Hyena Myths and Realities

Both male and female genitals are strikingly similar. Why?

by Stephen Jay Gould. ***Natural History, 1981.***

I freely admit that the spotted, or laughing, hyena is not the loveliest animal to behold. Still, it scarcely deserved the poor reputation imposed upon it by our illustrious forebears. Three myths about hyenas helped to inspire the loathing commentary of ancient texts.

Hyenas, first of all, were regarded as scavengers and consumers of carrion. In his *Natural History,* Pliny the Elder (A.D. 23-79) spoke of them as the only animals that dig up graves in search of corpses (*ab uno animali sepulchra erui inquisitione corporum*). Conrad Gesner, the great sixteenth-century cataloger of natural history, reported that they gorge themselves so gluttonously after finding a corpse that their bellies swell to become taut as a drum. They then seek a narrow place between two trees or stones, force themselves through it, and extrude the remains of their meal simultaneously at both ends.

Hans Kruuk, who spent years studying spotted hyenas on their home turf (the plains of East Africa), has labored to dispel these ancient myths (see his book *The Spotted Hyena,* University of Chicago Press, 1972). He reports that hyenas will scavenge when they get the opportunity. (Almost all carnivores, including the noble lion, will happily feast upon the dead product of another animal's labor.) But spotted hyenas live in hunting clans of up to eighty animals. Each clan controls a territory and kills most of its own food -mainly zebra and wildebeest in communal, nocturnal pursuit.

As a second insult, hyenas were widely regarded as hybrids. Sir Walter Raleigh excluded them from Noah's ark in 1614 since he believed that God had only saved the purely bred. Hyenas were reconstituted after the flood through the unnatural union of a dog and cat. In fact, the three living species of hyena form a family of their own within the order Carnivora. They are most closely related to the viverrids (weasels and their allies).

As a final, phony blot on their escutcheon, and in the unkindest cut of all, many ancient writers charged that hyenas were hermaphrodites, bearing both male and female organs. The medieval bestiaries, always trying to draw a moral lesson from the depravity of beasts, focused on this supposed sexual ambivalence. A twelfth-century document, translated by T. H. White, declared:

> Since they are neither male nor female, they are neither faithful nor pagan, but are obviously the people concerning whom Solomon said: "A man of double mind is inconstant in all his ways." About whom also the Lord said: "Thou canst not serve God and Mammon."

But hyenas also had some formidable defenders against this particular calumny. Aristotle himself had declared in the *Historia animalium*: "The statement is made that the hyena has both male and female sexual organs; but this is untrue."

Aristotle -- and not for the first time -- was right of course. But the legend had arisen for a good reason. Female hyenas are virtually indistinguishable from males. Their clitoris is enlarged and extended to form an organ of the same size, shape, and position as the male penis. It can also be erected. Their labia have folded up and fused to form a false scrotum that is not discernibly different in external form or location from the true scrotum of males. It even contains fatty tissue forming two swellings easily mistaken for testicles. Authors of the most recent paper on spotted hyenas found the appearance of males and females "so close that sex could only be determined with certainty by palpation of the scrotum. Testes could be located in the scrotum of the male compared with soft adipose tissue in the false scrotum of the female."

British zoologist L. Harrison Matthews wrote the most extensive anatomical description of the hyena's sexual anatomy in 1939 (*Philosophical Transactions of the Royal Society of London*, vol. 230). He described the peniform clitoris, emphasizing that it is no smaller than the male penis, is equally constricted to a single slitlike opening at the tip, and is as subject to erection as its male counterpart. He concluded his dry and precise pages of description with as forceful a statement of wonder as measured British scientific prose would allow: "It is probably one of the most unusual of the forms which the external orifice of the urogenital canal takes amongst female mammals."

Matthews also investigated the interesting question of how hyenas do it, given a female orifice no larger than the slit of a male's penis. "In the pre-pubertal state," he writes, "these functions are obviously impossible, owing to the minute size of the opening." But as the female matures the slit gradually lengthens and "creeps down round the ventral surface ... travelling down the midline" until it forms an orifice 1.5 cm long and extending from the tip of the clittoris to its base. This lengthening of the slit and a subsequent enlargement of the nipples following pregnancy and parturition help distinguish older females from males. We can now understand the basis for ancient myths that hyenas were either simultaneous hermaphrodites (bearing male and female organs at the same time) or male for part of their life and then female.

Nature's oddities cry out for explanation, and we must ask what advantages females gain from looking like males. Immediately, we come upon the other most striking oddity of hyena biology: females not only resemble males; they are also larger than males, contrary to the usual pattern in mammals, including humans. Females in Kruuk's East African clans averaged 120 pounds in body weight versus 107 pounds for males. Moreover, they lead the clans in hunting and defense of territory and are generally dominant over males in individual contacts. Dominance is not merely a result of larger size because females also rank higher than larger males if the discrepancy in size is not too great.

Although the female hyena's assumption of what are usually male roles in mammals is probably related to its evolution of sexual structures that mimic male organs, the link between these phenomena is not immediately clear. It cannot have much to do with sexual performance

itself for, if anything, the female "penis" is a hindrance to copulation until its opening enlarges and its form departs from that of the male.

Kruuk suggests that the strong mimicry arose in connection with a common behavior in hyenas called the "meeting ceremony." Hyenas live in clans that defend territories and engage in communal hunting. But individuals also spend much of their time as solitary wanderers searching the landscape for carrion. To maintain the cohesion of the clan and to keep strangers away, hyenas must develop a mechanism for recognizing each other and reintegrating solitary wanderers into their proper clan.

When two hyenas of the same clan meet, they stand side to side, facing in opposite directions. They each lift their inside hind leg, subordinate individual first, exposing either an erect penis or clitoris, one of the most vulnerable parts of the body, to their partner's teeth. They then sniff and lick each other's genitals for ten to fifteen seconds, primarily at the base of the penis or clitoris and in front of the scrotum or false scrotum.

Kruuk believes that the female clitoris and false scrotum evolved to provide a conspicuous structure serving for recognition in the meeting ceremony. He writes:

> It is impossible to think of any other purpose for this special female feature than for use in the meeting ceremony. ... It may also be, then, that an individual with a familiar but relatively complex and conspicuous structure sniffed at during the meeting has an advantage over others; the structure would often facilitate this reestablishment of social bonds by keeping partners together over a longer meeting period. This could be the selective advantage that has caused the evolution of the females' and cubs' genital structure.

Speculation about adaptive significance is a favorite, and surely entertaining, ploy among evolutionary biologists. But the question, "What is it for?" often diverts attention from the more mundane but often more enlightening issue, "How is it built?" In this case, speculations about adaptive significance have been in the literature for a long time, yet no one bothered to tread the obvious path for hypotheses of anatomical construction until 1979: What sexual hormones are maintained at what levels by female hyenas from conception to maturity? (See P. A. Racey and J. D. Skinner, "Endocrine Aspects of Sexual Mimicry in Spotted Hyenas, *Crocuta crocuta*," vol. 187, *Journal of Zoology*, 1979, pages 315-26.)

Racey and Skinner found, in short, that two androgens (male-producing hormones) had higher concentrations in testicles than in ovaries of adult spotted hyenas (scarcely surprising). Yet, when they investigated levels of the same hormones in blood plasma, they detected no differences between males and females. One female contained two twin female fetuses, and both, despite their tiny size relative to their mother, contained about the same level of testosterone as adult females. Racey and Skinner therefore conclude "that high foetal androgen levels are responsible for the appearance of the male sexual facies in adult female spotted hyenas."

Confirmation for their hypothesis arises from their study of brown and striped hyenas, the other two species of the family Hyaenidae. Neither brown nor striped hyenas develop peniform clitorises or false scrotums. In both species, androgen levels in blood plasma are much lower for

females than for males. (Aristotle, by the way, defended hyenas against the charge of hermaphroditism by correctly describing the genitalia of these other species-something of a dodge with respect to the spotted hyena, the source of the legend, but "the master of them that know" was right in any case.)

But why should high levels of androgenic hormones lead to the building of false penises and scrotums. The animals that construct them are still, after all, genetically female. How can female genes produce mimics of male structures, even under the influence of unusually high levels of androgenic hormones. A look at the developmental basis of sexual anatomy resolves this dilemma.

Mammals share a common pattern for the embryology of sexual organs, and we may therefore use humans as an example. The early embryo is sexually indifferent and contains all pre- cursors and structures necessary for the development of either male or female organs. After about the eighth week following conception, the gonads begin to differentiate as either ovaries or testes. The developing testes secrete androgens, which induce the development of male genitalia. If androgens are absent, or present at low levels, female genitalia are formed.

The internal and external genitalia develop in different ways. For internal genitalia, the early embryo contains precursors of both sexes: the Mullerian ducts (which form the Fallopian tubes and ovaries of females) and the Wolffian ducts (which form the vas deferens--the ducts that carry sperm from the testes to the penis--in males). In females, the Wolffian ducts degenerate and the Mullerian ducts differentiate; males develop by the opposite route.

The external genitalia follow a markedly different pattern. Individuals do not begin with two distinct sets of precursors and then lose one while strengthening the other. Rather, the different organs of male and female develop along diverging routes from the same precursor. The male's penis is the same organ as the female's clitoris-they form from the same tissues, are indistinguishable in the early embryo, and follow different pathways later. The male's scrotum is the same organ as the female's labia majora. The two lips simply grow longer, fold over and fuse along the midline, forming the scrotal sac.

The female course of development is, in a sense, biologically intrinsic to all mammals. It is the pattern that unfolds in the absence of any hormonal influence. The male route is a modification induced by secretion of androgens from the developing testes.

The mystery of male mimicry in female hyenas may be solved by recognizing these fundamental facts of developmental anatomy. We know from the work of Racey and Skinner that female hyenas maintain high levels of androgenic hormones. We may therefore conclude that the striking and complex peculiarities of sexual anatomy in female spotted hyenas are simply, indeed almost automatically, produced by a single, underlying effect: the secretion of unusually large amounts of androgens by females.

The automatic nature of peniform clitorises and false scrotums in female mammals with high androgen levels is confirmed by several related examples. Female spider monkeys also have an enlarged clitoris and a false scrotum produced by overgrowth of the labial folds. Although their levels of androgen have not been measured (to my knowledge), they do use their enlarged clitoris

in a male form of genital display and dominance. Better examples arise from unusual patterns of development within our own species. The adrenal glands also secrete androgens, usually in small amounts. In some genetic females, adrenals are abnormally enlarged and produce high levels of androgens. These baby girls are born with a penis and false scrotum. Several years ago a drug was placed on the market to prevent miscarriages. It had the unfortunate side effect of mimicking the action of natural androgens. Female babies were born with a greatly enlarged clitoris and an empty scrotal sac formed from the fused labia.

I believe that these facts of developmental anatomy must force a revision in the usual interpretation of male mimicry in female spotted hyenas. Evolutionary biologists have too often slipped into a seductively appealing mode of argument about the phenomenon of adaptation. We tend to view every structure as designed for a definite purpose, thus building (in our imagination) a world of perfect design not much different from that concocted by eighteenth-century natural theologians who "proved" God's existence by the perfect architecture of organisms. Adaptationists might allow a little flexibility for tiny and apparently inconsequential structures, but surely anything big, complex, and obviously useful must be built directly by natural selection. Indeed, previous literature on spotted hyenas has assumed that female sexual organs evolved directly for a definite function -- as in Kruuk's speculation about the adaptive advantages of conspicuous external genitalia for recognition in the meeting ceremony.

But another scenario is possible and strikes me as more likely. I don't doubt that the basic peculiarity of hyena social organization--the larger size and dominance of females is an adaptation to something. The easiest pathway to such an adaptation would be a marked rise in the production of androgenic hormones by females (these exist in small amounts in all mammalian females). High levels of androgens would entail complex secondary effects as automatic consequences among them, a peniform clitoris and a false scrotum (we cannot, after all, label the very same condition in some abnormal human baby girls as an adaptation). Once they are present, some use might be evolved for them as in the meeting ceremony. But their current utility does not imply that they were built directly by natural selection for the purpose they now serve. (Yes, I know that my scenario might be run in reverse: conspicuous female genitalia are required for the meeting ceremony, are evolved by enhanced androgen levels, thus yielding large female size and dominance as a consequence. I do, however, point out that under our usual preferences for seeing direct adaptation everywhere, my scenario would not even be considered. Indeed, it wasn't in the major works on spotted hyenas.)

My columns have the nasty habit of discoursing on funny facts of natural history, and then, only at the end, reaching the general argument that inspired the disquisition. This article is no exception, for I designed it to make a point about adaptation and the evolutionary analysis of form, not as a treatise on hyena penises.

We do not inhabit a perfected world in which natural selection ruthlessly scrutinizes all organic structures and then molds them for optimal utility. Organisms inherit a body form and a style of embryonic development; these impose constraints upon future change and adaptation. In many cases, the direction that evolution takes is more a result of inherited patterns than of current environmental demands. These inheritances constrain, but they also provide opportunity. A potentially minor genetic change a rise in androgen level in this case---entails a host of

complex, nonadaptive consequences. The primary flexibility of evolution may arise from nonadaptive byproducts that occasionally permit organisms to strike out in new and unpredictable directions. What "play" would evolution have if each structure were built for a restricted purpose and could be used for nothing else? How could humans learn to write if our brain had evolved for hunting, social cohesion, or whatever, and could not transcend the adaptive boundaries of its original purpose?

In the second show of his Cosmos series, Carl Sagan told the tale of a Japanese crab that carries a portrait of a samurai warrior on its back. He argued that humans have built this face after their own image because local fisherman have been throwing back the most facelike crabs for centuries, thus imposing strong selection pressure for samurai look-alikes (the others get eaten). He used this example as his lead-in for a rapture discourse on the pervasive power o natural selection.

I doubt this story very much and suspect that the conventional explanation is correct: that the resemblance is accidental and, at best, only slightly strengthened by human intervention. But even if Sagan were right I believe that he is marveling at the wrong item (or at least failing to give equal time to another remarkable aspect of the case). I am most impress by a crab's ability to do such an un-crabbily thing in the first place-just as the capacity of an inherited developmental system to produce (and so easily) such marked changes m the sexual anatomy of female hyenas grabs me far more than any putative adaptive significance for the change

The capacity of crabs to produce, a face can have nothing to do wit any selective value such a face might have since crabs do not routinely u this latent ability. It arises from several facts of crab biology: the bilateral symmetry of the carapace (corresponding by analogy with the bilateral symmetry of the human face), an the fact that many crabs are ornamented by creases along the midline (where a "nose" might form) and perpendicular to it (where "eyes" and mouths" might be constructed).

The (probably accidental) production of a human portrait represents a stunning example of the evolutionary flexibility arising from nonadaptive consequences of an inherited design. Organic material is not putty and natural selection is not omnipotent. Each organic design is pregnant with evolutionary possibilities, but restricted in its paths of potential change. Fishermen might throw back selected starfishes with their five-part symmetry, or snails with their spiral design for tens of millions of years and never carve a samurai into their hard parts.

Peter Medawar has described science as the "art of the soluble." Evolution might be labeled "the transformation of the possible."

Stephen Jay Gould teaches biology, geology, and the history of science at Harvard University.