

Spotted Hyenas

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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. These animals provide scientists with rich data to address questions at all four of Tinbergen's levels of analysis, including 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 Carnivore suborder Feliformia, which also contains cats, mongooses, civets, and allies. 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 so 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. Recent

molecular data indicate that *Crocuta* is the sister taxon to the monophyletic clade containing *Parahyaena* and *Hyaena* and also that *Proteles* represents a separate lineage that last shared a common ancestor with the bone-cracking hyenas some 10.6 Ma.

All four extant hyaenid species apparently originated in Africa, their ancestors having arrived there earlier from Eurasia via the Gomphothere land bridge at what is now Saudi Arabia. Bone-cracking forms appeared relatively late in the history of the hyena family, during the Late Miocene, and the extant bone-cracking forms all first appear in the fossil record in the Late Pliocene. The aardwolf (*Proteles*) is also apparently recently derived, first appearing in the Pleistocene. Modern spotted hyenas first appear in the fossil record less than 1 000 000 years ago.

Members of Hyaenidae and Their Ecological Niches

The four extant hyena species occupy three different feeding niches. 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. 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 (Figure 1). Spotted hyenas are impressively versatile in their choice of prey and use a number of different hunting techniques.

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. 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. Bone-cracking hyenas, particularly the spotted hyena, can generate enormous bite forces. In fact, wild spotted hyenas can even break open the leg bones of giraffe.



Figure 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).

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 (**Figure 2**), they are substantially more aggressive than adult males, and they are socially dominant to all adult immigrant males (**Figure 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 (**Figure 4**). Social rank strongly influences female reproductive performance. High-ranking females enjoy longer reproductive lifespans, experience shorter intervals between litters, and produce more surviving offspring than do lower-ranking females.

Perhaps the most unusual role-reversed trait in this species is the external genital morphology of the female spotted hyena. 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 (**Figure 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 **Figure 6**.

Many of the mysteries associated with sex-role reversed traits among extant spotted hyenas can only be unraveled in the 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. In stark contrast to any other hyaenid, however, spotted hyenas experience intense competition associated with feeding on fresh ungulate carcasses (**Figure 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. 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 hour. Thus, ungulate carcasses represent 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 (**Figure 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 (**Figure 9**) that favored the evolution of large, aggressive 'role-reversed' females capable of allowing their handicapped cubs access to food.



Figure 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).

A simplified hyena dominance hierarchy

		Loser								
		MRPH	SEIN	WHO	MP	NAV	BAIL	MIG	BP	BOS
Winner	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
Immigrant males

Note: Cubs slot into the hierarchy immediately below their mothers

Figure 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.

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. Why females with such heavily ‘masculinized’ genitalia evolved in spotted hyenas remains one of the most fascinating unanswered questions posed by this species (Figures 5 and 6). We are unlikely ever to know 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



Figure 4 A hyena's relative rank position in the social dominance hierarchy of the clan determines its priority of access to food at kill scenes. 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).



Figure 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 transverse the enlarged clitoris (Drawing by Christine Drea).

female spotted hyenas more complete control over which sperm fertilizes their eggs, and thus permits females to engage in 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. 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 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. All the existing alternative hypotheses can be ruled out, suggesting that the female's pseudopenis might indeed be involved in enhancing female control over fertilization.



Figure 6 The female hyena's clitoris is elongated, and distinguishable from the male's penis based on the shape of the penile glans. The glans of the juvenile female shown here is blunt, whereas those of males are pointed (Photo by Kay Holekamp and Laura Smale).



Figure 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 Laura Smale).

Social Organization

Spotted hyenas live in permanent complex, female-dominated societies, called clans, containing 6–90 individuals. The mean clan size across Africa is around 21 hyenas, but abundance of local prey animals determines clan size. 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, clans are

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.

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

(Figure 10), yet clan members spend much of their time alone or in small subgroups. Each clan is structured by a linear dominance hierarchy, and an individual's position in this hierarchy determines its priority of access to food (Figures 3 and 4). Although small clans may contain only a single matriline and a single breeding male, large clans may contain several different matrilineal comprising related females and their offspring, as well as a number of adult immigrant males that are generally unrelated to one another. 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 matrilineal, but on average, clan members are only very distantly related because of high levels of male-mediated gene flow among clans. In most respects, clans of spotted hyenas bear little resemblance to canid packs, lion prides, or groups of any



Figure 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. Eng).

other social carnivores. Instead, they are remarkably similar in their structure, size, and complexity to the female-bonded societies of cercopitheine primates.

Life History

The life histories of spotted hyenas exhibit many notable similarities to those of cercopitheine primates. Like monkeys, spotted hyenas have slow life histories. Hyenas live up to 19 years in the wild. At isolated natal dens (Figure 11), female hyenas bear litters containing one, two, or very rarely three cubs. 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. Here cubs are first introduced to the other members of the clan and learn their places in the clan's dominance hierarchy. Cubs become independent of the communal den when they are 9–12 months old. At this point, they start traveling around the clan's territory with their mother. On average, weaning occurs at around 13 months of age, but mothers may continue to nurse their cubs for up to 24 months. Mothers also help their offspring gain access to food at ungulate kills long after weaning, and even after puberty. 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. 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. 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 of the new hyenas encountered outside the natal area. This is



Figure 9 An ontogenetic series of *Crocuta* 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 (Photo by Jeremy Herliczek).

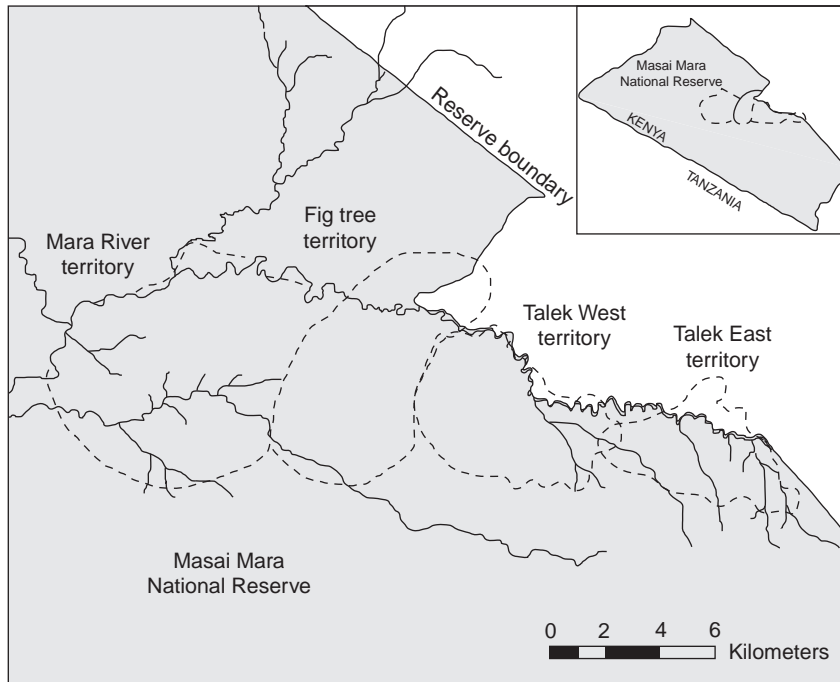


Figure 10 Dashed lines indicate the territorial boundaries of four clans of spotted hyenas in the Masai Mara National Reserve, Kenya (Image by Audrey Derose Wilson).

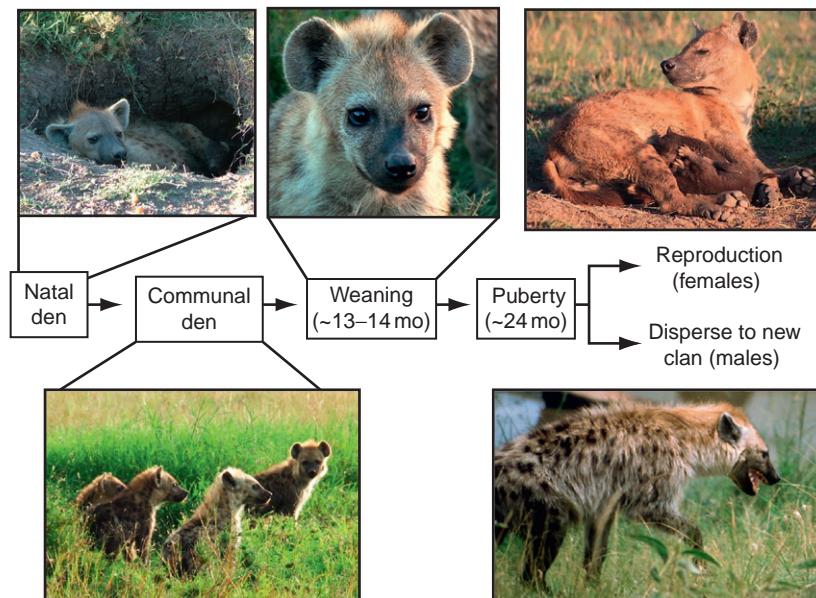


Figure 11 Spotted hyenas experience several discrete life history stages during their ontogeny. They are born at natal dens, and then are transferred to the communal den where they reside until they are 8–9 months of age. Subadults continue to nurse until 13.5 months of age, on average, and then undergo puberty around 24 months of age. After puberty, males disperse to join a new clan whereas females begin to reproduce in their natal clan.

the phase of ontogenetic development during which females come to dominate males. When a male joins a new clan, he assumes the lowest rank in that clan's dominance hierarchy (Figure 3). 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. The highest-ranking males are those that arrived first in the clan, and the lowest-ranking immigrants, most recently. Males rise in rank only when higher-ranking immigrants die or engage in secondary dispersal. Due to the female's male-like genitalia, coercive

sex is impossible. Among spotted hyenas, females strongly prefer to mate with immigrant males, which sire nearly all the offspring in every clan. Thus, mate choice by females apparently drives natal dispersal by males. 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 each other 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. Spotted hyenas are often referred to as laughing hyenas because of their submissive ‘giggle’ vocalizations that 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. 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. Spotted hyenas also sometimes whoop to recruit hunting partners, or to reunite mothers and offspring. Finally, whoops are also used as a form of individual display, particularly by adult immigrant males of high rank.

Olfactory communication plays an important role in advertising territorial borders (Figure 10), but also functions to signal intrasexual social status among immigrant males, and to maintain social cohesion among adult females. 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 (Figure 12). Individuals also paste deep within their territories. Bacterial communities inhabiting hyena subcaudal glands vary among clans, and bacteria may be largely responsible for generating clan-specific odors. In addition to signaling clan membership, paste also transmits information about an individual’s sex, reproductive state, and identity. 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 each other and face in opposite directions to sniff each other’s anogenital region (Figure 13). Greetings are most common when clan members reunite after being separated. The unique aspect of greetings in the spotted hyena is the prominent role of the erect phallus



Figure 12 Pasting behavior is the deposition of a strong-smelling, yellowish buttery secretion from the anal gland onto a grass stalk (Photo by Anne Engh).

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. Greetings represent affiliative gestures that reacquaint clan mates, strengthen social bonds, and affirm rank relationships. Directly following fights, greetings serve a conciliatory function by reducing rates of subsequent aggression between former opponents. Hyenas typically initiate greetings with higher-ranking social partners, and they do so with their phallus erect. Therefore the display of the erect phallus during greetings is often called a flag of submission.

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. 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. In fact, development of this strange organ is androgen-independent except for some finishing touches to the final shape of the penile glans. Furthermore, there is no evidence that activational effects of androgens or other steroid hormones mediate aggressive behavior emitted by female hyenas. However, there is some support for the idea that organizational effects of androgens mediate female aggressiveness in this species.



Figure 13 Ritualized greetings signal submission by the subordinate hyena and occur when two spotted hyenas stand parallel to each other with phallic erections and face in opposite directions to sniff each other's anogenital region (Photo by Heather Watts).

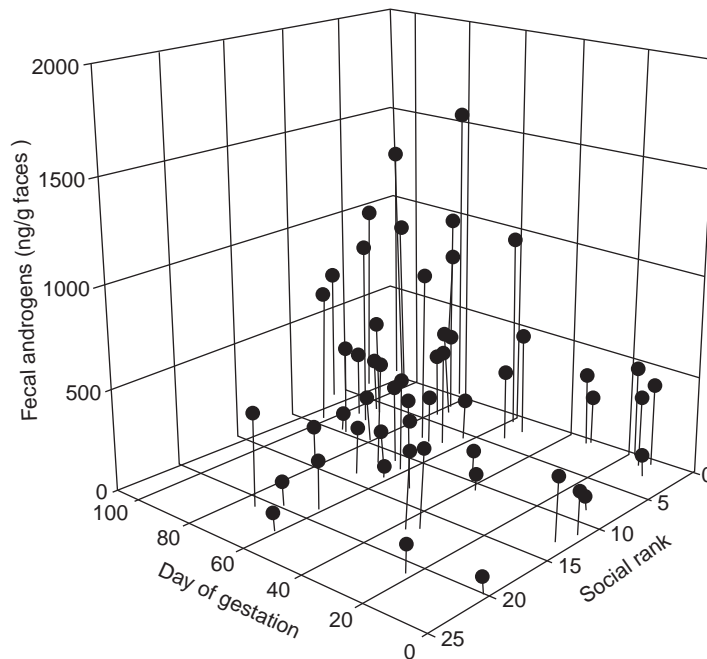


Figure 14 The relationships among social rank, day of gestation, and fecal androgen metabolite concentration in pregnant wild spotted hyenas. The highest social rank possible is 1. Reproduced from [Dloniak SM, French JA, and Holekamp KE \(2006\)](#) Rank-related maternal effects of androgens on behaviour in wild spotted hyenas. *Nature* 440: 1190–1193. Figure printed with permission by Macmillan Publishers Ltd: Nature Publishing Group.

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. Dominant females have higher concentrations of androgens during late pregnancy than do subordinate females ([Figure 14](#)). 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. 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. Enhanced aggressiveness may help females dominate males and compete for food at kills. Thus, prenatal androgen exposure appears to adaptively influence offspring phenotype.

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 sibling (Figure 15). 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 (Figures 16 and 17). 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

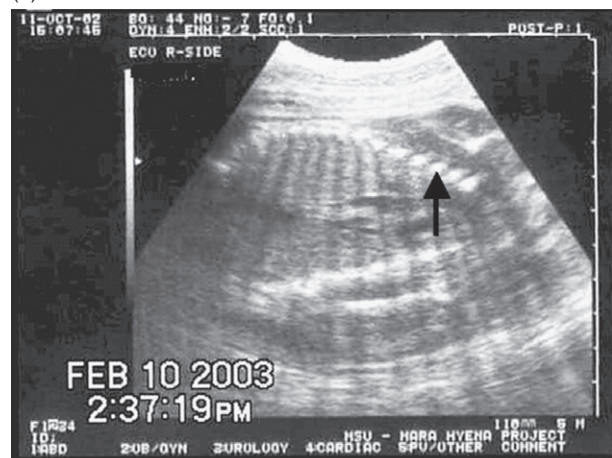


Figure 15 Black hyena cubs are born with their eyes open and teeth fully erupted, characteristics that are rare amongst carnivores (top). Littermates engage in aggressive interactions within minutes after birth (bottom), which quickly leads to the establishment of a dominance hierarchy between littermates (Photos by S.E. Glickman and L.G. Frank).

access to the mother's milk. 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. 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



(a)



(b)

Figure 16 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 SA, Place NJ, Weldele ML, Glickman SE, and Holekamp KE (2007) Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive I individuals. *Behavioral Ecology* 18: 974–984.

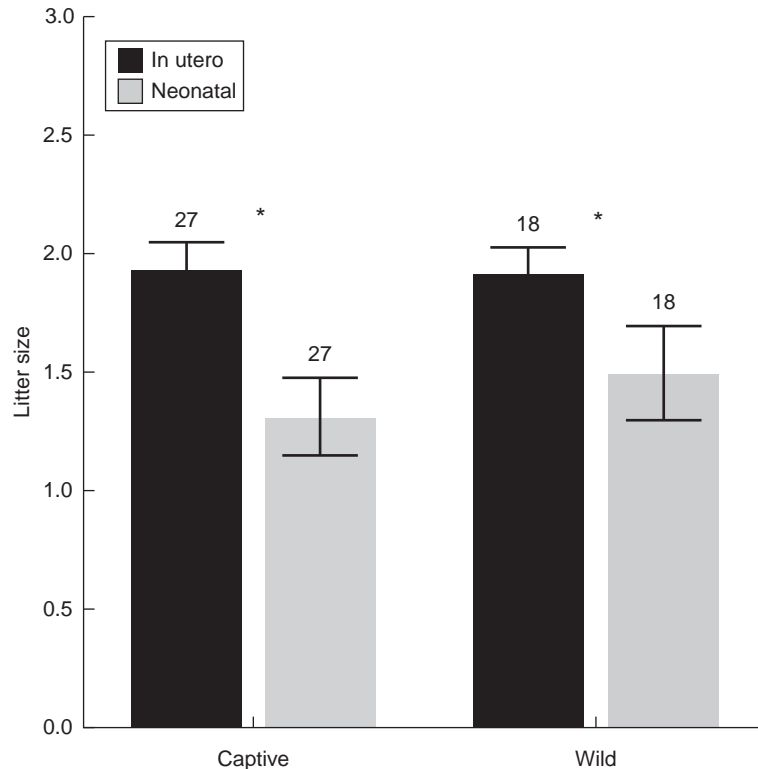


Figure 17 A comparison of litter sizes within pregnancies before and after birth in captive and wild hyena populations. Significant differences are indicated with asterisks. Numbers above bars represent numbers of pregnant females examined via ultrasonography. Reproduced from Wahaj SA, Place NJ, Weldele ML, Glickman SE, and Holekamp KE (2007) Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive individuals. *Behavioral Ecology* 18: 974–984.

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 (Figure 3). Dominance relations among adult female spotted hyenas are extremely stable across a variety of contexts and over periods of many years. Early in life, young spotted hyenas of both sexes assume the social rank directly below that of their mother. 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. 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 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. 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 proved to be a useful model for studying the evolution of brains and intelligence. 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 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 non-primates living in large, elaborate societies in which social dexterity enhances individual fitness. Because spotted hyenas live in large, complex societies, they offer an excellent nonprimate model in which to test predictions of the social complexity hypothesis (Figure 18).

Many workers agree that the most challenging societies are those in which animals live in stable multigenerational units, group members recognize each other individually, individuals form cooperative coalitions and compete for access to resources, and juveniles engage in a substantial amount of social learning during development. Spotted hyenas face all these challenges. 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. As in cercopithecine primates, spotted hyenas use multiple sensory modalities to recognize their maternal and paternal kin, and other conspecifics, as individuals. 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; they track changes in the composition of their current subgroup; and they implement this knowledge to make adaptive social decisions. Hyenas also form coalitions with group members to acquire and

reinforce their dominance status. 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 frontal cortex of the extant species of hyenas, even after correcting for its relatively large body size. Thus the available data strongly suggest convergent evolution of brains and social intelligence between spotted hyenas and primates.

Fission–Fusion Sociality

Like chimpanzees, spider monkeys, elephants, lions, many canids and dolphins, spotted hyenas live in fluid, fission–fusion societies. Although up to 90 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) group-mates belonging to the larger social unit. On average, subgroups contain four individuals. Subgroup composition changes once every hour and hyenas spend one-third of their time alone. However, low-ranking individuals spend considerably more time alone than do high-ranking conspecifics. Adult females generally prefer to associate with members of their own matriline. 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



Figure 18 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).

associate most often. Immigrant males join subgroups containing potential mates, and they prefer high- to low-ranking females as companions. Their 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.

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 neighboring groups of hyenas (Figure 19). 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 (Figures 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. In Kenya, clan members defend the same territory boundaries year-round, but they are most gregarious during months when local prey are superabundant (Figure 20). Although hunting pairs capture 20% more prey than do lone hunters, noise generated when hunting partners squabble over the carcass attracts numerous competitors to kills. As a result, hyenas, especially low-ranking ones, consume the most energy when they hunt alone (Figure 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. Instead, group living may have been favored to permit cooperative defense of shared resources, including both space and food. 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. 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. Spotted hyenas also occupy an



Figure 19 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 Kate Shaw).

extremely diverse array of habitats in Africa, including savanna, desert, swamps, woodland and montane forest up to 4000 m of elevation. Although spotted hyenas need water for drinking, they can make do with very little water, and seldom require access to it. Even lactating females can survive without water for over 1 week. 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.

Global expansion of human populations has caused alarming declines in, or extirpation of, many carnivore populations. Despite their remarkable plasticity and the

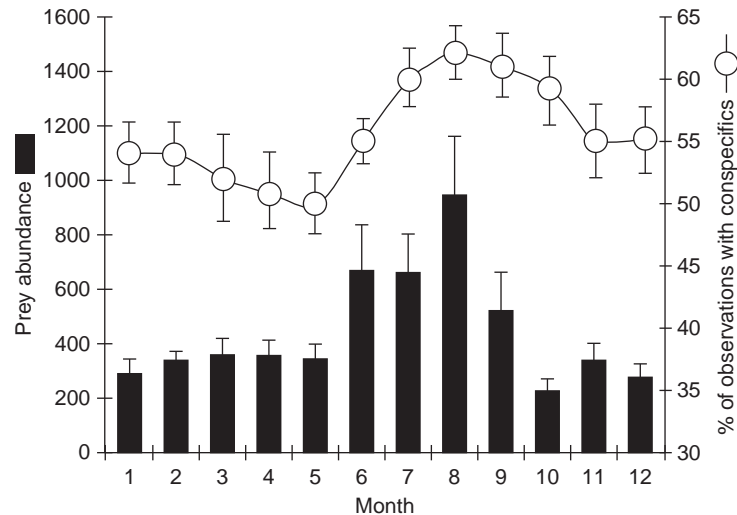


Figure 20 Monthly mean \pm SE numbers of local prey animals counted each month during biweekly ungulate censuses within one hyena territory in the Massai Mara Reserve (left vertical axis and histogram bars) and percentage of observation sessions in which spotted hyenas were found in subgroups containing more than one individual (right vertical axis and open circles). Reproduced from [Smith JE, Kolowski JM, Graham KE, Dawes SE, and Holekamp KE \(2008\)](#) Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619–636.



Figure 21 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).

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 (Figure 21). Humans also have nonlethal effects on spotted hyenas that occur before hyena population size declines. Recent work 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. 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. Furthermore, presence of pastoralists affects the stress physiology of spotted hyenas, as indicated by higher concentrations of glucocorticoid hormones. Interestingly, these negative effects do not occur in response to visitation by tourists, perhaps because tourists do not represent a threat to spotted hyenas.

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 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: Aggression and Territoriality; Body Size and Sexual Dimorphism; Communication Networks; Conflict Resolution; Conservation Behavior and Endocrinology; Cooperation and Sociality; Cryptic Female Choice; Decision-Making: Foraging; Dominance Relationships, Dominance Hierarchies and Rankings; Ethology in Europe; Group Living; Hormones and Behavior: Basic Concepts; Kin Selection and Relatedness; Maternal Effects on Behavior; Multimodal Signaling; Predator's Perspective on Predator-Prey Interactions; Sex Change in Reef Fishes: Behavior and Physiology; Social Cognition and Theory of Mind; Social Selection, Sexual

Selection, and Sexual Conflict; Wintering Strategies: Molt and Behavior.

Further Reading

- Dloniak SM, French JA, and Holekamp KE (2006) Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. *Nature* 440: 1190–1193.
- Drea CM, Weldele ML, Forger NG, et al. (1998) Androgens and masculinization of genitalia in the spotted hyaena (*Crocuta crocuta*). 2. Effects of prenatal anti-androgens. *Journal of Reproduction and Fertility* 113: 117–127.
- East ML and Hofer H (1991) Loud calling in a female-dominated mammalian society: I and II. *Animal Behaviour* 42: 637–669.
- East ML, Hofer H, and 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 AL, Funk SM, Van Horn RC, et al. (2002) Reproductive skew among males in a female-dominated society. *Behavioral Ecology* 13: 193–200.
- Frank LG (1986) Social organization of the spotted hyaena (*Crocuta crocuta*): I and II. *Animal Behaviour* 34: 1500–1527.
- Hofer H and East ML (1993) The commuting system of Serengeti spotted hyaenas: How a predator copes with migratory prey. I, II, and III. *Animal Behaviour* 46: 547–589.
- Holekamp KE (in press) *Evolutionary Ecology of the Spotted Hyena*. Princeton, NJ: Princeton University Press.
- Holekamp KE, Sakai ST, and Lundrigan BL (2007) Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B-Biological Sciences* 362: 523–538.
- Holekamp KE and Smale L (2000) Feisty females and meek males: Reproductive strategies in the spotted hyena. In: Wallen K and Schneider J (eds.) *Reproduction in Context*, pp. 257–285. Cambridge, MA: MIT Press.
- Höner OP, Wachter B, East ML, et al. (2007) Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature* 448: 798–801.
- Kruuk H (1972) *The Spotted Hyena: A Study of the Predation and Social behavior*. Chicago: University of Chicago Press.
- Mills MGL (1990) *Kalahari Hyaenas: The Behavioral Ecology of Two Species*. London: Unwin Hyman.
- Smale L, Frank LG, and Holekamp KE (1993) Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with adult females and immigrant males. *Animal Behaviour* 46: 467–477.
- Smith JE, Kolowski JM, Graham KE, Dawes SE, and Holekamp KE (2008) Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76: 619–636.
- Tinbergen N (1963) On aims and methods in ethology. *Zeitschrift für Tierpsychologie* 20: 410–433.
- Van Meter PE, French JA, Dloniak SM, Watts HE, Kolowski JM, and Holekamp KE (2008) Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Hormones and Behavior* 55: 329–337.
- Wahaj SA, Place NJ, Weldele ML, Glickman SE, and Holekamp KE (2007) Siblicide in the spotted hyena: Analysis with ultrasonic examination of wild and captive I individuals. *Behavioral Ecology* 18: 974–984.

Relevant Websites

- <http://www.hyaenidae.org/> – IUCN Hyaena Specialist Group.
- <http://hyenas.zoology.msu.edu/> – Kay E. Holekamp Laboratory.
- <http://msuhyenas.blogspot.com/> – Michigan State University Hyena Research Blog.