Chapter 5
Sex, Gender, and Evolution Beyond Genes

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5.1 An Interesting Misunderstanding

Recently, over a beer with friends, I began speaking of the unfortunate way that biological determinism, or the idea of the gene at the center of our discourse in biology and evolution, is the foundation for the way that nonscientists think about evolution. Attributing our successes and our failures to our genes has become commonplace. People talk in earnest about the gay gene. A recent radio story on US National Public Radio touted the finding of the entrepreneurial gene, going as far as interviewing twins that share business interests and contrasting them to an older brother that does not [1]. Yet during this conversation, one friend thought I was talking about determinism in the sense of males and females having set sex roles, fixed by evolution and exacerbated by society.

This misunderstanding set me to thinking, because to a large extent, it may be the same sort of worldview that envisions "the gene" as the main basis for the traits we see and the target of evolutionary change that also portrays males and females as unchanging, inflexible entities whose evolutionary strategies are as simple as "be ardent" or "be coy." Both views are far too narrow to account for the stunning amounts of variation that exist in the natural world (human or otherwise) and represent outmoded dogmatic views that scientists have largely begun to move past.

Given what we know about the complex ways that genes work, most biologists recognize that biological determinism is not a realistic way to view the world. Even Richard Dawkins, one of the most vocal proponents of a gene-centered view of evolution, concedes that "expressions like 'gene for long legs' or 'gene for

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altruistic behavior' are convenient figures of speech [… but] there is no gene which single-handedly builds a leg, long or short" [2]. Indeed, to a large extent, biologists talk of "genes" and "genetic bases" for traits as shorthand for genetic networks that influence traits.

Nevertheless, views about how traits can change over evolutionary time (as opposed to the development of traits like "long legs" in a single lifetime) remain gene-centric. To hammer this point home, biology students are taught about the evolution of a giraffe's long neck. Giraffes' necks did not evolve because individuals stretched their necks over their lifetimes and passed those cumulative changes on to their offspring, but rather because of changes in the underlying genes coding for longer necks. Put another way, a neck may stretch over the lifetime of a giraffe, but that giraffes' children will start at the same point. To invoke anything contrary to this view is heretical.

This seems odd when you consider that when Darwin wrote *The Origin of Species*, he did not know about genes, and yet he was still able to describe evolution by natural selection. Nowadays, it is difficult to find textbook descriptions of evolution that don't invoke changes in the relative frequency of genes occurring in populations. However, there are only a few conditions necessary for evolution by natural selection to occur: (1) in a population there exists variation in some trait; (2) in a given environment, individuals with one trait variant do better (e.g., leave more offspring) than others; and (3) trait variants have a hereditary basis. Nowhere does this include anything about genes, but since genes are passed in a predictable way from parents to their offspring, most scientists long considered genes to be the only mechanism of heredity that is important for evolutionary change.

Recently, however, many biologists have objected to the gene-centered approach. Two big flaws in this approach are (1) ignoring the existence of nongenetic ways in which traits can be inherited and (2) deeming the environmental determination of many traits as irrelevant to evolution.[1]

How is any of this related to myths about the sexes? Too often, biologists mention the strategies of the sexes in light of simple, genetically based views of evolution. The message of evolutionary biology, according to them, is that the sexes behave in such a way as to pass their genes to the next generation. Since males produce "cheap" sperm and females produce "expensive" eggs, this often means that males ought to be "eager" and "promiscuous" while females ought to be "coy." Not surprisingly, popular media often portrays a caricature of human behavior as falling in line with these evolutionary "principles." Example after example counters this view of evolution, and it points to an underlying flaw in the myth that stereotypical

[1] This may sound familiar. The idea of environmental versus genetic determination of traits is essentially nurture versus nature. However, to say that a trait is either one or the other is entirely wrong (all traits are a mixture of the two), and as such that language is misleading. A more apt view is nature *is* nurture. Throughout the article, I mention examples of traits that are more environmentally determined than others, but no trait is entirely so.

sex behavior is encoded in our genes. In this article, there are two main points that I would like to argue, both points related to each other[2]:

1. By focusing solely on genes and ignoring other ways that traits can be inherited, we miss out on much of the interesting and important details of the process of evolution.
2. Evolution can act on complex regulatory processes in such a way as to increase the environmentally induced aspects of a trait. Understanding evolutionary processes as dynamic and contingent upon both social interactions and other environmental factors is a much more compelling and truthful view of evolution than one of genes steering the sexes to behave in stereotyped ways.

5.2 Natural Selection on Nongenetic "Sex" Traits

The dogma about cheap sperm and expensive eggs and the sex-typical behavior that results is one whose conception is based on gene-centered ideas. Yet evolution does not solely result from genetic change. In the definition of natural selection that I mentioned above, one of the key ingredients to evolution is inheritance of traits. Although genes are certainly important entities through which information is passed between generations, they are not the only ones. A recent book by Eva Jablonka and Marion Lamb called *Evolution in Four Dimensions* describes several other so-called mechanisms of heredity, or systems that, like genes, can pass traits from parents to offspring [3]. These systems can exist inside of bodies yet outside of genes (think, e.g., of a zygote that inherits not only DNA from its mother but also all of the proteins and organelles that exist inside of an egg). Additionally, behavior can provide material on which natural selection can act when behavioral traits increase the fitness of their bearers even with no underlying genetic variation. These alternative mechanisms of heredity make it possible for natural selection to shape evolutionary outcomes in more ways than narrowly focused genetical models predict.

An example of hereditary, nongenetic variation inside of cells is called methylation. Methylation is simply the addition of a molecule to a particular spot on DNA. This methyl group changes the expression of the gene to which it is attached, often silencing the gene. The basis and inheritance of methylation process is not determined by genes, yet the patterns of imprinting can be passed along to offspring. Sometimes, which parts of DNA are methylated depends on which parent contributed that particular stretch of DNA—a phenomenon called genomic

[2] Though the focus of this article is about how new ways of thinking among scientists challenge narrow views of the sexes, it is worth nothing that not all scientists adhere to such views. Many scientists still fail to take into account variation among males and females, and many scientists are reluctant to discuss evolution without assuming changes in genes. Furthermore, in a self-perpetuating way, societal assumptions of the way that the sexes should behave can (unconsciously) shape the research programs that look to study such behavior. Nevertheless, much change in scientific views about the sexes has occurred in the last several decades, and this change is bound to continue.

imprinting. One way that genomic imprinting can influence reproductive success sounds more like something out of a science fiction movie than out of a biology textbook. In certain cases, males may benefit (increase their reproductive success) by having offspring that extract more resources from females than what is optimal for females to invest, since doing so will come at the cost to females of future offspring. As a result, several genes are imprinted differently depending on whether they are inherited from the father or the mother. The patterns of methylation in fetuses set the stage for a tug-of-war between fetus and mother over resources, the outcome of which influences traits such as the birth weight of offspring [4].

Jablonka and Lamb provide several examples of how a behavior, not the product of genes, can be passed from parent to offspring. One striking example comes from a study on European rabbits (*Oryctolagus cuniculus*), where investigators found that the diet of mother rabbits while they were pregnant influenced the food preference of their offspring later on [5]. It is easy to imagine how selection could act on this behavior: a pregnant rabbit that eats food that will be abundant or nutritious when her offspring are born will likely leave more and healthier offspring than a female that does not.

Among the more wanton examples of a behavioral trait favored by selection is genito-genito (G-G) rubbing in bonobo females (*Pan paniscus*). G-G rubbing is when female bonobos rub their clitorises together, generally in the context of food sharing and maintaining friendships [6]. Without any underlying G-G rubbing genes (though imagining just what such genes would code for is an amusing exercise), females that participate in the behavior are able to access resources such as food and babysitters.

Finally, my favorite example of a behavioral trait increasing the fitness of the individuals expressing it comes from house mice (*Mus domesticus*). Investigators determined which female mice associated with each other (let's call them "friends") by monitoring with whom everyone in an experimental population spent their time. They then allowed some females to reproduce in the same nest as their friends and other females they did not. Females who were allowed to reproduce near their friends weaned more pups than those that did not [7]. This example clearly illustrates how a behavioral trait (with whom female mice spend their time) can influence the number of offspring they leave.

Traits for which there is no underlying genetic variation can result in an increased number of offspring for individuals expressing those traits relative to individuals without those traits (e.g., mice that associate with friends versus those that do not). So, in the end, an individual's "genes" can be passed to the next generation without any help from any of those genes along the way. The interesting factors for a discussion of natural selection in such cases, then, are not genes but traits (e.g., behaviors, patterns of methylation), how they are transmitted to different individuals, and how those traits influence the reproductive success of their bearers. This paints a different picture of evolution, where the sexes interact with cues from their external environment, either because of cues from resources (e.g., pregnant rabbits and food) or from other individuals (e.g., house mice females and their friends), to increase their reproductive success. In other words, to say that natural selection favors individuals that act in such a way as to get their genes into the next generation is misleading. Selection has favored individuals that maximize their reproductive success, and the outcome of selection need not be changes in genes.

5.3 Environment, Genes, and the Evolution of the Sexes

Emerging discoveries about the way that genes can interact with environments over evolutionary time also have profound implications for views of the evolution of the sexes. As I've mentioned already, one of the greatest oversights of the last century of evolutionary biology is the insistence on "the gene" as a metaphor for the sole basis of evolutionary change. Paradoxically, Darwin knew nothing about genes, yet history has touted the modern synthesis, or the inclusion of gene-centered thinking into an evolutionary framework, as the missing piece of Darwin's puzzle. This approach unfortunately led to a nearly wholesale dismissal of the environment as an important factor in the appearance of new traits. In other words, the idea that a single mutation in a single gene causes a beneficial (i.e., adaptive) trait variant that spreads to an entire population or species has been the primary vision of how new traits arise. And so it is taught in high schools and universities.

But let's step back for a minute. As a thought experiment, imagine that our genomes were operating in the very simplest of ways (a view which no biologist would subscribe to): DNA is making proteins that are encoded in its pattern of nucleotides. We'd end up a pile of proteins with no rhyme or reason. Fortunately for us, there is a vastly complex regulatory system that directs the timing and location of DNA expression and as a result makes eyes show up on our head rather than our arm. This regulatory system is incredibly sensitive to the environment, and by "environment" I mean the area inside of the cell (where other genes are turning on and off), outside of the cell (where different tissues communicate information about the entire organism to one another), and outside of an organism itself (where the world contains information that an organism can exploit to make decisions about behavior and physiology). Furthermore, this regulatory system consists of many different genes, acting in concert with one another and in many different contexts.

Given this regulatory complexity, it is hard to imagine the mutational view, in which a single beneficial mutation acts in just the right place and at just the right time, can really account for all the vast amount of the adaptive evolution that we can see in nature. Seeing this problem clearly, evolutionary biologist and specialist on social wasps Mary Jane West-Eberhard spent nearly 15 years working on a sea-changing book titled *Developmental Plasticity and Evolution* [8]. In it, she describes a process called "genetic accommodation," wherein natural selection acts on the regulatory mechanisms of traits such that they can move along a continuum from being environmentally induced to genetically induced and vice versa. Sounds like a mouthful, but understanding this is key to the topics I'll pick up shortly with respect to the evolution of sexual behavior.

A famous example of this process comes from an experiment performed by C.H. Waddington in the 1950s. Waddington exposed fruit fly (*Drosophila melanogaster*) eggs to a chemical called ether, which caused some of those flies to hatch with deformed thoraxes, that is, midbodies (he called them "bithorax" individuals). He picked individuals with deformed thoraxes in each generation, let them breed with each other, and then exposed their offspring to the same ether treatment. After several cycles of doing this, some offspring were bithorax *without* exposure to ether [9]. A trait initially determined entirely by an environmental input (ether) soon became under the control of a non-environmental, hereditary mechanism (genes).

For another, fictional example of this process, let's return to the giraffes' necks that I mentioned earlier. The gene-centered view proposes that giraffes' necks evolved because of selection favoring individuals with genetic networks that produced longer necks. The genetic accommodation view, however, wouldn't immediately jump to this conclusion. Imagine, for example, there exists some environmental substance that helps induce the formation of larger necks, like a chemical in the leaves of a particular tree. Let's also imagine that there is variation in the amount of influence these leaves have on neck length: in some individuals, the leaves are the primary means of getting a long neck, yet other individuals have genetic architecture that overrides input from the leaves and gives a similar neck length whether that individual eats the leaves or not. If longer necked individuals leave more offspring than short-necked individuals, then one could imagine selection favoring a reduced genetic input, favoring those individuals in which the environmental signal overrides the genetic architecture for neck length. In other words, natural selection can act to decrease the genetic input for a trait.

In these examples, much of the selection that changes the determination of traits from being under genetic to environmental control is indeed acting on genes in the complex regulatory networks that produce traits. Yet in viewing evolution as acting only as changes in gene frequencies over time, much of the interesting story of how individuals respond flexibly to the environment is completely lost.

5.3.1 Genetic Accommodation and Flexible Reproductive Behavior

How can understanding selection as a process that changes the relative importance of environmental inputs over time shed light on the way that selection acts on the sexes? Several biologists have made groundbreaking discoveries in how individuals can respond to the environment to make reproductive decisions that increase their fitness. In many cases, selection favors increased sensitivity to environmental cues. In a cooperatively breeding bird species, red-backed fairy wrens (*Malurus melanocephalus*), for example, the plumage coloration of first-year males is entirely dependent on the social environment they inhabit. Some males stay at the nests from which they fledged and help raise their mothers' offspring. These males look much like females, while "dull" males look different from such helper males and "bright" males are mature and have showy plumage. Which of these plumage types a male has is a function of its social environment: when breeding opportunities become available, helper males begin to molt into dull or showy plumage depending on how much time is left in the breeding season [10, 11].

Individuals of both sexes can respond to variation in their social environments to maximize the number of offspring they leave. Evolutionary biologist Patricia Gowaty, for example, has posited that individuals should be able to detect the complementarity of their potential mates (to optimize the health of their offspring) and invest more in offspring resulting from pairings when individuals are constrained to reproduce with non-preferred partners.[3] This hypothesis has borne out in organisms ranging from fruit flies (*Drosophila pseudoobscura*) to ducks (*Anas platyrhynchos*), and this provides a remarkable example of how individuals must rely on environmental cues (i.e., mate complementarity) to make flexible decisions about reproductive strategies [12, 13].

Decisions with drastic evolutionary consequences such as whether or not to even reproduce can be under surprising environmental control. In several social mammals, such as meerkats (*Suricata suricatta*) [14] and tamarin monkeys (*Saguinus oedipus*) [15], social groups can have single "dominantly" breeding females who, through social interactions and hormonal signaling, suppress the breeding activity of other females in the groups. Even in human females, environmental cues such as diet can influence the age at which individuals have their first periods [16].

Even sex itself is subject to environmental influence. It turns out that the systems that control sex determination prove to be flexible over evolutionary history. In turtles, which have largely environmental sex-determination mechanisms (e.g., males result when eggs experience high temperature while females result when eggs experience intermediate temperatures), some species have evolved genetic sex determination [17]. Conversely, in lizards, which mostly have genetic sex determination, some species have evolved environmental sex determination [18]. Furthermore, in many species, including several species of fish that live on coral reefs, individuals can change from one sex to another over the course of their lifetimes, depending entirely on ecological and social stimuli [19].

These examples highlight the extreme importance of the environment not only in shaping the selection pressures that individual face, but also in dynamic, long-term evolutionary strategies. Such environmental input and subsequent behavioral flexibility is the norm rather than the exception, yet popular conceptions of the evolution of the sexes often ignore variation. This variation is the cornerstone of evolution, one of the main ingredients in the process of natural selection.

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[3] Mate preferences are often self-referential. By that I mean that the preferred mate for one individual may not be optimal, in terms of producing viable offspring, for another individual. In the context of the experiments on compensation, individuals mated to non-preferred mates compensated by either laying bigger or larger eggs, ejaculating more sperm, or providing more parental care.

5.4 Beyond Genes, Beyond Determinism

Despite the fact that many evolutionary biologists do not subscribe to the popular media perceptions of the way that genes influence behavior, most widely discussed evolutionary theory depicts selection as acting only upon genetic variation. As a result, people often discuss males and females as acting in ways to get their genes into the next generation. I've mentioned specific reasons why this view is misleading, namely because adaptive evolution can occur without genes and selection can act in ways that increase the input of environmental signals during trait development. Understanding evolution this way allows for a more nuanced and realistic view of the sexes.

Using nature to justify or bolster human behavior is fallacious. No one would point to chimpanzee infanticide to justify the murder of human infants (discussions about right and wrong fall outside of the realm of evolutionary biology), yet time and time again popular media depictions of normal males and females rely on tenuous, gene-centered views of evolution. These views are wrong, and the way that evolution actually works, with mice hanging out with their friends and red-backed fairy wrens changing their costumes when breeding opportunities present themselves, are far more interesting and relevant to discussions of the evolution of reproductive behavior.

Conversely, these tools can help us examine (though not to justify or ascribe morality to) how evolution has shaped human behavior. This may be particularly important for trying to understand patterns of behavior related to gender that are much more a result of selection acting on behavior and culture rather than on genes. Countless examples abound, such as female genital mutilation, sex-specific infanticide, and veiling. Indeed, understanding these societal problems in the context of evolution may point to novel ways to solve them [20].

The notion that selection has shaped the sexes into narrowly defined behavioral roles is just a myth. Natural selection has not shaped males and females as gene-driven machines trying to create new gene-driven machines. Rather, individuals of both sexes are active participants in the evolutionary process, behaving in ways that increase their reproductive success based on information from their environment, not their genes.

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Glossary

Biological determinism is the idea that any trait can be traced to either a single underlying gene or network of genes and that variation in such genes is the only target of natural selection.

Genetic accommodation is an evolutionary process resulting from natural selection modifying the relative importance of environmental and/or genetic input to the production of a trait. Sometimes this results from an increase in genetic control of a trait, while other times this results from a decrease in genetic control of a trait.

Mechanisms of heredity are ways in which traits are passed from parents to their offspring. Genes are one mechanism of heredity, but other, not genetic mechanisms include genomic imprinting and social behavior.

Natural selection is a process that results in evolution wherein individuals with some trait variant survive more and/or leave more offspring than individuals with a different trait variant.

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