Behavioral Development in the Spotted Hyena

Hyena development teaches us much about selection pressures shaping age-related variation in mammalian behavior

Kay E. Holekamp and Laura Smale

In many animal species, adults and juveniles occupy different ecological niches. The selection pressures operating within each niche favor morphological and behavioral traits that may differ dramatically from those expressed in younger or older individuals. In organisms as diverse as trematodes, butterflies, and frogs, the behavior and morphology of larval forms bear little resemblance to those of adults. In such animals, all of which undergo metamorphosis, it is readily apparent that structures and functions of immature forms are not necessarily mere precursors of adult traits, but represent specific adaptations to life in the niches occupied by juveniles. For example, the tail, gills, and lateral line system of tadpoles are critical for larval growth and survival but do not contribute to survival or reproductive success of adult animals (Oppenheim 1981, Stehouwer 1991). Therefore, at metamorphosis, these traits fall away like scaffolding from a completed building (Bateson 1986). At the same time, a variety of novel characteristics emerge that enable the adult frog to survive and reproduce in its new terrestrial environment.

Some juvenile behaviors are temporary adaptations to a specific set of selection pressures that animals ultimately outgrow

Similarly striking reorganizations of the phenotype also occur during mammalian development. An obvious example is the impressive morphological reorganization occurring in humans at puberty, when secondary sex characteristics like breasts or facial hair first appear. Although less easily observed than these dramatic changes in morphology, reorganizations of the behavioral phenotype also occur throughout mammalian development. For example, patterns of play behavior in domestic cats change abruptly at 7–8 weeks of age (Bateson 1981, Caro 1981), a "sensitive period" for forming social bonds occurs in dogs between 3 and 12 weeks of age (Scott et al. 1974), and "separation anxiety" first appears in human infants at 8–9 months of age (Kagen 1991). Studying such developmental discontinuities may reveal how behavior expressed at a particular ontogenetic stage is adaptive in the physical and social environments typically encountered by individuals at that stage. But which mammals should be selected for study?

Most research on mammalian behavioral development uses rodents or primates as model organisms (e.g., Myers 1991, Robinson and Smotherman 1992, Pereira and Fairbanks 1993). However, in both taxa, particularly primates, behavioral development often appears to unfold as a continuous, gradual process because there are few, if any, abrupt changes in the infant's environment as it matures. For example, as an infant primate grows, it becomes independent of its mother, spending less and less time each day in physical proximity to her (Hinde and Spencer-Booth 1967, Chalmers 1987). The daily changes in mother–infant interaction are nearly imperceptible. Nevertheless, over a period of several months, the infant ceases to cling continuously to its mother and eventually visits her only occasionally for nursing or grooming. Such patterns of continuous change suggest that behavioral development is a process in which new behaviors emerge gradually from older ones, and that this process ultimately culminates in the emergence of the adult behavioral repertoire (Klopfer 1988). Unfortunately, however, research that focuses exclusively on continuous developmental processes sometimes leads to the misconception that young animals are merely imperfect adults, with incomplete behavioral repertoires, rather than individuals behaving in ways that promote their immediate competence and survival (Lee and Bateson 1986).

Mammalian carnivores in general,

Kay E. Holekamp (e-mail: holekamp@pilot.msu.edu) and Laura Smale (smale@pilot.msu.edu) are associate professors in the Departments of Zoology and Psychology, Michigan State University, East Lansing, MI 48824-1115. Both authors study spotted hyenas in Kenya; in addition, Holekamp works on the behavioral ecology and endocrinology of ground squirrels, and Smale studies the neural substrates of biological rhythms in mammals.

Figure 1. A female hyena cub, showing her male-like genitalia.

and social carnivores in particular, are uniquely suited for the study of behavioral change during development because, in contrast to most mammals, gregarious carnivores have life histories that are often naturally partitioned into discrete stages. During each developmental stage, an individual carnivore may confront a different suite of social and ecological challenges imposed by its immediate environment. Consequently, natural selection has molded behaviors that adapt the young carnivore to the particular environment it inhabits at each developmental stage.

We use the spotted hyena (*Crocuta crocuta*) as a model organism in which to examine patterns of behavioral development. Spotted hyenas are large, gregarious carnivores that live throughout sub-Saharan Africa. In this article, we describe the discrete stages that are characteristic of hyena life histories and relate behavior patterns that are expressed during each developmental stage to the specific ecological and social demands imposed at that time by the animal's environment. As in most mammals, sexually dimorphic behavior patterns emerge during hyena development, and we consider how these behavioral sex differences reflect different sets of socioecological challenges faced by males and females at each stage. Finally, we explore the question of whether specific behaviors enhance individual welfare exclusively during the developmental stage in which they first appear, at later stages of development, or both.

The natural history of the spotted hyena

Spotted hyenas have some unique attributes that make them especially interesting subjects of behavioral studies. In contrast to other female mammals, female spotted hyenas are exposed to high levels of androgenic hormones in utero, and they exhibit dramatic masculinization of their morphology and behavior (Glickman et al. 1987, 1992, Frank et al. 1991, Licht et al. 1992). Females have external genitalia that look virtually identical to those of the male (Figure 1), they are more aggressive than males (Frank et al. 1989, Smale et al. 1993), and they are socially dominant to males (Kruuk 1972).

Spotted hyenas live in social groups, called clans, of 5–90 members. Clan members recognize each other by sight, scent, and vocalization (Kruuk 1972, East and Hofer 1993). They rear their cubs together at a communal den, jointly defend food against theft by lions, and defend the group's territory against incursion by neighboring hyena clans. Alien hyenas discovered within the clan's home range are often viciously attacked. A few of the most persistent and submissive males are the only hyenas that ever manage to penetrate this barrier of aggression when they join a new clan after dispersal.

The social organization of the spotted hyena is more similar to that of macaques and baboons than that of other carnivores, such as lions, wolves, wild dogs, or mongooses (Frank 1986, Holekamp and Smale 1991). In contrast to these other gregarious carnivores, spotted hyenas live in groups containing multiple breeding animals of both sexes whose interactions are strongly influenced by linear hierarchical dominance relationships. A typical hyena clan in eastern Africa contains several different matrilines, each composed of closely related adult females and their offspring as well as several immigrant adult males. The mating system is polygynous; there are usually roughly twice as many adult females as adult males present in the clan, and each breeding male may mate with multiple females. Adult females may also mate with multiple males within a single estrus period. Hyena clans are rigidly structured by stable, linear rank relationships in which members of each matriline occupy adjacent positions in the clan's dominance hierarchy (Kruuk 1972, Tilson and Hamilton 1984, Frank 1986, Mills 1990, Holekamp and Smale 1990, 1993).

The social rank of an individual hyena determines its priority of access to food and other critical resources (Tilson and Hamilton 1984, Frank 1986, Henschel and Skinner 1987). Before cubs reach reproductive maturity, they attain ranks in the clan's dominance hierarchy immediately below those of their mothers (Holekamp and Smale 1993, Smale et al. 1993). Adult females and their young consistently outrank all adult immigrant males (Smale et al. 1993). Subadult hyenas of both sexes maintain their maternal ranks as long as they remain in the natal clan (Smale et al. 1993, 1997). Females generally spend their entire lives in their natal clans (Frank 1986), but all males emigrate and join new clans between the ages of 2 and 5 years (Smale et al. 1997). A hyena's lifespan in the wild can exceed 18 years.

Spotted hyenas feed mainly on medium- or large-bodied ungulates, which they hunt themselves (Kruuk

1972). Although they are widely believed to be skulking carrion eaters and, in fact, have carrion-eating ancestors (Werdelin and Solounias 1991), modern spotted hyenas are actually effective hunters. An adult hyena can single-handedly bring down an antelope weighing three to four times its own body mass. Several hyenas join forces to hunt difficult prey, such as zebra or giraffe, whereas more common prey, such as gazelle and wildebeest, are usually hunted by lone hyenas or pairs (Holekamp et al. 1997).

Fresh ungulate carcasses represent rich, ephemeral food patches that occur unpredictably in space and time. After one or more hyenas kills an antelope, many other hyenas typically converge on the carcass, competing aggressively for the food and feeding so rapidly that several hungry hyenas can devour a 400-pound antelope in as little as 13 minutes. Thus, feeding competition among hyenas at kills is extraordinarily intense. Among hyenas of similar social rank, a competitive advantage accrues to individuals who can quickly tear off and swallow chunks of meat from the carcass. Because juveniles are smaller than adults and have less well developed skull bones and jaw muscles (Figure 2), they fare relatively poorly in these feeding competitions.

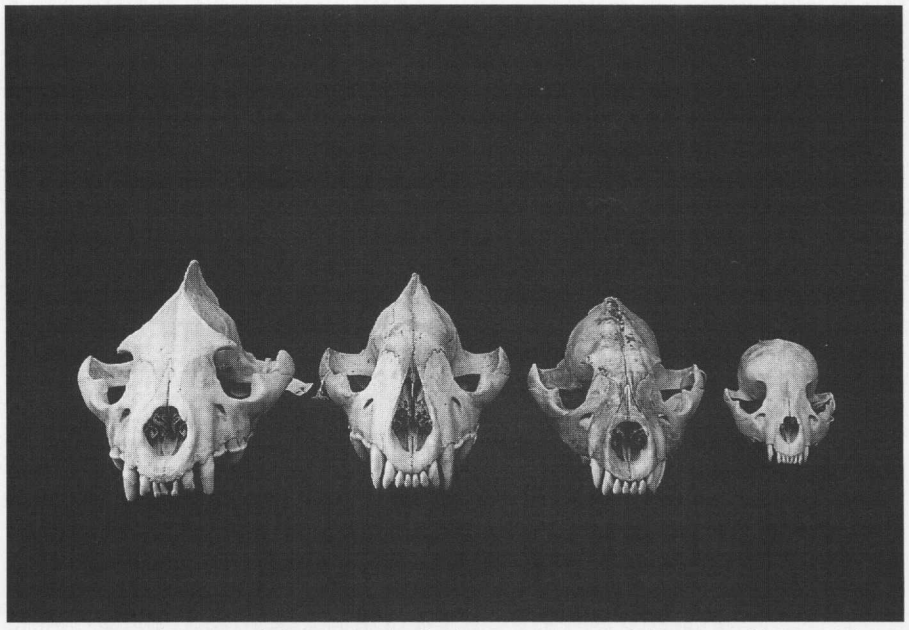

Figure 2. Developmental change in the feeding apparatus of the spotted hyena. These skulls were collected from hyenas of known age that died in our study population. From right to left, the ages of these animals at death were 3 months, 13 months, 24 months, and 11 years. In particular, changes are evident in the appearance of the sagittal crest, zygomatic arches, and bony processes on the forehead—all important attachment sites for feeding muscles.

In contrast to females of most other social carnivore species, all adult female members of a spotted hyena clan produce offspring. At all times of year, females bear litters of one or two cubs in isolated natal dens (East et al. 1989). Although females bearing their first litters often give birth to single cubs, experienced females are more likely to produce twins. Cubs reside at the natal den for the first 3–4 weeks of life. Mothers then carry their infants to the clan's communal den, where up to 20 cubs live together until they are 8 or 9 months old (Kruuk 1972). The communal den is a social focal point for clan members and is frequently visited by adults of both sexes as well as by immature individuals that no longer use the den for shelter. Cubs begin feeding at kills when they leave the communal den, but they also continue nursing for several more months. Females first bear litters when they are approximately 36 months old, and males can sire litters at 24 months (Matthews 1939). A female's social rank profoundly influences her reproductive success. High-ranking females have longer reproductive lifespans and produce litters more frequently than lower-ranking females. Effects of female social rank on fertility appear to be mediated by differential access to food (Holekamp et al. 1996).

Since early 1988, we have been studying behavioral development in one large clan of spotted hyenas inhabiting a 65 km^2 home range along the Talek River in the Masai Mara National Reserve in southwest Kenya. The Talek region is characterized by open grassland that is grazed year round by large concentrations of ungulates. At any given time, the Talek clan usually contains 21 or 22 adult females, 10 or 11 adult immigrant males, and 30–40 youngsters. We recognize individual members of the study clan by their unique spot patterns. Before the spots of young cubs emerge through their black natal fur, they are identified by their patterns of ear nicks and scarring. Males and females are distinguishable based on the dimorphic glans morphology of the erect phallus (Frank et al. 1990). We know the ages, kin relations, and social ranks of all animals born in the clan since the beginning of our study. Social ranks are assigned to adults of each sex based on outcomes of fights among clan members (Holekamp and Smale 1990). Winners in fights are considered to be dominant to losers, so we rank each hyena in a dominance hierarchy based on which other clan members it can regularly defeat. The "maternal rank" of a juvenile refers to its mother's position in the adult female hierarchy.

Stages of hyena development

Postnatal development in the spotted hyena takes place in five discrete stages, each of which begins and ends with observable milestones (Table 1). These five stages differ in length, with stage length increasing as the hyena matures. At each developmental transition, the hyena's environment changes and the animal is confronted with a different suite of challenges. Some behavior patterns appear to help the young animal face specific challenges encountered during one or more developmental stages. Other behavior patterns change slowly and continuously throughout a hyena's early years and ultimately

Table 1. Stages of behavioral development in the spotted hyena.

Age interval	Developmental stage	Primary challenges
0–4 weeks	Natal den	Establishing rank within litter; growth
1–8 months	Communal den	Gathering information about social environment; improving motor skills; establishing rank within peer group; growth
8–14 months	Communal den to weaning	Gathering information about the physical environment; completing establishment of rank relations; growth
14–24 months (males); 14–36 months (females)	Weaning to reproductive maturity	Acquiring food independently; growth
Remainder of the life span	Reproductive maturity to death	Dispersing and integrating into new clan (males); rearing own offspring (females); mating (both sexes)

develop into adult behaviors that are critical for survival and reproduction.

Stage 1: The natal den. A spotted hyena typically spends its first few weeks of life in an abandoned aardvark burrow. Although the mother may lie nestled in the entrance of this burrow to nurse her cubs, the narrow diameter of the den hole prevents the mother and other adults from entering. A newborn hyena has a coat of short, black fur and weighs approximately 1 kg. In contrast to most other mammals, spotted hyenas are born with fully erupted canine and incisor teeth, their eyes are open, and they are immediately capable of directed movement, albeit in a rather slow and uncoordinated fashion (Frank et al. 1991). During this first stage, the infant's physical world consists exclusively of the natal den and the area within 3–4 meters of its entrance. Infants at this stage are vulnerable to predation and to infanticidal attacks from adult clan members of both sexes (Kruuk 1972, East et al. 1989). The mother therefore remains almost constantly at the natal den, leaving only for brief periods to eat or drink.

In the natal den, an infant's social world consists almost exclusively of its mother and its littermate, if it has one. The most daunting task facing the newborn hyena at the natal den is to establish its rank relationship with its littermate. Starting within moments of birth, siblings engage in exceptionally intense fighting (Frank et al. 1991). Within a day or two, this neonatal aggression leads to the establishment of clear and stable dominance relationships between littermates (Smale et al. 1995). As soon as one cub begins to exhibit avoidance or appeasement behavior in response to aggression from its sibling, the frequency and intensity of aggressive behavior declines sharply (Frank et al. 1991, Smale et al. 1995, Drea et al. 1996). Thus, intense competition for food starts at birth in this species, and the young are born fully armed with the teeth, sensory capabilities, and behavioral repertoire needed to engage in neonatal combat.

The establishment of dominance over a littermate immediately improves a cub's access to its mother's teats during nursing, and dominant cubs therefore grow much faster than their subordinates. Winning neonatal fights for intralitter dominance also has other positive effects that may last many years. The rank relationship between siblings established at the natal den endures as long as both cubs remain together in the natal clan. Thus, for female littermates, this relationship persists for the rest of their lives, whereas for mixed-sex twins it persists until the male disperses. When food is abundant in the home range, and particularly when the mother is ranked high in the female dominance hierarchy, intralitter fighting is rare after the first weeks of life (Smale et al. 1995). However, if the mother's food supply becomes limited, such that she can produce enough milk to support only one cub, then fighting may continue, and the dominant littermate's ability to displace its sibling from the mother's two teats may result in the death of the subordinate by starvation (Frank et al. 1991, Hofer and East 1997).

Whereas the neonatal fighting characteristic of spotted hyenas is highly unusual among mammals, the other environmental challenges facing hyena cubs at the natal den are more typical of those confronting the young of other species. Like other neonatal mammals, hyena cubs need to stay warm and dry, avoid danger, develop the ability to recognize their mothers and siblings, gain motor coordination, and grow as rapidly as possible. Cubs find warm, dry shelter deep in the den, and they gain warmth above ground from their mother's body while nursing against her belly. Cubs at the natal den go to the surface only when their mother calls them out, with a soft groaning vocalization. Once above ground, they sometimes wander within a meter or two of the mouth of the den, sniffing and chewing on plants, but when they are frightened they quickly scuttle back into the den. Although well-nourished cubs occasionally romp around briefly beside the den, play behavior is seldom observed during this stage of development, possibly because cubs need to use most of their energy for maintenance and growth. Evidence that the development of play behavior is influenced by energy availability comes from observations of well-fed captive hyenas, which engage in play behavior 1–2 weeks earlier than hyenas in nature (Drea et al. 1996). Moreover, our field data suggest that cubs of well-fed, high-ranking mothers play at higher rates than their low-ranking peers, and that subordinate littermates play less frequently than their dominant siblings.

When a hyena other than the mother visits the natal den, cubs are initially fearful and flee underground, but they may eventually emerge to interact with the new arrival if it is tolerated by the mother. Cub behavior during such interactions invariably involves headbobbing, an extreme form of appeasement in hyenas. In addition to appeasing conspecifics, cubs at this stage may also headbob to guinea fowl strutting near the den, and even to plants waving in the wind. Thus, the strategies that cubs adopt at

this stage when dealing with animate objects other then the mother and sibling inevitably involve either flight or submission. This behavioral pattern changes dramatically during the next phase of the hyena's life history, when cubs start to establish their own positions in the clan's hierarchy.

Stage 2: The communal den. One day, after calling her cubs out of the natal den, the mother gently picks them up one at a time in her bone-crushing jaws and carries them to the clan's communal den. The communal den is usually a complex of burrows with an extensive network of underground tunnels and chambers providing shelter for several hyena cubs at a time. As they did at the natal den, cubs use the communal den for warmth and protection from predators, and they flee into it when frightened. Here, too, the interior of the den is entirely inaccessible to adult hyenas.

The mothers and older siblings of den-dwelling cubs typically visit the communal den every day, as do a host of unrelated clan members. Therefore, the social world of the young hyena now undergoes a dramatic change. Upon its arrival at the communal den, the young cub is abruptly confronted with dozens of unfamiliar hyenas with whom it will later compete for food and cooperate to defend resources from lions and alien hyenas. Thus, some of the cub's most pressing needs during its 8-month period of residence at the communal den are to gather information about its clanmates, to introduce itself to them so that it will never be mistaken for an alien, and to begin establishing rank relationships with them. In addition to acquiring these important social skills, cubs at this stage also need to develop an array of critical motor skills that will allow them to function effectively when they eventually leave the den.

Rates of play behavior are much higher at the communal den than during any other stage in hyena development (Laura Smale and Kay Holekamp, unpublished data). Cubs of both sexes engage in extensive play with objects found around the den. For example, they often play tug-of-war over bones or scraps of antelope skin. Cubs at the communal den spend a great deal of time chewing on such things as plants, feathers, bones, and one another. Most of this incessant jaw exercise yields no nutritional return to the cub, but it promotes development of the jaw muscles and skull bones that will later be used to devour antelope carcasses (Figure 2; Herring 1993). At the communal den, cubs also engage in a great deal of social play in which they race around in circles, chasing and pouncing on one another.

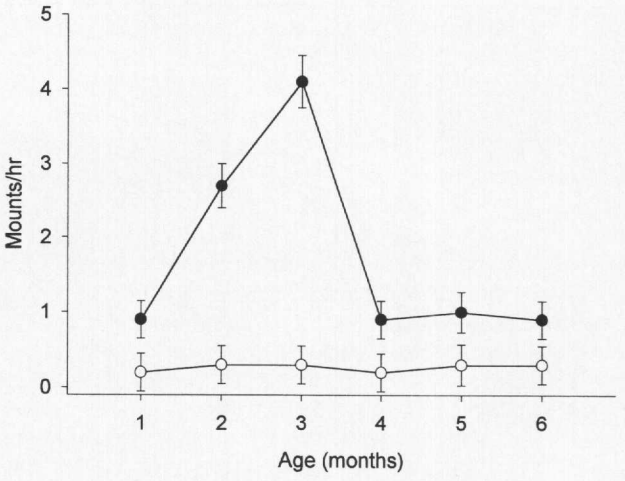

Figure 3. Sex differences in mounting behavior as a function of age. Hourly rates of mounting behavior are always very low in females (open circles), whereas males exhibit an early phase of frequent mounting (solid circles). Eight individuals of each sex are represented, all from mixed-sex twin litters.

Play behavior has a variety of functions in other mammals (Fagen 1981), and hyena play likewise has multiple functions, yielding both immediate and longer-term benefits. One immediate function may be to enable cubs to establish affiliative relations with other clan members (Drea et al. 1996). In addition, like all vigorous exercise, hyena play builds strength and endurance in the short term. Play also provides young hyenas with opportunities to practice motor patterns that are critical for future survival and reproduction. For example, play mounting, which is generally observed exclusively in male cubs, occurs frequently (although for only a few weeks) at the communal den (Figure 3). After this stage, mounting behavior rarely occurs again until years later, when the male is an adult and actively tries to inseminate females. Because the female's external genitalia are so heavily masculinized, successful mating requires that the male maneuver his penis into the female's pseudopenis. The communal den apparently offers a safe environment in which males can practice parts of this difficult behavior sequence without incurring any costs in terms of survival or reproduction.

Cubs at the communal den are intensely interested in the body odors of clanmates, and they spend much of their time above ground sniffing every new arrival (Figure 4). They also introduce themselves to others by nervously lifting a hindleg to initiate greeting ceremonies, thereby exposing clanmates to their own odors. Visiting hyenas are usually interested in meeting cubs, but sometimes cubs are so eager to introduce themselves that they even lift their legs over the noses of clanmates who are sound asleep and entirely unresponsive. Such behavior indicates that cubs at this stage are driven by the need to gather information about the identities of their clanmates and to ensure that they themselves are recognized and accepted by others.

The information transmitted and received by cubs at the communal den appears to be useful in promoting individual survival, both during this developmental stage and in later stages. It is immediately useful as cubs begin establishing their social ranks. Social ranks cannot be established until cubs can identify and discriminate among their clanmates and until other clan members can recognize each cub. Youngsters begin acquiring their ranks several weeks after they arrive at the communal den (Holekamp and Smale 1993). This process marks the first time that cubs behave aggressively toward hyenas other than their littermates. Thus, motor patterns that first appeared at the natal den in one restricted social context now appear in diverse new contexts.

Figure 4. The den-dwelling cub on the left is intensely interested in the scent of the older hyena on the right, who is marking a grass stalk near the den with a secretion from his anal glands. This scent-marking behavior is called "pasting."

At first, cubs direct aggressive behavior toward peers at the den, without regard for the relative maternal ranks of their targets (Holekamp and Smale 1993). That is, juveniles are initially just as likely to attack the cubs of females of higher rank as they are to attack cubs of females of lower rank. However, before leaving the communal den, cubs come to direct their aggression exclusively toward peers of lower maternal rank. This pattern suggests that rank acquisition involves associative learning, during which aggression directed at lower-ranking cubs is reinforced, whereas that directed at higher-ranking cubs is extinguished (Holekamp and Smale 1993). The establishment of rank relationships among cubs appears to be guided by each cub's tendency to do what its mother is doing, and by maternal interventions in fights (Anne Engh, Michigan State University, unpublished observations). That is, when one adult female attacks another at the communal den, the cubs of the aggressor soon begin to join her in the attack, while the offspring of the target female cower under their mother. Later, cubs begin to initiate attacks on their own, and their mothers then often rush to join the cub in its attack if the target animal belongs to a lower-ranking matriline. Mothers reinforce the aggressive behavior of their cubs only when it is directed toward appropriate target animals. Eventually cubs attack clanmates of lower maternal rank and win these fights, unaided by their mothers.

While living at the communal den, cubs also start establishing their rank relationships with the many older hyenas who regularly visit the den (Smale et al. 1993). The process of rank acquisition continues throughout this stage of development and the next, when cubs leave the communal den. The rank position attained in the clan's dominance hierarchy by each juvenile will affect its priority of resource access for many years to come.

Stage 3: Communal den to weaning. Eventually a day comes when the mother leaves the communal den and her cubs follow her out into the larger world and begin to explore it with her. After leaving the communal den, the cubs' physical world expands from the immediate vicinity of the den to the clan's entire home range. A major challenge facing the cub at this stage is to acquire information about its new physical environment and to figure out how to find food, water, and shelter. Cubs of both sexes engage in a great deal of exploratory behavior as they travel around the home range. They often return to the communal den to meet up with their mothers or siblings or to socialize with other hyenas, but they no longer use the den for shelter. Indeed, one dramatic change occurring early during this developmental stage is that cubs cease fleeing into a den when frightened. Even though they are still small enough to enter the den, cubs do not attempt to escape danger by dashing into a den hole but rather flee actively from danger above ground. When a lion or human approaches, even if the cub is near a den hole, it usually runs away as fast as it can, vocalizing loudly to recruit assistance from other clan members. Flight into a den hole rapidly becomes maladaptive for cubs, who will soon be too large to easily enter the den. Indeed, we once saw lions kill a subadult hyena who was attempting to squeeze into a den when it should have run away. Consequently, a behavior pattern that was adaptive at earlier developmental stages has not only lost its survival value but actually become a deadly liability.

Another new challenge a cub faces when it leaves the communal den is to learn the boundaries of its clan's territory and to distinguish its clanmates from members of neighboring clans. The cub has now entered a world in which clans are frequently at war with each other, and clan wars can be especially dangerous for young, relatively naive individuals. Life in general appears to take on a more serious tone during this stage of development, and far less time is spent at social play. Perhaps the energy previously spent on play must now be dedicated to other needs. Cubs never chew sticks or plants during this or any subsequent stage of development. Their skullbones and jaw musculature continue to develop, but the jaws now receive plenty of exercise as the young hyenas try to acquire adequate nutrition for survival and growth. They continue to chew on old carcass parts they find on the plain; this behavior is likely to provide some nutrients for the cub as well as to stimulate growth of skull bones and jaw muscles.

Cubs continue to nurse during this stage, but they also start to feed at ungulate kills with other clan mem-

bers. Feeding at kills undoubtedly represents the most daunting and critical new challenge a young hyena faces as it enters the third stage of its development. Cubs initially appear to be intimidated by the throng of hungry, blood-covered hyenas tearing at the carcass, and they approach the kill only if their mother is feeding. Early in this stage, mothers and cubs often feed side by side, and mothers frequently snap at lower-ranking hyenas who try to encroach on the part of the carcass where their cubs are feeding. These maternal interventions have an important function in this final phase of rank acquisition, when cubs must compete for food with adult females (Anne Engh, Michigan State University, unpublished observations).

During this stage, when separated from their mothers, cubs occasionally unwittingly attack larger hyenas of higher maternal rank with whom they may not have interacted previously. The penalties for such mistakes underscore the adaptive value of all the information gathering that occurred at the communal den during the previous stage. For example, we once saw a low-ranking cub threaten a higher-ranking adult female with whom the cub was clearly not familiar. The adult backed off momentarily, as if in surprise, but then counterattacked with such ferocity that the cub was wounded and fled limping and bleeding, with her tail between her legs. Had the cub acquired all the information at the communal den that she required for this encounter, she would not have risked serious injury by attacking a larger animal of higher rank than her own mother.

Stage 4: Weaning to reproductive maturity. Weaning usually occurs at approximately 14 months of age in our study population, but it can occur as early as 7 months, if the mother is high ranking, or as late as 21 months, if she is low ranking and food is scarce. This variability suggests that energy reserves available to females and their cubs may influence the timing of weaning. Although hyena cubs ingest some solid food during earlier developmental stages, they generally rely heavily on their mother's milk for several months after leaving the communal den. Eventually, however, the mother begins to reject her cub's attempts to nurse. Some cubs respond with noisy tantrums that persist for many days or weeks. Other cubs accept this change much more quickly and quietly. Several irreversible physiological changes accompany the transition from a diet composed largely of milk to an adult diet, including reversals in the relative availability of particular gut enzymes required to extract different nutrients from milk and meat (Bateson 1994).

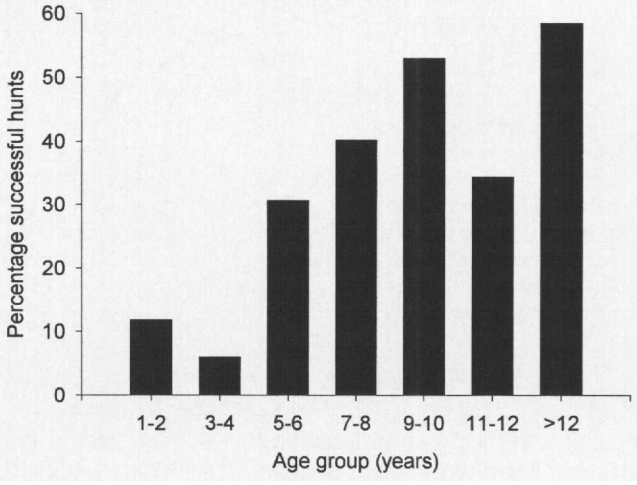

Figure 5. Percentage of hunts that are successful (i.e., that end in the capture of a live antelope) observed for spotted hyenas of different ages. Hunting success among hyenas younger than 5 years is very low.

The major challenge confronting cubs after weaning is obtaining enough solid food to survive and grow. This problem is compounded by the fact that young hyenas are ineffectual hunters (Figure 5). Even when they join their clanmates at fresh kills, they are still inferior competitors for food because of their poorly developed ability to rip meat from the carcass. Thus, during this developmental stage their only recourse is often to revert to the ancestral pattern of feeding on carrion. Presumably because carrion contains fewer nutrients and more pathogenic organisms than fresh meat, adults in our study area rarely feed on old carcasses unless they are unable to hunt due to sickness or injury. However, it is probably because young hyenas are rarely able to capture live antelope prey that they rely more heavily on carrion than do healthy adults. Although young hyenas occasionally catch hares and gazelle fawns, their competence at hunting antelope does not reach adult levels until they are well into the next and final stage of their development (Figure 5).

Stage 5: Reproductive maturity to death. Male hyenas become reproductively mature several months before females, and post-pubertal animals of each sex confront different reproductive demands. During this stage, females must develop adequate energy reserves to initiate reproduction, modify their aggressive responses to adult males so that mating can occur, and develop the parenting skills needed to rear their own offspring. Male hyenas do not contribute at all to parental care, but male behavior is nevertheless shaped by reproductive demands during this developmental stage. That is, adult females appear to be unreceptive to the sexual advances made by post-pubertal males born in their clan, so males must apparently leave the natal clan in order to breed (Smale et al. 1997). Thus, striking sex differences in the use of space emerge for the first time (Figure 6).

Post-pubertal males make frequent excursions into the home ranges of neighboring clans, where they appear to evaluate resource availability and the probability of becoming successfully integrated into each new clan (Smale et al. 1997). At the same time, males also adopt a behavioral strategy that bears a striking resemblance to that seen in cubs living at the natal den. That is, males that have left their natal clans always behave submissively to any new hyena encountered, regardless of the other animal's relative body size. We suspect that males may find it impossible to become socially integrated into a new clan unless they adopt this pattern of highly obsequious behavior. Although it is not yet known precisely how this behavioral reorganization helps the dispersing male, one sig-

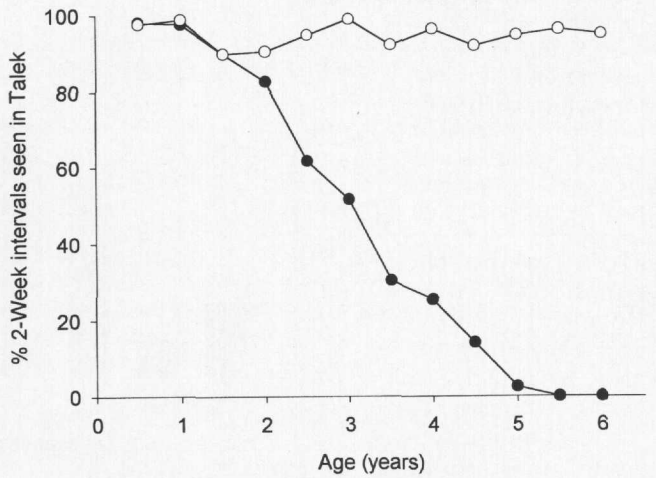

Figure 6. Disappearances of natal hyenas from the Talek study clan's home range as a function of age. If a hyena was not seen during a 2-week observation period, it was said to have "disappeared" during that interval. These disappearances represent periods when animals are on excursions, exploring habitat beyond the boundaries of their natal home range. Males (solid circles) begin to go on these excursions at 2 years of age and are sighted in the natal area significantly less often than females (open circles) by 2.5 years of age ($t = -4.72$; $df = 41$; $P < 0.001$). Females continue to be seen regularly in the natal home range throughout their lives. Data points represent mean values in each interval for 21 males and 22 females.

nificant result is that emigration represents the point during ontogenetic development at which females come to dominate males (Smale et al. 1993). In fact, because immigrant males even initiate their social interactions with small cubs by appeasing them, all natal animals can dominate immigrants.

Conclusions and future directions

Our brief summary of development in the spotted hyena reveals a variety of patterns of behavioral change (Figure 7). Play behavior and behavioral responses to danger show marked discontinuities at the milestones separating developmental stages. By contrast, feeding behavior starts with chewing on plants and sticks at the natal den and then continues to develop slowly and gradually, finally reaching adult competence levels in the final stage of development. Although the immediate usefulness of the incessant chewing behavior cubs exhibit while living at dens is not yet understood, over the long term it undoubtedly enhances individuals' ability to use their jaws to rapidly tear meat from carcasses and thereby compete effectively for food at kills as adults. Play behavior and the establishment of rank relationships occur only during brief periods of development, but these transient behavioral phenomena appear to have both immediate and long-term utility. Still other behaviors, such as flight into den holes, are present at birth but vanish from the behavioral repertoire when their utility expires. The discontinuities in hyena behavioral development strongly suggest that some juvenile behaviors are temporary adaptations to a specific set of selection pressures that animals ultimately "outgrow," such that behaviors that are useful at one stage may prove useless or maladaptive at the next.

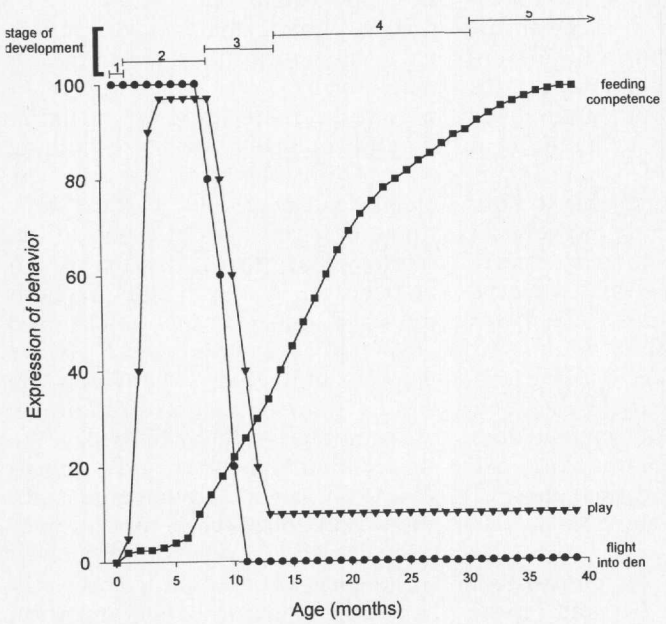

Figure 7. A schematized representation of contrasting patterns of behavioral development, as expressed in three behavior patterns observed in free-living spotted hyenas: the tendency to flee into a den hole when frightened, play behavior, and competence at removing meat from antelope carcasses. Percentages of individuals expressing each behavior are indicated on the y-axis. Circles, flight into den; triangles, play; squares, feeding competence. The five stages of hyena development (see Table 1) are indicated by the horizontal lines above the figure.

Our studies of patterns of ontogenetic change in hyena behavior leave many questions unanswered. Perhaps the most intriguing of these have to do with the mechanisms mediating transitions between developmental stages. Although little is known about developmental changes in the hyena's nervous system, it would be fascinating to relate shifts in neural structure or function to behavioral changes observed in hyena cubs, as has previously been done for dogs (e.g., Scott et al. 1974) and humans (e.g., Herschkowitz et al. 1997). It is also possible that transitions between stages are mediated by stores of available energy. Energy stores might take the form of body fat or other oxidizable metabolic fuels. Our finding that well-fed cubs of high-ranking females progress through the five developmental stages more rapidly than their leaner, low-ranking peers is consistent with the hypothesis that energy availability, which is strongly influenced by social rank, regulates developmental transitions. Metabolic cues affect the timing of puberty in many mammals (e.g., Bronson 1989, Wilson 1992). It thus seems reasonable to expect that metabolic cues signaling energy availability might similarly influence the timing of transitions between earlier ontogenetic stages in hyenas and other mammals.

Acknowledgments

The authors thank the Office of the President of Kenya for its permission

to conduct the research described in this article. We also thank the Kenya Wildlife Service, the Narok County Council, and the Senior Warden of the Masai Mara National Reserve for their cooperation. This work was supported by National Science Foundation grants BNS-8706939, BNS-9021461, IBN-9309805, and IBN-9630667; by fellowships to Kay E. Holekamp from the David and Lucille Packard Foundation and the Searle Scholars Program/Chicago Community Trust; and by a fellowship to Laura Smale from the American Association of University Women.

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