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Sex within Bodies

Ithough the binary in gamete size is practically universal, the way male and female functions are packaged into individual bodies does not fit into any consistent polarity. We tend to think that males and females must be in separate bodies because most of us are, as are most of the animals we live with, such as our pets, domesticated stock, and the birds and bees around our parks. However, many species have other ways of organizing sexual functions.

An individual body who makes both small and large gametes at some point in life is called a hermaphrodite. An individual who makes both sizes at the same time is a simultaneous hermaphrodite, and one who makes them at different times is a sequential hermaphrodite. Most flowering plants are simultaneous hermaphrodites because they make pollen and seeds at the same time. Pollen is the male part of a plant and the ovule is the female part. A pollinated ovule turns into a tiny embryo that detaches, to be blown away by the wind or carried away by an animal.

Among animals, hermaphrodism is common in the ocean. Most marine invertebrates, such as barnacles, snails, starfish, fan worms, and sea anemones, are hermaphroditic. Many fish are too. If you go snorkeling at a coral reef in Hawaii, the Caribbean, Australia, or the Red Sea, chances are that about a quarter of the fish you see will be hermaphroditic. Or take a look at some of the colorful fish popular in tropical

aquaria—they are often sequential hermaphrodites. Most species of wrasses, parrot fish, and larger groupers are hermaphroditic, as are some damselfish, angelfish, gobies, porgies, emperors, soapfishes, dottybacks, and moray eels (all from shallow waters), and many deep-sea fish as well.²

Hermaphrodism is a successful way of life for many species; my guess is that hermaphrodism is more common in the world than species who maintain separate sexes in separate bodies (called gonochorism). The separate-sex/separate-body state is often viewed as "normal," suggesting that something unusual favors hermaphrodism in plants, on coral reefs, and in the deep sea. Alternatively, hermaphrodism may be viewed as the original norm, prompting us to ask what there is in mobile organisms in the terrestrial environment that favors separate sexes in separate bodies.

WHAT FISH CAN TELL US

FEMALES CHANGING TO MAIF

Sex change is only one of several interesting aspects of coral reef fish society. The bluehead wrasse is named for the blue head of the largest males. When small and just entering sexual maturity, fish of both sexes look similar. Later three genders develop. One gender consists of individuals who begin life as a male and remain so for life. Another gender consists of individuals who begin as females and later change into males. These sexchanged males are larger than those who have been male from the beginning. The third gender consists of females who remain female. We'll call the two male genders the "small unchanged males" and the "large sexchanged males," respectively. The large sex-changed males are the biggest individuals of the three genders, and they attempt to control the females. In some species, the large sex-changed males maintain and defend the females, and in others they defend locations that females appear to prefer.

Fertilization is external—a female releases eggs into the water and a male then releases a cloud of sperm around the eggs to fertilize them. The unfertilized eggs are out in the open and can potentially be fertilized by any male in the vicinity.

The small unchanged and large sex-changed males are hostile to each other. The large sex-changed males chase the small unchanged males

away from the territory or from females they control. The small unchanged males are more numerous than the large sex-changed males and may form coalitions to mate with females that a large sex-changed male is trying to control. The small unchanged males mate by darting in and fertilizing the eggs that a large sex-changed male was intending to fertilize. Some small unchanged males keep the large sex-changed male busy while others are mating.

Different ecological circumstances favor unchanged and sex-changed males. The wrasses live both on coral reefs and in the seagrass beds nearby. In seagrass, females nestled among grass blades can't be guarded very well, and the balance of hostilities tips in favor of the small unchanged males. This situation leads to only two genders, unchanged males and females. On the coral reef, clear water and an open habitat structure permit the large sex-changed males to control the females, and the balance tips in their favor.³ This situation encourages the presence of all three genders. Simple population density also shifts the gender ratios. At high densities females are difficult to guard and small unchanged males predominate, whereas at low densities a large sex-changed male can control a "harem." Whether females prefer either type of male isn't known.

The sex changes are triggered by changes in social organization. Another type of wrasse is the cleaner wrasse, named for its occupation of gleaning ectoparasites from other fish. When a large sex-changed male is removed from his harem, the largest female changes sex and takes over. Within a few hours, she adopts male behavior, including courtship and spawning with the remaining females. Within ten days, this new male is producing active sperm. Meanwhile the other females in the harem remain unchanged.⁵ I haven't been able to find out whether any female can turn into a male if she is the biggest female when the existing male dies, or whether females divide into two groups—those who remain female no matter what and those who change sex when circumstances are right.

Does this animal society seem oh-so-bizarre? It isn't. Aspects of this system appear again and again among vertebrates, especially the themes of male control of females or their eggs, multiple male genders, hostility among some of the male genders, flexible sexual identity, and social organization that changes with ecological context. Still, if you think the

coral reef fish scene is bizarre, you're not alone—so did the biologists who first witnessed it. We're only just realizing that the concepts of gender and sexuality we grew up with are seriously flawed.

MALES CHANGING TO FFMALE

Sex changes from male to female also occur. A group of damselfish are called clown fish because their bold white strips remind one of the white makeup used by clowns. These fish live among the tentacles of sea anemones, which have cells in their tentacles that sting any animal who touches them. To survive in this lethal home, a clown fish secretes a mucus that inhibits the anemone from discharging its stinging cells. Although living within the anemone's tentacles provides safety for the clown fish, the size of its house is limited by how big its sea anemone grows. An anemone has space for only one pair of adult clown fish and a few juveniles.

The female is larger than the male. If she is removed, the remaining male turns into a female, and one of the juveniles matures into a male.⁶ The pair is monogamous. Female egg production increases with body size. A monogamous male finds no advantage in being large because he's not controlling a harem of females. The advantage for males of remaining small and for females of becoming large may account for the developmental progression from male to female.⁷

MALE AND FEMALE SIMULTANEOUSLY

Hamlets, which are small coral reef basses, don't have to worry about choosing their sex: they are both sexes at the same time. However, they cross-fertilize and must mate with a partner to reproduce. These simultaneous hermaphrodites change between male and female roles several times as they mate. One individual releases a few eggs and the other fertilizes them with sperm. Then the other releases some eggs, which the first fertilizes with sperm, and so on, back and forth.⁸

No one has offered any suggestions about why hamlets are simultaneous hermaphrodites. Deep-sea fish also tend toward simultaneous hermaphrodism, which for these species is viewed as an adaptation to extremely low population density. Hamlets don't have a strange appearance.

nor do any other hermaphroditic fish. Hermaphroditic fish look like, well, just fish. Hamlets are not particularly rare, nor are they derived from ancestors who were rare or lived in the deep sea. So just why hamlets are simultaneously hermaphroditic remains mysterious.

MALE AND FEMALE CRISSCROSSING

Changing sex once may seem a big deal, but some fish do it several times during their life span. An individual may change from an unsexed juvenile to a female, then to a male, and then back to a female. Or it may change from a juvenile to a male, then to a female, and then back to a male. In certain species, sexual identity can be changed as easily as a new coat.

Sex crisscrossing was first discovered in a species of goby, which is the largest family of fish. Gobies are tiny and often live on coral reefs—in this case, on the Pacific island of Okinawa. These gobies live as monogamous pairs on branching coral, and the males care for the eggs. About 80 percent of the juveniles mature female, and the rest mature male. Some of the females later switch to male, and some of the males later switch to female. Of those that have switched once, a small fraction later switch back again—the crisscrossers.

Why go to the expense of changing one's sexual wardrobe? One theory envisages pair formation in gobies as resulting when two larvae drop out of the plankton together onto a piece of coral.¹¹ They awake after metamorphosis to discover that they are both the same sex. What to do? Well, one of them changes sex. Changing sex has been suggested as a better way of obtaining a heterosexual pairing than moving somewhere else to find a partner of the opposite sex when traveling around is risky. Thus this theory comes down to a choice: switch or move. This theory is rather heterosexist, though. As the hamlets show, a heterosexual pair is not necessary for reproduction, because both could be simultaneously hermaphroditic and not have to bother with crisscrossing.

A species of goby from Lizard Island on Australia's Great Barrier Reef has recently been discovered to crisscross, but in a way that is interestingly different from the Okinawan goby. 12 In the Australian goby, all the juveniles mature into females, with some later becoming males. The males, however, can change back into females. In fact, the meaning of

male is ambiguous here. The investigators defined a male to be any fish with at least some sperm production. All males, however, contain early-stage oocytes—cells that develop into eggs—in their gonads. So all the males remain part female. The species therefore consists of two genders at any one time: all-female fish and part-male-part-female fish.

Among flowering plants, populations with hermaphrodites and females are common, ¹³ more so than populations with males and females. These mixed hermaphrodite/single-sex species contrast with most plant species, which are entirely hermaphroditic. (Perhaps as more gobies are investigated, a species will be found consisting of females and hermaphrodites, just as in plants.)

Plants also offer the most amusing examples of crisscrossing sex changes. In a tropical ginger from China, some individuals are male in the morning, making pollen, while others are female in the morning, receiving pollen. Then they switch sexes in the afternoon. This phenomenon, called flexistyly, is known in eleven families of flowering plants. ¹⁴ The ginger's diurnal sex change is not too different from how hamlets mate, where members of a mating pair switch back and forth between male and female once a minute.

These examples of sequential, simultaneous, and crisscrossing hermaphrodism show that male and female functions don't need to be packaged into lifelong distinct bodies. Hermaphroditic vertebrate species are successful and common.

INTERSEXES IN MAMMALS

Can mammals be hermaphroditic too, or have we been left out? Not entirely. Mammals described as hermaphrodites are often reported, although the word "hermaphrodite" is misleading.

Let's work out some definitions. The reproductive system in mammals consists of gonads—the place where eggs and sperm develop—and plumbing, which transports gametes from the gonads to their destination. The plumbing consists of internal pipes and external valves. The internal pipes are fallopian tubes, muellerian ducts, and so forth. External valves include the penis, clitoris, scrotum, labia, and so on. An "inter-

sexed" individual has gonads to make both eggs and sperm and/or combinations of sperm-related and egg-related plumbing parts. With so many parts in the overall system, many combinations are possible.

To be more specific, we can distinguish intersexed gonads, with some combination of ovarian and testicular tissue, from intersexed genitals, with some combination of egg- and sperm-related plumbing.¹⁵ We could even distinguish internal genitally intersexed and external genitally intersexed to pinpoint where the combined plumbing is located. Although the gamete-size binary implies that only two sexed functions exist, many body types occur, ranging from all-sperm parts, through various combinations of both sperm- and egg-related parts, to all-egg parts.

To manufacture a hermaphrodite using mammalian components on a vertebrate chassis, two entire sets of gonadal and plumbing parts are needed, one for eggs and one for sperm. Mammals show many partial combinations of sperm- and egg-related parts. All the partial combinations could be stirred together into a putty from which evolution might someday mold a full mammalian hermaphrodite if selection pressure for that arose, a pressure such as those to which coral reef fish have already responded. In some mammalian species, intesexed bodies are a minority; in others, the majority.

Antlers offer easy-to-see clues for possible intersexed individuals. White-tailed deer (Odocoileus virginianus) possess a male body type, called a velvet-horn because these deer retain the special velvet skin over the antlers that is usually shed after the antlers have aged. Velvet-horn males have small antlers, doelike body proportions and facial features, and small testes; they are said to be infertile. Females typically don't have antlers, but there is a type of female deer with hard, bony antlers and extensively combined plumbing parts, which is believed to be infertile. A distinct fertile antlerless male morph and a distinct fertile antlered female morph occur as well.

The mention of infertility plays to the prejudice that something is "wrong" with intersexes. But the story is more complicated. The frequency of velvet-horns in white-tailed deer is around 10 percent in some areas and can reach as high as 40 to 80 percent. Numbers this big contradict the idea that velvet-horns represent a deleterious mutation.

Similarly, a male morph in black-tailed deer (Odocoileus hemionus) called a cactus buck may be a form of intersex as well. Elk (Cervus ela-

phus, also called red-tailed deer), swamp deer (Cervus duvauceli), Sika deer (Cervus nippon), roe deer (Capreolus capreolus), and fallow deer (Dama dama) all have a male morph with velvet-covered antlers, called a peruke, that is described as nonreproductive. Moose (Alces alces) have males with velvet-covered antlers, called velericorn antlers, as well as perukes and a small number of velvet-antlered females.¹⁷

Because female kangaroos incubate their embryos in a pouch rather than a uterus, an intersexed individual might have both a penis and a pouch, mammary glands and testes. Intersexed kangaroos are known among eastern gray kangaroos (Macropus giganteus), red kangaroos (Macropus rufus), euros (Macropus robustus), tammar wallabies (Macropus eugenii), and quokkas (Setonix brachyurus). 18

Kangaroo rats are small mammals that are not marsupials at all, but rather rodents native to the American Southwest. Kangaroo rats hop around on their hind feet, reminding one of real kangaroos. Not to be outdone by the better-known kangaroos, kangaroo rats (Dipodomys ordii) have lots of intersexes. About 16 percent of the animals have both sperm- and egg-related plumbing, including a vagina, a penis, a uterus, and testes in the same individual.¹⁹

Pigs in the South Pacific islands of Vanuatu (formerly the New Hebrides) have been bred for their intersex expressions. Typically, these pigs have male gonads and sperm-related internal plumbing, intermediate or mixed external genitalia, and tusks like boars. In Vanuatu cultures, the pigs are prized as status symbols, and among the people of Sakao, seven distinct genders are named, ranging from those with the most egg-related external genitalia to those with the most sperm-related external genitalia. The indigenous classification of gradations in intersexuality is said to be more complete than any system of names yet developed by Western scientists and was adopted by the scientist who wrote the first descriptions of the culture. In the past, 10 to 20 percent of the domesticated pigs consisted of intersexed individuals.²⁰

Bears, including the grizzly bear (*Ursus arctos*, also called the brown bear), the American black bear (*Ursus americanus*), and the polar bear (*Ursus maritimus*), have long been symbols of gender mixing for Native American tribes. The Bimin-Kuskusmin and Inuit peoples have stories of bears who are "male mothers," giving birth through a penis-clitoris.²¹ Indeed, 10 to 20 percent of the female bears in some populations have a

birth canal that runs through the clitoris, rather than forming a separate vagina. An intersex female bear actually mates and gives birth through the tip of her penis.²²

This form of intersexed plumbing is found in all females of the spotted hyena (Crocuta crocuta) of Tanzania-in which the females have penises nearly indistinguishable from those of the males.²³ Aristotle believed these animals to be hermaphrodites, but he was only half right. The first scientific investigation in 1939 showed that a spotted hyena makes only one-size gamete throughout its life, either an egg or sperm.²⁴ Thus these hyenas are not hermaphrodites. Rather, female spotted hyenas are intersexed, like some female bears. The females have a phallus 90 percent as long and the same diameter as a male penis (yes, somebody measured, 171 millimeters long and 22 millimeters in diameter). The labia are fused to form a scrotum containing fat and connective tissue resembling testicles. The urogenital canal runs the length of the clitoris, rather than venting from below. The animal can pee with the organ, making it a penis. Completing the picture, the female penis contains erectile tissue (corpus spongiosum) that allows erections like those of a male penis.

A female spotted hyena mates and gives birth through her penile canal. When mating, a female retracts the penis on itself, "much like pushing up a shirtsleeve," and creates an opening into which the male inserts his own penis. The female's penis is located in the same spot as the male's penis, higher on the belly than the vagina in most mammals. Therefore, the male must slide his rear under the female when mating so that his penis lines up with hers. During birth, the embryo traverses a long and narrow birth canal with a sharp bend in it. About 15 percent of the females die during their first birth, and they lose over 60 percent of their firstborn young. These obvious disadvantages lead us to the question of why female spotted hyenas have this penis instead of a clitoris.

Female spotted hyenas have a dominance hierarchy, and the erect penis is a signal of submission. When two females interact with each other in a struggle for dominance, the one who wants to back down signals by erecting her penis.²⁶ No one knows why female hyenas evolved this method of signaling, but then signals always seem arbitrary in themselves. Why are traffic lights red, yellow, and green? The female penile erection of hyenas is an "honest signal." Erections occur in the "meet-

ing ceremony" when animals greet after having been apart. The animals approach each other and stand alongside one another, head-to-tail, one or both lifting her hind leg to allow inspection of her erect penis. When only one member of a greeting pair displays an erection, she is normally the subordinate. Each hyena puts her reproductive organs next to powerful jaws. Greetings between captive females that have been separated for a week are tense and frequently wind up in a fight that starts when one bites the genitals of the other, doing occasional damage to the reproductive capability of the injured party.

The masculinized genitals of female hyenas are an example of what I call a social-inclusionary trait, which allows a female hyena access to resources needed for reproduction and survival. If a female were not to participate in social interactions using her penis for signaling, she would not be able to function in hyena society and presumably would either die or fail to breed.

It has been suggested that the enlarged clitoris is a side effect of high testosterone levels in female spotted hyenas.²⁷ Social life among female spotted hyenas involves lots of aggression, possibly caused by elevated blood testosterone. This testosterone might produce incidental "excess" masculinization during development. I don't buy this theory. Aggressiveness doesn't require testosterone. We're not talking about a slightly larger clitoris, but a full-fledged replica of male genital anatomy, complete with scrotal sacs and fat bodies resembling testicles. This structure can't develop from a few extra splashes of testosterone in the blood. I believe this case demonstrates that mammalian genitals have a symbolic function. In fact, displaying genitals is a mammal thing. Fish, frogs, lizards, snakes, and birds rarely have external genitals pigmented with bright colors to wave around at one another. Mammals do.

Penises can be seen in various female primates, such as bush babies, nocturnal squirrel-like primates from central Africa. Among the dozen or so known species of bush babies, all the females have a penis—that is, a long pendulous clitoris with a urethra extending through the tip so that they can pee through it.²⁸ The males have a bone in their penis called a baculum. Copulation is unusually slow in these primates, lasting one to two hours.²⁹

Field guides to spider monkeys of South America refer to a pendulous and erectile clitoris long enough to be mistaken for a penis.³⁰ Over half

a dozen species of these monkeys exist, named for their spectacular ability to hang from prehensile tails and move around the treetops using their hands, feet, and tails as though they were five-legged creatures. Because the clitoris looks like a penis, the presence of a scrotum is used as a field mark to indicate whether the subject is male. Scent-marking glands may also be present on the clitoris of spider monkeys.

In woolly monkeys, close relatives of the spider monkeys, the clitoris is actually longer than the penis.³¹ In still another close relative, the muriqui, nipples are located along the sides, under the arms. Thus, even in primates, a gendered body can be assembled on a vertebrate chassis in many ways.

One reason the public presentation of genitals is such an emotionally charged issue for us humans is that primates use their genitals in displays even more than other mammals do. Picture books about animals often feature baboons called drills and mandrills, showing the male's colorful snout. A full-body photo, rather than just a head shot, would reveal that the color extends to the genitals. Both males and females have bright red genitals. The male displays a crimson-red penis riding astride a snow-white scrotum, and an estrous female displays large red bulbous swellings surrounding her vagina. The drills provocatively present these areas to one another's view.³² Our own practice of covering the genitals with clothes except in particular evocative situations bespeaks the symbolic power of genital design and decoration for us too. Medicine's peculiar history of assigning gender based on genital anatomy can undoubtedly be traced to our primate dependence on genitals as symbols.

How about feminized male genitals? Spotted hyenas, bush babies, and spider monkeys offer cases of masculinized female genitals. What about the reverse? The genitals of male dolphins and whales apparently represent a different type of intersex. For the purposes of hydrodynamic streamlining, male dolphins and whales don't have external genitals. Instead, paired testes are located within the body cavity. The penis is cradled inside a "genital slit" and covered by flaps unless it is erect. Male cetaceans have no scrotum.

What would be the easiest way to develop this genital architecture for males, using mammalian body parts and a vertebrate chassis? Some of the steps ordinarily taken by terrestrial mammalian males when their genitals are developing could simply be omitted. On land, a male mammal's testes descend from the body cavity into the scrotum, whereupon they become testicles. The scrotum is derived by fusing the tissues that in females become the labia covering the vagina and clitoris. By not bothering to fuse the labial tissue into a scrotum and leaving the testes in the abdominal cavity, a developing male dolphin or whale keeps his testes protected, using the labial tissues as protective flaps. The clitoris continues to develop into a penis, as the urethra becomes included along its axis. If these steps took place on land, a mammalian male would be classified as intersexed. Thus, we might speculate that male dolphins and whales have achieved their genital architecture by making a norm out of what would otherwise be considered an exceptional intersex morphology.

Both genital and gonadal intersexes are documented in wild cetaceans. The striped dolphin (Stenella coeruleoalba) has some individuals who display external female genitals along with testes and internal male plumbing. The bowhead whale (Balaena mysticetus) has individuals with female external genitalia and mammary glands combined with male chromosomes, testes, and male internal plumbing. A fin whale (Balaenoptera physalus) has been described with both male and female reproductive organs, including uterus, vagina, elongated clitoris, and testes. A beluga whale (Delphinapterus leucas) in the St. Lawrence seaway had male external genitals combined with a complete set of two ovaries and two testes.³³

Although a recent report on intersexes among cetaceans raises the specter of pollution causing genital deformity, the early reports on intersexes predate dangerous levels of pollution. Perhaps cetaceans are on their evolutionary way to the state that hermaphroditic fish have already attained.

The examples so far have focused on intersexed genital plumbing. What about intersexed gonads? In four species of burrowing mammals from Europe called old world moles, males have testes typical of other mammals, whereas *all* the females have ovotestes, containing both ovarian and testicular tissue. The females make eggs in the ovarian part of their ovotestes, whereas the testicular portion has no sperm, although the testicular portion does actively secrete hormones. These species come close to being hermaphroditic.³⁴

Thus a number of mammalian species have recombined genital plumbing and gonads in surprising and successful ways. More generally,

we see that among vertebrates, from fish through mammals, the binary distinction in gamete size does not generally extend to the entire body. Many body plans include production of both sizes of gamete at different times or the same time, as well as various genital sculptures and mixtures of genital plumbing—all as a way of serving social functions important in the society of the species.