*, 2008). Although up to 130 individuals may concurrently belong to a single clan of spotted hyenas, all clan members are rarely, if ever, found together in one place. Instead, individuals make active decisions to leave (fission) or join (fusion) groupmates belonging to the larger social unit (Smith *et al.*, 2008; Holekamp *et al.*2015). On average in large clans, subgroups contain four individuals. Subgroup composition changes roughly once every hour and the average hyena spends one-third of its time alone. However, low-ranking individuals spend considerably more time alone than do high-ranking conspecifics (Smith *et al.*, 2008). Adult females generally prefer to associate with members of their own matriline (Holekamp *et al.*, 2012). Among nonkin, adult females actively join subgroups containing social companions higher-ranking than themselves; this enhances the social and feeding tolerance enjoyed by females from the dominant animals with which they associate most often (Smith *et al.*, 2007). Immigrant males join subgroups containing potential mates, and they prefer high- to low-ranking females as companions (Szykman *et al.*, 2001), although we do not know yet how males distinguish high- from low-ranking females. Nevertheless, the male hyenas' ability to discriminate among females on the basis of rank, and their preference for females who's young are likeliest to survive to adulthood, permit males to make adaptive mate-choice decisions.

Fig. 22 Spotted hyenas routinely join forces with clan members to direct coalitionary aggression toward lions (which are three to five times larger than a single hyena), and hyenas belonging to neighboring clans in defense of group resources (Photo by Stephanie Dloniak).

The flexible lifestyle of spotted hyenas limits the costs of group living while allowing group members to aggregate when the benefits of sociality are high or the costs of grouping are low. Spotted hyenas gain direct benefits from forming large subgroups during cooperative defense of resources from lions or members from neighboring groups of hyenas (**Fig. 22**). Nonetheless, ecological constraints limit gregariousness such that intraspecific competition among clan-mates generally promotes solitary behavior. Resource limitation operates at virtually all times in the lives of spotted hyenas, occurring in the short term at kills (**Figs. 4 and 7**), but also in the long term during periods of food scarcity that may last several months. In Tanzania and Namibia, hyenas commute long distances to follow migratory prey, redistributing themselves from less profitable areas to more profitable areas (e.g., Hofer and East, 1993). In Kenya, clan members defend the same territory boundaries year-round, but they are most gregarious during months when local prey are superabundant (Smith *et al.*, 2008; Holekamp *et al.*2012) (**Fig. 23**). Although hunting pairs capture 20% more prey than do lone hunters (Holekamp *et al.*, 1997), noise generated when hunting partners squabble over the carcass attracts numerous competitors to kills (Smith *et al.*, 2008). As a result, hyenas, especially low-ranking ones, consume the most energy when they hunt alone (Smith *et al.*, 2008) (**Fig. 1**).

Extant spotted hyenas descended from a carrion-feeding ancestor with a solitary lifestyle much like that of the modern striped hyena. Although the ability to capture a larger array of prey animals more successfully presumably emerged as a by-product of group living, it appears that the benefits of cooperative hunting did not promote the evolution of group living in spotted hyenas (Smith *et al.*, 2008). Instead, group living may have been favored to permit cooperative defense of shared resources, including both space and food (Smith *et al.*, 2008). Nevertheless, constraints imposed by limited food resources might explain retention of the tendency for spotted hyenas to spend much of their time alone.

Behavioral Plasticity and Conservation

Behavioral plasticity is the ability of an animal of a given genotype to modify its behavior in response to changes in environmental conditions. As in many carnivores, the fission–fusion lifestyle of spotted hyenas permits individuals to make plastic decisions with respect to current subgroup size. However, spotted hyenas also exhibit extraordinary plasticity in a suite of other behavioral traits that set them apart from most other large terrestrial carnivores. For instance, spotted hyenas can breed at any time of year; they can be active day or night; and they can survive on foods ranging from insects to elephants (Kruuk, 1972; Holekamp and Dloniak, 2010).

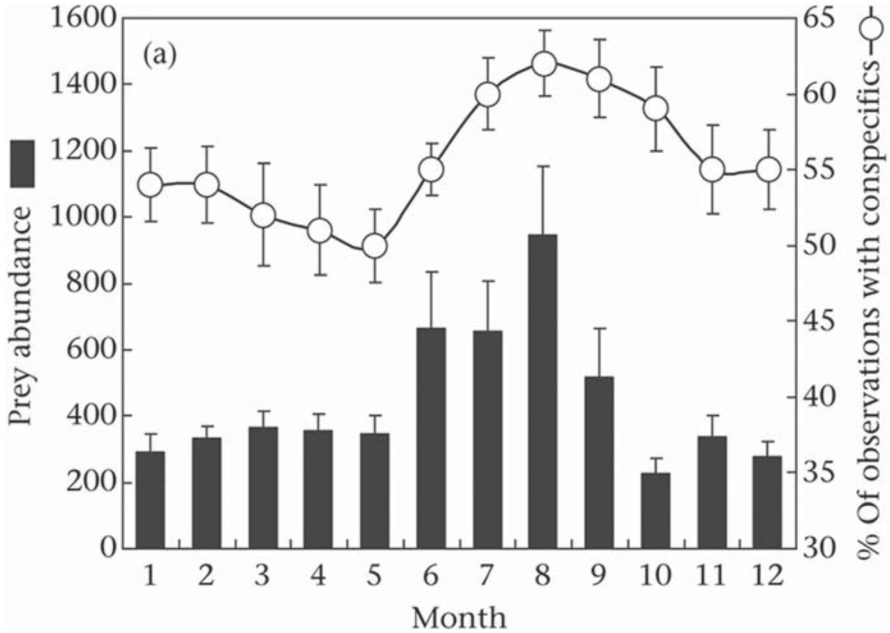

Fig. 23 Monthly mean±SE numbers of local prey animals counted each month during biweekly ungulate censuses within one hyena territory in the Massai Mara Reserve (left vertical axis and histogram bars) and percentage of observation sessions in which spotted hyenas were found in subgroups containing more than one individual (right vertical axis and open circles). Reproduced from Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E., Holekamp, K.E., 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. Animal Behavior 76, 619–636.

Perhaps because spotted hyenas descended recently from carrion-feeding ancestors, their immune systems appear to cope far better with bacteria and diseases than do those of sympatric carnivores (Flies *et al.*, 2016). Samples collected from free-living spotted hyenas as part of a long-term study offer unique insights into their immune systems. For example, whereas two measures of immunity, complement-mediated bacterial killing capacity and concentrations of the antibody immunoglobulin M are positively associated with social rank, immunoglobin G concentrations are rank-independent (Flies *et al.*, 2016).

Spotted hyenas also occupy an extremely diverse array of habitats in Africa, including savanna, desert, swamps, woodland and montane forest up to 4000 m of elevation (Holekamp and Dloniak, 2010). Although spotted hyenas need water for drinking, they can make do with very little water, and seldom require access to it. Plasticity in all of these domains permits spotted hyenas to be unusually resilient to environmental perturbations. Thus, because their behavioral plasticity far exceeds that of other large African carnivores, and because spotted hyenas are relatively easy to monitor, their responses to environmental change should represent convenient and conservative indicators of ecosystem health (Holekamp and Dloniak, 2010).

Global expansion of human populations has caused alarming declines in, or extirpation of, many carnivore populations. Despite their remarkable plasticity and the fact that they are more abundant than any other large carnivore in Africa, populations of spotted hyenas living outside of protected areas are also declining. Disease is an important mortality source for hyenas in some areas, but humans and lions cause most adult mortality. Spotted hyenas are commonly killed by humans in response to, or in fear of, livestock depredation (Kolowski and Holekamp, 2006) (**Fig. 24**). Interestingly, anthropogenic disturbances against lions indirectly benefit spotted hyenas in a highly disturbed reserve (Green *et al.*, 2018).

Humans also have nonlethal effects on spotted hyenas that occur before hyena population size declines. Long-term study suggests that anthropogenic activity, particularly that occurring in the form of pastoralists grazing livestock within the boundaries of protected areas, alters the behavior of spotted hyenas and forces them to make energetic compromises not observed where pastoralists are absent (Boydston *et al.*, 2003). To avoid potentially lethal encounters with humans, hyenas in areas used by pastoralists alter their activity and movement patterns, and they also spend more time being vigilant than do hyenas living in undisturbed areas (Kolowski *et al.*, 2007). Furthermore, presence of pastoralists affects the stress physiology of spotted hyenas, as indicated by higher concentrations of glucocorticoid hormones (Van Meter *et al.*, 2008). Interestingly, these negative effects do not occur in response to visitation by tourists, perhaps because tourists do not represent a threat to spotted hyenas (Van Meter *et al.*, 2008).

The disappearance of this extremely resilient species from an African ecosystem indicates that the habitat has become very severely degraded, perhaps irreversibly so. In areas where spotted hyenas still occur, their behavior, stress physiology, and demography can be monitored to reveal warning indications of deleterious trends. If such trends can be identified and quantified, then they can potentially be halted or reversed. This is particularly important in sub-Saharan Africa, where loss of large carnivores would remove an important incentive for tourists to visit from abroad, and thus eliminate a key source of foreign exchange for many

Fig. 24 Like many large carnivores, spotted hyenas are in conflict with humans over resources, and they sometimes kill livestock such as the cow shown here. Spotted hyenas are commonly killed in response to livestock depredation, even within protected areas (Photo by Joseph M. Kolowski).

developing nations. As human population density continues to increase, and habitats continue to be modified by human activity, spotted hyenas will continue to serve as visible and conservative indicators of how these and more specialized large carnivores in the same ecosystems are responding to environmental change.

See also: **Reproductive Behavior:** Reproductive Behavior in the Hyaenidae.

References

Arsznov, B.M., Lundrigan, B.L., Holekamp, K.E., Sakai, S.T., 2010. Sex and the frontal cortex: A developmental study in the spotted hyena. Brain, Behavior and Evolution 76, 185–197.

Benson-Amram, S., Holekamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. Proceedings of the Royal Society of B-Biological Sciences 279, 4087–4095.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M., Holekamp, K.E., 2003. Altered behaviour in spotted hyenas associated with increased human activity. In: Proceedings of Animal Conservation Forum, pp. 207–219. Cambridge University Press.

Boydston, E.E., Morelli, T.L., Holekamp, K.E., 2001. Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). Ethology 107 (5), 369–385.

Curren, L.J., Weldele, M.L., Holekamp, K.E., 2003. Ejaculate quality in spotted hyenas: Intraspecific variation in relation to life-history traits. Journal of Mammalogy 94 (1), 90–99.

Dloniak, S.M., French, J.A., Holekamp, K.E., 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. Nature 440, 1190–1193.

East, M.L., Hofer, H., 2001. Male spotted hyenas (Crocuta crocuta) queue for status in social groups dominated by females. Behavioral Ecology 12(5), 558–568.

East, M.L., Burke, T., Wilhelm, K., Greig, C., Hofer, H., 2003. Sexual conflicts in spotted hyenas: Male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. Proceedings of the Royal Society of London B: Biological Sciences 270 (1521), 1247–1254.

East, M.L., Hofer, H., 1991. Loud calling in a female-dominated mammalian society: I and II. Animal Behaviour 42, 637–669.

East, M.L., Hofer, H., Wickler, W., 1993. The erect 'penis' as a flag of submission in a female-dominated society: Greetings in Serengeti spotted hyenas. Behavioral Ecology and Sociobiology 33, 355–370.

Engh, A.L., Esch, K., Smale, L., Holekamp, K.E., 2000a. Mechanisms of maternal rank 'inheritance' in the spotted hyaena, *Crocuta crocuta*. Animal Behaviour 60 (3), 323–332.

Engh, A.L., Funk, S.M., Horn, R.C.V., et al., 2002. Reproductive skew among males in a female-dominated mammalian society. Behavioral Ecology 13(2), 193–200.

Engh, A.L., Funk, S.M., Van Horn, R.C., et al., 2000b. Reproductive skew in a female-dominated society. Behavioral Ecology 13 (2), 193–200.

Engh, A.L., Siebert, E.R., Greenberg, D.A., Holekamp, K.E., 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. Animal Behaviour 69 (1), 209–217.

Flies, A.S., Mansfield, L.S., Flies, E.J., Grant, C.K., Holekamp, K.E., 2016. Socioecological predictors of immune defences in wild spotted hyenas. Functional Ecology 30 (9), 1549–1557.

Frank, L.G., 1986. Social organization of the spotted hyaena (*Crocuta crocuta*): I and II. Animal Behaviour 34, 1500–1527.

Glickman, S.E., Cunha, G.R., Drea, C.M., Conley, A.J., Place, N.J., 2006. Mammalian sexual differentiation: Lessons from the spotted hyena. Trends in Endocrinology and Metabolism 17 (9), 349–356.

Gould, S.J., 1981. Hyena myths and realities. Natural History 90 (2), 16.

Green, D.S., Johnson-Ulrich, L., Couraud, H.E., Holekamp, K.E., 2018. Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. Biodiversity and Conservation 27, 1–19.

Hofer, H., East, M.L., 1993. The commuting system of Serengeti spotted hyaenas: How a predator copes with migratory prey. I, II, and III. Animal Behaviour 46 (3), 547–589.

Holekamp, K.E., Danzter, B., Stricker, G., Yoshida, K.C.S., Benson-Amram, S., 2015. Brains, brawn and sociality: A hyaena's tale. Animal Behaviour 103, 237–248.

Holekamp, K.E., Dloniak, S.M., 2010. Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. Advances in the Study of Behavior 42, 189–229.

Holekamp, K.E., Smale, L., Berg, R., Cooper, S.M., 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). Journal of Zoology 242 (1), 1–15.

Holekamp, K.E., Smale, L., Szykman, M., 1996. Rank and reproduction in the female spotted hyaena. Journal of Reproduction and Fertility 108 (2), 229–237.

Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., Watts, H.E., 2012. Society, demography and genetic structure in the spotted hyena. Molecular Ecology 21 (3), 613–632.

Holekamp, K.E., Swanson, E.M., Van Meter, P.E., 2013a. Developmental constraints on behavioural flexibility. Philosophical Transactions of the Royal Society 368 (1618), 20120350.

Holekamp, K.E., Van Meter, P.E., Swanson, E.M., 2013b. Developmental constraints on behavioral flexibility. Philosophical Transactions of the Royal Society B, Biological Sciences 368 (1618), 20120350.

Höner, O.P., Wachter, B., East, M.L., et al., 2007. Female mate-choice drives the evolution of male-biased dispersal in a social mammal. Nature 448, 798–801.

Kolowski, J.M., Holekamp, K.E., 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. Biological Conservation 128 (4), 529–541.

Kolowski, J.M., Katan, D., Theis, K.R., Holekamp, K.E., 2007. Daily patterns of activity in the spotted hyena. Journal of Mammalogy 88 (4), 1017–1028.

Kruuk, H., 1972. The Spotted Hyena: A Study of the Predation and Social behavior. University of Chicago Press, Chicago.

Lewin, N., Swanson, E.M., Williams, B.L., Holekamp, K.E., 2017. Juvenile concentrations of IGF-1 predict life-history trade-offs in a wild mammal. Functional Ecology 31 (4), 894–902.

Mills, M.G.L., 1990. Kalahari Hyaenas: The Behavioral Ecology of Two Species. Unwin Hyman, London.

Smale, L., Frank, L.G., Holekamp, K.E., 1993. Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with adult females and immigrant males. Animal Behaviour 46, 467–477.

Smith, J.E., Estrada, J.R., Richards, H.C., et al., 2015. Collective movements, leadership and consensus costs at reunions in spotted hyaenas. Animal Behaviour 105, 187–200.

Smith, J.E., Kolowski., J.M., Graham, K.E., Dawes, S.E., Holekamp, K.E., 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. Animal Behaviour 76, 619–636.

Smith, J.E., Lehmann, K.D.S., Montgomery, T.M., Strauss., E.D., Holekamp, K.E., 2017. Insights from long-term field studies of mammalian carnivores. Journal of Mammalogy 98, 631–641.

Smith, J.E., Memenis, S.K., Holekamp, K.E., 2007. Rank-related partner choice in the fission-fusion society of the spotted hyena. Behavioral Ecology and Sociobiology 61 (5), 753–765.

Smith, J.E., Powning, K.S., Dawes, S.E., et al., 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. Animal Behaviour 81, 401–415.

Smith, J.E., Van Horn, R.C., Powning, K.S., et al., 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. Behavioral Ecology 21 (2), 284–303.

Swanson, E.M., McElhinny, T.L., Dworkin, I., et al., 2013. Ontogeny of sexual size dimorphism in the spotted hyena (*Crocuta crocuta*). Journal of Mammalogy 94 (6), 1298–1310.

Szykman, M., Engh, A.L., Van Horn, R.C., et al., 2001. Association patterns among male and female spotted hyenas (*Crocuta crocuta*) reflect male mate choice. Behavioral Ecology and Sociobiology 50 (3), 231–238.

Tanner, J.B., Dumont, E.R., Sakai, S.T., Lundrigan., B.L., Holekamp., K.E., 2008. Of arcs and vaults: The biomechanics of bone-cracking in spotted hyenas (*Crocuta crocuta*). Biological Journal of the Linnean Society 95 (2), 246–255.

Theis, K.R., Schmidt, T.M., Holekamp, K.E., 2012. Evidence for a bacterial mechanism for group-specific social odors among hyenas. Scientific Reports 2, 615.

Tinbergen, N., 1963. On aims and methods in ethology. Zeitschrift für Tierpsychologie 20, 410–433.

Van Horn, R.C., Engh, A.L., Scribner, K.T., Funk, S.M., Holekamp, K.E., 2004. Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan level cooperation. Molecular Ecology 13 (2), 449–458.

Van Meter, P.E., French, J.A., Dloniak, S.M., et al., 2008. Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. Hormones and Behavior 55, 329–337.

Wahaj, S.A., Guse, K.R., Holekamp, K.E., 2001. Reconciliation in the spotted hyena (*Crocuta crocuta*). Ethology 107 (12), 1057–1074.

Wahaj, S.A., Place, N.J., Weldele, M.L., Glickman, S.E., Holekamp, K.E., 2007. Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive l individuals. Behavioral Ecology 18, 974–984.

Wahaj, S.A., Van Horn, R.C., Van Horn, T.L., et al., 2004. Kin discrimination in the spotted hyena (*Crocuta crocuta*): Nepotism among siblings. Behavioral Ecology and Sociobiology 56 (3), 237–247.

Watts, H.E., Tanner, J.B., Lundrigan, B.L., Holekamp, K.E., 2009. Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. Proceedings of the Royal Society of London B: Biological Sciences 276 (1665), 2291–2298.

Wilson, D.E.M., Russell, A., 2009. Handbook of the Mammals of the World. Lynx Editions, Barcelona.

Relevant Websites

www.youtube.com/watch?v=a7knYbhe0_8. –Adult Female Hyenas Greeting.wmv.
www.youtube.com/watch?v=S6T752_EXno. –Hyena Aggression: The Scapegoat-Chain.
http://www.hyaenidae.org/. –IUCN Hyaena Specialist Group.
http://www.holekamplab.org/. –Kay E. Holekamp Laboratory.
www.youtube.com/watch?v=0ZowlS5zo1o&lc=z23jjpu4dvrpu3vq204t1aokgr4spswngahmdijznbkjrk0h00410. –Lion Hyena Interaction.
www.youtube.com/watch?v=1uazjU54suM. –Mating Hyenas.
http://msuhyenas.blogspot.com/. –Michigan State University Hyena Research Blog.
www.youtube.com/watch?v=xtOBJ0EjJlY. –MSUToday: Hyena Puzzle Box.
www.youtube.com/watch?v=IsCLyqMbSgY&feature=youtu.be. –MSUToday: Learning About Hyenas.
www.youtube.com/watch?v=Rs7AXFa4sN0. –Spotted hyenas join forces to collectively mob a group of lionesses to defend their kill from left by lions.
www.youtube.com/watch?v=MYULS7zGbqk. –Spotted hyenas join forces to usurp carcass from a pride of lionesses.
https://www.youtube.com/watch?v=w5waide171I. Sunrise- Hyena Stand off in the Mara.
www.youtube.com/watch?v=PBCNWmU5apE. –Why It Sucks to Be a Male Hyena.