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The Theory of Evolution

Diversity in gender expression and sexuality undercuts Darwin's theory of sexual selection. Saying this, however, does not mean *all* of Darwin's writings are incorrect. Indeed, I feel we should not lose sight of his overwhelming contribution, even though I believe one of his theories is seriously mistaken.

Perhaps Darwin's most important discovery is that all species are related to all other species through shared descent from common ancestors. The most grand and most lowly share in the unity of life. Darwin came to this insight as a young man, during his travels as a naturalist on a sailing ship called the *Beagle*. In his diary, Darwin compared the animals of an archipelago, the Galápagos Islands, with those of South America, which he had previously visited.[1] He wrote, "We see that this archipelago, though standing in the Pacific Ocean, is zoologically part of America. If this character were owing merely to immigrants from America, there would be little remarkable in it; but we see that a vast majority of all the land animals, and that more than half the flowering plants, are aboriginal productions. It was most striking to be surrounded by new birds, new reptiles, new shells, new insects, new plants, and yet by innumerable trifling details of structure, and even by tone of voice and plumage of the birds, to have the temperate plains of Patagonia, or the hot dry deserts of Northern Chile, vividly brought before my eyes." Thus

Darwin observed that the species unique to the Galápagos, which he called aboriginal productions, are nonetheless related to South American species.

Darwin continues by comparing the animals on different islands within the Galápagos: "I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would have been differently tenanted . . . one is astonished at the amount of creative force, if such an expression may be used, displayed on these small, barren, and rocky islands; and still more so, at its diverse yet analagous action on points so near each other." Here Darwin further observes that species diverge even within a group of islands, not only between the group and the mainland.

Today, one could not improve on Darwin's formulation. Darwin perfectly expressed the idea of evolution through common descent. He focused on *populations* of plants or animals rather than on single individuals. Strictly speaking, Darwin might have concluded only that the species he personally saw were related to one another by descent from common ancestors. Although at present the possibility of more than one independent origin for life perhaps can't be ruled out after considering the enormous diversity of single-celled organisms, all the organisms people are generally familiar with do share descent from common ancestors.[2]

DARWIN'S NATURAL SELECTION

Darwin's next task was to understand what "creative force" produces the diversity of new species. Darwin identified a force he named "natural selection," which causes species to change over time. Darwin's theory of natural selection is correct overall, although our contemporary understanding of the process is somewhat different from the way Darwin wrote about it.

Living in an agricultural setting, Darwin was well aware of animal and plant breeding—cows, horses, and crops for yield and dogs, roosters, and flowers for show. Animal and plant breeding was done every day and could obviously change the properties of a stock. Animal and plant breeding is based on selecting certain individuals to reproduce and eliminating the remainder. This process is now called "artificial selection" to indicate that a farmer, rather than the natural environment, determines who gets to survive and/or to breed.

Darwin was also aware that a contemporary, Thomas Malthus, was developing scenarios about the consequences of population growth. Darwin wrote, "On the principle of geometrical increase . . . more individuals are produced than can possibly survive, there must in every case be a struggle for existence. . . . It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms."[3] Darwin realized that if only certain types of individuals survive in crowded conditions, then the population will consist of descendants of those survivors. Thus was born the idea of "natural selection," the process by which the natural environment determines who gets to survive and/or breed. Natural selection is nature's equivalent of artificial selection for yield. Furthermore, if nature selects for different types of individuals in different locations, then the populations in those locations will diverge over time, eventually accumulating enough differences to be distinguished as different species.

A technical difficulty in Darwin's original account concerns how diversity is maintained. Darwin had not heard of Mendelian genes and could not account for why variation persists in a natural population rather than simply dissolving. Fifty years later, population geneticists Ronald Fisher and J. B. S. Haldane in the United Kingdom and Sewall Wright in the United States rescued Darwin's theory of natural selection using mathematical equations that incorporated Mendelian inheritance. Today, evolutionary textbooks all triumphantly teach how early population genetics theory provided Darwin's natural selection with a rigorous mathematical basis.

Although scientists are perhaps justly proud of early population genetics, they rarely bother to mention that those equations also fundamentally change the interpretation of how natural selection works. In the Malthusian scenario, the "struggle for existence" emphasizes competition for scarce resources, making aggressive combat the theme of natural selection. Yet the equations for natural selection do not concern a struggle for limited resources at all. Instead, each genetic type is associated with a measure of net reproductive productivity—fecundity times probability of survival, the so-called Darwinian fitness. Natural selection

is today best described as survival of the productive based on the progressive improvement of natural yield. Evolution by natural selection takes place even in a population unlimited by resources, because some genetic types are inherently more productive than others, regardless of the scarcity or abundance of resources. A genetic type may become more productive by being cooperative, forming friendships, being frugal or innovative, or any number of strategies having nothing to do with "struggle." I believe scientists have failed to publicize effectively that the notion of a tooth-and-claw struggle for existence was discarded over fifty years ago as the central metaphor of mathematical natural selection theory. What actually happens in nature is much kinder than people have been led to believe.

Thus Darwin's concept of natural selection has been modified and invested with new meaning, showing that he was on the right track. However, evolution by natural selection is not completely settled even to this day. The issue remains of where the variation among individuals comes from. This has been the most problematic area of evolutionary biology.

In the 1970s the distinguished biologist Lynn Margulis discovered that all the plants and animals above the level of bacteria—so-called eukaryotic organisms—are really partnerships at the cellular level.[4] I vividly remember when, as a teenager in biology class, I peeled an onion's skin, placed the thin sheet under a microscope, and saw cells for the first time. I was taught that cells are the elemental building blocks of organisms, and there I was, looking at the building blocks of an onion. Well, it's now clear that the cell is not a unitary building block after all, but rather a partnership of many subunits, some of which lived separately by themselves at some time in the past. The places within a plant cell where the green chlorophyll is located and photosynthesis occurs—the chloroplasts—were once bacteria that lived on their own. The places within a cell where our food is broken down and converted into energy (the mitochondria) were also once bacteria existing independently. The genes in an onion's cells, and in our cells too, are located not only in the nucleus, but also in other places that were once free-living cells. A cell is thus a partnership, and its overall genome is distributed across all the formerly independent partners and not solely contained in the nucleus.

Biologists have been reluctant to think through what this partnership implies. If every one of our cells is a symbiosis among formerly free-

living bacterial elements, then we are but clusters of bacteria ourselves. We're not only descended from bacteria—we still *are* bacteria, a deeply humbling thought. And cellular function is not the simple story of a nucleus whose genes impose its wishes on the cytoplasm. Instead, some subcellular negotiation was required to form our cells to begin with, and may still take place. Perhaps the nucleus and mitochondria have an ongoing biochemical discussion, whose breakdown shows up as disease.

Most genes in our cells are in fact located in the nucleus, and those few residing in mitochondria and elsewhere are exceptional. This fact allows the narrative of nuclear genetic control to persist unchallenged. One wonders, though, how long this biological fiction can be sustained. Traditional population genetics views genetic variation as blindly popping up through random mutation of nuclear genes, and natural selection as operating on these new genes to fashion innovative adaptations. This view implicitly accepts the story of nuclear genetic control.

Suppose instead that genes arrive by negotiation with other organisms: one cell says to another, "I need some of your genes," and the other replies, "Sure, and I need a home to live in." Well, this collaboration is exactly what occurs in corals. The coral is an invertebrate animal like a hydra, capable of catching food with tiny tentacles. But corals also welcome single-celled algae called zooxanthellae into their bodies. At any time, the genes in a coral cell may include those in the coral nucleus plus those in the algae nucleus. However, the zooxanthellae of a coral are still quite capable of leaving the coral and surviving alone, unlike the chloroplasts of land plants. The coral-zooxanthellae relationship breaks down in low light, where corals rely on what they can catch with their tentacles. No one knows what zooxanthellae do when living on their own. Many strains of zooxanthellae exist, and the total genetic composition within a coral cell varies as different strains of zooxanthellae shuffle in and out. The genetic variation in a coral cell thus does not depend on the blind mutation of single genes, as envisioned by traditional population genetics theory. Instead, a cell can adaptively negotiate its genome with other cells.

Evolutionary biology is nowhere close to engaging the implications of a genome whose composition originates by negotiation with other genomes instead of by blind mutation. I feel the discovery of the partnership basis of cells is as important as the discovery of DNA. But the DNA

story has been relatively easy for people to absorb, a refinement of the narrative of genetic control we've been taught since grade school. The partnership theory of cellular function is wholly unexpected, and scientists haven't known what to do with the finding. The situation is analogous to gender and sexuality, where also no one was prepared for the findings, and there, too, cooperative relationships have been underestimated.

Thus Darwin's theory of natural selection as the creative force molding diversity seems certain to continue as the major element of evolutionary theory, even as discussion continues about the source of variation. By contrast, the third component of Darwin's theory, sexual selection, should not, in my opinion, be resuscitated.

DARWIN'S SEXUAL SELECTION

I appreciate the gravity of discrediting a discipline's master text. However, I doubt that the factual difficulties in Darwin's theory of sexual selection can be easily smoothed over. I also believe that this theory has promoted social injustice and that overall we'd be better off both scientifically and ethically if we jettisoned it. I am far from the first to call for a thorough overhaul of sexual selection theory. I join a tradition initiated in the courageous studies by Sarah Hrdy of female choice in Indian monkeys and continued today in the writings and the experimental and field studies of Patricia Gowaty.[5] I am, I confess, more extreme than they in calling for the outright abandonment of sexual selection theory.

Darwin's sexual selection is evolutionary biology's first universal theory of gender.[6] Darwin claimed, based on his empirical studies, that males and females obey nearly universal templates. He wrote, "Males of almost all animals have stronger passions than females," and "The female . . . with the rarest of exceptions is less eager than the male . . . she is coy."

Darwin offered sexual selection as an explanation for why males and females should obey these universal templates. Whereas artificial breeding for yield was the model for natural selection, artificial breeding for show was the model for sexual selection. Darwin proposed that females, like the farmer, choose showy and virile males. Females choose males who are, he wrote, "vigorous and well-armed. . . . Just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit, so . . . the strongest and most vigorous males, or those provided with the best weapons . . . have led to the improvement of the . . . species." Beauty, too, could be a factor. In particular, "Many female progenitors of the peacock must . . . by the continued preference of the most beautiful males, [have] rendered the peacock the most splendid of living birds." Thus Darwin imagined that males come to be the way they universally are because these males are what females universally want, and the species is better off as a result.

Darwin further proposed a universal template for social life in animals: "It is certain that amongst almost all animals there is a struggle between males for the possession of the female. . . . The strongest, and . . . best armed of the males . . . unite with the more vigorous and better-nourished females . . . [and] surely rear a larger number of offspring than the retarded females, which would be compelled to unite with the conquered and less powerful males." In these writings, Darwin pejoratively viewed diversity within a species as a hierarchy beginning with superior individuals and winding down to the "retarded," a view that is diversity-repressing and elitist, stressing a weeding out of the weak and sickly and naturalizing male domination of females. In his earlier writings, however, Darwin viewed diversity favorably across species within an ecological community, imagining that each species fills a special niche in nature. The contradiction evident in Darwin's attitude to diversity within species, as opposed to diversity between species, plagues our society today, from biology and medicine to politics and law.

However, Darwin didn't ignore diversity altogether. Juxtaposed with universalist claims are acknowledgments of "exceptions" to the general pattern. In some species, males "acquire" females by defeating their rivals. In other species, males cannot unilaterally capture females but must allow for female choice instead. "In very many cases the males which conquer their rivals do not obtain possession of the females, independent of the choice of the latter." In such cases, "the females . . . prefer pairing with the more ornamented males, or those which are the best songsters, or play the best antics . . . [and] at the same time prefer the more vigorous and lively males." In still other species, males and females are equals, and male choice of females is as important as female choice of males. Darwin wrote that in the "much rarer case of the males select-

ing particular females . . . those which . . . had conquered others . . . would select vigorous as well as attractive females." Darwin was an experienced naturalist who knew of diversity in mating behavior but dealt with this diversity by privileging the narrative of the handsome warrior, relegating everything else to exceptions. Darwin made no attempt to explain why "exceptions" occur or why species vary in the balance of power between the sexes. His labeling of this diversity as exceptional sidestepped the need to explain.

Darwin also acknowledged that many animals do not align with a simple sexual binary. Although Darwin worked at length on barnacles, which are simultaneously hermaphroditic, he never tried to fit them into his theory. Instead, he simply set barnacle-like species aside and asserted that all the remaining species do obey the universal male and female templates: "On the whole there can be no doubt that with almost all animals, in which the sexes are separate, there is a constantly recurrent struggle between the males for the possession of the females."

Similarly, Darwin knew of sex-role reversal but offered no explanation other than to say that such reversals are rare: "With birds there has sometimes been a complete transposition of the ordinary charters proper to each sex; the females having become the more eager in courtship, the males remaining comparatively passive, but apparently selecting the more attractive females. . . . Certain hen birds have thus been rendered more highly colored or otherwise ornamented, as well as more powerful and pugnacious than the cocks." After reviewing the sex-role reversed cassowary, emu, tree-creeper, and nightjar, Darwin concluded, "Taking as our guide the habits of most male birds . . . [females] endeavor to drive away rival females, in order to gain possession of the male. . . . [Here] the males would probably be most charmed or excited by the females which were the most attractive by their bright colors, other ornaments, or vocal powers. Sexual selection would then do its work, steadily adding to the attractions of the females; the males and the young being left not at all, or but little modified." Even today, sex-role reversals are "explained" as resulting from a higher parental investment from males than females in raising the young. Yet even today no theory has been proposed that explains when this transposition of the sex-role binary occurs.

Darwin does not appear to have been aware of natural same-sex sexuality, or of gender multiplicity in the sense of coexisting alternative reproductive and/or life history strategies within each sex. Nor does Darwin consider any functions for mating that are not directly linked to reproduction. Yet Darwin did anticipate the theory of parental investment based on the relative cost of egg and sperm: "The female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals, in wandering about in search of the female, in exerting his voice. . . . on the whole the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates."

Darwin should be credited for distinguishing between traits contributing mostly to survival in the physical environment and those contributing mostly to reproduction in the social environment, for acknowledging many exceptions, and for anticipating many of the concepts still employed today. Darwin should also be credited with attributing evolutionary status to females. The possibility that females were even capable of choice was controversial at the time. Yet Darwin wrote, "Females have the opportunity of selecting one out of several males, on the supposition that their mental capacity suffices for the exertion of a choice. . . . No doubt this implies powers of discrimination and taste on the part of the female which will at first appear extremely improbable; but by the facts . . . I hope . . . to show that the females actually have these powers."

What then are we to make of Darwin's theory of sexual selection? The matter comes down to whether the underlying metaphor is correct. Is selection in a social context the natural counterpart of artificial selection for show? Does social life in animals consist of discreetly discerning damsels seeking horny, handsome, healthy warriors? Is the social dynamic between males limited to fighting over the possession of females? Does diversity within a species reflect a hierarchy of genetic quality?

Is today's sexual selection theory any better than Darwin's? No. Today's theory makes matters worse by adding new mistakes, morphing what Darwin actually wrote into a caricature of male hubris. According to today's version, males are supposed to be more promiscuous than females because sperm are cheap, and hence males are continually roaming around looking for females to fertilize. Conversely, females are supposed to be choosy because their eggs are expensive, and hence they must

guard their investment from being diluted with bad genes from an inferior male. A male is naturally entitled to overpower a female's reluctance lest reproduction cease, extinguishing the species. In fact, Darwin's writings do not endorse the expensive-egg-cheap-sperm principle. Today's sexual selection lore is based on an accounting mistake that Darwin did not make. Darwin referred to the total energy expended by each sex in reproductive effort over a lifetime as being equal.[7]

The second contemporary mistake is elevating deceit into an evolutionary principle. Darwin claimed that warfare to secure control over females is the universal social dynamic among males. Therefore, cooperative relations, especially those between members of the same sex, appear to falsify the social template that Darwin claims is universal. The contemporary work-around is to postulate deceit. Today's sexual-selectionists have produced a proliferation of "mimicries": sexual mimicry, female mimicry, egg mimicry, and so forth. By postulating these types of mimicry, the spirit of warfare and conflict is preserved but driven underground, turned into guerrilla combat. Yet in no case have any of the mimics been shown to be fooling any other animal, and the circumstances suggest that the animals are in fact perfectly aware of what is happening. The sexual-selectionist picture of nature is not pretty. Not correct either.

Darwin conceived his theory in a society that glamorized a colonial military and assigned dutiful, sexually passive roles to proper wives. In modern times, a desire to advertise sexual prowess, justify a roving eye, and disregard the female perspective has propelled some scientists to continue championing sexual selection theory despite criticism of its accuracy.

SEXUAL SELECTION FALSIFIED

Contemporary sexual selection theory predicts that the baseline outcome of social evolution is horny, handsome, healthy warriors paired with discreetly discerning damsels. Deviations from this norm must then be explained away using some special argument. But is the theory that makes this prediction correct to begin with? How many exceptions are needed before sexual selection theory is itself seen as suspect?

The time has come to set the glass on the table: to declare that sexual theory is indeed false and to stop shoe-horning one exception after another into a sexual selection framework. We need to face the fact that sexual selection theory is both inaccurate and inadequate. To do otherwise suggests that sexual selection theory is unfalsifiable, not subject to refutation.

The universal claims of sexual selection theory are inaccurate. Males are not universally passionate, nor females universally coy. The social dynamic between males is not universally combat to control females. Diversity among males and among females does not universally fit a hierarchy of genetic quality. Females do not universally select males for their genetic quality. Moreover, sexual selection theory is inadequate to address the diversity in bodies, behaviors, and life histories that actually exists. Darwin didn't bother to explain the exceptions he recognized, and as data on diversity in gender and sex continue to accumulate, sexual selection theory, which addressed only a subset of the facts to begin with, becomes increasingly inadequate.

Let's record, then, the many ways we've seen in which real species depart from the sexual selection norm:

1. *Bodies do not conform to a binary model.* Gametic dimorphism doesn't imply a binary of body types. The individuals in many species don't make only eggs or sperm for the duration of their lives. In most species, distinct "male" and "female" bodies are undefined or unstable. Sexual selection theory doesn't apply to many species because distinct male and female individuals as envisioned in the theory simply don't exist in those species, a point Darwin recognized.
2. *Genders do not conform to a binary model.* Gametic dimorphism does not imply a binary of gender roles either. The two sexes, even if located in separate bodies, may each entail more than two genders, defined as distinct morphologies, behavioral roles, and life histories in sexed bodies. Societies with one, two, and three male genders, together with one or two female genders, have been extensively described. However, sexual selection theory is a two-gender theory.
3. *Sex roles are reversible.* Even when distinct male and female bodies exist, with one gender per sex, the behavioral roles these genders carry out may be the reverse of what sexual selection theory envisions. Pipefish and jacana sperm are tiny and their eggs

large, just as in other metazoan species, yet the overall parental investment by the male exceeds that of the female in these species, resulting in a reversed operational sex ratio leading to female-female competition for males and male choice of females. Neither today's extensions to sexual selection theory nor Darwin's original treatment offer any prediction for when this occurs.

4. *Sperm are not cheap.* According to well-known primatologist Meredith Small, "Non-human primates show us what many single women in America today already know—sometimes it's very hard to get a date. Female rhesus monkeys and baboons often present to males, a clear sign of preference and choice, but males regularly refuse. Lion-tail macaque females, especially subadults, share this rejection. Females of this species initiate almost 70 percent of the copulations but only 59 percent end up in mounts. No one is sure why these males refuse, inasmuch as sperm is supposed to be so cheap, but males often ignore estrous females."[8] Why should males refuse the invitation to sex when sperm are supposedly so cheap, as sexual selection theory requires? Because sleeping together is meaningful in itself. Animal sex is not anonymous. Mating is a public symbol. Animal "gossip" ensures everyone knows who's sleeping with whom. Therefore, mate choice, including male mate choice, manages and publicizes relationships. A male may not want the commitment that accepting a new girlfriend entails.

5. *Females do not choose "great genes."* Females choose mates for many reasons, but rarely or never to acquire the great genes that a male is supposed to have according to sexual selection theory. Low-ranking males have offspring just as capable as those of high-ranking males. Females select for males who deliver on their promises of parental care and spread the probability of paternity among males to ensure offspring safety. Physical characteristics in a male serve to endow offspring with the bodily markers of a powerful lineage, not to acquire attractiveness; females are buying their offspring membership in the old genes club.

6. *Family size is negotiated.* Egg and sperm production are not necessarily independent, as sexual selection theory envisions. Males don't have to run around trying to fertilize a fixed number of eggs. Males and females can negotiate to increase the number

of eggs a female produces beyond those she would make if she were to raise them by herself. In addition, males need to make sure the eggs they do fertilize are successfully raised—it doesn't matter how much sperm they produce if the quality of parental care is compromised.

7. *Social deceit is not demonstrated.* The deceit required by sexual selection theory has never been demonstrated. Despite scientists' invention of many categories of social deceit, such as sexual mimicry and egg mimicry, it has never been proved that the mimetic traits are not simply social symbols. Perhaps animals do lie to each other now and then, but biologists have yet to catch them in a lie, so a presumption of honesty is appropriate.

8. *Same-sex sexuality is common.* Same-sex sexuality is contrary to sexual selection theory, so the existence of homosexuality must be explained away as either an aberration or a deception. Instead, the extensive documentation of same-sex sexuality among vertebrates rules out any further denial of homosexuality and contradicts sexual selection theory.

9. *Mating is not primarily for sperm transfer.* The purpose of mating, both heterosexual and homosexual, is more often to create and to maintain relationships than to transfer sperm. Sexual selection theory requires that mating be primarily about sperm transfer, whereas the amount of mating that actually takes place is a hundred to a thousand times more frequent than that needed for conception alone.

10. *Secondary sex characteristics are not just for heterosexual mating.* Sexual selection theory limits the meaningfulness of secondary sex characteristics to heterosexual mating. In species with common homosexual matings, secondary sex characteristics, including genital geometry, are shaped to facilitate all types of mating, including homosexual matings.

The sheer number of difficulties with sexual selection theory precludes plugging all the leaks. An occasional leak might be fixable, but this many leaks make repair impossible. The theory of sexual selection was taking on water long before evidence was found of widespread homosexuality, but homosexuality is the final torpedo.

The uncritical acceptance of sexual selection theory has led to underestimation of the extent of cooperation among animals, forcing scientists to construe all interactions between organisms as somehow competitive. From a scientific standpoint, sexual selection theory is inaccurate in its claims and unable to account, even by extension, for the diversity of bodies, genders, sexualities, and life histories.

Most important, sexual selection theory is diversity-repressing. Sexual selection theory envisions male-male competition as weeding out the frail and sickly, and female choice as welcoming to bed the winners of male-male competition so that their children may inherit great genes. This elitist, regressive stance incorrectly views gene pool diversity as consisting of mostly bad genes that males must eliminate and females avoid.

SEXUAL SELECTION CORRUPTED

Sexual selection theory has long been used to perpetuate ethically dubious gender stereotypes that demean women and anyone else who doesn't identify as a gender-normative heterosexual male. By hesitating to declare sexual selection theory scientifically false, scientists prolong the injustice that emanates from this theory, as the writings of contemporary evolutionary psychologists illustrate.

Evolutionary psychology extrapolates the cheap-sperm-expensive-egg principle of today's sexual selection theory to "explain" human desire. One psychologist writes, "Because women in our evolutionary past risked enormous investment as a consequence of having sex, evolution favored women who were highly selective about their mates. . . . A man in human evolution history could walk away from a casual coupling having lost only a few hours of time. . . . A woman in evolutionary history could also walk away from a casual encounter, but if she got pregnant as a result, she bore the costs of that decision for months, years, and even decades afterward."[9] This view implies that motherhood is a punishment for sex rather than a desirable end in itself. If women do wind up having to abide with more severe consequences from a casual encounter than men, this reflects a social inequity in the division of childcare, not some universal difference between the sizes of egg and sperm. We thus see how psychologists attempt to naturalize gender inequality.

Another psychologist writes, "Differences in mating strategies can be traced to the minimum 'parental investment' required to produce an offspring. In our species, parental investment required to produce offspring is much greater for females (i.e., nine months for females vs. minutes for males). Given that females can only produce a maximum of 20 offspring in a lifetime, having sex with a relatively large number of males is unlikely to have adaptive advantages. It is generally far better to invest more in each offspring by carefully selecting a mate with good genes who will participate in the raising of the offspring. For males, having intercourse with a larger number of fertile females was likely correlated with reproductive success since in ancestral environments contraceptive devices were not available."[10] Apart from asserting a natural right to promiscuity, this quotation also manages to suggest that nonprocreative sex awaited the invention of condoms. Drawings on Greek pottery, not to mention the behavior of our primate relatives, demonstrate many nonprocreative heterosexual positions.

These quotations illustrate how Darwin's theory, which might otherwise be written off as merely incorrect, is open to corruption by psychologists, yielding a stimulating fantasy. The assertions by psychologists claiming to speak biological truth have finally come to the attention of professional evolutionary biologists and are being refuted with uncharacteristic vehemence. One of the most accomplished experimental population geneticists today, Jerry Coyne, writes, "Evolutionary psychologists routinely confuse theory with idle speculation. . . . Evolutionary psychology . . . is utterly lacking in sound scientific grounding." Its "stories do not qualify as science, and they do not deserve the assent, or even the respect, of the public."[11]

What provoked such an unusual declaration? The recent publication of yet another theory of the naturalness of rape supposedly based on evolutionary biology.[12] The idea is that men unable to find mates in the "usual way" can reproduce through rape. Genes for rape then increase, leading to the brain's acquisition of a "rape chip." All men are therefore potential rapists, although they do not necessarily act on this potential, depending on external circumstances. Coyne points out that this I-can't-fight-evolution theory is falsified by the facts that one-third of all rapes are of women too young or too old to reproduce; 20 percent do not involve vaginal penetration; 50 percent do not include ejaculation in the vagina; 22 percent involve violence in excess of that needed to force cop-

ulation; 10 percent of peacetime rapes are in gangs, thus diluting each man's chance of reproducing; wartime rapes usually culminate in the murder and sexual mutilation of the victim; some rapists are wealthy, giving them access to women without coercion; and many rapes are homosexual. So many rapes are nonreproductive that rape can't plausibly be viewed as a means of sperm transfer for disadvantaged men to achieve reproduction. Like other mating acts, rape is about relationships—in this case, domination.

The assertion that all men are potential rapists is offensive enough to make men angry about the misuse of sexual selection theory—as women and others outside the sexual selection templates have been for years. Coyne has been prompted to say publicly what many have already observed: that evolutionary psychology "is not science, but advocacy," that evolutionary psychologists "are guilty of indifference to scientific standards. They buttress strong claims with weak reasoning, weak data, and finagled statistics . . . [and] choose ideology over knowledge." Coyne points out, "Freud's views lost credibility when people realized that they were not based on science, but were actually an ideological edifice, a myth about human life, that was utterly resistant to scientific refutation. . . . Evolutionary psychologists are now building a similar edifice. They, too, deal in dogmas rather than propositions of science." Worse even than being theorized as a latent rapist, the misuse of science offends Coyne: "To a scientist, the scientific errors . . . are far more inflammatory than . . . its ideological implications."

Thus Darwin's sexual selection theory uses an incorrect model of social life in animals—that when not busy looking for food or escaping from predators, discreetly discerning females are busy selecting for horny, handsome warriors. This theory that social life boils down to a selection for showy traits is both inaccurate in its universalist claims and inadequate to address the diversity of bodies, gender expression, and sexuality that actually occurs in nature. Furthermore, the theory has been corrupted by evolutionary psychologists and others to naturalize injustice and deny freedom of expression.

Still, some may feel that denying sexual selection theory is too drastic. I get responses like "She throws out a very healthy baby with some slightly soiled bathwater"[13] to my proposal that sexual selection theory should be discarded. Couldn't we just substitute new wording for Darwin's—invest the theory of sexual selection with new meaning—much as we have done with the theory of natural selection? Well, from my perspective, the crux is that the underlying model of sexual selection—selecting for show—is incorrect. To me, all that's floating in the dishwater of sexual selection theory is dirt—no baby there, never was.

I invite you to make your own judgment on retaining sexual selection theory as a scientific principle. I've been clear about where I'm coming from. I'm a transgendered woman; I have standing, as lawyers say, to sue for damage against this theory: it denies me my place in nature, squeezes me into a stereotype I can't possibly live with—I've tried. For me, discrediting sexual selection is not an academic exercise. By now, nearly everyone can claim to be misrepresented by sexual selection theory. Today we have a call-to-action from society to scientifically audit sexual selection theory. I have done this audit, and found the books cooked. If we're serious that scientific principles are open to falsification by facts, then I believe we're compelled to rule that sexual selection theory has now been discredited. I propose a different theory.

SOCIAL SELECTION

My underlying assumption is that animal species with distinct males and females interact socially to acquire opportunities for reproduction—that is, through trade or other exchanges, they obtain access to resources that enable the production and survival of young. Animals are not seeking each other's genes; they are seeking access to the resources that each controls. Each animal has a time budget to allocate among between-sex and same-sex relationships. Together, these relationships further the expected number of offspring successfully placed in the next generation.

Females may be thought of as starting with total control of reproductive opportunity, and males none, because an egg can potentially develop without any male contribution (as in the case of parthenogenesis). What benefit, then, do males offer to make sexual reproduction advantageous to females? They allow a continual rebalancing of the species' genetic portfolio. This benefit must be substantial, because—instead of producing 100 percent daughters, each of whom can lay eggs—females dilute their future reproductive rates by one-half, producing 50 percent

sons, who don't lay eggs, along with 50 percent daughters, who do lay eggs. However, by negotiating male parental care in return for male input into the offspring, a female can increase, even double, the number of offspring that she could produce by herself, thus partly compensating for the 50 percent loss that the invitation to sex originally cost. Courtship therefore consists of exchanging information about ability to pay, likelihood of payment, and transfer of control. Meanwhile, the ability to pay, for both males and females, depends on the same-sex relationships each is engaged in. Males interact with one another to acquire and defend the resources they pay out as parental care, and females interact with one another to acquire the circumstances in which they can safely rear the young under their control.

The packaging of male and female functions in one body type—as seen in plants, many invertebrates, and coral reef fish—may be thought of as the initial and more general condition. Confining one sex to one body emerges as a specialization for the "home delivery" of sperm. Wind-pollinated plants and broadcast spawners like sea urchins suffer substantial sperm loss, opening a niche for specialized delivery systems. Barnacles glued to rocks in the intertidal zone, for example, remain simultaneously hermaphroditic but have evolved a very long penis, typically three or more times the body diameter, to deliver sperm to adjacent barnacles without losing any to the pounding surf. Plants, which are sessile and can't carry out home delivery by themselves, contract with insects and birds to deliver their sperm to other plants. Mobile animals have the option of locating sperm in a separate body type for delivery to females. But once males exist as separate bodies, they assume an agenda of their own. Males may find their interests furthered by offering parental care to females to increase successful paternity. Because males must negotiate with females and with one another, the delivery of sperm itself can assume a secondary and almost incidental function to the act of mating. Mating is then more about maintaining the between-sex and same-sex relationships needed to provide food and safety for the young than about sperm transfer as such.

If social life in animals is primarily about acquiring and trading the opportunity to reproduce, then the dynamics of animal societies are complex, nonlinear, and unpredictable. I'm struck by the unpredictability of how social evolution has played out in closely related species. Take

our two closest relatives, the bonobo and the common chimp: they differ slightly in chin hair and habitat. Yet one is peaceful, the other violent. Female spotted hyenas have a penis, but their closest relative doesn't. The Idaho ground squirrel performs mate guarding, Belding's ground squirrel doesn't. These pairs of very closely related species have developed societies with diametrically opposed power relations. Why? Traditionally, it is thought that a society's organization reflects properties of the environment, that a society is somehow put together for overall efficiency, a great machine organized for a collective function.[14] Instead, I suggest that social evolution is turbulent, that an animal society is throbbing, vibrating, and energetic, and that the unpredictability of the power relations emerging in closely related species is the evolutionary signature of turbulent social dynamics. The outcome of social evolution seems as uncertain as where a white-water stream deposits a floating leaf.

If social evolution results from complex nonlinear dynamics, then phenomena like sex-role reversal, which Darwin noted in passing, are not so anomalous. A common feature of nonlinear systems is the presence of alternative multiply stable attracting states. The axes of gendered morphology and gendered behavior may each have two simultaneously stable evolutionary states and give rise to many combinations of morphology and behavior that are evolutionarily stable. Some would be sexually monomorphic, some dimorphic, some with typical gender roles and others with reversed roles. Similarly, various family arrangements, either monogamy, polyandry, or polygyny, may emerge as the diverse outcomes of social negotiations about how to control access to various kinds of resources needed for reproduction and safety. This suggestion is pure conjecture on my part, but I believe this is the direction in which we should start thinking.

When we focus on social life as a continual exchange of control over resources to reproduce, then complex multigendered societies are not anomalous. The genders emerge as occupational categories, with gendered symbolism to signal occupational roles in bringing about matings, raising young, or tending resources, much as a worker's uniform does in human society. The payment for services rendered is in terms of increased opportunity to reproduce. While some genders reach a market-based accommodation of their needs, others linger on the outside of their political economy, taking the opportunity to reproduce by force and ag-

gression. Social violence is not nature's baseline state, but a special case of failing to strike a successful bargain in an animal society's marketplace for access to reproductive opportunity.

As ever-increasing similarities between animals and humans are revealed, do animal societies become more relevant to human societies than previously believed? Should political science and sociology, basic subjects in the human social sciences, be widened to include investigations of how animal societies function? I think so. People are not demeaned by the comparison with animals, but animals are elevated by the comparison to people.

SOCIAL-INCLUSIONARY TRAITS

Finally, we are left with the one issue on which many feel that Darwin's sexual selection theory was correct—the peacock's tail, an example of a so-called secondary sex characteristic. Other supposed examples would include the long nose on an elephant seal, the antlers on a deer, and countless other male ornaments. As Darwin wrote, the female peacock's "preference for beautiful males, [has] rendered the peacock the most splendid of living birds." Is female preference for beautiful tails why male peacocks have them? Even if one grants that Darwin's sexual selection theory is inaccurate in its claims of universality and inadequate to address the diversity of bodies, gender expression, and sexuality that actually exists, perhaps Darwin is still correct about peacocks. Perhaps sexual selection applies solely to those few species like the peacock, in which the males, and the males alone, are highly ornamented, and where the males actually do display these ornaments to a female during courtship.

If I were settling out of court with Darwin's lawyer, I'd happily concede peacocks to obtain a compromise. Someday, though, someone will challenge Darwin on peacocks too, and I'll bet they'll win. Here's the problem. Let's turn our gaze for the moment from ornamented males to species where females are the sex with unusual structures. Some species with female ornaments are sex-role reversed, like the pipefish and the jacana. However, other species with female-limited ornaments are not sex-role reversed. Take the spotted hyena, in which females all have penises.

No one suggests that females have these structures because male hyenas prefer females with a large penis. The female penis in hyenas is used for social interaction among females and has nothing to do with what males want. This case raises the possibility that some structures are used as a condition for inclusion in the same-sex social groups that control the resources needed to reproduce. If a female hyena lacks a penis, she has no chance of effectively interacting with other females. She would therefore be excluded from the all-female groups that control resources in hyena society: she would not be able to reproduce, the evolutionary equivalent of death.

Candidates for social-inclusionary traits include the masculine genitals on female spotted hyenas, female same-sex sexuality in bonobos and Japanese macaques, and the human brain (as we will see in chapter 12). Social-inclusionary traits evolve fast because, once a trait takes hold, anyone without it is excluded from the group—a lethal situation. Unique to the group in which they occur, they are a bodily manifestation of animal prejudice. Social-inclusionary traits are to social selection what secondary sex traits are to Darwin's sexual selection, but social-inclusionary traits pertain to both within- and between-sex social dynamics, and to relationships distributed across many individuals, not just dyadic relationships. Selection for social-inclusionary traits would seem to account for traits found solely in females of species that are not sex-role reversed, traits that presently lack any explanation. The idea of social-inclusionary selection thus fills an explanatory vacuum.

Social-inclusionary traits also provide an alternative explanation for many, if not all, of the traits conventionally interpreted as secondary sex characteristics in males, which, like the peacock's tail, females are supposed to prefer. The problem is that the traits of the males with whom females wind up mating may be intended more for the attention of other males than for display to the females. Antlers, for example, serve as weapons by which males can physically beat up other males, but they may also be symbolic to other males of what they seek in companions and allies. In short, these traits may be "medals" valued by other males rather than ornaments valued by females. A female might not necessarily care if a male held another male in high regard, unless that regard correlated with the amount and reliability of parental care he would provide her. But a male not held in high regard by other males might never have

the opportunity to court a female. Thus an illusion emerges that the female prefers the male who is victorious, or otherwise held in high regard among males, when she is in fact indifferent to those characteristics except insofar as her own direct reproductive success is affected. Here it is male-male social dynamics that determine who qualifies as an eligible suitor. Thus the test of whether a male's showy trait is an ornament resulting from sexual selection or a medal resulting from social-inclusionary selection is whether the trait is valued by the females or by other males, and not whether males lacking the trait don't mate. For this reason, I wouldn't bet money that Darwin is correct about peacocks, because we don't know how male peacocks regard each other's tails—whether male peacocks require beautiful tails on each other as a condition for participating in whatever male-male social dynamic establishes eligibility to become a suitor.

Social-inclusionary medals are within-species counterparts of what evolutionary biologists call premating isolating mechanisms. Animals use color spots and vocalizations to tell what species they belong to and avoid hybridizing with other species. These traits reinforce the distinction between species. Biologists have long wondered how species become distinct from one another. The selection pressure to reduce hybridization gradually disappears as species become more distinct from each other, stalling the evolution before completion and leaving a residual hybridization rate. If the traits that separate species also function as social-inclusionary medals, then selection for social inclusion augments selection to lower hybridization and propels the evolution of species distinctness to completion. Species are more distinct in animals than in plants, where extensive hybridization takes place across the species in many genera. If premating isolating mechanisms in animals are also social inclusionary medals, then animal species should evolve sharper between-species distinctions than plant species for this reason.

This review of diverse gender expression and sexuality among the vertebrates demonstrates that biology need not tell one single, simple, and boring story. Biology need not be a purveyor of essentialism, of rigid universals. Biology need not limit our potential. Nature offers a smorgasbord of possibilities for how to live, and an endless list of solutions for every context, some of which we'll wish to reject, and others to adopt or modify.

The true story of nature is profoundly empowering for peoples of minority gender expressions and sexualities. Yet this truth has been suppressed by biologists, and the few accounts that do surface are embedded in pejorative language. To remove the conceptual rot, we've had to excavate deep into the foundation of evolutionary theory, identify the collapsing member—Darwin's theory of sexual selection—and replace it with new ideas that may be better able to carry the load as the future unfolds.