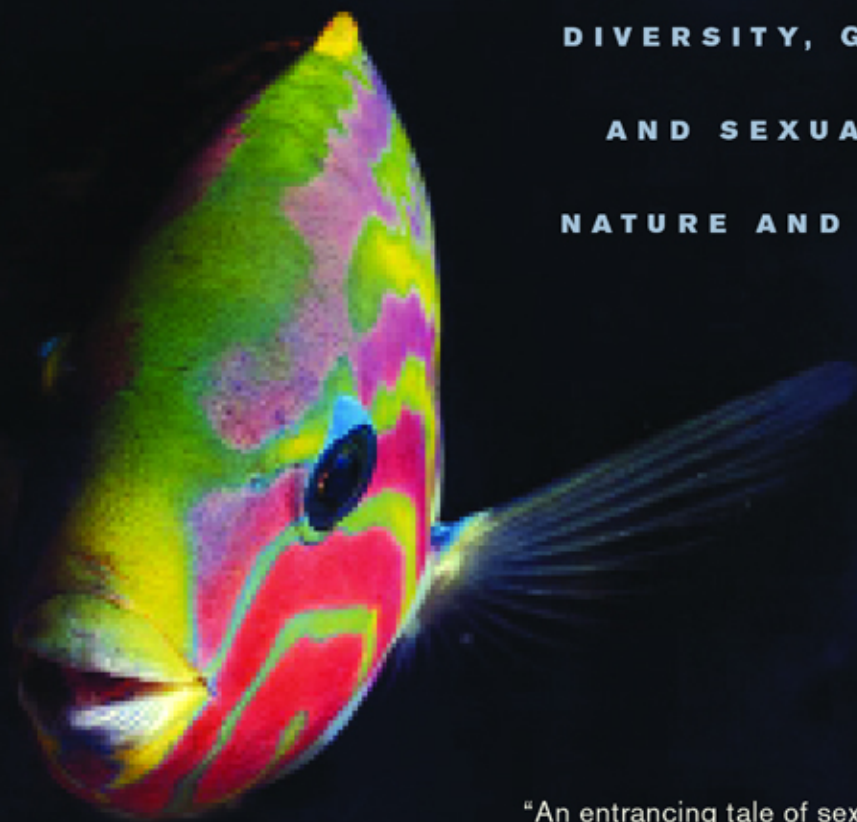


JOAN ROUGHGARDEN

EVOLUTION'S RAINBOW

DIVERSITY, GENDER,
AND SEXUALITY IN
NATURE AND PEOPLE



"An entrancing tale of sexual ambiguity
in animals and people, but also that rarest of
literary beasts—a science book written from the heart."

STEVE JONES, author of *Darwin's Ghost*

1

Sex and Diversity

All species have genetic diversity—their biological rainbow. No exceptions. Biological rainbows are universal and eternal. Yet biological rainbows have posed difficulties for biologists since the beginnings of evolutionary theory. The founder of evolutionary biology, Charles Darwin, details his own struggle to come to terms with natural variation in his diaries from *The Voyage of the Beagle*.¹

In the mid 1800s, living species were thought to be the biological equivalent of chemical species, such as water or salt. Water is the same everywhere. Countries don't each have water with a unique color and boiling temperature. For biological species, though, often each country does have a unique variant. Darwin saw that finches change in body size from island to island in the Galápagos. We can see that robins in California are squat compared to robins in New England, and lizards of western Puerto Rico are gray compared to the brownish ones near San Juan. Darwin recognized that the defining properties of biological species, unlike physical species, aren't the same everywhere. This realization, new and perplexing in the mid 1800s, remains at times perplexing today.

In Darwin's time, the Linnaean classification system, which is based on phyla, genera, species, and so forth, was just becoming established. Naturalists mounted expeditions to foreign places, collecting specimens

for museums and then pigeonholing them into Linnaeus's classification system. At the same time, physicists were developing a periodic table for elements—their classification scheme for physical species—and chemists were classifying recipes for various compounds on the basis of chemical bonds. But the biological counterpart of physical classification didn't work very well. If Boston's robin is different San Francisco's, and if intermediates live at each gas station along Route 80, what do we classify? Who is the "true" robin? What does "robin" mean? Biological names remain problematic in zoology and botany today. Biological rainbows interfere with any attempt to stuff living beings into neat categories. Biology doesn't have a periodic table for its species. Organisms flow across the bounds of any category we construct. In biology, nature abhors a category.

Still, a robin is obviously different from a blue jay. Without names, how can we say whether it is a robin or a blue jay at the bird feeder? The work-around is to collect enough specimens to span the full range of colors in the species' rainbow. Then specialists in biological classification, taxonomists, can say something like, "A robin is any bird between six and seven inches in length with a red to orange breast."² No single robin models the "true robin"; *all* robins are true robins. Every robin has first-class status as a robin. No robin is privileged over others as the exemplar of the species.

DIVERSITY—GOOD OR BAD?

Rainbows subvert the human goal of classifying nature. Even worse, variability in a species might signify something wrong, a screwup. In chemistry a variation means impurity, a flaw in the diamond. Doesn't variability within a species also indicate impurity and imperfection? The most basic question faced by evolutionary biology is whether variation within a species is good in its own right or whether it is simply a collection of impurities every species is stuck with. Evolutionary biologists are divided on this issue.

Many evolutionary biologists are positive about the rainbow. They view it as a reservoir of genes that can come to the forefront at different times and places to guarantee a species' survival under changing condi-

tions. The rainbow represents the species' genetic assets.³ According to this view, the rainbow is decidedly good. This view is optimistic about the capability of species to respond to ever-changing environmental conditions. This view affirms diversity.

Other evolutionary biologists are negative about the rainbow, believing that all gene pools—even our own—are loaded with deleterious mutations, or bad genes. During the 1950s, studies claimed that every person has three to five lethal recessive genes that would surface if they chose the wrong marriage partner, causing their children to die.⁴ This view is pessimistic about the future, suggesting that evolution has already reached its pinnacle and all variation is useless or harmful.⁵ This school of evolutionists believed in a genetic elite, advocating artificial insemination from sperm banks stocked with genes from great men. This view represses diversity.

Darwin himself was ambivalent on the value of rainbows. Darwin argued that natural selection is the mechanism that causes species to evolve. On the one hand, because natural selection depends on variation, Darwin viewed the rainbow as a spectrum of possibilities constituting the species' future. A species without variability has no evolutionary potential, like a firm with no new products in the pipeline. On the other hand, Darwin viewed females as shopping around for mates with desirable genes while rejecting those with inferior genes. This view demeans the variation among males and implies a hierarchy of quality, suggesting that female choice is about finding the best male rather than the best match. Darwin both affirmed and repressed diversity at different times within his career.

The philosophical conflict over whether to affirm or to repress diversity is still with us today, permeating everything from the way biologists interpret motives for an animal's choice of a particular mate to how medical doctors handle newborn babies in the hospital.

THE COSTS VERSUS THE BENEFITS OF SEX

How, then, are we to decide whether rainbows are good or bad? Who is correct, the diversity affirmers or the diversity repressers? To answer this most fundamental question of evolutionary biology, let's compare species

with full rainbows to species with very limited rainbows. Species who manage to reproduce without sex have limited rainbows. By sex, I mean two parents mixing genes to produce offspring. Lots of species propagate without sex. In such species, everyone is female and offspring are produced without fertilization. In addition, in many species offspring may be produced either with or without fertilization, depending on the season.

If you go to Hawaii, look at the cute geckoes on the walls. You're seeing an asexual species—all these geckoes are female.⁶ Females in all-female species produce eggs that have all the needed genetic material to begin with. In sexual species, like humans, an egg has only half the genetic material needed to produce a baby; a sperm has the other half, so combining these yields the required material. In addition, eggs from an all-female species don't need fertilization by a sperm to trigger the cell divisions that generate an embryo. Females in all-female species clone themselves when they reproduce.

The Hawaiian all-female geckoes are locally abundant and widespread throughout the South Pacific, from the lovely Society Islands of French Polynesia to the Marianas Islands near New Guinea. More all-female species live in Mexico, New Mexico, and Texas—all varieties of whiptail lizards. These small, sleek tan and brown-striped animals dart quickly along the ground looking for food. The all-female species of whiptail lizards live along streambeds, while sexually reproducing relatives typically live up-slope from the streams in adjacent woods or other vegetation. Every major river drainage basin in southwestern North America is a site where an all-female whiptail lizard species has evolved. More than eight all-female species are found in this area. Still more all-female species of lizards are found in the Caucasus Mountains of Armenia and along the Amazon River in Brazil. All-female fish occur too. Indeed, all-female animal species are found among most major groups of vertebrates.⁷

Also, some species have two kinds of females: those who don't mate when reproducing and those who do mate. Examples include grasshoppers, locusts, moths, mosquitoes, roaches, fruit flies, and bees among insects, as well as turkeys and chickens.⁸ Fruit flies grow easily in the laboratory and are especially well studied. Over 80 percent of fruit fly species have at least some females that reproduce entirely asexually. Although the majority of females in these species reproduce through mat-

ing, selection in the laboratory increased sixtyfold the proportion of females not needing to mate, yielding a vigorous all-female strain.⁹

Thus all-female species are well known among animals. So why don't even more all-female species exist? Indeed, why aren't *all* species all-female? To answer this question, let's look at the costs and benefits of reproducing with and without sex.

Sexual reproduction cuts the population's growth rate in half—this is the cost of sex. Only females produce offspring, not males. If half the population is male, then the speed of population growth is half that of an all-female population. An all-female species can quickly outproduce a male/female species, allowing an all-female species to survive in high-mortality habitats where a male/female species can't succeed. (This result is also true in hermaphrodite species, in which the fifty-fifty allocation of reproductive effort to male and female function reduces the female allocation used to make eggs by half.)

The potential for doubling production in an all-female species hasn't escaped the attention of agricultural scientists. In the 1960s, turkeys and chickens were bred to make all-female strains.¹⁰ Indeed, the cloning of a sheep in Scotland reflected a fifty-year-old aspiration to increase agricultural production by taking the sex out of reproduction. However, despite the big advantage in population growth rate that all-female species enjoy and the many examples of all-female species that do occur, clonally reproducing species remain a tiny minority. Far and away most species are sexual. Nature has experimented many times and keeps experimenting with clonal species, but with little success. Sex does work. Why?

The benefit of sex is survival over evolutionary time. Lacking sex, clonal species are evolutionary dead ends. On an evolutionary time scale, almost all clonal species are recently derived from sexual ancestors. On the family tree of species, asexual species are only short twigs, not the long branches.¹¹ The advantages of sex are also demonstrated by species who can use sex or not, depending on the time of year. Aphids (tiny insects that live on garden plants) reproduce clonally at the beginning of the growing season, switching to sexual reproduction at the end of the season. Aphids benefit from fast reproduction when colonizing an empty rose bush, but the anticipated change of conditions at the end of the season makes sexual reproduction more attractive.¹²

Clonally reproducing species are “weeds”—species specialized for quick growth and fast dispersal, like plants that locate and colonize new patches of ground. The common dandelion of North America is a clonal reproducer whose sexual ancestors live in Europe.¹³ Weeds eventually give up their territory to species who are poorer colonizers but more effective over the long term.¹⁴ The geckoes who colonized the South Pacific and the whiptail lizards of New Mexico streambeds make sense in these contexts, where dispersal is at a premium or the habitat is continually disturbed.

Clonal reproduction is a specialized mode of life, not recommended for any species that fancies itself a permanent resident of this planet. But we haven’t answered *why* sexual reproduction is good over the long term. Two theories have been offered for why sex benefits a species, one diversity-affirming, the other diversity-repressing. Both theories agree that asexual species are short-lived in evolutionary time relative to sexual species and that sex guarantees the longer species survival. Both theories therefore agree that sex is beneficial to a species. Both theories also agree that the purpose of sex isn’t reproduction as such, because asexual species are perfectly capable of reproducing. But the theories have different perceptions of why sex is good. The diversity-affirming theory views diversity itself as good and sex as maintaining that diversity. The diversity-repressing theory views diversity as bad and sex as keeping the diversity pruned back.¹⁵ Let’s start with the diversity-affirming theory.

THE DIVERSITY-AFFIRMING THEORY

According to the diversity-affirming theory for the benefit of sex, sex continually rebalances the genetic portfolio of a species. Think of a savings account and jewelry—a rainbow with two colors. How much can both colors earn together? When demand for jewelry is low, one can’t sell jewelry, even to a pawnshop, and earning 2 percent from a bank account looks great. When jewelry is hot, interest on a bank account looks cheap and selling jewelry turns a good profit. The overall earnings are the total from both investments.

A species earns offspring instead of money from its investments. The long-term survival of a species depends on being sufficiently diversified to always have some offspring-earning colors. Although biologists may

talk about the rainbow as a source of genes for new environments, it is in fact more important for surviving the regular fluctuations between hot and cold, wet and dry, and the arrival and departure of new predators, competitors, and pathogens like the bubonic plague or AIDS.¹⁶

The social environment within a species is always changing too. Concepts of the “ideal” mate change through time. Among humans, men have sometimes preferred the amply proportioned *Mama Casses* among us, at other times the skinny *Twiggy*s, as recorded in the portraits of women from art museums. Other aspects of our social environment have also changed over the centuries, like the fraction of time spent with others of the same sex or the opposite sex, or the number of sex partners a person has. Changes in the social setting within a species, as well as changes in the ecological and physical environment, all affect which colors of the rainbow shine the brightest at any one time.

A clonal species can accumulate diversity through mutation, or it may have multiple origins, thereby starting out with a limited rainbow. In fact, several genetically distinct clones have been detected among the South Pacific geckoes and dandelions. Still, these mutation-based and origin-based rainbows are nearly monochromatic.¹⁷

Furthermore, even the limited rainbow of a clonal species is continually endangered. The colors that shine brightly are always crowding out the colors that don’t, causing diversity to contract over time. Recall the jewelry and the savings account. If diamonds are valuable for a long time, their value grows and comes to overshadow the savings account. If profits are automatically reinvested in the most immediately successful venture, the portfolio gradually loses its diversity. Then when the demand for jewelry drops—say because a new find of diamonds floods the market—the portfolio takes a big hit. This progression is similar to that of the clonal reproducer, which courts danger by concentrating on only a few investments. Instead, one should redistribute some earnings each year across the investments. If jewelry has a good year, sell some and put the proceeds in the savings account. If interest is high one year, then withdraw some funds and buy jewelry. Shuffling money across investments in this way maintains the portfolio’s diversity, and a bad year for one investment doesn’t cause disastrous losses in the portfolio. Wall Street investors call this shuffling “rebalancing a portfolio.” This is the strategy of the sexual reproducer. Every generation when sexually re-

producing animals mate, they mix genes with one another and resynthesize the colors in short supply. Thus, according to the diversity-affirming theory, sex serves to maintain the biological rainbow, which conserves the species.¹⁸

THE DIVERSITY-REPRESSING THEORY

According to the diversity-repressing theory for the benefit of sex, sex protects the genetic quality of the species. The diversity-repressing theory envisions that asexual species accumulate harmful mutations over time and gradually become less functional, as though asexual lizards gradually lost the ability to run fast or digest some food. Sex supposedly counteracts this danger by allowing family lines that have picked up harmful mutations to recombine, producing offspring free of bad mutations. According to this theory, some offspring will possess both families' mutations and will die even more quickly, but other offspring will have none of the mutations, and will prosper on behalf of the species. According to this theory, without sex each and every family line inexorably accumulates mutations, leading eventually to species extinction.

ENDING THE DEBATE

Although both the diversity-affirming and diversity-repressing views have a long history, the time has come for closure. The time has come to reject the diversity-repressing view as both theoretically impossible and empirically vacuous. The scenario envisioned by the diversity-repressing theory can't exist. In an asexual species, when a bad gene arises, the line where the mutation originated is lost to natural selection, whereas the lines without the mutation prosper. The entire stock never deteriorates, because natural selection doesn't look the other way while a bad gene spreads. Instead, natural selection eliminates a bad gene when it first appears, preserving the overall functionality of the species. No evidence whatsoever shows asexual species becoming extinct because of a progressive accumulation of disabilities and loss of functionality. A bad gene never gets going in an asexual species, and sex's supposed pruning of the gene pool is unnecessary and mythical.

On the other hand, the environment does change from year to year,

and individuals who don't do well one year may shine when conditions change, and vice versa. Butterflies whose enzymes work at cold temperatures thrive in dark, damp years, while butterflies whose enzymes function best at hot temperatures do better in sunny drought years. All butterflies are perfectly good butterflies, even if the abilities of some don't match the opportunities currently supplied by the environment.

I don't see any grounds for dignifying the diversity-repressing view for the benefit of sex as a viable alternative to the diversity-affirming view. To be agreeable, one might say both theories are valid. But this compromise isn't true. Conceding, even slightly, that one function of sex is to prune diversity puts forth a view that hasn't earned its place scientifically. Accepting a diversity-repressing view of sex simply to be polite admits through the back door a philosophical stance that may later be used to justify discrimination.

Therefore, I accept as a working premise that a species' biological rainbow is good—good because diversity allows a species to survive and prosper in continually changing conditions. I further accept that the purpose of sex is to maintain the rainbow's diversity, resynthesizing that diversity each generation in order to continually rebalance the genetic portfolio of the species. I reject the alternative theory that sex exists to prune the gene pool of bad diversity.

Darwinists have to take a consistent stand on the value of diversity. They can't maintain on the one hand that most variation is good because it's needed for natural selection and on the other hand also maintain that females must continually shop for males with the best genes as though most genes could be ranked from good to bad. Instead, I argue that almost all diversity is good and that female choice is more for the best match than for the best male.

How then should we assess the rainbows in our own species? We should be grateful that we do reproduce sexually, although we probably take this gift for granted. I feel too that we should conserve and embrace our rainbows. Affirming diversity is hard, very hard. We must come to accept ourselves and love our neighbors, regardless of color in the rainbow.

Overall, sex is essentially cooperative—a natural covenant to share genetic wealth. Sexual reproduction is not a battle.

2

Sex versus Gender

To most people, “sex” automatically implies “male” or “female.” Not to a biologist. As we saw in the last chapter, sex means mixing genes when reproducing. Sexual reproduction is producing offspring by mixing genes from two parents, whereas asexual reproduction is producing offspring by one parent only, as in cloning. The definition of sexual reproduction makes no mention of “male” and “female.” So what do “male” and “female” have to do with sex? The answer, one might suppose, is that when sexual reproduction does occur, one parent is male and the other female. But how do we know which one is the male? What makes a male, male, and a female, female? Indeed, are there only two sexes? Could there be a third sex? How do we define male and female anyway?

“Gender” also automatically implies “male” and “female” to most people. Therefore, if we define male and female biologically, do we wind up defining gender as well? Similarly, for adjectives like “masculine” and “feminine,” can we define these biologically? Moreover, among humans, is a “man” automatically male and a “woman” necessarily female? One might think, yes, of course, but on reflection these key words admit lots of wiggle room. This chapter develops some definitions for all these words, definitions that will come in handy later on.

When speaking about humans, I find it’s helpful to distinguish between

social categories and biological categories. “Men” and “women” are social categories. We have the freedom to decide who counts as a man and who counts as a woman. The criteria change from time to time. In some circles, a “real man” can’t eat quiche. In other circles, people seize on physical traits to define manhood: height, voice, Y chromosome, or penis. Yet these traits don’t always go together: some men are short, others are tenors, some don’t have a Y chromosome, and others don’t have a penis. Still, we may choose to consider all such people as men anyway for purposes like deciding which jobs they can apply for, which clubs they can join, which sports they may play, and whom they may marry.

For biological categories we don’t have the same freedom. “Male” and “female” are biological categories, and the criteria for classifying an organism as male or female have to work with worms to whales, with red seaweed to redwood trees. When it comes to humans, the biological criteria for male and female don’t coincide 100 percent with present-day social criteria for man and woman. Indeed, using biological categories as though they were social categories is a mistake called “essentialism.” Essentialism amounts to passing the buck. Instead of taking responsibility for who counts socially as a man or woman, people turn to science, trying to use the biological criteria for male to define a man and the biological criteria for female to define a woman. However, the definition of social categories rests with society, not science, and social categories can’t be made to coincide with biological categories except by fiat.

MALE AND FEMALE DEFINED

To a biologist, “*male*” means making small gametes, and “*female*” means making large gametes. Period! By definition, the smaller of the two gametes is called a sperm, and the larger an egg.* Beyond gamete size, biologists don’t recognize any other universal difference between male and female. Of course, indirect markers of gamete size may exist in some species. In mammals, males usually have a Y chromosome. But

*A gamete is a cell containing half of its parent’s genes. Fusing two gametes, each with half the needed number of genes, produces a new individual. A gamete is made through a special kind of cell division called meiosis, whereas other cells are made through the regular kind of cell division, called mitosis. When two gametes fuse, the resulting cell is called a zygote. A fertilized egg is a zygote.

whether an individual is male or not comes down to making sperm, and the males in some mammalian species don't have a Y chromosome. Moreover, in birds, reptiles, and amphibians, the Y chromosome doesn't occur. However, the gamete-size definition is general and works throughout the plant and animal kingdoms.

Talk of gamete size may seem anticlimactic. Among humans, for example, centuries of poetry and art speak of strength and valor among men, matched by beauty and motherhood among women. Saying that the only essential difference between male and female is gamete size seems so trivial. The key point here is that "male" and "female" are biological categories, whereas "man" and "woman" are social categories. Poetry and art are about men and women, not males and females. Men and women differ in many social dimensions in addition to the biological dimension of gamete size.

Yet, biologically, the gamete-size definition of "male" and "female" is far from anticlimactic. In fact, this definition is downright exciting. One could imagine species whose members all make gametes of the same size, or several gamete sizes—small, medium, and large—or a continuum of gamete sizes ranging from small to large. Are there any such species? Almost none. Some species of algae, fungi, and protozoans have gametes all the same size. Mating typically occurs only between individuals in genetic categories called "mating types." Often there are more than two mating types.¹ In these cases, sex takes place between the mating types, but the distinctions of male and female don't apply because there is only one gamete size.² By contrast, when gametes do come in more than one size, then there are generally only two sizes, one very small and the other very large. Multicellular organisms with three or more distinct gamete sizes are exceedingly rare, and none is known to have a continuum of gamete sizes.

More than two gamete sizes occur in some colonial single-celled organisms, the protozoans. In the green ciliate *Clamydomonas euchlora*, the cells producing gametes may divide from four to sixty-four times. Four divisions result in relatively big gametes, whereas sixty-four divisions produce lots of small gametes. The cells that divide more than four times but less than sixty-four make various intermediate-sized gametes. Another ciliate, *Pandorina*, lives in colonies of sixteen cells. At repro-

duction, some cells divide into eight big gametes and others into sixteen small gametes. However, any two of these can fuse: two big ones, one big and one small, or two small ones.³ These species are at the borderline between single-celled and multicellular organisms.

In the fruit fly *Drosophila bifurca* of the southwestern United States, the sperm is twenty (yes, twenty) times longer than the size of the male who made it! These sperm don't come cheap. The testes that make these sperm comprise 11 percent of the adult male's weight. The sperm take a long time to produce, and males take twice as long to mature as females. The sperm are so expensive that males conserve them, "offering" them to females in small amounts, leading to a one-to-one gamete ratio.⁴ So much for the vision of one huge egg surrounded by zillions of tiny sperm. Although giant sperm are a marvelous curiosity, the important finding is that some species of *Drosophila* have three sperm sizes—one giant type and two smaller varieties that overlap somewhat, totaling four gamete sizes (three sperm sizes plus one egg size). In *Drosophila pseudoobscura* from Tempe, Arizona, the tail of the big sperm is $1/3$ millimeter long, and the tail lengths of the two small types are $1/10$ and $1/20$ millimeter.

Female *Drosophila* in some species can store sperm for several days or even up to a month after mating. About one-third of the sperm are the giant type; the remaining two-thirds are small. Females preferentially store the large sperm, although some small sperm are stored too. Females also control which sperm are used for fertilization and preferentially select the large sperm. Whether the small sperm are ever used for fertilization has been hard to demonstrate. The amount of material in a large sperm is about one hundred times that of a small sperm. Therefore, to break even, the fertilization rate for small sperm needs to be only $1/100$ of the fertilization rate of large sperm, and this low rate would be hard to detect.⁵

If different individuals made the different-size gametes, we could have as many as four sexes in *Drosophila*, one for each gamete size. In this species, however, every male apparently makes all three of the sperm sizes in the same ratio, so all the males are apparently the same. If further research reveals that the sperm makers differ in the ratio of sperm sizes they produce, we will have discovered a species with more than two sexes. Such a discovery would not violate any law of nature, but it would

be very rare and would certainly make headlines. So, for practical purposes, male and female are universal biological categories defined by a binary distinction between small and large gametes, sperm and egg.

Why are two gamete sizes practically universal in sexually reproducing species? The current theory imagines a hypothetical species starting with two mating types that produce gametes of the same size. These gametes fuse with each other to produce a zygote, and each gamete contributes half the genes and half the cytoplasm needed by the zygote. Then the gamete in one of the mating types is hypothesized to evolve a smaller size to increase quantity while sacrificing quality. The gamete in the other mating type responds by evolving a larger gamete size to compensate for the lowered quality of the small gametes now being made by its counterpart. Overall, this back-and-forth evolutionary negotiation between the mating types with respect to gamete size culminates in one mating type making the tiniest gametes possible—gametes that provide genes and nothing else, whereas the other mating type makes gametes large enough to provide genes as well as all the cytoplasm the zygote needs to start life.⁶

This little story of how the gamete binary originates is completely conjectural and untested, and points to the need for much further thought on such an important issue. This story also leaves unexplained why some groups, such as fungi, persist with only one gamete size, and why rare groups such as *Drosophila* occur with multiple sperm sizes.

GENDER DEFINED

Up to now, we've come up with two generalizations: (1) Most species reproduce sexually. (2) Among the species that do reproduce sexually, gamete size obeys a near-universal binary between very small (sperm) and large (egg), so that male and female can be defined biologically as the production of small and large gametes, respectively. Beyond these two generalizations, the generalizing stops and diversity begins!

The binary in gamete size doesn't extend outward. The biggest error of biology today is uncritically assuming that the gamete size binary implies a corresponding binary in body type, behavior, and life history. No binary governs the whole individuals who make gametes, who bring

them to one another for fertilization, and who interact with one another to survive in a native social context. In fact, the very sexual process that maintains the rainbow of a species and facilitates long-term survival automatically brings a cornucopia of colorful sexual behaviors. Gender, unlike gamete size, is not limited to two.⁷

“Gender” usually refers to the way a person expresses sexual identity in a cultural context. Gender reflects both the individual reaching out to cultural norms and society imposing its expectations on the individual. Gender is usually thought to be uniquely human—any species has sexes, but only people have genders. With your permission, though, I’d like to widen the meaning of gender to refer to nonhuman species as well. As a definition, I suggest: *Gender is the appearance, behavior, and life history of a sexed body.* A body becomes “sexed” when classified with respect to the size of the gametes produced. Thus, gender is appearance plus action, how an organism uses morphology, including color and shape, plus behavior to carry out a sexual role.

Now we’re free to explore the zoological (and botanical!) counterpart of human gender studies. So, we may ask: How much variety occurs in gender expression among other species? Let’s take some favorite stereotypes and see. We’ll look mostly at vertebrates; even more variety occurs with invertebrates and plants.

An organism is solely male or female for life. No, the most common body form among plants and in perhaps half of the animal kingdom is for an individual to be both male and female at the same, or at different times during its life. These individuals make both small and large gametes during their lives.

Males are bigger than females, on the average. No, in lots of species, especially fish, the female is bigger than the male.

Females, not males, give birth. No, in many species the female deposits the eggs in the pouch of the male, who incubates them until birth. In many species, males, not females, tend the nest.

Males have XY chromosomes and females XX chromosomes. No, in birds, including domesticated poultry like chickens, the reverse is true. In many other species, males and females show no difference in chromosomes. In all alligators and crocodiles, some turtles and lizards, and the occasional fish, sex is determined by

the temperature at which the eggs are raised. A female can control the sex ratio among her offspring by laying eggs in a shady or a sunny spot.

Only two genders occur, corresponding to the two sexes. No, many species have three or more genders, with individuals of each sex occurring in two or more forms.

Males and females look different from one another. No, in some species, males and females are almost indistinguishable. In other species, males occur in two or more forms, one of which resembles a female, while the others are different from the female.

The male has the penis and the female lactates. No, in the spotted hyena, females have a penislike structure externally identical to that of males, and in the fruit bat of Malaysia and Borneo, the males have milk-producing mammary glands.⁸

Males control females. No, in some species females control males, and in many, mating is a dynamic interaction between female and male choice. Females may or may not prefer a dominant male.

Females prefer monogamy and males want to play around. No, depending on the species, either or both sexes may play around. Lifelong monogamy is rare, and even within monogamous species, females may initiate divorce to acquire a higher-ranking male.

One could tick off even more examples of gender stereotypes that are often thought to be “nature’s way” but that have no generality within biology. Instead, let’s look closer at the lives of these organisms to see whether what they do makes sense to us. Be prepared, though, to shrug your shoulders and wonder about the mystery of life.

Note that by defining gender as how an organism presents and carries out a sexual role, we can also define masculine and feminine in ways unique to each species. “Masculine” and “feminine” refer to the distinguishing traits possessed by most males and females respectively. Cross-gender appearance and behavior are also possible. For example, if most females have vertical stripes on their bodies and males do not, then a male with vertical stripes is a “feminine male.” If most males have antlers and females do not, then a doe with antlers is a “masculine female.”

Politically, locating the definition of male and female with gamete size

keeps society's gender categories at arm's length from biology's sex binary. We don't have to deny the universality of the biological male/female distinction in order to challenge whether the gender of whole organisms also sorts into a male/female binary. In humans specifically, a gender binary for whole people is not clear-cut even though the difference between human sperm and egg is obvious—a size ratio of about one million to one.

3

Sex within Bodies

Although 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, hermaphroditism is common in the ocean.¹ 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

Hermaphroditism is a successful way of life for many species; my guess is that hermaphroditism 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 hermaphroditism in plants, on coral reefs, and in the deep sea. Alternatively, hermaphroditism 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 MALE

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 sex-changed 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 sex-changed 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."⁴ 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 FEMALE

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 hermaphroditism, which for these species is viewed as an adaptation to extremely low population density.⁹ 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.¹⁰ 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 hermaphroditism 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, intersexed 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.¹⁶ 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.²⁵ 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.

4

Sex Roles

Even species thought of as typical, with one gender per sex and individuals who maintain a single sex throughout life, often have gender roles quite different from the traditional template. Indeed, in some species, males (apart from making sperm) look and behave much as females do in other species, and females (apart from making eggs) look and behave much as males do in other species. If these species could express their thoughts about us, they would describe our gender distinctions as reversed.

BODY SIZES REVERSED

Anglerfish are deep-sea fish who have what looks like a tiny fishing pole attached to their head. A spine projects out in front of the fish, and somewhat upward, with a frilly or luminescent bulb at its tip to lure prey. When prey comes near, the anglerfish lunges forward, “angling” and then gobbling it up.

Predators catch prey in countless tricky ways. The anglerfish’s fishing pole is a neat curiosity, but what is more interesting is that the anglerfish just described are all female—fisherwomen, not fishermen. Is the anglerfish another example of an all-female species? Nope. Anglerfish males

exist, but they are tiny and are called “dwarf males.” These anglerfish males are incapable of independent existence. They have large nostrils for homing in on perfumes released by the females and pinchers, instead of teeth, to grasp little projections on the female. After a male attaches to the back or side of a female, their epidermal tissues fuse and their circulatory systems unite, and the male becomes an organ of the female. Multiple males may attach to one female, a case of polyandry. They thereby turn into two or more genetically distinct individuals in one body, a colony.¹

These fish were discovered in 1922 by an Icelandic biologist who observed two small fish attached by their snouts to the belly of a large female. He thought the small fish were juveniles being suckled by their mother—which mammals do all the time, but which would be big news for fish.² Three years later, the small attached fishes were discovered to be reproductively mature males.

An attached male was called a “parasite,” by analogy to the small ectoparasites on the outside of large individuals, such as the barnacles attached to whales or leeches that cling to people who bathe in tropical streams. The terminology is unfortunate, because here the relationship is presumably reciprocal. The anglerfish male is “merely an appendage of the female, and entirely dependent on her for nutrition. . . . [S]o perfect and complete is the union of husband and wife that one may almost be sure that their genital glands ripen simultaneously, and it is perhaps not too fanciful to think that the female may possibly be able to control the seminal discharge of the male and to ensure that it takes place at the right time for fertilization of her eggs.”³

Over one hundred species of anglerfish are distributed throughout the world at depths below one mile. For all anglerfish, the females are much larger than the males. In other respects, though, anglerfish are diverse, exhibiting a rainbow of their own. Some species have attaching dwarf males that fuse with the body of a female, as just described; others have both free-living males and attaching males; and still other species have males who are exclusively free-living. Indeed, whenever one looks deeply into any biological category, a rainbow is revealed. The living world is made of rainbows within rainbows within rainbows, in an endless progression.

SEX ROLES REVERSED

The pipefish is a small pencil-like fish with a circular mouth that resembles a small musical pipe, like a flute. In some species of pipefish, the embryos are “glued” to the male’s underside. The young fish develop there and swim away when they are mature. In other pipefish species, the males have protective skin flaps that partially cover the fertilized eggs.

In their close relative the seahorse, the skin flap is elaborated into a pouch that fully encloses the developing embryos. A female seahorse places eggs in a male’s pouch. The eggs are fertilized there, forming embryos, and the male becomes “pregnant.” The male provides oxygen, maintains the right salt balance, and nourishes and protects the embryos in his sac.⁴

We might think that seahorses and pipefish reverse male and female roles relative to mammals. To determine whether this impression is correct, we must consider the “parental investment” made by males and females in the raising of young. A male contributes a sperm to the embryo, which provides little energy or nutrients. A female contributes a full-sized egg to the embryo. A female therefore starts out by putting a larger investment in the embryo than the male does.

Biologists define “sex-role reversal” as occurring when the total parental investment by males in raising the young exceeds that of females.⁵ Male seahorses and pipefish provide a great deal of parental investment in terms of time spent rearing the young in their pouches or glued to their undersides. Does what the males do for the young by the time the embryos mature add up to more than what the females do, given that females invested more at the beginning?

Simply having males provide some care for the young doesn’t qualify as sex-role reversal. Species showing some male parental care are too numerous to mention. Many male fish watch over and nourish eggs in nests on the sea floor or lake bottom, and others even store the eggs in their cheeks (called mouth brooders). The specific way males provide parental care depends on the species, and the seahorse’s pouch is one of many curious delivery styles. The style of care doesn’t matter, the amount does. So, are seahorses sex-role reversed? That is, does

the cumulative parental investment by male seahorses exceed that of females?

How could one tell which sex was contributing the most overall to the raising of offspring? An indication comes from the supply and demand of each sex at the time of mating. We're all familiar with supply and demand during courtship. A belle at an Alaskan mining camp has men entreating her with bags of gold dust and promises of trips to Paris. A bachelor on a love-boat cruise is entertained by women offering duty-free Cuban cigars and football lore memorized from the 49ers playbook. Let's extend this idea.

If one sex, say A, is providing most of the parental care, then few are receptive to mating at any particular time because most are occupied with raising offspring. Conversely, the other sex, B, is not very involved with raising offspring and has many individuals ready and willing to mate. This asymmetry in the supply and demand of mates leads to a dynamic tension between the sexes. The Bs compete for access to and control of the As. Provided their freedom of choice is not thwarted by the Bs' control, the As choose which B they wish to mate with.

Biologists call the ratio of receptive females to willing males the "operational sex ratio." The operational sex ratio isn't fifty-fifty because the sex with the higher parental investment is occupied with raising the offspring and is relatively unavailable for mating compared with the other sex.⁶

Returning to the seahorses and pipefish, we can ask which sex is relatively unavailable for mating because of their efforts in raising offspring. Swedish investigators found two nearby North Sea pipefish species that are indeed sex-role reversed. The females from both these species produce enough eggs for about two males during the time it takes for one male to raise his young. In the wild, the number of females with ripe eggs consistently exceeds the number of receptive males. Females in these species are polyandrous, with a harem of males. In addition, these females are larger than the males and develop bright colors at courtship time, presumably for the males to choose among, reversing Darwin's classic peacock story. Furthermore, the females, not the males, compete with one another, forming dominance hierarchies for access to the males who will tend their eggs. Nine other pipefish species in which the females

alone have sexual coloration and/or grow larger than the males are thought to be sex-role reversed as well.

On the other hand, seahorses and certain other pipefish species are not sex-role reversed; they follow the model of Darwin's peacocks. Male seahorses can raise their young and get ready for the next embryos faster than female seahorses can produce egg batches. The result is a net surplus of males wanting eggs compared to females offering eggs. Males aggressively tail-wrestle and snout-snap one another for access to females, whereas females don't have any specific aggressive behaviors among themselves. Male seahorses tend to be larger, more colorful, and more distinctly patterned than females.⁷

Thus sex-role reversal definitely occurs in nature. Many feel that the concept of an operational sex ratio effectively extends Darwin's theory of sexual selection to cover sex-role reversed species—after all, the logic is the same for the mating strategies in both sex-role-typical species and sex-role-reversed species, with the identities of the excess sex and rate-limiting sex simply flipped. But no theory has been proposed to explain why sex-role reversal occurs in the first place.

Sex-role reversal is found in birds, especially aquatic and sea birds. When sex-role reversal occurs, the double standard can reverse too. Wattled jacanas from the Chagres River in Panama are large, squat black birds with white wing tips, a red face, and a long, yellow probing bill used to feed among shallow freshwater plants like hyacinths. The raucous, beefy females spend their days jousting with one another at the borders of their territories. Within these territories, harems of smaller males tend the eggs and chicks.

DNA fingerprinting has shown that males raise eggs laid by the female who controls their harem, even when the eggs were fathered by males outside the harem. The females clearly went outside their harem to obtain matings and yet burdened the males within their harem with the job of raising the young. The investigators, themselves male, were outraged, asserting that male jacanas were being "cuckolded" in spite of contributing so much parental care. One investigator stated, "It's about as bad as it can be for these guys."⁸

The converse probably wouldn't have provoked such outrage. A female in a harem controlled by a male might raise a chick fathered by that

male and placed there by a female from a neighboring harem. We could imagine many reasons for such an adoption. The female might find it advantageous to raise the chick in return for the controlling male's provisioning and protection of the young she has mothered herself. Similarly, a male jacana might find it advantageous to raise a chick mothered by the controlling female in return for the controlling female's provisioning and protection of the young he has fathered himself. Thus, sex-role reversal implies that the double standard also reverses. This idea takes some getting used to.

Other birds showing sex-role reversal include two shore birds, Wilson's phalarope and the spotted sandpiper.⁹ Apparently, no mammals exhibit sex-role reversal, presumably because of the very high parental investment by mammalian females. In addition to the egg, a mammalian female supplies milk to the embryo and carries the young to term, either in a placenta or a pouch. For a mammalian male, this act is hard to follow. To exceed this already high parental investment by a female, a male would require a social system allowing him to care for his offspring well beyond the age of weaning, as may be approached in humans.

The evolution of the mammalian placenta and pouch is usually presented as a physiological advance, an adaptation for nurturing embryonic development in a climate that has cooled globally since the time of dinosaurs. Alternatively, the evolutionary force behind the placenta and pouch may have been for females to assume control of their offspring. A side effect is that males then acquire an incentive to control females.