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ASEXUAL REPRODUCTION; CNIDARIA; MARINE INVERTEBRATES, MODES OF REPRODUCTION IN; PARTHENOGENESIS AND NATURAL CLONES

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Hyenas

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- I. Reproduction in the Hyenidae: An Overview
- II. Reproduction in the Spotted Hyena
- III. Sexual Differentiation in the Spotted Hyena
- IV. Summary: Mechanisms and Implications of Sexual Differentiation in the Spotted Hyena

GLOSSARY

- androstenedione** An androgenic steroid secreted by the ovaries and adrenals that is involved in the synthesis of testosterone.
- clitoris** A small, sensitive erectile organ in the female corresponding to the male penis and located at the ventral end of the vulva.
- masculinize** To cause an individual to develop the secondary sexual characteristics of a mature male, as by the administration of androgens.

- placenta** A structure formed by fusion of the chorion with the wall of the uterus that serves to attach the embryo to the uterine wall and to exchange nutrients, wastes, and gases between the maternal blood and the embryonic blood.
- prohormone** A precursor of a hormone.
- sexual differentiation** The process by which the two sexes become different; whereby a bipotential embryo develops along either male or female lines, as determined initially by the chromosomes and subsequently by hormones.

The family Hyenidae, a lineage that separated from viverrid ancestors 25–30 million years ago, comprises four extant species: striped hyenas (*Hyaena hyaena*), brown hyenas (*Hyaena brunnea*), spotted hyenas (*Crocuta crocuta*), and the aardwolf (*Pro-*

teles cristatus). Although there is substantial variation in the details of mating systems, gestation, parental care, and diet, three of these species present traditional, sexually dimorphic, external genitalia. In the fourth species, the spotted hyena, females exhibit remarkably "masculinized" external genitalia. Because of the extraordinary similarity between male and female genital morphology, the common belief that these animals were hermaphrodites persisted well into the nineteenth century. Recently, it was discovered that female spotted hyenas are also behaviorally male-like, being very aggressive and totally dominating adult males in social situations. This suite of "masculine" characters has directed attention to the process of sexual differentiation in the female spotted hyena: Either there are androgens circulating during fetal life that create the unusual external genitalia of these animals (and might enhance their aggressiveness) or there is a hitherto unrecognized mechanism for the production of male-like genital morphology in a female mammal. This article is, accordingly, focused on reproduction and sexual differentiation in the spotted hyena, although first a brief outline is provided of the major features of reproductive behavior in the four extant hyenid species.

I. REPRODUCTION IN THE HYENIDAE: AN OVERVIEW

In all four hyenid species (Table 1)—aardwolf (*Proteles cristatus*), striped hyenas (*Hyaena hyaena*), brown hyenas (*Hyaena brunnea*), and spotted hyenas (*Crocuta crocuta*)—males have internal testes, there is no baculum, and both sexes have anal scent glands contained within an anal pouch. Males and females of all four species engage in scent-marking behavior, which presumably plays a role in sexual advertisement. Regarding generalizations on reproduction, the similarities across species end here. Teat number varies individually and by species. Notably, in spotted hyenas, only the caudal pair of teats is functional, a factor contributing to sibling rivalry in triplet litters. Also, only spotted hyenas show sexual size dimorphism favoring the female and only female crocuta display highly specialized sexual organs. In all other

hyenids, adults are sexually size monomorphic and the sexual organs are not specialized.

A. The Aardwolf

For such a small family, hyenids show fairly diverse reproductive behavior and mating strategies, including both monogamy and promiscuity. The least typical member of Hyenidae, the aardwolf, is socially monogamous, forming pair bonds that can last from 2 to 5 years. Aardwolves are the smallest, the shortest lived, and the only seasonal breeders among Hyenidae. Females have a single yearly estrus in July and give birth to between one and four cubs in October. Because of this species' exclusive termite diet, cubs are entirely dependent on maternal milk for the first 4 months of life. Though fathers guard and defend their young, they do not provide food.

B. Striped Hyenas and Brown Hyenas

Striped and brown hyenas are the most closely related and, consequently, the most similar in their reproductive biology. They are of equal size and longevity and have similar lifestyles (both are solitary foragers and scavengers). In contrast to the aardwolf, these two species are aseasonal breeders, with females being polyestrous. Neonatal mass in striped and brown hyenas is at least threefold that in the aardwolf, but cubs of all three species are born with their eyes closed. The most prominent differences in reproduction between striped and brown hyenas are evidenced by adult behavior. Though generally loners, striped hyenas form short-term pair bonds for breeding and the resulting family unit may endure for several years. There is biparental care as both parents provision their young. The "single family" approach of striped hyenas contrasts with the "cooperative venture" of brown hyenas. The latter occur in small social groups in which members are related to each other. Females mate with nongroup-living, nomadic males; nevertheless, resident males provide care for the young they did not sire. Mothers are also cooperative, suckling the cubs of other females along with their own. Although striped and brown

TABLE 1
Comparative Reproductive Biology and Life Histories of Hyenids

Feature	Hyenid species			
	Aardwolf (<i>Proteles cristatus</i>)	Striped hyena (<i>Hyaena hyaena</i>)	Brown hyena (<i>Hyaena brunnea</i>)	Spotted hyena (<i>Crocuta crocuta</i>)
Age at maturity (years)	M = 1.8 F = 1.8	M = 2-3 F = 2-3	M = ? F = 2	M = 2 F = 3
Life span (years)	Wild: 7 Captive: 15	Wild: >8 Captive: 24	Wild: 12 Captive: 20	Wild: 20-25 Captive: >40
Adult mass (kg)	Size monomorphism M = 7.8-10 F = 7.7-10	Size monomorphism M = 28.0-43.2 F = 27.5-36.0	Size monomorphism M = 35-49.5 F = 28-47.5	Size dimorphism M = 40-62.5 F = 44-75.0
Sexual organs and secondary sexual characteristics	Unspecialized sexual dimorphism Internal testes No baculum Anal glands and pouch	Unspecialized sexual dimorphism Internal testes No baculum Anal glands and pouch Teats: 2-3 pairs	Unspecialized sexual dimorphism Internal testes No baculum Anal glands and pouch Teats: 2-6 pairs	Specialized sexual monomorphism Internal testes No baculum Anal glands and pouch Teats: 1-2 pairs
Mating system	Monogamy	Monogamy	Promiscuity (F mates with nongroup-living M)	Promiscuity (F mates with group-living M)
Breeding	Seasonal	Aseasonal	Aseasonal	Aseasonal
Estrus cycle	Monoestrous Estrus: 1-3 days	Polyestrous Estrus: 1 day	Polyestrous Estrus: 1 week	Polyestrous Estrus: unknown
Mating behavior	Multiple mounting	Multiple mounting No thrusting	Multiple mounting No thrusting	Multiple mounting Thrusting
Gestation (days)	90	91	96	110
Litter size	1-4 ($x = 3$)	1-6 ($x = 2.4$)	1-5 ($x = 2.3$)	1-3 ($x = 2$)
Neonatal mass	223 g	600-700 g	630-812 g	1.5 kg
Parental care	F suckles own cubs Biparental care No provisioning of cubs	F suckles own cubs Biparental care Provisioning by both parents	F allosuckles Cooperative care Provisioning by mother and adults	F suckles own cubs No paternal care Limited or no provisioning
Age at weaning (months)	4	4-5	10-12	12-18
Interlitter interval (months)	12	14	12-41	16-19

hyenas have multiple pairs of teats, only the two caudal pairs are functional.

C. The Spotted Hyena

Unlike their relatives, spotted hyenas are pack hunters and live in the largest social groups of any carnivore. Within this complex social network, there is no extended pair bonding of the sort seen in other

hyenas: Mating is promiscuous and there is no paternal care. Spotted hyenas are aseasonal breeders, but there is little information on their estrus cycle. They have an exceptionally long period of gestation (97-132 days) and give birth to young that are unusually precocial. Despite this "head start," spotted hyenas have longer lactation periods than do most other carnivores, which places a substantial energetic burden on mothers and, by extension, puts lower-rank-

ing females at a disadvantage. Not surprisingly, therefore, mothers suckle their own young exclusively. Details of spotted hyena reproductive biology are described in the following sections.

II. REPRODUCTION IN THE SPOTTED HYENA

A. Morphology

In the female, the clitoris has hypertrophied, approximating the size and shape of the male penis. It is traversed by a central urogenital canal, through which the female spotted hyena urinates, copulates, and gives birth. There is no external vagina: The external labia have fused to form a pseudoscrotum, marked by two pads of fibrous/fatty tissue which are visible externally and might be mistaken for testes. Moreover, this elongated clitoris is fully erectile and females display erections similar to those of the male. The internal reproductive system follows the standard mammalian pattern. Careful examination of the external genitalia reveals sex differences in "phallic" structure. The clitoris is shorter and thicker than the penis, and the central urogenital canal ends in an opening (the urogenital meatus) that is larger and more elastic in the female than in the male. This elasticity is prerequisite for mating and birth. The shape of the glans is also sexually dimorphic: The glans clitoridis has a rounded contour, whereas the glans penis has a more angular profile. These differences in the shape of the glans are used by field researchers to distinguish male from female spotted hyenas.

B. Mating Behavior

Mating occurs in the social context of the hyena clan. Unlike the social canids, in which breeding is commonly restricted to the dominant female, all female spotted hyenas mate and give birth. Females achieve sexual maturity at approximately 30–36 months of age and typically reproduce in the clan of their birth. Males generally disperse at the time of puberty (18–24 months of age) and mate only after joining a new clan. Currently, little is known

of the spotted hyena estrous or ovulatory cycle (if, in fact, there is a cycle). The presence of spines on the glans penis of spotted hyenas is characteristic of other species of induced ovulators, suggesting the possibility of induced ovulation in spotted hyenas. There is no sharply defined breeding season. Although there are seasonal peaks in frequency of births, associated with rainy seasons in Sub-Saharan Africa, mating occurs throughout the year.

Because of their unusual external anatomy, the act of mating requires unusual cooperation on the part of the female and some agility on the part of the male (Fig. 1). During the sexual act, the female retracts her

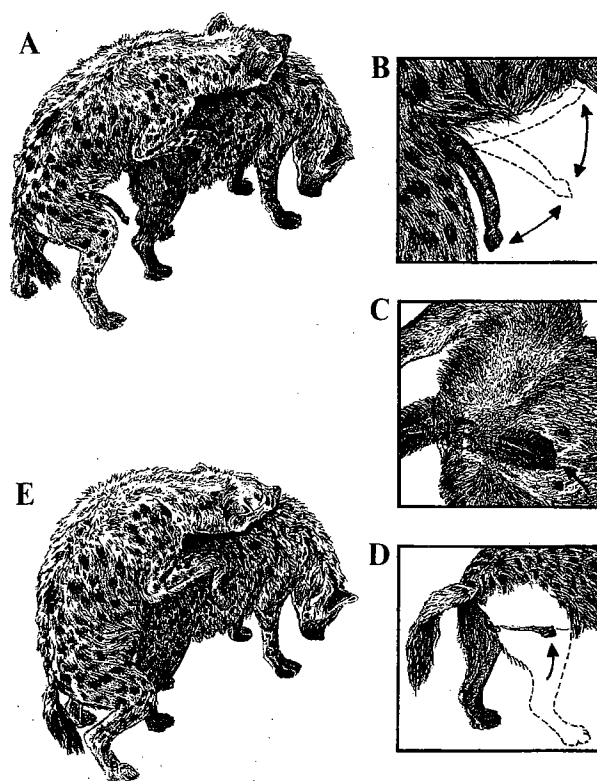


FIGURE 1 The mating sequence in spotted hyenas. (A) The male mounts the female, who stands still with her head lowered and her clitoris retracted into her abdomen. (B) The male shows penile "flips," as indicated by arrows. (C) Under-side view and (D) lateral view of a female spotted hyena, with arrows showing the site of the clitoral opening, which is located anterior to the point of entry in other female mammals. (E) Once the male locates the opening, he squats down and scoots forward to enable intromission, which is followed by pelvic thrusting (illustration by Christine M. Drea).

clitoris into the abdomen and, standing exceptionally still, assumes a head-down posture. The male mounts the female and stands on his hindlegs with his forepaws on her flanks (Fig. 1A). He then "flips" his erect penis against her lower abdomen (Fig. 1B), searching for the clitoral opening (Fig. 1C), which is well anterior to the position normally occupied by the external vagina (Fig. 1D). To achieve entry, the male must squat down on his haunches, move forward, and reposition his pelvis (Fig. 1E). After achieving entry there is an interval of pelvic thrusting followed by ejaculation. During the minutes following ejaculation, the male maintains insertion and often assumes a posture in which he leans forward resting his head on the back of the female. A number of additional ejaculatory sequences may follow, with the female taking an active role in soliciting the male's attention.

C. Gestation and Parturition

As noted previously, gestation is prolonged in the spotted hyena, relative to the other hyenids. Elevated concentrations of plasma progesterone can be detected within the first 2 weeks of gestation. As pregnancy proceeds, plasma levels of estrogen and testosterone, as well as the peptide hormone relaxin, also exhibit a substantial rise from prepregnancy values. A marked increase in the size of the nipples is often the first external indicator of pregnancy, particularly in primiparous animals. In nature, as the female proceeds toward term, she locates a site removed from the communal den of the clan and gives birth in this "natal den." The young will be nursed and maintained in this den for a variable period (2–4 weeks) before being carried by the mother to the communal den and introduced to the clan.

D. Costs of Clitoral Delivery

Giving birth to a large (1–2 kg) fetus through the clitoris is a mechanically challenging feat. The urogenital meatus, although highly elastic, is not adequately large to permit passage of the fetus and must tear before an initial birth can occur. The process is further complicated by the presence of a short

umbilical cord and a rather tortuous route from the point of placental attachment in a uterine horn. The fetus must travel through the uterus and upper vagina before finally reaching the clitoris. If delivery of the fetus does not proceed in a timely fashion, the infant will be stillborn (presumably due to anoxia, consequent to detachment of the placenta from the uterine wall). In captivity, approximately 60% of first births result in stillborn offspring due to the time required for passage of the fetus. Moreover, in some primiparous females, the fetus was lodged in the birth canal and would have taken the life of the mother without veterinary intervention. Such intervention is obviously not available for female hyenas in nature. In subsequent pregnancies, after a fetus has successfully passed through the clitoris, infant mortality (and indeed maternal mortality) is much lower. Because there are substantial costs to clitoral delivery in this species, it is probably not surprising that this process has evolved only once.

E. Behavior of Infants

The twins that generally constitute a hyena litter are quite precocial. At birth, their eyes are open, they are highly mobile, and they possess an impressive array of needle-like teeth. In addition, within minutes of the birth of the second cub, the twins begin to fight. The fighting is intense and, if not interrupted, wounds result from the vigorous biting. At a minimum, fighting during the first days of life establishes a dominance relationship between the siblings that lasts, at least, for several years. In nature, if the dominant sibling can keep its young twin sequestered in a burrow and prevent it from emerging to nurse, death will result from a combination of starvation and wounding. If both infants survive, however, the intense aggression is largely replaced by playful, prosocial interactions. The development of these prosocial behavior patterns is also precocial, emerging in the second week of life and increasing over subsequent months. This schedule ensures that both aggressive and prosocial behavior patterns will be in the infant's repertoire when it joins the clan. As outlined later, the exposure of all fetuses to high levels of androgens during fetal life might be expected to facilitate the aggression observed at birth in this species.

