



Sex Differences in Spotted Hyenas

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The apparent virilization of the female spotted hyena raises questions about sex differences in behavior and morphology. We review these sex differences to find a mosaic of dimorphic traits, some of which conform to mammalian norms. These include space-use, dispersal behavior, sexual behavior, and parental behavior. By contrast, sex differences are reversed from mammalian norms in the hyena's aggressive behavior, social dominance, and territory defense. Androgen exposure early in development appears to enhance aggressiveness in female hyenas. Weapons, hunting behavior, and neonatal body mass do not differ between males and females, but females are slightly larger than males as adults. Sex differences in the hyena's nervous system are relatively subtle. Overall, it appears that the "masculinized" behavioral traits in female spotted hyenas are those, such as aggression, that are essential to ensuring consistent access to food; food critically limits female reproductive success in this species because female spotted hyenas have the highest energetic investment per litter of any mammalian carnivore. Evidently, natural selection has acted to modify traits related to food access, but has left intact those traits that are unrelated to acquiring food, such that they conform to patterns of sexual dimorphism in other mammals.

Spotted hyenas (*Crocuta crocuta*) are large mammalian carnivores that occur throughout sub-Saharan Africa. They show many unique and fascinating characteristics, such as living in large, complex societies in which they must compete and cooperate with non-kin as well as kin. However, the aspect of the biology

of spotted hyenas that many people find most intriguing is the apparent "masculinization" of females. This female virilization manifests itself in several obvious ways. For example, in contrast to the situation characteristic of most other mammalian species, female spotted hyenas are larger than males, they are socially dominant to

⁶Deceased.

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S.K. McCormick et al.

males, and they show genitalia that are astonishingly male-like. These “sex-role-reversed” traits coexist in the same individuals with other sexually dimorphic traits that are much like those shown by virtually all “typical” female mammals, such as dogs, antelope, rats, and baboons. The hyena’s chimeric blend of feminine and “masculinized” traits is particularly intriguing because it raises so many questions about how and why some traits have been “masculinized” in this species, whereas others have not. Here, we summarize existing information about sexually dimorphic traits in the behavior and morphology of spotted hyenas. We will consider sexually dimorphic traits in adults of this species, including both those that are “reversed” from patterns found in most other mammals and those known to show the same patterns of dimorphism typical of other mammals. Wherever possible, we also briefly review what is known about the development of sexually dimorphic traits in spotted hyenas. Finally, we discuss the adaptive significance of sexually dimorphic traits in this species.

SEX DIFFERENCES IN BEHAVIOR

Sex Differences in Space Use, Territory Defense, and Dispersal

Spotted hyenas live in stable social groups, called “clans,” which may contain up to 130 individuals. They defend group territories against encroachment by neighboring conspecifics. They engage in border patrols and “wars” with neighboring clans. In contrast to many other mammals that defend group territories, female hyenas initiate and lead most territorial advertisement and defense efforts. Females are more likely than males to lead border patrols and clan wars, and females tend to scent-mark along territorial boundaries at higher hourly rates than do adult males (Henschel and Skinner 1991; Boydston et al. 2001). Thus, female hyenas are willing to assume more risks and expend more energy during territorial defense than are males. These sex differences are consistent with the hypothesis that male and female clan members derive different selective benefits from advertisement and defense of group territories. Defense of food re-

sources appears to be the primary function of territoriality in spotted hyenas (Kruuk 1972; Henschel and Skinner 1991). Indeed, it appears that natural selection has favored female spotted hyenas to maintain boundaries of a territory that supports enough herbivore prey to feed themselves and their young throughout the year.

In other respects, the territorial and space-use behavior of spotted hyenas resembles that of other territorial mammals. For instance, during territorial encounters between residents and aliens, residents are more likely to attack same-sex than opposite-sex intruders (Boydston et al. 2001). As also occurs in most other social mammals, male spotted hyenas disperse from their natal clans after they reach reproductive maturity, whereas females are philopatric and spend their entire lives in the natal clan (Smale et al. 1997; Höner et al. 2007). No measures of space use are sexually dimorphic among young hyenas until these animals are ~30 mo of age, which is roughly 6 mo after they reach reproductive maturity. Late in the third year of life, males start making exploratory excursions into the territories of neighboring clans, whereas females do not; these sex differences in space-use persist throughout the remainder of the life span. Males are found farther from the geographic center of their natal territory than are females, and the mean size of individual home ranges is larger for males than females (Boydston et al. 2005). As adults, male spotted hyenas travel 17.7 km/d, whereas females travel only 12.36 km/d (Kolowski et al. 2007).

Sex Differences in Reproductive Behavior

Although copulation is rather challenging for male spotted hyenas because of the female’s unusual external genitalia (see below), otherwise spotted hyenas show the same suite of sex differences in reproductive behavior as those typical of other mammals. For instance, males approach females at higher rates than vice versa (Szykman et al. 2007), although, in contrast to most other male mammals, male spotted hyenas appear to be extremely nervous when courting females. Copulation involves the male mounting the female and inserting his erect penis into the

female's flaccid clitoris. Both males and females mate promiscuously (Szykman et al. 2007).

Hyenas are born in litters that usually contain only one or two cubs, but maternal investment in each cub is enormous. As occurs in most mammals, female spotted hyenas do all the parenting; the low social status of sires effectively prevents them from being able to assist their offspring even to the same small extent as males can assist their young in other polygynous, group-living mammals (e.g., baboons; Buchan et al. 2003). Spotted hyena cubs rely exclusively on their mother's milk during the first 6 mo of life, and although they then start eating some solid food, cubs continue to rely largely on milk until they are weaned, which typically occurs at 12–20 mo of age (Kruuk 1972; Hofer and East 1995; Holekamp et al. 1997); this represents an extremely protracted lactation period relative to those of other carnivores of similar body mass. For example, canid and felid species the same size as, or larger than, spotted hyenas wean their young when they are only 1.1 to 6 mo of age, including species as large as wolves, lions, and tigers (Watts et al. 2009). The milk produced by spotted hyenas is also unusually rich; it has the highest protein content of milk from any fissiped carnivore (Hofer and East 1996), a fat content exceeded only by that of milk produced by palarctic bears and sea otters, and a higher gross energy density than the milk of most other terrestrial carnivores (Hofer and East 1995). Because of the high energy content of their milk and the long period of lactation, spotted hyenas have the highest energetic investment per litter of any mammalian carnivore (Oftedal and Gittleman 1989; Hofer et al. 2016). It follows that two critical factors affecting cub growth and survival are maternal access to food (Swanson et al. 2011; Holekamp and Strauss 2020) and nursing frequency (Hofer et al. 2016), both of which vary with maternal social rank.

Sex Differences in Aggression and Dominance among Adults

Adult female spotted hyenas are socially dominant to all adult males not born in the females' natal clan, so females can straightforwardly dis-

place immigrant males from desired resources such as food (Kruuk 1972; Mills 1990). Natal animals of both sexes acquire ranks immediately below those of their mothers via a prolonged learning process early in development, so they can dominate all immigrant males. However, most males disperse before breeding and behave submissively to all new hyenas encountered outside the natal territory. Thus, the mechanisms by which adult social rank is acquired differ between male and female hyenas. Females maintain their natal ranks as long as they live in the natal clan; females do this largely by behaving aggressively to lower-ranking clan mates. In contrast, when males disperse to new clans, they assume the lowest possible rank in the new clan, where they follow a queuing convention in which the most recent immigrant is the lowest-ranking animal in the entire clan (Smale et al. 1997; East and Hofer 2001). Males only improve their status when higher-ranking immigrants die or engage in secondary dispersal, which occurs in roughly 40% of males (Van Horn et al. 2003).

Although some have argued that female dominance among spotted hyenas is strictly the result of more social support for females than males (e.g., Vulliamd et al. 2019), compelling evidence indicates that behaviors associated with the acquisition and maintenance of social rank are strongly sexually dimorphic in this species, and in fact require no social support. Female spotted hyenas emit aggressive acts at higher rates than do males (Fig. 1A), they emit more intense aggressive acts (Fig. 1B), they are more tenacious fighters (Fig. 2), and they show unambiguous "role-reversed" sex differences in aggressive behavior from a very young age. Thus, in contrast to most mammals, female spotted hyenas are substantially more aggressive than males (Szykman et al. 2003; McCormick and Holekamp, in review). This notion is also supported by wounding data obtained from the several hundred spotted hyenas we have immobilized in Kenya (Fig. 3). These data show clearly that adult females bear many more wounds, on average, than do adult males; this is the opposite of the pattern found in most other mammals (e.g., primates [Holekamp 1984]; rodents

S.K. McCormick et al.

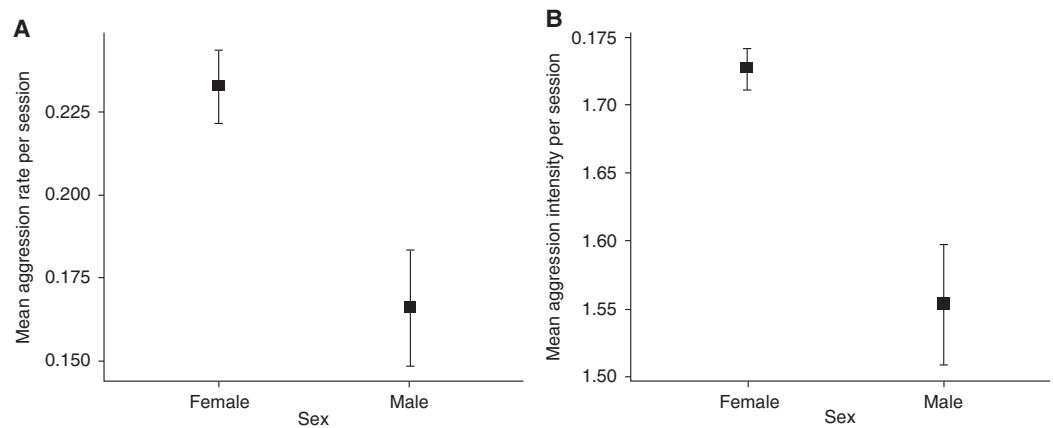


Figure 1. Sex differences in the mean (A) rates of emission of aggressive acts by adult hyenas per observation session, and (B) intensity of aggressive behaviors emitted by adult natal females and immigrant males, controlled for social rank, time observed, and immigration status. Sampled hyenas include 57 adult immigrant males and 128 adult females. Error bars represent 95% confidence intervals.

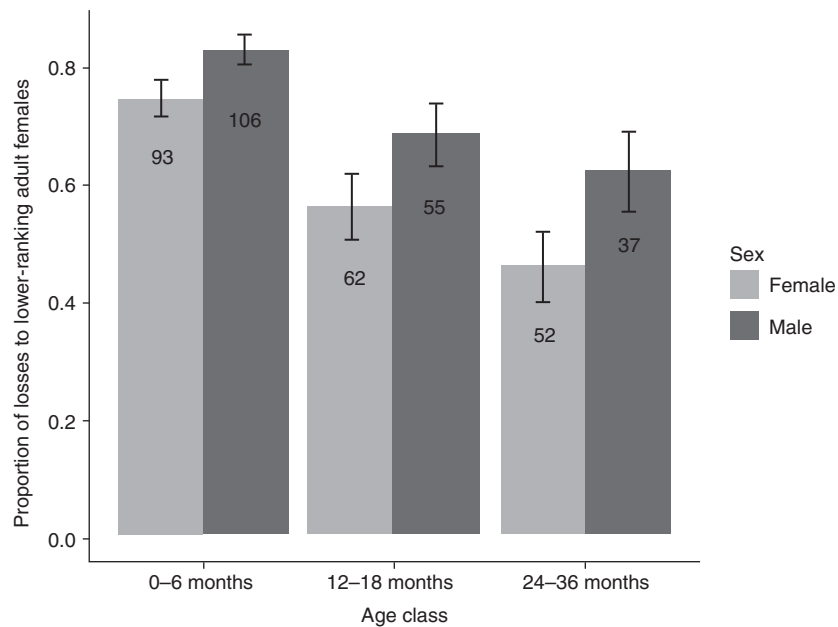


Figure 2. Sex differences in losses by juvenile hyenas in aggressive interactions initiated by lower-ranking adult females. Bars represent the proportion of fights lost per individual in each sex and age class, error bars represent standard error of the mean, and the numbers above the error bars represent the number of individuals included. Females are represented by pale gray bars, and males by dark gray bars. Significant differences were found based on sex ($F = 9.71$, $P = 0.002$) and age class ($F = 19.05$, $P < 0.001$). Modified from Smale et al. (1993).

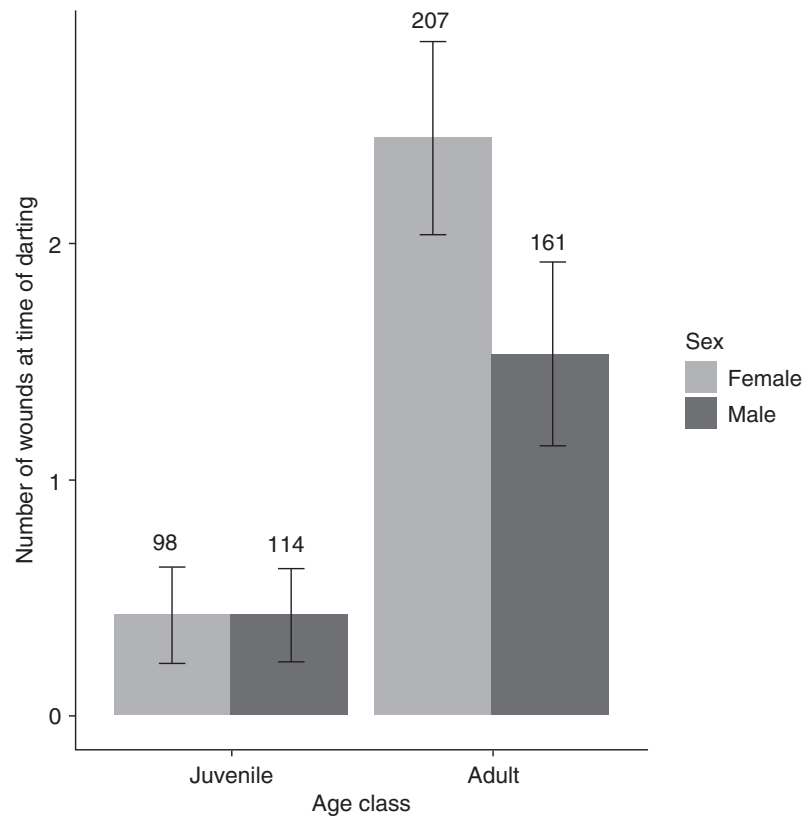


Figure 3. Sex differences in wounding among juvenile (pale gray, younger than 24 mo) and adult (dark gray, older than 24 mo) spotted hyenas of each sex. Numbers above bars indicate individuals sampled. Significant differences were found based on sex ($F = 5.17$, $P = 0.024$), age class ($F = 72.34$, $P < 0.001$), and an interaction between sex and age class ($F = 6.64$, $P = 0.01$).

[Pusey and Packer 1978]). Interestingly, the sex difference in wounding among hyenas does not emerge until adulthood, as males and females 24 mo of age or less do not differ in wounding frequency (Fig. 3). If most wounds were caused by prey animals during capture, we would expect male and female hyenas to show similar rates of wounding because adults of both sexes are equally successful at hunting their own prey (Holekamp et al. 1997). However, the finding that females sustain so many more wounds than males is consistent with the idea that most wounding occurs during fights over carcasses. Males almost invariably defer to females at kills, whereas other females often do not (Kruuk 1972), and fights among males are typically far less intense than those among females. Our

wounding data are consistent with both of these behavioral tendencies.

Ontogenetic Development of Sex Differences in Aggression

Sex differences in aggressive behavior emerge during the first days of life in young spotted hyenas. Newborn spotted hyenas often fight vigorously with their siblings during the first days or weeks after birth to establish intralitter ranks (Frank et al. 1991; Smale et al. 1999; Wachter et al. 2002; Wahaj and Holekamp 2006). Once intralitter ranks have been established, the rates and intensities at which siblings fight decline; intralitter aggression rates also decline with increasing maternal rank (Golla et al. 1999; Smale

S.K. McCormick et al.

et al. 1999). When litters are of mixed sex, females dominate their male siblings 67% to 84% of the time (Smale et al. 1995; Golla et al. 1999; Wahaj and Holekamp 2006; Benhaïem et al. 2012). Thus, female spotted hyenas evidently come into the world behaving more aggressively than their male peers.

This trend persists throughout ontogeny. The proportion of dyadic fights with lower-born adult females won by hyenas 6–36 mo of age is significantly greater for young females than for their male peers (Smale et al. 1993). Subadult females also dominate lower-born adult females more consistently than do subadult males. That is, although young males can often displace lower-born adult females from desired resources, their rank relationships with lower-born adult females often remain unstable until males disperse from their natal clans (Smale et al. 1993). Furthermore, juvenile females are more persistent than their male peers in their attempts to outrank adult females. For instance, juvenile females are more likely than their male peers to counterattack lower-born females who attack them (Fig. 2; also see Smale et al. 1993). Thus, although aggression rates come to be strongly affected by social rank in adulthood (McCormick and Holekamp, in review), sex differences in aggressive behavior are apparent from birth in this species.

Exposure to androgens early in development appears to enhance aggressiveness in female spotted hyenas. In the wild, both juvenile and adult females whose mothers have higher androgen concentrations during gestation are considerably more aggressive than are same-age females exposed to lower androgen concentrations in utero (Dloniak et al. 2006; Holekamp et al. 2013). Furthermore, experimental exposure to anti-androgens (AAs) during development in utero reduced female aggressiveness later in life among captive hyenas at the Berkeley hyena colony. Pregnant females were treated throughout gestation with a cocktail of AAs (flutamide and finasteride), and the behavior of the offspring from those pregnancies was assessed throughout development. For many years after the AA-treated hyenas reached adulthood, investigators were unable to identify any obvious effects of the pre-

natal AA treatment on aggressive behavior. In particular, AA-treated females were always the winners over control and AA-treated males in single-bone dyadic tests, wherein two hyenas compete for a single bone tethered to a fence within an enclosure, as described by Beach et al. (1982). However, as the Berkeley Hyena Project neared its end, the bone dyad test was modified to include two bones. Only two double-bone dyad tests were completed before the colony closed, one with a control female and the other with an AA-treated female, in which each was paired with an untreated male. In their single-bone dyad tests with these same males, both females always won, securing all bones for themselves by aggressively displacing the males from proximity to the tethered bones. However, whereas the control female secured both bones for herself in the double-bone test while keeping the male at bay, the AA-treated female allowed the male to have the second bone and feed on it beside her. No untreated captive females or females in the wild ever share food with unrelated males, so even with a sample size of only one, the experimental treatment effects here were highly suggestive. A video showing both control and treatment trials is available (see online Movie S1).

The striking sex differences seen in aggression and dominance in spotted hyenas have clear adaptive value, as higher rates of aggressive behavior enhance reproductive success among females (Watts et al. 2009; Yoshida et al. 2016; McCormick and Holekamp, in review) but not among males (East and Hofer 2001). Furthermore, the establishment of dominance over other females has a much greater influence on the fitness of females than males. Similarly, although rank reversals among adult females are rare in this species, improving one's social status via rank reversals is far more critical to females than males, as the effects of rank reversals are amplified in later generations (Strauss and Holekamp 2019). The uniquely heavy energetic demands of lactation in this species (Oftedal and Gittleman 1989) cause improved access to food resources, often accomplished via aggressive displacement of group-mates from carcasses, to be far more important for female than males (Holekamp and Strauss 2020), and females are

clearly willing to fight to maintain or improve their priority of access to food.

SEX DIFFERENCES IN MORPHOLOGY

Body Size and Shape

Sexual size dimorphism is common among mammals; in most species, including most other mammalian carnivores, males on average are larger than females. In contrast, the spotted hyena is one of the rare species in which females are generally larger than males. We took 14 different body measurements from several hundred wild hyenas in Kenya, and found that, although many body size measures differ only by 1% to 5% between the sexes, and although distributions of most size measures overlap for males and females, these sex differences are strongly statistically significant (Swanson et al. 2013). The largest sex differences in body size in spotted hyenas appear in measures of head and neck circumferences, body mass and girth, indicating that adult females are roughly 10% brawnier than males. These traits are larger in adult female hyenas than adult males even when the two sexes are fed identical diets while housed alone throughout development in captivity, allowing us to rule out a strictly environmental explanation for this dimorphism (Swanson et al. 2013). Because the fundamental frequencies of some hyena vocalizations vary with girth measurements and because girth is strongly sexually dimorphic in this species, adult females have deeper voices than adult males in their whoop and groan vocalizations (Theis et al. 2007; Mathevon et al. 2010), so these calls inform listeners about the sex of callers.

Female spotted hyenas are larger than males because they grow faster, rather than showing a longer period of growth (Swanson et al. 2013). Eleven sets of male and female littermates born as mixed sex twins at the Berkeley hyena colony did not differ in mass at birth; on average, both sexes weighed 1.5 kg at birth (Fig. 4A). However, there was a significant effect of litter size on mass at birth, with singletons being heaviest and members of triplet litters being lightest (Fig. 4B). Early in postnatal life males and females

appear to grow similarly, but between weaning and reproductive maturity their ontogenetic growth trajectories diverge. Female growth rates increase relative to those of males as animals approach sexual maturity. Traits that mature before divergence of these ontogenetic trajectories are monomorphic, whereas traits that mature later are dimorphic (Swanson et al. 2013). Although it is difficult to distinguish young males from young females, in adulthood, female spotted hyenas are visibly brawnier than their male peers (Fig. 5).

The teeth of a spotted hyena, particularly the incisors and canine teeth, are its primary weapons, but neither the canines nor the incisors differ significantly between the sexes in spotted hyenas (Van Horn et al. 2003). However, in adulthood, the height of the lower canine tooth tends to be slightly larger in females than males, so if any sexual dimorphism exists at all in weaponry in this species, females may have a slight advantage.

External Genitalia

The external genitalia of female spotted hyenas are unique among mammals. The clitoris is greatly elongated to form a fully erectile structure (Fig. 6), with a single urogenital (UG) tract passing from the tip of this structure into the caudal region of the abdomen (Matthews 1939; Neaves et al. 1980; Henschel and Skinner 1991). The female's enlarged clitoris is not as slender as the male's penis (Glickman et al. 2006), and the clitoris is slightly shorter (mean = 17 cm) than the male's penis (mean = 19 cm) (Neaves et al. 1980; Drea et al. 2002). Furthermore, the glans of the phallus is blunt and barrel-shaped in females, whereas it is angular and pointed in males (Fig. 7; Frank et al. 1990; Cunha et al. 2003). Nevertheless, the female's external genitalia look remarkably like those of the male (Figs. 5–7). In female spotted hyenas, these unusual genitalia are present at birth. "Masculinization" of their genitalia is not as strictly androgen-dependent (Drea et al. 1998; Cunha et al. 2005; Conley et al. 2020) as it is in other mammals. Initial prenatal development of the external genitalia in both sexes is

S.K. McCormick et al.

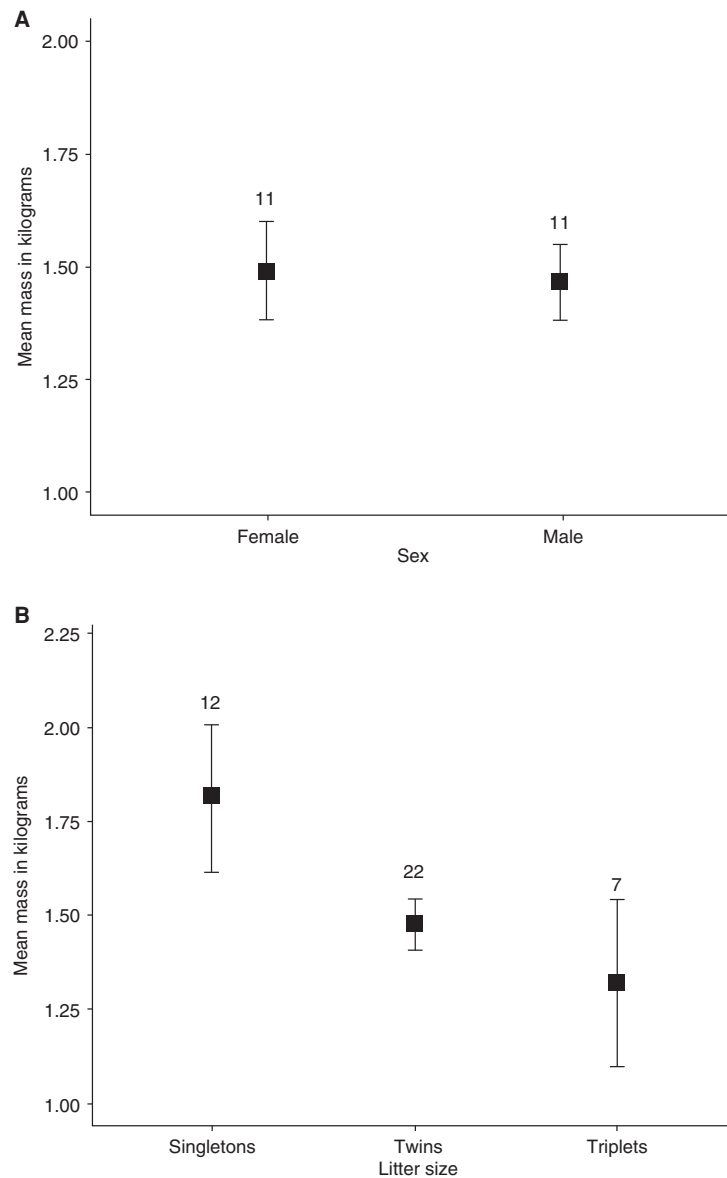


Figure 4. (A) There is no sex difference in body mass at birth among twin cubs born in mixed sex litters in captivity at the Berkeley hyena colony (Wilcoxon Rank Sum Test: $P = 0.553$); each litter contained one male and one female cub. (B) Litter size does have a significant effect on cub birthweights (Kruskal Wallance Test: $P = 0.0007$). Error bars represent 95% confidence intervals. Numbers above the error bars indicate individuals sampled.

largely free of androgenic influence (Glickman et al. 2006); however, elevated androgen concentrations in late gestation influence the development of both genital morphology and behavior (Drea et al. 2002; Dlonek et al. 2006; Holekamp et al. 2013). Furthermore, AA treatment of preg-

nant females reduces the developmental influence of androgens on their fetuses (Conley et al. 2020). No adult females in other members of the hyena family have unusual genitalia, so the enlargement of the clitoris is unique to spotted hyenas. In contrast to other carnivores, includ-

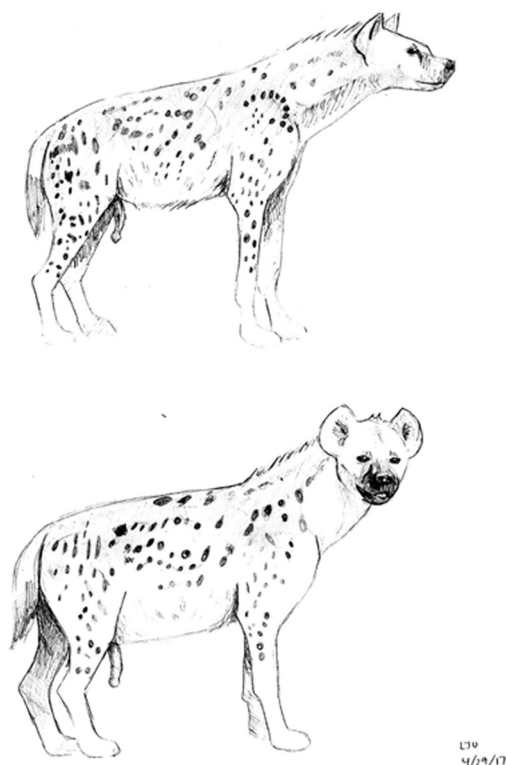


Figure 5. Adult male (*top*) and adult female hyena (*bottom*) showing sex differences in body shape and genital morphology. (Drawing by Lily Johnson-Ulrich.)

ing the other hyena species, the female spotted hyena has no external vaginal opening. Instead, she urinates, copulates, and gives birth through the tip of her elongated clitoris. Her vaginal labia are fused together and filled with fat and connective tissue to form a bilobed structure (Fig. 6) that resembles the scrotal sac and testes of the male (Frank et al. 1990).

Although the spotted hyena's clitoris and penis are similar in length, their internal anatomies are strikingly different to match their different functions (Cunha et al. 2005). The male urethra needs only to allow for the passage of urine and ejaculate, but in addition to passing urine, the female UG canal that traverses the clitoris must enable her to receive the male during copulation and to give birth to cubs that weigh ~1.5 kg. In contrast to the male urethra, which is narrow and surrounded by the corpus

spongiosum, the female UG canal is more pleated, voluminous, and expandable because it is surrounded by loose connective tissue, which facilitates the birthing process. The spotted hyena's penis and clitoris are retractable organs as a result of retractor muscles that span their lengths. However, the position of the retractor muscles relative to the urethra and the UG canal are quite different in the two sexes, with the retractor muscles being ventral to the urethra in males and dorsal to the UG canal in females. If not for this sex difference, the retractor muscles within the clitoris would surely be damaged during parturition, because the distal clitoris tears along its ventral midline (Fig. 6) during the first birth of a cub, which has a cranial diameter substantially exceeding the diameter of the clitoral meatus. Interestingly, the differences in the internal anatomies of the penis and clitoris are androgen dependent, as indicated by the ef-

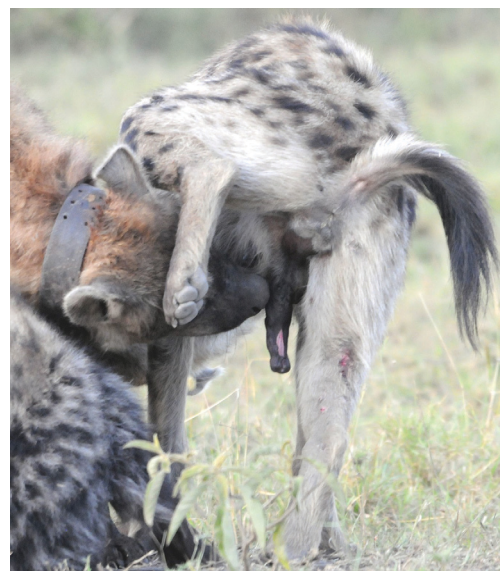


Figure 6. External genitalia of the female spotted hyena seen while this female engages in a greeting ceremony with another female, who sniffs her anogenital region. The vaginal labia form structures that resemble the male's scrotal sac, and the clitoris is elongated to form a fully erectile "pseudopenis." The strip of pink scar tissue running down the posterior surface of the clitoris was caused by tearing during parturition, and indicates that the female has borne at least one litter in the past.

S.K. McCormick et al.

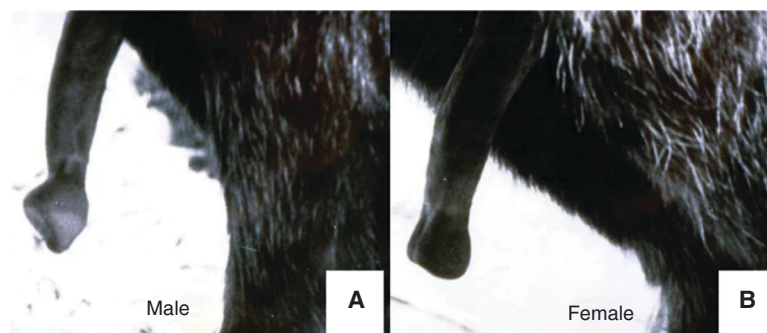


Figure 7. The gross anatomy of the male and female genitalia of the spotted hyena (*Crocota crocuta*). Shown are the penis (A), and clitoris (B) in the erect state.

fects of AAs that were administered to pregnant dams starting in early gestation. Most striking was the finding that the internal penile anatomy of AA-treated males was almost completely “feminized”—the urethra was more pleated and voluminous, because it was surrounded by loose connective tissue rather than the corpus spongiosum, and the retractor muscles had shifted from the ventral to dorsal position relative to the urethra (Cunha et al. 2005). Many of the external differences between the penis and clitoris (as described above) were also erased by in utero AA treatment, in that the penis was reduced in length, and the shape of the glans was feminized. This alteration proved to be functionally significant, because the males that had received the most intensive AA treatment during fetal development were incapable of copulating with receptive females (Drea et al. 2002).

In both sexes, the phallus is erect during greeting ceremonies, but during copulation, only the penis is erect while the clitoris is flaccid and retracted. The location of the clitoral opening is far more rostral than in more typical mammals, and as such, males perform penile “flips” that are used to locate the flaccid and retracted clitoris, and then pull the opening caudally so that he can intromit. The ability of an AA-treated male to reach the clitoral opening was largely negated by the reduced length of his feminized penis. And the AA treatment also feminized the perineal muscles that contribute to the flipping behavior (i.e., the bulbocavernosus [BC] muscles) (Forger et al. 1996). As a result, AA-treated

males are more likely to misdirect their flips (NJ Place and SE Glickman, unpubl.). Similar to the internal anatomy of the phallus, the morphology of the BC muscles is sexually dimorphic in spotted hyenas and in utero AA treatment feminized the BC muscles in males. The BC muscles are innervated by spinal motoneurons located in Onuf’s nucleus (see below), and the male advantage in the number of motoneurons was negated in AA-treated males.

Nervous System

Sex differences in behavior are of course mediated by differences in the nervous system. One would therefore expect to see a mosaic pattern of typical and atypical sex differences in the spinal cords and brains of spotted hyenas, as we do in the behavior and morphology of these animals. Regions such as those mediating sexual behavior (e.g., male-typical mounting and erection of the phallus), aggression, and dispersal are of special interest in this regard. Although there are major obstacles impeding research on the hyena’s nervous system, we are aware of five such studies. We begin with three that focused on specialized subpopulations of cells within the nervous system, and then turn to two that have taken a broader “whole brain” approach.

The first study to compare the nervous systems of male and female hyenas described spinal motor neurons located in Onuf’s nucleus (Forger et al. 1996). These cells project to muscles at the base of the penis, and in most mammals,

they are more numerous in males than females (Sakamoto 2014). This is also the case in spotted hyenas; adult males have ~20% more Onuf's neurons than do females. This difference is present at birth, and prenatal AA treatment feminizes the nucleus in males (Forger et al. 1996). These data might suggest that hyenas are not unusual with respect to Onuf's nucleus. However, both male and female hyenas frequently engage in greeting ceremonies in which the erect phallus of one animal is presented to another for sniffing (Fig. 6), so perhaps motor neurons in Onuf's nucleus play a role in this behavior in both sexes (Forger et al. 1996). As male hyenas face unusual challenges associated with copulation that females do not, these behaviors may depend on the additional neurons found in the male's Onuf's nucleus. This suggests that the development of the motor neurons projecting to muscles controlling the phallus in females follows the same "rules" as the development of the phallus itself; this in turn suggests considerable masculinization via androgen-independent mechanisms. The additional development of Onuf's nucleus in males may be mediated by androgens produced in the testes, which is the case for the phallus (Glickman et al. 2006).

The first subcortical region of the brain examined in spotted hyenas is the sexually dimorphic nucleus (SDN) in the preoptic area (Fenstermaker et al. 1999), which is larger in males than females in the many species in which it has been examined (McCarthy et al. 2017). This is also the case in spotted hyenas. In other species, the SDN is associated with mounting, intromission, and ejaculation, as well as partner preference (for review, see Pfaff and Baum 2018). Although the motor coordination of copulation may seem especially challenging for male hyenas, it can be decomposed into the same basic elements as seen in other species, and it is directed toward females. It is therefore not surprising that the sex difference in the SDN of hyenas would resemble that found in other mammals (i.e., that it is larger in males than in females). However, the two-fold sex difference in size of the hyena's SDN is considered modest compared with those in other species (Fenstermaker et al. 1999).

Rosen et al. (2006) assessed sex differences in four forebrain regions of captive hyenas with

respect to the density of fibers containing the peptide vasopressin (VP). In many other species, VP innervation of the forebrain, particularly that of the lateral septum, is associated with social behaviors such as aggression and dominance (Albers 2012), and VP innervation of the lateral septum is consistently greater in males than in females (De Vries and Panzica 2006). Rosen et al. (2006) found no sex differences in the sub-paraventricular region of the hypothalamus, anterior hypothalamic region, or anterior supraoptic region, nor was there a significant sex difference in the lateral septum, but they observed a bimodal distribution of VP fibers in this brain region in males. Specifically, they found that VP fibers were heavily concentrated in the lateral septum of all three females examined and in two of the four males, but that these fibers were virtually absent in the other two males. These investigators suggested that in a natural setting, VP may contribute to the heightened aggression of adult females relative to adult males that have dispersed from their natal clans, but that their two captive males with elevated VP, which were both living with peers, may have been in a predispersal state, in which their aggressive behavior had not yet declined to facilitate immigration into a neighboring clan.

Sex differences have also been examined with respect to whole brains, endocranial volumes and "virtual brains" of spotted hyenas (Arsznov et al. 2010; Mann et al. 2018). Mann et al. (2018) reached the conclusion that "females have smaller brains despite having bodies that are (on average) longer and heavier," whereas Arsznov et al. (2010) found no evidence of a sex difference in overall brain size but did see regional sex differences. The methods used to collect and analyze data were quite different in these two studies so it is difficult to compare them.

Mann et al. (2018) found no sex difference in the weight of brains dissected from nine hyenas in Northern Kenya or in endocranial volumes in a collection of 60 skulls in the British Museum of Natural History (BMNH), but they did find a difference, favoring males, in a sample of 19 skulls in the Museum of Vertebrate Zoology (MVZ) at UC Berkeley. Body lengths were greater in females than males in the BMNH collec-

S.K. McCormick et al.

Table 1. A summary of traits reviewed here, indicating which conform to a typical mammalian pattern of sexual dimorphism, which show a “role-reversed” pattern of dimorphism, and which show no sex differences

Category	Typical mammalian pattern	Role-reversed pattern	No sex difference
Behavior	Space-use	Aggressive behavior	Cognition
	Dispersal behavior	Social dominance	Hunting
	Sexual behavior	Territory defense	
	Parental behavior		
Morphology	Onuf’s nucleus	Body size	Weaponry
	SDN		

(SDN) Sexually dimorphic nucleus of the hypothalamus.



tion, but there was no difference in the MVZ collection. These patterns thus suggest a difference favoring males in the BMNH sample because body size was greater in females, and in the MVZ sample because brain size was smaller in females. Reasons for these interpopulation differences are not obvious. In contrast, Arsznov et al. (2010) found no evidence of a sex difference in overall brain sizes measured from a sample of 22 adult hyena skulls in the Michigan State University Museum. Here, brain volumes were measured in “virtual” brains (endocasts) created from CAT scans of skulls; these volumes were divided by skull basal length to take body size into account. There were many differences between the protocols used by Mann et al. (2018) and Arsznov et al. (2010) that might account for what appear to be conflicting results. For example, the former study evaluated sex differences in brain size and in body length but not in brain size corrected for body length, whereas investigators of the latter study used skull length as a proxy for body size and conducted their analysis on the corrected values.

When Arsznov et al. (2010) examined regional brain volumes (as a proportion of total brain volume) in virtual hyena brains, they found clear and interesting differences between the sexes. Specifically, the anterior cerebrum was larger in males than females, and the posterior cerebrum was larger in females than males. The latter difference is difficult to interpret because this portion of the brain contains a multitude of subregions that have a diverse array of functions but that were impossible to delineate with the endocast method. The anterior cerebrum contains primarily frontal cortex, which is associat-

ed with a variety of measures of social cognition, as well as inhibitory control. However, no differences between male and female hyenas have been found to date in either of these domains in behavioral tests (Benson-Amram and Holekamp 2012; Johnson-Ulrich and Holekamp 2020).

CONCLUSIONS

In the domains of both behavior and morphology, we find in spotted hyenas a mosaic of traits: some conform to sex differences in other mammals, whereas others do not (Table 1). We find that spotted hyenas show sexually dimorphic behavior that conforms to mammalian norms with respect to space-use, dispersal behavior, sexual behavior, and parental behavior. However, we also find sex differences that are reversed from mammalian norms in the hyena’s aggressive behavior, social dominance, and territory defense. Neither weapons nor hunting behavior differ between males and females, but sexual size dimorphism is distinctly reversed from mammalian norms. However, as in other mammals, the SDN in spotted hyenas is larger in males than in females (Fenstemaker et al. 1999). Similarly, the number of motoneurons innervating the perineal muscles associated with the phallus is sexually dimorphic in the conventional manner (Forger et al. 1996). Several features of VP immunoreactivity in the spotted hyena forebrain are similar to what has been described in other mammals (Rosen et al. 2006). However, contrary to what has been reported in many other species (De Vries and Panzica 2006), the density of VP innervation of the lateral septum



is not sexually dimorphic. Whether there are sex differences in overall brain size remains controversial. In any case, it is clear that “sex role-reversed” or “masculinized” traits coexist in the same females with other sexually dimorphic traits that are like those shown by virtually all “typical” female mammals.

The female spotted hyena’s chimeric blend of feminine and “masculinized” traits raises questions about how and why some traits have been “reversed” in this species, whereas others have not. Overall it appears that the behavioral traits that have been “masculinized” in female spotted hyenas are those critical to ensuring consistent access to food resources, which is the critical factor limiting reproductive success in females of this species (Holekamp and Strauss 2020). Aggressive behavior, social dominance, and territory defense are all very important in this regard. Furthermore, because body size is not a good predictor of fight outcomes among spotted hyenas (Smale et al. 1993), larger body size does not help female hyenas win fights; instead, larger body size most likely helps females capture larger prey to help satisfy the enormous energetic demands imposed by pregnancy and lactation. Evidently, natural selection has acted to modify those traits related to food access from the ancestral condition, but has left intact those behavioral and morphological traits that are unrelated to accessing food, such that they conform to patterns of sexual dimorphism in other mammals. The adaptive significance of the female’s odd genitalia remains uncertain, although they may play a role in allowing females to determine which sperm fertilize her ova.

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S.K. McCormick et al.



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Sex Differences in Spotted Hyenas



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