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Sexual Monomorphism in Spotted Hyenas, *Crocuta crocuta*

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Abstract

Intersexual and intrasexual interactions by female spotted hyenas, (*Crocuta crocuta*), are correlated with the ability of the heavier and more aggressive females to dominate males at large carcasses, the principal food of spotted hyenas.

Female spotted hyenas have a modified clitoris closely resembling a penis. A slightly bilobed scrotum containing fat and connective tissue contributes to the male-like appearance of the female sexual facies. Penile and pseudopenis erection by spotted hyenas occurs primarily during social encounters at carcasses and elsewhere.

Analyses here, based on interspecies comparisons of spotted hyena, brown hyena (*Hyaena brunnea*) and striped hyena (*H. hyaena*) morphology, behavior and ecology and interpopulation comparisons of spotted hyenas suggest possible gradualistic evolutionary interpretations of the pseudopenis.

Introduction

Female spotted hyenas (*Crocuta crocuta*) possess a characteristic unique among mammals — a peniform clitoris which is the anatomical basis of enduring legends identifying these animals as hermaphrodites (Watson 1877; Chapman 1888; Grimpe 1916; Davies & Story 1949). Female resemblance to males is enhanced by the absence of body size sexual dimorphism (see later discussion). Male penile and female clitoral erection occur during social encounters, most commonly when individuals meet (Wickler 1965; Kruuk 1972).

This unusual female spotted hyena morphological development has been related to serum androgen levels which, for females, equals that of males (Racey & Skinner 1979). Gould (1981, 1983) and Gould & Vrba (1982) conclude that the pseudopenis may have developed as a direct and functionless consequence of elevated female androgen levels, and that only during subsequent evolution did the structure come to be functional. Gould & Vrba (1982: 10) suggest: "... that female(s) attain their status by secreting androgens and that the peniform clitoris and false scrotal sac are automatic, secondary by-products. Since they are formed anyway, a later and secondary utility might ensue; they may be coöpted to enhance fitness in the meeting ceremony and then secondarily modified for this new role. We suggest that the peniform clitoris and false scrotal sac arose as nonadaptive consequences of high androgen levels (a primary adaptation related to the unusual behavioral role of females)." The theoretical implications of this argument, that the pseudopenis was once a nonadaptive structure, are substantial. Here we evaluate evidence related to this and other hypotheses concerned with the evolution of the spotted hyena pseudopenis development, both ontogenetic and evolutionary. These hypotheses include:

1. *The pseudopenis is an incidental consequence of the action of high blood androgen levels upon fetal sexual development* (Racey & Skinner 1979; Gould 1981, 1983; Gould & Vrba 1982). This hypothesis is in part based upon correlations which show that high mammalian fetal blood androgen levels may lead to virilization of female external sexual organs (Jost 1972; Wilson et al. 1980, 1981). Selection, according to this hypothesis, was based upon elevated female androgen levels, which served initially to regulate the expression of female aggression.

2. *The pseudopenis and its association with social greeting facilitates* "... reestablishment of social bonds by keeping partners together often over a longer meeting period" (Kruuk 1972: 229—230). According to Kruuk (1972), the female peniform clitoris and false scrotal sac function in greeting displays to facilitate individual recognition and clan reintegration of solitary foragers. This behavioral explanation does not deal with the question of evolutionary origins, and while this may be a part of the utility of the pseudopenis and penis in association with meetings, penile and pseudopenile displays are also commonly associated with interactions between familiar associates.

3. *The pseudopenis has evolved as an organ for signalling social status.* Erection of the penis or clitoris is one of a suite of displays used by subordinates of both sexes to identify their status and inhibit aggression by dominants in a variety of social contexts. This hypothesis also stresses current function, and may be alternative or complementary to Kruuk's (1972) greeting ceremony hypothesis.

In our analyses of these alternatives we will also consider the question of origins.

Methods

Our analysis is based on behavioral observations of the context of penile erections by male, female and juvenile spotted hyenas living in the Namib-Naukluft Park, Namibia (Tilson et al. 1980; Tilson 1983; Tilson & Hamilton 1984) and a population of the same species in Masai Mara National Reserve, Kenya (Frank unpubl.). Our conclusions are related to (1) interspecies comparisons of the three extant hyenas: spotted hyenas, brown hyenas (*Hyaena brunnea*) and striped hyenas (*H. hyaena*); and (2) interpopulation comparisons of the Namib and Masai Mara hyena population with the Ngorongoro and Serengetti spotted hyena populations in Tanzania (Kruuk 1972). Our focus here is upon the evolution of the pseudopenis and the selective consequences of its elaboration in extant spotted hyenas.

Results

Greeting Ceremonies and Phallic Erection

Both striped and brown hyenas have well differentiated male and female external genitalia (Racey & Skinner 1979). In the female spotted hyena, a peniform clitoris and false scrotal sac develop from undifferentiated genital primordia (Jost 1972; Short 1972; Wilson, J. D., 1978; Wilson et al. 1980, 1981) to form an erectable organ of approximately the same shape, size and position as a male penis (Matthews 1939; Neaves et al. 1980).

One of the several features of the pseudopenis distinguishing it from other mammalian genitalia, male and female, is its precocious development. It is already large, erectile, and actively used in greeting ceremonies by the time spotted hyenas are one month old (Kruuk 1972, pers. obs.). During these greetings, participants stand parallel to one another, head to tail, and lift the hind leg on the side towards the greeting partner. Genital sniffing and occasional licking follow. Then, both individuals drop their legs and walk away. By contrast, brown hyenas raise their tails and smell one another's anal gland areas during greetings (Owens & Owens 1979), while in striped hyenas one member of the pair typically lies down while the standing individual smells the anal gland region of the other (Racey & Skinner 1979).

Phallic erection is not exclusively confined to the greeting ceremony but its use is correlated with lower social status (Frank, pers. obs.). Males consorting with estrous females are submissive and maintain a constant erection. Penile and pseudopenis erection are characteristic of cubs when they greet one another, subadults and adult females. Cubs maintain erections when wandering about the den area and during rough play. Subadults, up to the age of at least two years, often maintain an erection when playing with cubs and as they approach the den area where other hyenas — mostly cubs, adult females and subadults — congregate. During active interactions at kills where females are feeding, lower ranking individuals of both sexes frequently dive beneath the most dominant female, grovelling in front of her (Kruuk's [1972] carpal crawl) and performing a variety of displays, including clitoral or penile erection. Clitoral and penile erection also occur during pasting (Kruuk 1972), when anal gland secretions are deposited by straddling grass stalks and dragging the everted rectum over them. Most pasting is done by subadults and young low-ranking females in den areas, the social focus of clans. Pasting, accompanied by erection, is a common behavior of males and high ranking females at kill sites after agonistic encounters. All individuals paste at clan border areas.

Body Size Dimorphism

The conclusion that female spotted hyenas are larger than males (Matthews 1939; Deane 1962; Wilson, V. J., 1968; Kruuk 1972; Racey & Skinner 1979) is questioned by Whateley (1980). In the Masai Mara National Reserve, Kenya, measurements of 18 adult females and 25 adult males show that adult female body mass ($t = 3.66$, 41 d.f., $p < 0.02$) and girth ($t = 2.68$, 31 d.f., $p < 0.02$) are significantly greater than those of males, but our other measurements are the same for males as for females (Table 1). Thus, the evidence for this population suggests that female spotted hyenas are heavier, but not larger bodied, than males. The greater mass of females may simply reflect their dominance as a class over males and consequently their priority of access to limited food (Tilson & Hamilton 1984). By comparison, both male brown and striped hyenas are heavier than females (Table 2).

Table 1: Sexual size dimorphism by body measurements for adult spotted hyenas in Masai Mara, Kenya

Body measurement	Males		Females		M/F
	X	N	X	N	
Mass (kg)	48.7	25	55.6*	18	0.88
Girth (cm)	84.5	16	88.8*	17	0.95
Total length (cm)	147.7	24	151.5	23	0.97
Tail length (cm)	23.2	24	23.1	22	1.00
Hind foot (cm)	23.8	24	23.6	23	1.01
Ear length (mm)	112.7	19	112.6	22	1.00
Neck diameter (cm)	52.1	20	53.3	21	0.98
Shoulder height (cm)	77.5	19	76.7	21	1.01

* Values significantly different: $p < 0.02$ (Student's t test). All other male-female values not significantly different.

Hyena Food and Feeding Behavior

Striped and brown hyenas feed on a variety of carcasses, none of which they produce by regularly killing prey themselves (Kruuk 1976; Skinner 1976; Mills 1977, 1978; MacDonald 1978; Owens & Owens 1978). Both brown hyenas (Owens & Owens 1978) and striped hyenas (Kruuk 1976; MacDonald 1978; Skinner & Ilani 1979) forage and hunt solitarily but may assemble at carcasses left by other predators, where they feed one at a time, with dominant males gaining first access.

By contrast, spotted hyenas hunt primarily in groups (Kruuk 1972; Bearder 1977; Tilson et al. 1980; Tilson 1983). In locations where lions leave partially eaten giraffe carcasses, spotted hyenas may scavenge more than they hunt (Bearder 1977).

Kruuk (1972) reports scramble competition (Nicholson 1954) among spotted hyenas at most large kills or discovered carcasses. Individuals do not attempt to exclude one another, but feed side by side as fast as possible (Van

Table 2: Sexual size dimorphism by mass for extant hyena populations. See also Table 1 for original data on spotted hyenas

Species	Sex	N	Mass (kg)		Ratio male/ female	Source
			$\bar{X}$ ± S.D.	Range		
Spotted hyena	M	11	66.6	55—79		
(*Crocuta crocuta*)	F	12	70.0	56—80	0.94	Whateley (1980)
	M	12	48.7 ± 2.3	41—55		
	F	8	55.3 ± 4.1	45—64	0.88	Kruuk (1972)
	M	5	56.2 ± 2.2	54—60		
	F	4	61.1 ± 4.9	62—67	0.92	Skinner (1976)
	M	5	43.6 ± 1.0	—		
	F	5	51.6 ± 1.2	—	0.84	Neaves et al. (1980)
Brown hyena	M	8	47.1 ± 1.9	43—50		
(*Hyaena brunnea*)	F	4	42.0 ± 3.6	37—46	1.12	Skinner & Ilani (1979)
Striped hyena	M	9	34.9 ± 4.6	28—43		
(*Hyaena hyaena*)	F	12	30.6 ± 4.2	28—36	1.14	Skinner & Ilani (1979)

Lawick-Goodall & Van Lawick-Goodall 1970). Under such circumstances an assembled group of spotted hyenas may rapidly devour carcasses. Feeding success under these conditions depends upon individual strength and speed in tearing apart and consuming a carcass.

In the Namib Desert, where lower population densities of both spotted hyenas and their prey prevail (Table 3), a different pattern of social interactions at carcasses is observed. Rather than feeding together in scramble competition, individuals replace one another at carcasses throughout the night. Thus, when small groups of spotted hyenas assamble at large carcasses, indi-

Table 3: Comparative feeding and density characteristics of spotted hyenas at three population densities

Characteristic	Serengeti[a]	Ngorongoro[a]	Namib[b]
Prey density (kg/km²)	16,200	7,100	130
Hyena density (hyenas/100 km²)	170.	12	0.5
Group size at carcasses ($\bar{X}$)	25	15	4
	Serengeti-Ngorongoro combined		
Group feeding rate (kg/h/grp)	431		6
Indiv. feeding rate (kg/h/hyena)	18		1.3

[a] Kruuk (1972); [b] Tilson et al. (1980); Tilson & Hamilton (1984).

vidual access may be more limited (Tilson 1983; Tilson & Hamilton 1984) than for large groups feeding at carcasses of similar size in East Africa (Kruuk 1972). Thus, unlike the scramble competition situation reported by Kruuk (1972), Namib Desert spotted hyenas are intra- and intersexually agonistic at carcasses, and adult females win all encounters (Tilson & Hamilton 1984). Adult females extend their status to accompanying offspring who, although subordinate to other adult females, dominate and supplant males, subadults and lower ranking adult females at carcasses with the support of their mothers. Proximity to the mother allows cubs as young as two months old and less than one-fifth the size of older males to gain access to carcasses.

Occasionally adult female spotted hyenas carry food to dens, but den cubs less than 2 months old depend mainly upon maternal milk (Kruuk 1972; but see Hill 1980). Adults do not regurgitate to cubs and males provide no parental care. Brown hyena females, but not males, transport plant and animal foods to cubs and immature relatives at communal dens (Owens & Owens 1979).

By comparison with Kruuk's (1972) observations, Masai Mara cubs as young as four months feed with their mothers at kills up to 2 km from dens. 7 month old cubs accompany adults on hunts, but do not take part in kills. Cubs of high ranking females begin feeding on kills at a younger age than cubs of lower ranking females. In the Masai Mara, as in the Namib, adult females and their offspring exclude males and subadults from carcasses.

Thus, the Namib and Mara observations reported here differ strikingly from those reported by Kruuk (1972) for the Ngorongoro and Serengetti where unweaned infants rarely attended carcasses. Cubs at these East African sites are not weaned until 12 to 16 months, or when they were almost fully grown. By comparison, Namib Desert and Masai Mara females wean their offspring 6—8 months earlier, apparently a consequence of an earlier introduction of meat into their diet.

Discussion

Classification of a behavior pattern as a "greeting ceremony" (Kruuk 1972) identifies the context, a meeting of unfamiliar individuals, in which this behavior appears. Kruuk (1972) noted that juvenile spotted hyenas initiated most greetings between individuals of different ages and sexes, and adult males initiated most greetings between adults. Because larger individuals dominate smaller ones and females dominate males, Kruuk concluded that it was subordinate individuals who initiated greetings.

These observations need to be considered during further speculation concerning the evolution of the female spotted hyena peniform clitoris. Some signal function of the current female, male and juvenile spotted hyena sexual anatomy is implied by observations of living populations. Gould (1981, 1983) suggests that selection for high androgen levels in females, associated with a reduction in body size dimorphism and increased female competitive ability, may in the past have *incidentally* produced peniform clitorises. According to this evolutionary scenario, the female structure was subsequently incorporated into the female's signalling repertoire (GOULD 1981, 1983).

Teratological hormonal effects may not influence mammalian evolutionary developments. An evolutionary cause and effect relationship between androgen levels and peniform clitorises is not established. Female spotted hyena pseudopenis ontogeny and evolution is compatible with interpretations other than that proposed by GOULD & VRBA (1982).

The Adaptationist Fallacy Hypothesis

GOULD (1981, 1983) challenges the "adaptationists' fallacy", i. e., invention of adaptive rationales for observed biological structures. It is not clear to us, however, that the evolutionary sequences he proposes for spotted hyenas are any less speculative than those suggested by us. Comparative ecological and behavioral data for extant hyena species do suggest adaptive interpretations of monomorphism and spotted hyena sexual facies. Comparative functional morphology suggests that there is strong selection against functionless structures of significant size. The spotted hyena pseudopenis is, by comparison with apparently vestigial structures, a relatively large, complex and vulnerable protuberance. We are unaware of convincing arguments for external organs of comparable mass (comprising 1% of the adults weight, NEAVES et al. 1980) which, *when carefully studied*, were found to be devoid of current function. If a well developed female pseudopenis were ever functionless, comparative evidence suggests to us that its size would be selected against, regardless of its hormonal milieu, unless there was countervailing positive selection.

Since the GOULD & VRBA (1982) hypothesis suggests a generalizable direct hormone-morphology relationship between hormone level and structure it follows that androgens acting upon female genital primordia would also produce in other mammalian species a similar penis-like structure. Experimentation with mammals, however, including introduction of androgens during pregnancy and early development, does not produce a penile structure as fully developed as that of the male (BEACH 1972; YOUNG et al. 1964; TELEGDY 1977). Human adrenal abnormalities can cause testosterone secretion resulting in virilization of genetic females, expressed in its extreme form by genitalia approximating functional male morphology. Perhaps an evolutionary increase in female testosterone levels increased slightly the expression of the male external sexual facies among females. Selection would then, in our view, either be against further increases if the organ were functionless or for further increases in size if it conveyed some behavioral or other advantage. That is, we suggest that structure and hormone levels are coupled during evolution only to the extent that there is active selection for structures. Direct effects of hormones upon behavior and anatomy have been advanced to explain reversed sexual dimorphism in all phalarope species, where high female androgen levels are also correlated with a high level of female aggressiveness (HÖHN 1969). Among mammals female aggression probably is mediated by the same hormones as those of the male (Floody & Pfaff 1974; Reinisch 1981). It follows that a simple evolutionary avenue to increased female aggressiveness would be through increased androgen levels, a relationship which has been well established in a number of species of birds (Searcy & Wingfield 1980) and mammals (Peretz et al. 1971; Goy & Resko 1972; Walker & Mooney 1972).

Masculinization of spotted hyena fetuses by the direct effect of adult female hormonal secretion is not supported by Lindeque & Skinner's (1982) measurements of maternal, placental, and embryonic testosterone and androstenedione concentrations. Concentrations of these hormones in the placental effluent were less than those in fetal circulation, leading Lindeque & Skinner (1982) to conclude that maternal testosterone can not be a major contributor to fetal hormone levels. They suggest that the male hormone is produced by the fetal gonads. These observations emphasize the potential for independent selection upon maternal and fetal hormone levels and their morphological targets.

Spotted Hyena Social Hunting

Spotted hyenas are the only one of the three living hyena species that are social hunters, i.e., group hunters of large prey. This practice accounts for the importance of large carcasses in their diet compared with that of the other two hyena species (Table 4), which scavenge carcasses and other foods. An increase in the proportion of large carcasses in the diet, made possible by social hunting, may have led to intensification of contest competition at carcasses and to the evolutionary developments of relatively large female body size and exaggerated signalling systems by females and juveniles.

The problem of how females managed to challenge the male hierarchy, if their ancestors were significantly smaller than males, remains. While saltatorial development through the incidental action of androgens is a possibility, there could also have been selection for small increments in female body size, enhancing the effectiveness of social hunting and/or intrasexual competition at carcasses. This intermediate development may have preceded the transition to female dominance.

The evolutionary scenario proposed here for spotted hyena monomorphism is that effective female competition with males at carcasses was advantageous. A comparable hypothesis is that monomorphism (Wolf 1969) or the mimicking of males by females (Geist 1974) provides females with access to male controlled resources. Selection for increased female body size, a major determinant of rank, was accompanied by selection for increased female aggression, mediated by increased androgen levels. Changes in female hormone levels could lead to initial virilization of the female external genitalia; these rudiments were incorporated into a novel genital display — or possibly one already occurring in males — leading to further selection for enlarged and fully erectile phalluses in females.

Table 4: Proportion of diets according to prey size based on scat analysis of hair types

Species	Prey size			N	Locality	Source
	small (< 12 kg)	medium (12—80 kg)	large (> 80 kg)			
Spotted hyena (*Crocuta crocuta*)	0.7	35.7	63.6	401	Serengeti (Tanzania)	Kruuk (1972)
	0.8	10.9	88.3	348	Ngorongoro (Tanzania)	Kruuk (1972)
	2.9	39.7	57.4	527	Timbavati (South Africa)	Bearder (1977)
	4.5	3.2	92.3	595	Namib Desert (Namibia)	Tilson et al. (1980)
	$\overline{X}$ = 2.2	22.4	75.4			
Brown hyena (*Hyaena brunnea*)	72.0	3.3	24.7	143	Kalahari Desert (South Africa)	Mills (1977)
	50.6	35.5	14.1	258	Kalahari Desert (Botswana)	Owens & Owens (1978)
	$\overline{X}$ = 63.5	19.3	19.4			
Striped hyena (*Hyaena hyaena*)	$\overline{X}$ = 72.1	19.0	8.9	50	Serengeti (Tanzania)	Kruuk (1976)

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