Crossroads of Knowledge

Malin Ah-King *Editor*

Challenging Popular Myths of Sex, Gender and Biology

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Chapter 1
Introduction

Malin Ah-King

Myths about gender and biology abound. We are constantly fed with ideas about essential differences between women and men in popular books such as *Men Are from Mars, Women Are from Venus*, telling us that we had better accept and approve of innate differences or we will make ourselves unhappy [1]. Biological facts have often been and are still being used to make claims about what is "natural" and morally acceptable, thereby justifying oppression based on a variety of grounds for discrimination such as sex, sexuality, race, and class. In the nineteenth century, it was considered a scientific fact that brain use in women would drain limited energy from their true reproductive roles [2]. Today, biological claims of differences between men and women turn up everywhere and are used both to justify why men are not suited to taking care of babies and to substantiate relationship advice.

Biological arguments are sometimes used to account for our behavior when we cannot control ourselves, and our understanding of biology is internalized when we reflect on ourselves as cavemen [3] or as driven by hormonal cravings [4]. There exist many popular conceptions about biology, sex, gender, and bodies that stem from supposedly common-sense notions of gender difference, human evolution, biological processes, and animals. Science often underpins popular understandings of female-male sexual difference, but current research in biology also opens up a space for variable and non-static views of sex and gender. Instead of emphasizing polar differences between females and males, the natural sciences may underscore variation, sameness, and a continuum of morphologies, behavior, and processes.

This edited volume presents contributions from international researchers from a variety of disciplines—biology, history of science, anthropology, human evolution, and social sciences—all with the aim of challenging popular misconceptions of sex

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differences. The chapters in this collection offer not only a critique of conventional understandings of sex and gender, but the authors also demonstrate that current research findings suggest alternative ways of conceiving of sex, gender, and biology. Our aim is to make current insights about sex and gender accessible to a broader audience. Popular beliefs are often not in accordance with the ideas developed and held by researchers in biology and medicine. Our goal is to question taken-for-granted assumptions and thereby deepen our readers' understanding of biology, sex, and gender by going beyond these popular conceptions.

1.1 Sex or Gender?

Sex and gender are often used interchangeably, but researchers in women's studies/gender studies use the term gender (as in gender identity or gender representation) as an analytical category which has enabled focusing on the social constructs of what it means to be a woman or a man, and to emphasize that these social constructs are changing over time and are variable across cultures. Notably, about a hundred years ago, the color pink was considered a "decided and strong" color suitable for boys, symbolizing "zeal and courage," while blue was considered "more delicate and dainty" signaling faith and constancy and thereby suitable for girls [5].

Among biologists, the term sex has several different meanings: the most common use is in the sense of sex as the female-male distinction, which is based on the size of the sex cells—females produce large sex cells (eggs), and males produce small ones (sperm). But there is also another term that is sometimes confused with the former one, namely, sexual reproduction. Sexual reproduction occurs when sex cells fuse to produce a new individual. There are species in which sexual reproduction occurs that have sex cells of the same size and that are therefore not categorized as males and females, such as *Chlamydomonas*, an algae.

The distinction between sex and gender is not clear-cut. We may think of biological sex differences that we can measure, but many measurable characteristics may be influenced by our ways of behaving as women or men, such as cultural ideals influencing the building of muscle mass. Even if we do find biological sex differences, for example, in brains, it is very difficult to distinguish between the cultural and biological influence producing these differences, because the brain develops in relation to how we use it [6].

In understanding and explaining sex differences, we often use stereotypes as a shortcut to process information [7] (see Chap. 4). Virginia Valian uses the term "gender schemas" to describe how our underlying generalizations about sex differences influence how we perceive and interpret different phenomena [8]. One example is how general knowledge of sex differences in body height influences how height in women and men is estimated. For instance, studies show that we tend to overestimate male height and to underestimate female height, despite the presence of reference objects. We tend to use these kinds of generalizations in our interpretation of the world, which probably has contributed to current taken-for-granted conceptions of sex, gender, and biology.

In debunking myths about sex, gender, and biology, we have many predecessors. In 1985, Anne Fausto-Sterling wrote her critique of biological theories entitled *Myths of Gender*, in which she critically analyzed biological research on hormones, aggression, menstruation, and adaptive theories of rape.

In her book *Sexing the Body*, she presents an illuminating meta-analysis of studies investigating sex differences in a part of the brain called the corpus callosum, the tissue connecting the brain halves, which is popularly referred to as the "highway between brain halves." Fausto-Sterling shows that even though some studies have revealed significant sex differences in measures of the corpus callosum and thereby gained media attention, the overall results do not show any consistent sex differences in the size or shape of the corpus callosum [9]. Recent endeavors to scrutinize the science of sex differences have resulted in two books: Cordelia Fine's *Delusions of Gender: How Our Minds, Society, and Neurosexism Create Difference* [5] and Rebecca Jordan-Young's *Brain Storms: The Flaws in the Science of Sex Differences* [6]. Cordelia Fine reviews research showing that preconceptions about how men and women perform in different tasks have substantial effects on the results. For instance, investigating gender differences in mathematical problem-solving abilities may show sex differences that are due to gender stereotypes about the very mathematical abilities that are being tested. Fine also makes the point that when we see stereotypical differences between boys and girls, we tend to fall back on biological sex differences as an explanation, overlooking the overwhelming social influence. Rebecca Jordan-Young, in turn, scrutinizes evidence that is claimed to support the hypothesis that hormonal influences early in life organize the brain and cause permanent masculine/feminine effects, leading to differences between masculine and feminine desires, personality, and cognition. Jordan-Young demonstrates the methodological deficiencies and questionable assumptions on which these studies are based and shows that there is a great discrepancy between the contradictory research findings and the grand conclusions that have been drawn from them [6].

Language research is another area that fails to support commonly held beliefs about women's and men's communication [7]. Throughout her book *The Myth of Mars and Venus: Do Men and Women Really Speak Different Languages?* Deborah Cameron shows that research provides little support for the notion of women using more words than men when talking, of women being more verbally skilled than men, or of men using language in a more instrumental way than women. Clearly, challenging myths of sex and gender are as urgent as ever and require scientific knowledge from many disciplines.

1.2 Cultural Influence on Science

Science historians and gender researchers have shown how cultural conceptions influence the interpretation of research results and what questions are considered worthy of pursuing at a certain time. Cultural norms also influence how we view biology. For example, the focus on reproduction in evolutionary theory has caused biologists to disregard how frequent same-sex sexuality is among animals [10, 11]. Science philosopher and science historian Evelyn Fox-Keller has analyzed how feminism has changed science. Keller's famous science historical account of Barbara McClintock's career is one example of this argument. McClintock showed that DNA restructures and changes, but her discovery was so radically different from the prevailing paradigm at the time she presented it that the scientific community did not understand it. This example shows that there are many theoretical approaches occurring simultaneously and that some perspectives are overlooked, and it is in this process that ideology in general may have its greatest impact. Therefore, Keller argues that feminist critique of science should make visible the history of science and that it also has the potential to transform science. Critical gender perspectives on science have the potential of decreasing biases and improving science [12]. Stereotypical portrayals of females and males in scientific models and in the scientific literature prevent researchers from approaching their research material with an open mind (see Chap. 4), and therefore gender-neutral models may lead to less biased scientific endeavors [12] (see Chap. 6).

1.3 Implications for Society

Why is it important to challenge myths of sex, gender, and biology? We think it is important because these myths are highly influential in human societies; they essentialize differences and make them seem natural and justifiable. Questioning the "essentials" or what constitute the fundamental sex differences is one way of taking on the task (see Chap. 2). Biological research on human nature is especially problematic in this sense, as it is concerned with examining what is "natural" for females and males. Priscille Touraille, in Chap. 7, problematizes the evolution of human sex differences in body height from an interdisciplinary perspective, including different cultural and biological perspectives. Furthermore, it is important to understand how developments in society and science are interdependent, and this volume includes historical perspectives on the science of sex hormones and evolutionary theory (see Chaps. 3 and 6). Finally, it is important to understand how arguments about nature and culture influence political debates and decisions and how we can understand policy as a reflection of traditions, ideologies, and local contexts (see Chap. 9).

1.4 The Chapters

The first chapters concern our understanding of sex differences, taking as a starting point the variation in sex among animals, fundamental sex differences, genes, and hormones. With reference to the huge variability in males and females among animals and plants, Root Gorelick, Jessica Carpinone, and Lindsay Jackson Derraugh go on a quest for the fundamental and unequivocal sex difference (Chap. 2). They reject sex chromosomes—many species do not have sex chromosomes and an individual's sex may instead be determined by temperature—and genitals; a penis is definitely not a universal among males of all species; in birds the majority of species lack penises. The quest ends in possible minute details of the sex cells (eggs and sperm) that need to be further investigated before we have a definitive answer to what the fundamental sex differences may be.

Daniella Crocetti's Chap. 3, on genes and hormones, contains a historical review of the importance of genes and hormones for our understanding of sex. The history starts with binary conceptions of hormones, labeled by sex, although they later were found to occur in both sexes, and ends with the acknowledgment that what determines a person's sex is an intricate interplay between genes, hormones, and gendered components of the body. These different components may or may not coincide with that person's gender identity. She argues that intersexuality, which in medical terms is called disorders of sex development (DSD), questions the conception of sex as a binary, and she discusses current medical hormone treatment practices in general.

The next three chapters look at scientific research in evolutionary biology: the relatively new field of sexual conflict within evolutionary biology (Chap. 4), new findings in evolutionary biology showing alternative ways of heredity than genetic inheritance (Chap. 5), and the history of ideas in evolutionary biology pertaining to sex differences (Chap. 6). In Chap. 4, Josefin Madjidian, Kristina Karlsson Green, and Åsa Lankinen describe stereotypes in a new field of evolutionary research, namely, sexual conflict that focuses on the conflicting interests of the sexes in relation to mating. They show that gendered notions pervade in models as well as descriptions of animal behavior. Words used to describe females and males in these conflicts fall in two almost mutually exclusive categories, reflecting classic stereotypes of active males and reactive females. Madjidian, Karlsson Green, and Lankinen argue for a more balanced use of terms to facilitate research that is more inclusive of variation outside of female and male stereotypes. Furthermore, avoidance of stereotypes in biological research is also beneficial to communication of scientific findings to the general public, as biological research shows that nature is much more flexible than is typically described.

Popular views hold that genes steer the sexes, causing them to behave in stereotypical ways. Since the 1930s, evolutionary biology has positioned genes as the focus of evolution. In Chap. 5, Jonathan P. Drury explores recent biological research showing different paths of heritability that have an important impact on how we view evolution. Drury draws on empirical studies to show how environmental and social factors influence the expression of traits and, consequently, evolution. Social interactions and environmental factors influence the expressions of genes, affecting, for example, sex determination, such as in many lizards whose sex is determined by temperature. In an experiment on fruit flies, a special appearance (bi-thorax) was induced by treating individuals with an environmental factor: ether. After pairing these bi-thorax individuals for some generations, the fruit flies produced bi-thorax individuals in the absence of treatment with ether. Thus, selection may influence regulatory processes to increase or decrease environmental effects on different characteristics. These research findings help us understand evolutionary processes as dynamic and dependent on both social interactions and other environmental factors, in stark contrast to the popular deterministic view of genes.

Evolutionary theory of sex differences, in particular the theory of sexual selection, has received a great deal of critique from gender perspectives, such as the overfocus on males and stereotypic portrayals of the sexes. In Chap. 6, on the development of evolutionary explanations for sex differences, Thierry Hoquet explores both stereotypic notions and Darwin's emphasis on male traits, critiques of them, and development of the theory of sexual selection. Darwin described females as generally coy and males as eager, in accordance with Victorian ideals, but he did not explain why this pattern had emerged. Subsequent biologists have tried to solve the question by relying on sex differences in investment in large versus small sex cells (eggs and sperm) and investment in parental care. These ideas have been challenged, and in the final part Hoquet reviews emerging models in evolutionary biology that do not build in taken-for-granted assumptions about what it means to be female or male.

The last three chapters deal with humans, the cultural and biological effects on sex differences in body height and how voices are gendered, and the last chapter addresses the political and cultural implications of the current debate on shared parental leave in Norway.

Human sex differences in body height are often discussed as a biological characteristic caused by ancient selection pressures, as a kind of remnant of our evolutionary history. In Chap. 7, Priscille Touraille problematizes this notion and explores different hypotheses about sex differences in human stature: selection on males to increase height and selection for women's increased height to decrease problems in childbirth, mate choice, and nutritional constraints. Finally Touraille provides a new hypothesis, positing that sex differences in height are a result of cultural gender systems that restrict nutrition for females and thereby influence biology and evolution. Using an interdisciplinary approach including anthropology, evolutionary biology, and gender studies, Touraille suggests that a cultural gender hierarchy may contribute to this biological characteristic.

In Chap. 8, "How do voices become gendered? A critical examination of everyday and medical constructions of the relationship between voice, sex, and gender identity," David Azul examines the often taken-for-granted assumption that voice characteristics have a biological basis in a person's physiology and morphology that results in a distinctive binary. This common-sense view has led to the medical pathologization of people who do not show "correctly" gendered voices and to the development of treatment approaches to what is perceived of as "gender-inappropriate" voices. Azul draws on empirical evidence contradicting the common-sense view that male/female vocal differences are straightforward reflections of a biological dimorphism. For example, sex differences in the fundamental frequency or pitch of the voice have been found to differ between cultures (one study showing that both female and male speakers of a dialect of Chinese speak on pitch levels above the "gender-dividing line"); there is a diversity of voices that do not conform to gender norms, and our perception of gendered voices is influenced by how we think about sex and gender. Azul proposes an alternative perspective on the "natural binary" of voices, namely, that the gendering of voices is the result of performance and interpretation practices that draw on conventional ideas about what constitutes "femaleness" and "maleness."

In the last chapter, Ole Jacob Madsen analyzes the arguments in the political debate around paternity leave in Norway, illustrating how nature-culture arguments influence politics and the debates, as an example of localized and situated negotiations of the meanings of gender in society. Scandinavian parental-leave politics, based on an ideological agenda to increase equal opportunities in society and women's participation in the workforce, has been progressive and led to unequaled leave benefits for parents. In the current debate about prolonging or abolishing the father's quota of parental leave in Norway, opinions differ. On the one hand, arguments about the naturalness of women doing the caring, how breastfeeding benefits children's health, how sex roles evolved during the Stone Age, and the stress caregiver change causes children are all used to advocate against a special father's quota of parental leave. In contrast, reports on equality and quality of life are used by other child psychologists to promote prolonged paternal leave. Nature and culture continue to be a hot topic for debate in contemporary Norway.

Different views on the role of individuals in society underlie the debate. Political ideology in Scandinavia has moved from stressing equal opportunities, societal context, and cultural influences on women's and men's roles in society toward an emphasis on individual autonomy, which is currently strong in the Euro-American political climate. The latter understanding of individuals as isolated from their social context has paved the way for increased emphasis on biological explanations, which has implications for individual citizens as well as the development of society.

With our diverse disciplinary backgrounds and approaches, we take on the task of questioning taken-for-granted assumptions about sex and gender and of encouraging critical thinking about sex differences. We show that conventional notions of females and males are not only a manifestation of cultural representation but also that gender bias in (supposedly objective) scientific research persists until today. We hope that this volume will broaden our readers' perspectives and give new insights into sex, gender, and biology.

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References

1. Gray, J. (1992). *Men are from Mars, women are from Venus*. New York: HarperCollins.
2. Bleier, R. (1984). *Science and gender, a critique of biology and its theories on women*. New York: Pergamon.
3. McCaughey, M. (2007). *The Caveman mystique, pop-Darwinism and the debates over sex, violence and science*. New York: Routledge.

4. Fausto-Sterling, A. (1992). *Myths of gender, biological theories about women and men*. New York: Basic books.
5. Fine, C. (2010). *Delusions of gender, the real science behind sex differences*. New York: W. W. Northon & Company Inc.
6. Jordan-Young, R. M. (2010). *Brain storms: The flaws in the science of sex differences*. Cambridge, MA: Harvard University Press.
7. Cameron, D. (2007). *The myth of Mars and Venus: Do men and women really speak different languages?* Oxford: Oxford University Press.
8. Valian, V. (1999). *Why so slow? The advancement of women*. Cambridge, MA: MIT Press.
9. Fausto-Sterling, A. (2000). *Sexing the body, gender politics and the construction of sexuality*. New York: Basic books.
10. Bagemihl, B. (1999). *Biological exuberance, animal homosexuality and natural diversity*. New York: St. Martin's Press.
11. Ah-King, M. (2009). Queer nature, towards a non-normative perspective on biological diversity. In J. Bromseth, L. Folkmarson Käll, & K. Mattsson (Eds.), *Body claims*. Uppsala: Centre for Gender Research, Uppsala University.
12. Ah-King, M., & Nylin, S. (2010). Sex in an evolutionary perspective: Just another reaction norm. *Evolutionary Biology, 37*, 234–246.

Chapter 2
Fundamental Differences Between Females and Males?

Root Gorelick, Jessica Carpinone, and Lindsay Jackson Derraugh

> *Hence, in regard to that most difficult question, what are the natural differences between the two sexes–a subject on which it is impossible in the present state of society to obtain complete and correct knowledge–while almost everybody dogmatizes upon it, almost all neglect and make light of the only means by which any partial insight can be obtained by it.*
>
> John Stuart Mill [1] (p. 22)

2.1 Introduction

John Stuart Mill's quote from *The Subjugation of Women* is as timely today as it was one and a half centuries ago. He approached differences between females and males from a purely human perspective, focusing on political science and psychology. From a modern perspective, Mill conflated sex and gender and, possibly for that reason, favored the role of nurture in the nature-nurture debates. By contrast,

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Charles Darwin, who was conservative with respect to sex (but very liberal with respect to race), especially in his epic *The Descent of Man, and Selection in Relation to Sex* [2], favored nature in the nature-nurture debates. Our purpose is not to rekindle the false nature-nurture dichotomy, which is an unfortunate historical artifact – nature and nurture interact far too much for a meaningful dichotomy. Instead we show that an evolutionary biological perspective can highlight problems with the customary differences between females and males and possibly illuminate previously unsuspected differences.

A definition of females and males should transcend as many species as possible. The act of sex (meiosis), vis-à-vis production of gametes (eggs and sperm) that have half the usual complement of chromosomes, is an ancient phenomenon that evolved before the diversification of life into animals, fungi, plants, and protists (single-celled organisms that have nuclei and other internal cell membranes). All animals and plants (by which we mean land plants, such as mosses, ferns, conifers, and flowers) have distinct eggs and sperm. Therefore, biological definitions of female and male should transcend all or most animals and plants.

Standard definitions of female and male when applied to humans are problematic, as anybody studying transsexuality and transgender can attest. There is simply too much fluidity, plasticity, and variation in human genitalia. We need look no further than the continuum of human phallic lengths to see that clitoris and penis are really the same (homologous) organs [3]. The location of the urinary opening is also variable, not always at the tip of the phallus in otherwise unambiguous males and not always near the base of the phallus in otherwise unambiguous females. For humans, Anne Fausto-Sterling [3] unmasked the false female-male dichotomy, at least for our diploid stage in which every cell nucleus has two copies of each chromosome. After extending her argument to all animals and plants, we then ask whether there is a female-male dichotomy for individuals with only one copy of each chromosome per nucleus (haploid), which for animals means eggs and sperm.

An overarching theme in women's and gender studies is elimination of essentialism, which is the notion that any entity, such as "female" or "male," has a fixed list of properties that it must possess. In tautological terms, essentialism means that there is some fixed essence of femaleness (or maleness) that all females (or males) possess.

Universal differences between the sexes are only expected if the evolution of two sexes from one sex only happened once (or, much less likely, via multiple origins of two sexes, followed by extinction of all species except those derived from one of the origination events). Multiple independent evolutionary origins of two sexes from a single sex would imply that differences between females and males should vary between organisms. With multiple independent origins, is it fair to use the same labels – female and male – for the resulting two sexes? In such instances, terminology would conflate and confound evolutionarily distinct events. Multiple evolutionary origins of sexes correspond with anti-essentialism, while single evolutionary origins correspond with essentialism.

2.2 Definitions

Our ideas will be easier to understand with the introduction of four technical biological terms describing a lifecycle (see glossary). All sexual organisms other than bacteria (which we do not consider sexual [4]) undergo the same cyclical process, known as alternation of generations. We begin by considering humans. Each cell nucleus in the zygote (in which egg and sperm nuclei have already fused in one cell), embryo, fetus, child, and adult has 46 chromosomes that come in 23 pairs – two copies of chromosome 1, two copies of chromosome 2, etc. – one copy inherited from each parent. Such organisms are known as *diploid*, where the prefix "di-" indicates that chromosomes come in twos. The diploid organism develops from the single-celled zygote all the way up to an adult by having each nucleus contain 46 chromosomes (a pair of each of 23 chromosomes), duplicating all 46 chromosomes, and then parsing those identical copies equally amongst two new nuclei. This copying process, preserving the number of chromosomes per nucleus, is called *mitosis*.

The diploid state alternates with the *haploid* state, in which each nucleus contains one copy of each chromosome (Fig. 2.1). The prefix "haplo-" means one. In humans and most other animals, haploid nuclei only exist in eggs and sperm

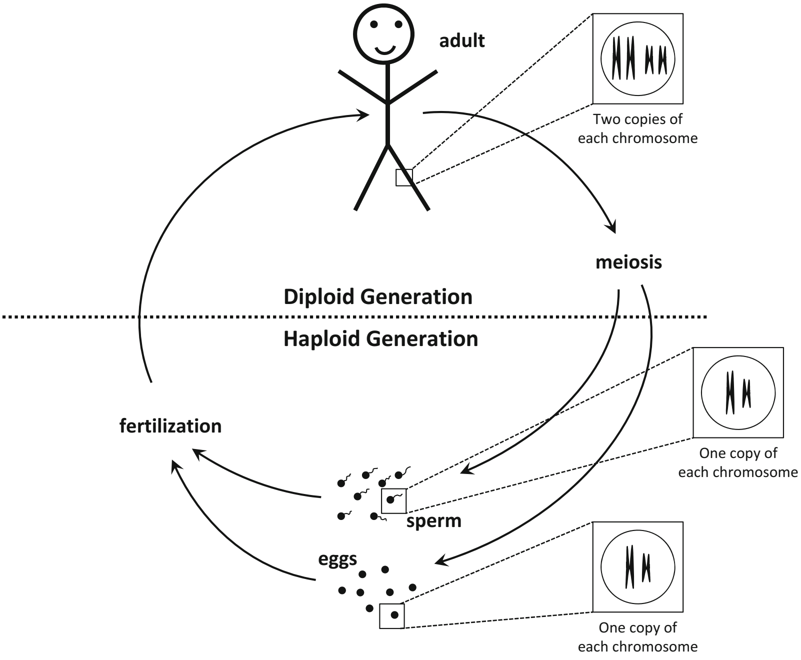

Fig. 2.1 Alternation of generations in animals

(human eggs and sperm contain one copy of each of the 23 chromosomes). Not all haploids are single celled. In haplodiploid animals, one sex (usually female) is diploid, but the other sex is haploid, with both sexes appearing morphologically similar, except for their genitalia. Haplodiploidy occurs frequently in insects and mites. Some plant stems and leaves can be composed of millions of cells with haploid nuclei, for example, the meter-long moss *Dawsonia superba*. These moss stems later produce haploid eggs and sperm via mitosis. The process by which an organism goes from diploid to haploid nuclei – that is, halving the number of copies of chromosomes per nucleus – is called *meiosis*.

There are two ways that an organism goes from a haploid back to a diploid state. The most common way is fertilization, where an egg and a sperm nucleus fuse, thereby restoring two copies of each chromosome. While much rarer and nonexistent in mammals, the diploid state can be restored by a haploid nucleus spontaneously duplicating all of its chromosomes at the start of meiosis, thereby producing diploid "gametes," which can start the next generation without fertilization, for example, whiptail lizards (*Aspidoscelis* spp.) [5]. In many ways it is surprising that this does not happen more often insofar as many cells in so-called diploid individuals have duplicated their chromosomes via the same mechanism and have four, eight, or more copies of each chromosome, such as cells in your liver and muscles, especially heart muscles. Organisms always use meiosis to go from diploid to haploid but can use either fertilization or simple chromosomal duplication to go from haploid to diploid states.

The purpose of this chapter is to determine whether there are fundamental ("essential") differences between females and males, differences that transcend as many different species as possible, such as all species but bacteria. We therefore take an evolutionary perspective to both debunk putative differences between the sexes and to construct possible unexplored differences.

2.3 Deconstruction: Debunking Accepted Differences Between Females and Males

We first examine traditional characterizations of female-male dimorphism, showing how these differences between the sexes break down in many instances. For a similar exposition applied to humans, see Fausto-Sterling [3]. We first look at macroscopic and microscopic differences between diploid parts of the lifecycle. The macroscopic differences encompass genitalia and secondary sexual characteristics, whereas microscopic differences encompass sex chromosomes (such as XY) and inheritance of portions of cells that are enveloped by internal membranes, such as mitochondria and chloroplasts. None of these circumscriptions of female and male work for defining sex based on fundamental differences; many of these even fail in mammals.

Alternatively, assuming that eggs and sperm are well-defined entities, we could try defining females as individuals that only produce eggs and males as individuals that only produce sperm. However, as Myra Hird [6] has elegantly detailed, there is way too much transsex – such as temperature-dependent sex determination and sequential hermaphroditism – to make these viable definitions, something brought home beautifully by Isabella Rossellini's video vignettes under the umbrella *Green Porno* (www.sundancechannel.com/greenporno).

Instead of looking at diploid individuals, maybe we would be better off looking at haploid individuals. For animals, this relegates us to the world of eggs and sperm, while plants have huge multicellular haploid parts. Nonetheless, conventional female-male dichotomies fail here too. The notions of eggs as large, rare, immobile, passive, long-lived entities and sperm as small, ubiquitous, mobile (with flagella), short-lived entities is incorrect in too many instances. What follows are details about female-male false dichotomies in both the diploid and haploid stage.

2.3.1 Sexual Differences in Diploid Individuals

A penis or lack thereof does not distinguish males from females. In mammals, clitoris and penis are essentially the same organs. Anne Fausto-Sterling has done an extraordinary job detailing the false dichotomy between the sexes in humans, especially in light of the huge number (1 in 60) of intersexuals [3]. While the typical human clitoris is shorter than the typical penis, some women have a clitoris that is sufficiently long to be used as an intromittent organ that can be inserted into female genitalia. It is more difficult to distinguish human females from males than it is in most other mammals because human males lack a penis bone, aka baculum. But not all male vertebrates have an intromittent organ. Male birds (except ducks) and amphibians lack any organ resembling a penis. Then there are some species in which males have a penis, but it is detachable: cephalopod (squid, octopus, etc.) hectocotyli, Malabar ricefish spermatophores, and banana slugs in which one copulating partner gnaws off the other's penis. Seed plants have pollen, which is a detachable "penis" (an expandable, intromittent organ) that grows through female tissues to deposit sperm near an egg. External genitalia are not a consistent difference between females and males across plants and animals. We will therefore have to look for more microscopic differences.

Female mammals (except for platypus and echidnas) have a pair of X chromosomes, while males have one X and one Y chromosome, with Y being shorter than X. This is in diploid individuals. By contrast, mature mammalian eggs only have one X chromosome, and sperm have either an X or Y chromosome. In birds, females are the sex with unequal length sex chromosomes, with W shorter than Z. Male birds have two Z chromosomes. Different length sex chromosomes in either females or males is, however, very unusual, only occurring in mammals, birds, a few reptiles, several fishes, a few insects, and a few plants. Almost all diploid animals and plants have both sex chromosomes of equal length, when they have sex chromosomes at all, rendering this an unacceptable way to distinguish females from males. Many species of animals have environmental sex determination and therefore no sex chromosomes, let alone sex chromosomes of different length [7].

Mitochondria – the metabolic power plants inside cells – are often said to be exclusively inherited from females, providing a way to distinguish female from male parents. While this is a more consistent criterion than any of the ones we have thus far discussed, there are still lots of exceptions. Many plants inherit mitochondria from both parents, many from just their female parent, many others just from their male parent. Mitochondrial inheritance patterns are largely maternal in animals, with the primary exceptions seen in mollusks with doubly uniparental inheritance, known as DUI [8]. Female DUI mollusks inherit all their mitochondria from their female parent. Male DUI mollusks have most tissues in which mitochondria are from their female parent, as is typical, but their gonads have mitochondria from their male parent. Looking at diploid individuals will not allow for unambiguous differentiation of females and males. Plus, as we will see below with ribosomes, determining sex by asking about inheritance of subcellular parts is not very practical because this would require examination of individuals in two successive generations and would require being certain about paternity of each offspring.

Maybe we would have better luck by simply defining females as individuals that produce eggs and males as individuals that produce sperm [9]. While a seemingly simple solution, this also has major problems. What sex is a hermaphrodite, who either simultaneously or sequentially produces both eggs and sperm? What sex are fish, such as members of the genus *Gobiodon*, which includes the coral gobies, that can change from producing sperm to producing eggs and back to producing sperm based on environmental cues, such as number of nearby individuals of the species producing eggs or sperm [10]? What sex should we call the many animals with environmental sex determination, such as turtles and crocodiles, who produce ovaries and eggs if as juveniles they are raised at one temperature, but who produce testes and sperm if raised at a different temperature?

There is no consistent way to define the sexes based on fundamental differences for diploid plant and animal individuals. We therefore shift gears and ask whether there is such a thing as female and male haploids, including sperm and mature eggs. Our motivation for examining haploid stages – and, in fact, our motivation for looking for fundamental differences between haploid females and males – arises from the realization that humans are exceptional in having such a dominant, long-lived, free-living diploid stage, with a haploid stage that is short-lived and highly dependent on the diploid individual. While the haploid stages may superficially appear relatively insignificant in any species, including humans, they are vital because the next generation cannot be created without them [4]. Compounding the relative importance of haploids, the haploid stage is large, long-lived, and free-living in almost all fungi and algae, in most single-celled species, many plants, and even some animals. Being that sex evolved before animals existed – in the progenitors of all plants, animals, fungi, protists, etc. – we should be able to garner insight about sex from these other organisms. Furthermore, we can think of no decent philosophical reason why haploid individuals, including single-celled human eggs and sperm, should not be considered individuals on equal footing with our large diploid selves, reiterating that we are taking a broad evolutionary perspective. Thus, it is irrelevant to us that diploid humans have a brain and a phallus, while haploid humans clearly can have neither.

2.3.2 Sexual Differences in Haploid Individuals

Conventional wisdom holds that all eggs and sperm are haploid, and that eggs and sperm can be readily distinguished. However, this is wrong. While most sperm are haploid, with very few exceptions, many eggs have additional copies of each chromosome (and so maybe should not be called gametes). In almost all animals, egg nuclei start out with two copies of each chromosome, double that to four copies, and then later halve this to two copies, and finally halve this again to become haploid (meiosis: $2n \rightarrow 4n \rightarrow 2n \rightarrow 1n$, where n represents the base number of chromosomes, e.g., $n = 23$ in humans). This fluctuation in number of copies is a normal part of the process – meiosis – that transitions organisms from diploid to haploid. In almost all animals except sea urchins and jellyfish (and their relatives), this process is arrested in eggs at some point in the process, before there is one copy per nucleus, and the process is only restarted and completed once an egg is fertilized by a sperm [11]. Thus, except in sea urchins and jellyfish, animal egg nuclei have either two or four copies of each chromosome when fertilized by a sperm whose nucleus has only one copy of each chromosome.

Even excepting sea urchins and jellyfish, requiring fertilization to halve their number of chromosomes is not a defining trait of females because there are many parthenogenetic (virgin birth) animals whose eggs complete meiosis without fertilization by sperm. In many animal groups, there exist a few species whose females manage to reduce their number of chromosomes down to one copy without fertilization. These individuals then take two of the four products of egg meiosis – namely, an egg cell and a polar body – and fuse these together to form a diploid zygote.

In all plants, eggs and sperm are haploid at the time of fertilization, but this is largely because the process of halving chromosomes (meiosis) occurs long before production of eggs and sperm. Plants produce a large multicellular stage in which every nucleus is haploid. It is from this stage that egg and sperm are later produced via mitosis. Sometimes a given haploid plant will produce only eggs, sometimes only sperm, and sometimes both. As with diploid animals, haploid plants can thus be female, male, or hermaphrodite. Consequently, instead of asking whether haploid individuals are female or male, we ask whether there are any fundamental and universal differences between eggs and sperm.

Before leaving the topic of sex differences between haploid individuals, we would be remiss to not presage that this tack does lead to one universal sexual difference: asymmetry of female meiosis versus symmetry of male meiosis. We defer discussion of this topic to the section on criteria that may work universally for distinguishing females from males.

2.3.3 Sex Differences Between Eggs and Sperm

Eggs are usually conceived of as large, passive, immobile, uncommon, and long-lived and sperm as small, active, mobile (propelled by flagella), common, and short-lived.

Unfortunately, none of these generalities are universally true. Below, we devote a short paragraph to each of these false dichotomies.

Humans are typical in that eggs are few, large, and very long-lived, while sperm are many, motile, and short-lived. Most eggs are produced prior to birth in humans, that is, they live for roughly a quarter to half a century – whereas sperm live for no more than one week. But sperm movement is not as efficient as many believe, largely moving from side to side (not forward) via their flagella [12]. Eggs also travel substantial distance, through fallopian tubes.

In some species, sperm are giant [13]. Some insects and cone-bearing seed plants produce enormous sperm with flagella. In these cone-bearing plants, sperm have thousands of flagella and grow to many times larger than the pollen grain that carried them to the female cone. In some small fruit flies (*Drosophila*), sperm are twelve times longer than the adult animals [14]. In the cases of insects with giant sperm, they usually produce very few sperm.

In some insects, males produce about the same number of sperm cells as females produce egg cells. Some species of ants produce colonies of several million individuals. A newly emerged (virgin) queen goes on a single mating flight during her lifetime, in which she mates with several males. She then lands on the ground, chews off her wings, and starts digging an underground colony from which she will never emerge and certainly never go on another mating flight. Over the next decade or two, she will form millions of eggs and fertilize them with the sperm that she stored from her one mating flight. Unlike in humans, these queen ants seem to undergo meiosis throughout their lives; hence their eggs may be shorter-lived than are the sperm the queens are storing. (Sue Bertram suggested that ant sperm may not be long-lived, but instead the queen ant may cryptically mate with her own sons while underground before her sons depart on their mating flight – but this has never been documented.)

Many animal and plant species have sperm that lack flagella. Flowering plants and conifers have sperm that lack flagella and are not independently motile. Their sperm are carried to the egg cell by the growing pollen tube, the erect detachable "penis" that grows through hollows in the female's tissues. Many groups of animals have amoeboid sperm, lacking flagella [15], including species of segmented worms, round worms, flat worms, crustaceans, spiders, insects, and even one group of fish, the freshwater elephant fish. While amoeboid sperm are somewhat mobile, they are very different looking from sperm with flagella.

While sperm may seem more active than eggs, their nuclei are not. After fertilization, sperm nuclei are passive, but egg nuclei are not. Sperm nuclei – of which there may be many per egg cell in many species – are relatively sedentary once inside an egg cell. By contrast, egg nuclei of at least one species of comb jelly (*Beroe ovata*) move about their own cytoplasm, querying other nuclei about suitability for fusing [16]. The path of the egg nucleus is very directed.

Thus far we have briefly debunked all the common female-male dichotomies or at least showed that these dichotomies are only applicable to small subsets of species, certainly not all animals and plants. It turns out that there may be universal ways to distinguish females from males, but these other dichotomies, if they exist, will be highly nuanced, taking a highly magnified and well-trained eye to possibly differentiate females from males.

2.4 Reconstruction: Possible Differences Between Females and Males

We hypothesize four fundamental differences between females and males, all four of which only work for haploid individuals and which derive from an evolutionary perspective. First, only females contribute the subcellular machinery (ribosomes) responsible for translating DNA into proteins. Unfortunately this requires us to keep track of inheritance between subsequent generations, which is not a convenient way to distinguish the sexes. Second, during the process of meiosis, both females and males go from one diploid nucleus to four haploid nuclei. However, in females, this cell division is always asymmetrical; in males it is always symmetrical. Third, only sperm have nuclei without any pores. All other cell nuclei have pores. Sperm nuclei also have some unique proteins and genes. Fourth, only sperm replace their nuclear membrane (without pores) without any chromosomal replication, replacing it with a membrane that has pores. Below, we devote a paragraph or two to each of these four hypothesized ways of distinguishing females from males. However, note that there is still a paucity of corroborative evidence for each hypothesis.

In most species, eggs are large and sperm are small. When there are exceptions, it turns out that sperm are relatively large, while eggs are still the relatively large cells that exist in all related species. This implies that there may be a reason for eggs being large. The difference in size is probably not due to mitochondria or chloroplasts because inheritance of these organelles is not strictly maternal, and when these organelles are inherited paternally, eggs are still relatively large and sperm relatively small. The egg supplies the next generation with lots of cytoplasm, including all the biochemical machinery needed to carry out most metabolic functions. This includes internal membranes (endoplasmic reticulum) and ribosomes on many of those membranes. Ribosomes are huge globs of protein and RNA that translate the genetic code into proteins. Tinker with cellular machinery other than nuclei and mitochondria, such as ribosomes, and you can get a radically different organism. We hypothesize that ribosomes are strictly inherited from the maternal parent (egg), although new ribosomes are later made under control of the zygote's or embryo's DNA and hence may then have paternal contributions. This will confound using these cellular components as a defining characteristic of females versus males. A more operational way of defining the sexes would be helpful.

We hypothesize that in males, meiosis is always symmetrical; in females, meiosis is always asymmetrical. In males, a nucleus with two of each chromosome undergoes a replication of each chromosome (four copies of each chromosome) followed by two successive partitions of those copies into four separate nuclei in separate cells. We hypothesize that the four male cells and four male nuclei are completely symmetrical and all completely functional. Females also undergo meiotic divisions; however, the four nuclei may be in one, two, or four cells; the cells may be of different sizes from one another; and only one of the nuclei will go on to form the next generation. Occasionally two nuclei go on to the next generation in which case it is always because these two fuse with one another rather than with a sperm nucleus.

We briefly discuss one apparent exception to the previous paragraph, which on closer inspection turns out not to be an exception. Some plants with so-called tetrasporic meiosis seem to have somewhat more symmetrical meiosis, but even here meiosis is fundamentally asymmetrical. Tetrasporic meiosis results in one cell containing four haploid nuclei [17]. However, one of these nuclei migrates to one side of the cell and will eventually give rise to an egg cell. Another nucleus moves toward the center of the cell and will eventually give rise to nutritional tissue (endosperm, product of double fertilization) that will not be inherited by the next generation. The remaining two nuclei move to the opposite end of the cell from the first cell and are effectively unused after fertilization, and thus they are not passed along to the next generation. The asymmetry in female meiosis is still evident with tetrasporic species, but is more subtle.

We hypothesize that sperm are the only cells lacking nuclear pores [18, 19]. Most nuclei, including egg nuclei, have pores to allow messenger RNA out of the nucleus. This allows the information of the DNA code held in the chromosomes to be shuttled to the ribosomes, thereby providing a template for protein production. Various signals that turn on and off genes also need to travel in the opposite direction through these nuclear pores, as does DNA itself. When a nucleus replicates, the DNA comes from outside the nucleus. Nuclear pores are not only holes (where passage of substances are highly controlled by protein in the pores) but also the place where the nuclear envelope is contiguous with the internal cell membranes of the rest of the cell. Sperm nuclei are utterly atypical in lacking pores and being quite compact. Messenger RNA cannot leave a sperm nucleus, and chromosomes cannot be replicated in sperm. We do not know of any exceptions. However, the place to look for exceptions may be in sperm of ants in which the female stores mature sperm for a decade or two. Another place to look may be flowering plants whose pollen can stay viable for many decades, especially if the sperm cells have already differentiated in the pollen grain (so-called trisporic, and not bisporic, pollen). Sperm nuclei also contain proteins that only seem to be found in sperm, such as the protein lamin B [20] and expression of the gene *BOULE* [21]. This may be correlated with sperm lacking nuclear pores.

Lack of nuclear pores in sperm poses a quandary after fertilization. In all species that people have looked at, egg and sperm nuclei replicate all their chromosomes before their nuclei fuse with one another to form a zygote nucleus (sand dollars, rabbits, mice, frogs, and humans [22]). We therefore suspect that pore-less sperm nuclei have to break open inside the egg cell and have all or a portion of their nuclear envelope replaced with a pore-laden nuclear envelope formed from the egg cell's internal membranes, aka the egg's endoplasmic reticulum. Once this occurs, the sperm nucleus is called a pronucleus. Only then can and does the sperm replicate its chromosomes. This is also an event that is unique to sperm. During all other cell divisions, including meiosis and mitosis, nuclear membranes are only replaced after a replication of all chromosomes [23]. With sperm pronuclear formation, membranes are replaced without any intervening chromosomal replication, which only occurs immediately after the new membrane is in place [24].

There does not yet exist a corpus of evidence for any of the above hypotheses for female-male differences between haploid individuals. But we also do not know of any evidence to debunk any of these hypotheses.

2.5 Concluding Remarks

How often have two sexes evolved from species with only one sex? For diploids, the standard answer is many times, where hermaphrodites evolved multiple times into separate diploid females and males [7]. This is completely consistent with an utter lack of *universal* differences between female and male diploid individuals. Remember, multiple evolutionary origins correspond with anti-essentialism.

How often did two sexes evolve at the haploid level? Isogamous and anisogamous literally mean equal gametes and unequal gametes, respectively. Humans are anisogamous because eggs and sperm are different from one another. There are, however, many algae and fungi in which fertilization occurs between gametes that appear to be identical, which is termed isogamous. The first sentence of this paragraph then translates as: How often did anisogamy evolve? The standard answer is many times [9, 25]. However, if any of our four hypothesized universal differences between haploid females and males is supported, then anisogamy probably only evolved once. This is both a biologically radical notion and also one that makes us haploid essentialists.

John Stuart Mill, Anne Fausto-Sterling, and Rebecca Jordan-Young [1, 3, 26] were right: It is not easy telling the two sexes apart. Even though sex change is more difficult in mammals than in many other animals, sexual ambiguity is still prevalent, even in humans. One of our goals is to emphasize that this sexual ambiguity is real. From an evolutionary perspective, any reasonable way of distinguishing females from males via fundamental differences fails unless we look at individuals whose cell nuclei are haploid. Thus, we cannot distinguish females from males in adult animals, newborn animals, nor fetuses but can only distinguish females from males in animal gametes. Even if an adult (i.e., diploid) individual is naked, their sex is indeterminate. If evolutionary biology provides a cogent way of distinguishing the sexes – and it is not obvious yet if it can – then this will require careful examination of haploid cells and their nuclei.

One reason for the ambiguity in distinguishing the sexes is that we insisted that definitions should apply as universally as possible. This forces us to look at some peculiar species, but that is the price that must be paid to come up with a universal and operational definition of the sexes. “Darwin admonished us not to ignore the ‘oddities and peculiarities’ of life as we see it today. It is by the analysis of such oddities that evolutionary history can be reconstructed” [27] (p. 26). It is also the price that must be paid because separate diploid sexes independently evolved multiple times from hermaphrodites. It is remotely possible that haploid female and male gametes (anisogamy) evolved independently multiple times from species with only one type of gamete (isogamy), although the evidence we presented here strongly implies that anisogamy only evolved once.

We hypothesize that there exists a female-male dichotomy only when examining haploid individuals. For animals, this means that eggs and sperm are conceptualized as individuals, albeit single-celled haploid individuals that may be dependent upon diploid individuals. For diploid individuals, there is no female-male dichotomy. We are thus diploid anti-essentialists, but reluctantly hypothesize an essentialist view of haploids. There is very little biological evidence in support of and none in opposition to our four hypothesized differences between haploid females and males (nuclear pores, nuclear proteins, symmetry of meiosis, inheritance of ribosomes). Further evidence could readily debunk any or all of these hypotheses. But existing biological evidence leaves us in the uncomfortable position of suspecting that there may be subtle but fundamental differences between haploid female and male individuals.

There are some curious societal implications to being diploid anti-essentialists but haploid essentialists, none of which we have the space to explore here. For instance, in law, there should be absolutely no basis for different treatment of diploid females and males. However, one could envision a biologically based unequal legal treatment of human haploid individuals, that is, eggs and sperm. While we certainly do not advocate basing normative (moral) legal decisions regarding storage of human gametes or contraceptive technologies on this science, others may try.

2.6 Summary

All well-known putative differences between females and males are ambiguous or with many exceptions. There is no female-male dichotomy when looking at individuals who have two or more copies of each chromosome per nucleus (diploid) because there are many hermaphroditic species, intersex individuals, and species with environmental sex determination. Not all males have an intromittent organ, such as a penis. We are diploid anti-essentialists. Even standard female-male differences are illusory when looking at individuals with only one copy of each chromosome per nucleus (haploid), such as animal eggs and sperm. Not all sperm are mobile with flagella, short-lived, small, nor have a Y chromosome. Not all mitochondria, nor other membrane-bound organelles, are inherited from eggs. However, here we hypothesize two essential differences between haploid females and males. (1) Sperm are the only cells whose nuclei lack pores in their nuclear membranes. Sperm nuclei uniquely contain certain proteins in their nuclear membranes, but this is probably due to lack of pores. Furthermore, due to lack of pores, sperm nuclear envelopes must be replaced prior to chromosomal replication. (2) Reduction from two to one copy of each chromosome per nucleus (meiosis) is always symmetrical in males, but never in females. If applicable, the terms female and male fundamentally apply only to haploid cells and their nuclei, not to diploid cells and their nuclei. Neither of our two hypotheses has been well tested, hence we are reluctant haploid essentialists.

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Glossary

Haploid A nucleus containing only one copy of each chromosome. A nucleus containing two copies of each chromosome (usually one from the mother and one from the father).

Mitosis A cell division that results in the production of two identical sets of chromosomes partitioned into two identical daughter cells. Both new cells have the exact same chromosomal content as the cell that produced them. Mitosis is akin to photocopying.

Meiosis A cell division that reduces the number of chromosomes by half (e.g., a diploid cell produces haploid cells). Each newly produced nucleus contains one copy of each chromosome (either maternal or paternal copy), although crossing over recombination can also produce chimeric chromosomes that are part maternal and part paternal. Meiosis is akin to shuffling cards.

Mitochondria Small completely symbiotic bacterial cells within every eukaryotic cell that are used for converting sugars to chemical energy.

Ribosomes Compact pieces of RNA and protein that translate messenger RNA (which itself was transcribed from DNA) into amino acids and proteins.

Endoplasmic Reticulum Internal cell membranes that form throughout the cell's cytoplasm and are used to construct the membrane of the cell nucleus. Presence of endoplasmic reticulum distinguishes eukaryotes from bacteria. Ribosomes are attached to a subset of the endoplasmic reticulum and the outer cell membrane.

References

1. Mill, J. S. (1869). *The subjugation of women*. London: Longmans, Green & Co. (Reprinted by Transaction Publishers in New Brunswick, NJ, 2001.)
2. Darwin, C. R. (1871). *The descent of man and selection in relation to sex*. London: John Murray.
3. Fausto-Sterling, A. (2000). *Sexing the body: Gender politics and the construction of sexuality*. New York: Basic Books.
4. Gorelick, R., & Carpinone, J. (2009). Origin and maintenance of sex: The evolutionary joys of self sex. *Biological Journal of the Linnean Society, 98*, 707–728.
5. Lutes, A. A., et al. (2010). Sister chromosome pairing maintains heterozygosity in parthenogenetic lizards. *Nature, 464*, 283–286.
6. Hird, M. J. (2006). Animal transex. *Australian Feminist Studies, 21*, 35–50.
7. Gorelick, R. (2003). Evolution of dioecy and sex chromosomes via methylation driving Muller's ratchet. *Biological Journal of the Linnean Society, 80*, 353–368.
8. Zouros, E., Freeman, K. R., Ball, A. O., & Pogson, G. H. (1992). Direct evidence for extensive paternal mitochondrial DNA inheritance in the marine mussel *Mytilus. Nature, 359*, 412–414.

9. Blute, M. (2010). *Darwinian sociocultural evolution: Solutions to dilemmas in cultural and social theory*. Cambridge: Cambridge University Press.
10. Nakashima, Y., Kuwamura, T., & Yogo, Y. (1996). Both-ways sex change in monogamous coral gobies, *Gobiodon* spp. *Environmental Biology of Fishes, 46*, 281–288.
11. Austin, C. R. (1965). *Fertilization*. Edgewood Cliffs: Prentice-Hall.
12. Martin, E. (1991). The egg and the sperm: How science has constructed a romance based on stereotypical male-female roles. *Signs, 16*, 485–501.
13. Matzke-Karasz, R. (2005). Giant spermatozoon coiled in small egg: Fertilization mechanisms and their implications for evolutionary studies on Ostracoda (Crustacea). *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, 304B*, 129–149.
14. Pitnick, S., Spicer, G. S., & Markow, T. A. (1995). How long is a giant sperm? *Nature, 375*, 109.
15. Morrow, E. H. (2004). How the sperm lost its tail: The evolution of aflagellate sperm. *Biological Reviews, 79*, 795–814.
16. Carré, D., & Sardet, C. (1984). Fertilization and early development in *Beroe ovata*. *Developmental Biology, 105*, 188–195.
17. Yadegari, R., & Drews, G. N. (2004). Female gametophyte development. *Plant Cell, 16*, S133–S141.
18. Lu, P., Zheng, H., & Zhai, Z. H. (2006). In vitro reassembly of nuclear envelopes and organelles in Xenopus egg extracts. *Cell Research, 16*, 632–640.
19. Iwamatsu, T. (2000). Fertilisation in fishes. In J. J. Tarín & A. Cano (Eds.), *Fertilization in protozoa and metazoan animals: Cellular and molecular aspects*. Berlin: Springer.
20. Poccia, D., & Collas, P. (1997). Nuclear envelope dynamics during male pronuclear development. *Development, Growth & Differentiation, 39*, 541–550.
21. Shah, C., et al. (2010). Widespread presence of human BOULE homologs among animals and conservation of their ancient reproductive function. *PLoS Genetics, 6*, e1001022.
22. Simmel, E. B., & Karnofsky, D. A. (1961). Observations on the uptake of tritiated thymidine in the pronuclei of fertilized sand dollar embryo. *Journal of Biophysical and Biochemical Cytology, 10*, 59–65.
23. Hartwell, L. H., & Weinert, T. A. (1989). Checkpoints: Controls that ensure the order of cell cycle events. *Science, 246*, 629–634.
24. Longo, F. J. (1987). *Fertilization*. London: Chapman & Hall.
25. Bell, G. (1978). Evolution of anisogamy. *Journal of Theoretical Biology, 73*, 247–270.
26. Jordan-Young, R. M. (2010). *Brainstorm: The flaws in the science of sex differences*. Cambridge: Harvard University Press.
27. Margulis, L., & Sagan, D. (1988). Sex: The cannibalistic legacy of primordial androgynes. In R. Bellig & G. Stevens (Eds.), *The evolution of sex*. San Francisco: Harper & Row.

Chapter 3
Genes and Hormones: What Make Up an Individual's Sex

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The twentieth century has seen the separation of sex and gender, separated at the hip in order to create ways of talking about the practical aspects of living in a gendered body in any given society [1]. Sex has come to refer to biological objects such as genes and hormones and gender to social aspects such as identity and behavior [2]. The word gender has given us an important tool to think about what was assumed to be natural or embedded in the body. We have come a long way from the end of the nineteenth century when anatomists claimed that women and certain races were naturally inferior to European men based on their brain size and other biological components [3].

Gender has given us a way to address disparity and prejudices by removing them from the "natural," or biological, body and placing them in the realm of social interaction where they best belong. Gender finds its place in the "social body," the concept of the body that interacts and performs a social role, and sex is placed in the "biological body," a world of molecular processes and interactions. However, this has often allowed the biological "facts" of sex to remain black boxes, un-scrutinized, and accepted "as they are." The biological myths that we will be looking at in this chapter are the relationship between chromosomes, hormones, and the biological image of sex in the body.

A professor once said to me, "Isn't it science's job to investigate differences, in this case gender differences in the body?"[1] It is important to understand how the social image of scientific information is being used when addressing the gendered body. Even if the intention is to help people, it is also used to establish a biological/natural rational for discrimination.

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[1] In reference to the Dorothy Sayers quote, "The first thing that strikes the careless observer is that women are unlike men. They are 'the opposite sex' (though why 'opposite' I do not know; what is the 'neighboring sex'?). But the fundamental thing is that women are more like men than anything else in the world." In Laqueur [4].

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Chromosomes and hormones obviously have a lot to do with how the body forms into male types and female types. What we will be looking at is how scientific research and medical practice frame chromosomes and hormones as creating absolute masculinity and femininity, as opposed to a spectrum of biological and physical gender types.

The first myth we will be looking at is the claim that sex chromosomes are the main biological factors determining phenotypic sex. Phenotype refers to the actual "type" into which the organism develops, representing the whole product of biological factors, where instead the genotype refers to the molecular material of the genes and chromosomes. In the early twentieth century, plant biologists realized there was a need for a separation of terms, seeing as the genotype did not always predict the phenotype.

The sex chromosomes, XX and XY, are called just that because they are considered to be the primary indicators of one's genetic, and therefore biological, sex [5, 6]. Since their discovery in the beginning of the twentieth century, they have come to represent the final argument as to what biological sex "really is," even though one might look or feel like one belongs in a different category. In specialized fields that deal directly with the development of the gendered body, it is recognized that the picture is much more complex. Intersexuality, which in the medical community is called disorders of sex development (DSD),[2] indicates the complexity that goes into forming gendered traits in the body, such as gonads, reproductive organs, and secondary sexual characteristics.

The second myth we will be looking at comes directly from experience following the medical care of people diagnosed with any of the myriad of syndromes that made up the medical category of DSD. The second commonly believed myth is that hormones have gender and belong to either the male body or the female body [8]. What we will see is that these two biological factors, genes and hormones, contribute to a wide spectrum of gendered bodies, as opposed to absolute and essential categories of male and female.

3.1 Chromosomal Sex

In biology we are taught that the XX chromosomes indicate a female individual and XY a male. We are told that the maternal egg contributes an X and the paternal sperm contributes either an X or a Y that then affects the sex of the developing tissue. In greater detail the Y chromosome is believed to contain a gene, the SRY, that suppresses Müllerian structures and female internal development, allowing for the creation of Wolffian structures[3] and male development [9]. In this model,

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[2] This name, coined in 2006, still receives a great deal of criticism for using of the word "disorder," Diamond, Reis, and others promoting instead the less stigmatizing term "divergence"; see Reis [7].

[3] Wolffian and Müllerian structures lead to formation of parts of the reproductive organs, named for Wolff who first describes the duct in 1759: Wolff, K. F., *Theoria generationis*. Doctoral dissertation, Halle and der Saale, 1759 and Müller in 1830 *Bildungsgeschichte der Genitalien.*

female development is seen as the default, while male development requires active intervention on the molecular and hormonal level. However, new research indicates that female fetal formation is also an "active" process,[4] requiring other genetic markers such as DAX-1 and WTN4 [12, 13].

However, individuals are extremely varied, and XX individuals are not always biologically female or XY individuals biologically male [11]. While any of these divergences are put into the DSD category, as pathological disorders, what is meant is that the gendered development of these individuals deviates from a statistical norm, not that they are sick or have life-threatening conditions. These divergences do not necessarily indicate potential health problems or gender dysphoria.

Gender dysphoria is a medicalized term for transgenderism, individuals who live a different gender role that the one assigned them at birth usually because of the appearance of their genitals. The medicalization of said gender dysphoria allows people to access medical resources such as hormone replacement therapy, but unfortunately stigmatizes transgender experiences as a mental disease category for people who are not mentally ill. Gender identity is related to the concept of gender role, but whereas gender role often represents culturally specific stereotypes and activities, gender identity refers to which of the gender categories one self-identifies with, regardless of stereotyped behavior. Most individuals who fall into the DSD category have consistent *gender identities*, much like non-DSD individuals, but may suffer from the stigma of the medical treatment they receive in childhood.

So what is biological sex then if not chromosomes? And how is it related to gender identity? To answer these questions, we need to step into one of the historical debates in the field of genetics. In the beginning of the twentieth century, the work of Gregor Mendel, of the famed plant breeding experiments, was rediscovered, and his theories were applied to the new visualization technologies that were identifying molecular structures inside the body. At first the gene was a concept, a unit of heredity, localized somewhere on the chromosome. Mendel had seen that not all plants had the same properties as their parents, but sometimes these traits appeared in future generations, leading to the belief that the information was passed along in the genes, but not necessarily expressed in one generation due to the other in the pair of genetic information being dominant. In 1911, Johansen developed the idea that living beings had genotypes, represented by the genetic or molecular material, and phenotypes, which instead was how they actually looked and functioned [14].

In the neo-Mendelian model, one gene determined one trait; therefore, the genotype directly codes for the phenotype. This model was embraced by Watson and Crick, famous for publicizing the double helix chromosomal form and also for establishing the central dogma of genetics that states that development is unidirectional. In this simplistic model, DNA creates RNA, which creates protein and then the organism itself. Following this central dogma, it should follow that an XY chromosome will always produce a body with the physical components

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[4] Butler poses the heterosexual binary as inherently hierarchical and insists that the search for the gene for sex (like the chromosome for sex) imposed a gender binary on the research question from the start [10] – a binary that reflects the Aristotelian paradigm that sees "male" as active and therefore superior. For an in-depth discussion, see Holmes [11].

associated with the male body, Wolffian structures, testicles, testosterone, penile structures with a urethra that exits at the tip, facial hair, lower fat-to-muscle ratio, not to mention all of the behavioral components that are associated with maleness. Whereas this direct link between XY chromosomes and male gender identity (as for transgender women) is not always the case, neither is the direct link between XY chromosomes and the development of a "male" body with all of the previously mentioned components. And not only that, sometimes a body has three sex chromosomes or only one.

Developmental models and epigenetics[5] address this discrepancy between what is considered the genotype, the genetic material, and the phenotype, referring to not just how a body looks but also its functional components [14]. In these newer models, the development of the body is seen to be highly influenced by the functions and processes of development, not just genetic material. Epigenetics draws on early *Drosophila* fly experiments that showed how flies would be born with different eye color and different wing types based on the environmental factors, such as heat or humidity, in which they developed.

One of the important factors of this research for our interest in the gendered body is that the experiments produced flies that showed how varied the results of genetic material can be, without producing nonfunctional or impaired bodies. Variations in the biological manifestation of the gendered body as is the case of DSD are believed to occur in 1 in 2,000 people [2, 15]. This statistic continues to increase based on increased knowledge about the body that expands our knowledge of physical variance and increased genetic testing. DSDs are often considered medical emergencies when they manifest what are considered either "ambiguous" genitals or genitals that do not conform with the assigned gender. Genital appearance is intensely private but also highly relevant to how we think about gendered bodies. The surgical manipulation of children's genitals to conform to social expectations is still a highly contested part of DSD treatment.

Generally when talking about DSDs, we are not talking about bodies that have functional problems, but bodies that are different in their gendered components. Genetic technology has "discovered" many more of these differences that do not fall in the realm of the social anxiety provoked by the genitals. In Italy, the two most visible patient groups represent two syndromes that have less to do with genitals and more to do with hormones and genetics. Androgen insensitivity syndrome (AIS/Morris syndrome) and Klinefelter's syndrome were both "discovered" in the 1940s [16]. Without the chromosomal information, many of the people with these diagnoses would not have any idea they were different from any other man or woman. The main functional problem they experience is sterility. However, the gendered body is made up of many different biological components besides just its reproductive capabilities.

AIS is a syndrome in which the XY chromosomes do not produce a recognizable male. As the body develops, Wolffian structures and "male" gonads form internally,

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[5] Epigenetics looks at how internal environmental factors affect genetic expression and development of the organism.

while externally "female" genitals and secondary sex characteristics develop. Clinically it seems that 1 in 20,000 people have AIS [2], although it also seems possible that there are many more who have not been diagnosed. Testicles are differentiated from ovaries through the function they perform in reproduction and their tissue differences. However, having "male" gonads does not make a person a man, especially when other female biological components are present. When doctors discover AIS, they often recommend the removal of the gonads, claiming they want to avoid identity problems in the woman diagnosed.

However, the identity problems reported by patients are based on the language the doctor chooses. If the doctor believes chromosomes dictate sex and gender, the doctor might tell patients they are biologically or genetically a man but physically a woman. However, as we have seen, chromosomal material is not the primary determining factor in the gendered biological body. In the case of AIS, other factors lead to a different developmental path. The gendered body has many different components from gonads to genitals to timbre of the voice. The vast majority of people with AIS have female gender identities, while some XX individuals reared as women do not.

In Klinefelter's syndrome individuals have three sex chromosomes, XXY, with the primary symptom being infertility. There are certain mutations that may also be associated with cognitive developmental issues. However, with the increase of genetic testing, Klinefelter's syndrome is now estimated to occur in 1 in 700 people, increasing the number of cases that have symptoms that disturb the person diagnosed. The Klinefelter body has been seen as feminine, with breast growth, or with an increased body fat-to-muscle ratio. Doctors recommend hormone replacement therapy, which does not affect cognitive development or sterility, but can masculinize the appearance of the body and affect mood and behavior. We will talk more about this aspect in the next part on hormones.

Klinefelter's syndrome reveals how common genetic variety can be, but specifically it also reveals that this biological variety still produces a healthy body. The variety in the gendered physical manifestation becomes a problem when it is measured against an idealized norm of the gendered body. There is still not much data on other health aspects related to Klinefelter's syndrome that are not in some way related to gendered expectations.

3.2 Hormones Make the Man, or the Myth That Hormones Have Gender

Endocrinology is the medical science that deals with the endocrine system, its diseases, and its specific secretions called hormones and is a fairly recent discipline in the history of Western medicine,[6] born in the twentieth century. The idea that there was a chemical substance that induced changes in the body related to

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[6] There is evidence that hormones were isolated from human urine in China in 200 BCE; see Temple [17].

reproduction and sexual behavior originated with the naming of the difference between the testicle and the ovary in the eighteenth century [4]. The gonads were used in experiments on animals, establishing their effects on the reproductive system in the nineteenth century [8, 18]. It was in the beginning of the twentieth century that the idea was accepted that hormones were a chemical secretion that circulated in the body, instead of being directly tied to the material of the gonads [19].

Historians such as Chandak Sengoopta have pointed out how medicine promoted the idea that the ovary and the womb were inherently linked to womanliness and behavior. However, this womanliness was imbued with social concepts about the negative aspects of so-called feminine traits such as weakness, mania, and hysteria. Early research into sex hormones instead focused on what is considered a positive trait of the male domain: sex drive. Biologist Charles-Edouard Brown-Sequard was initially ridiculed in 1889 when he addressed the Société de Biologie stating that he had injected himself with animal testicles as an experimental therapy to renew vigor and mental clarity [20]. However, soon afterward there was a rash of therapies and treatments that treated mostly men, but also women, with gonadal mixtures. These mixtures claimed rejuvenation properties in a manner that linked sexual prowess with energy and intellectual prowess [20, 21].

In the 1920s, the chemical structures of certain hormones were identified and the search for their sources to mass-produce them was on. The first striking discovery was that large quantities of estrogenic hormone (estrogen) were found not only in pregnant mares (but not in nonpregnant females) but also in stallions. Estrogens and progestogens were thought to be directly linked to the female reproductive process; therefore there was no good explanation for its appearance in male horse urine [20]. In the 1930s, “male” hormones were also found in female animals. So strong was the belief that hormones were gendered that researchers began looking for causes outside the body for the presence of “heterosexual” hormones, such as in food sources or environmental factors [20].

In the late 1930s, Lillie Research Laboratories was commissioned by the Rockefeller Foundation to perform detailed research on hormones and sexuality (meaning reproduction more than behavior) [21]. Some of Frank Lillie’s theories were founded on earlier experimental research with freemartins, pairs of calf twins, one XX, and one XY, in which the XX calf often developed male and female genitals. This led him to believe that in complex organisms, sex development is “taken over” by hormonal influences [20]. However, the explosion of hormone research continued to blur the clear link between male and female hormones and their corresponding sex hormones. Hormones were shown to have multiple effects on the body, regardless of gender, on the fat ratio, cardiac health, bone density, etc. Another prominent research group in Amsterdam started pushing for a change in terminology that would remove sex and the gendered labels from hormones [18, 20].

Lillie’s affirmations about the role of hormones in sex development served to dismantle eighteenth-century ideas about the dual-sexed deterministic nature of the gonads,[7] but now gave the hormones a determining role, that was also linked to the brain, and Lillie was opposed to desexing their terminology. Lillie saw sex as merely a name for our total impression of differences and therefore argued to maintain the sexed terminology [20].

Whereas the early history of hormone research focused on male sexuality and rejuvenation, from the 1930s onward, the focus turned on the female body, no longer through ovary removal but by hormonal therapies. Premenstrual syndrome (PMS) was defined in the 1930s and debated as to its causes throughout the 1950s. The idea of PMS, however, was never liberated from early hypotheses of hormonal intoxication and the image of the biologically irrational female. Historian Nelly Oudshoorn states that hormones became drugs looking for diseases [20], and in fact female reproduction now has hormonal products for everything from pregnancy prevention to increasing fertility.

So what happened to the debate surrounding the gendered nature of hormones and hormonal effects on nonreproductive systems? Well, they remain slightly hidden behind social concepts about the gendered body. In the medical clinic, one talks about male hormones and female hormones and theories such as hormonal imprinting, but in practice doctors use experimental data as best as they can to help people, which often means liberating "sex" hormones from their obligation to create absolute male and female bodies.

One highly influential idea about the gendered body is that behavior, intelligence, and the brain are different between the biological sexes. This is certainly true in part, but not in ways, that means one gender will have behavior or abilities that the other will not. In the 1970s, it was discovered that androgens are converted (aromatized) to estrogens before they interact with brain tissue [23]. Since then, researchers have proved and disproved gendered brain differences many times over.[8] The hormonal imprinting theory correlates gender identity with crucial time periods in early childhood and high hormone production periods, yet this too remains hypothetical. People who have hormone replacement therapy certainly report changes in mood, energy, and sexual desire (but not necessarily sexual orientation), but rarely changes in cognitive performance or ability or their own gender identity.

Hormones certainly shift what we consider secondary sex characteristics, the physical traits we see as male and female. Hormonal therapy can make a person feel and look more like their actual gender identity; however, hormonal therapy will not change a person's idea of who they are. Hormones are instead catalysts for physical,

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[7] In the eighteenth century, the "discovery" of the difference of the gonads in a precise quality (type of tissue, productive cycles, although not yet hormonal secretion) shifted the discourse on the gendered body from external qualities, such as genitals, to internal qualities, such as gonads [4]. In the case of what we now consider DSD/Intersex, medical practitioners were then known to insist that one adopt the social gender indicated by the gonads [22]; however, some doctors maintained that while the gonads indicated biological sex, one should have the legal/social gender that allowed one to be heterosexual [3].

[8] See Pinker/Spelke debate http://www.edge.org/3rd_culture/debate05/debate05_index.html

mood, and energy changes. These hypotheses about hormones are put into practice in different arenas. For transgendered people, hormones help adjust their body to fit their identity. The relationship of androgens to mood and depression has been explored in psychology, and androgens have been used to treat depression in women, obviously without the hormones having any effect on their gender identity.

"Male" and "female" hormones are not only found in all bodies but are necessary for all bodies. We saw earlier that in androgen insensitivity syndrome, doctors often wanted to remove the patients' gonads so as not to threaten their gender identity. Unfortunately patients have reported the disastrous results of having their autonomous hormone production removed, especially before puberty. As the syndrome name implies, people with this syndrome are insensitive to androgens; however, their body still uses and needs them, not for reproductive functions but for all the other processes in which hormones are involved, such as bone density, heart regulation, endocrine regulation, metabolism, mood, and energy, to name a few. Because these patients are women, they are then prescribed female hormone replacement therapy to help their body function. Researchers are increasingly proposing a mix of "male" and "female" hormones, so as to better replicate what bodies actually produce. In some countries, however, women have difficulty accessing therapies based on "male" hormones and are forced to use only estrogens and progestogens.

In Klinefelter's syndrome, one can see the physical effects of low testosterone levels. Certain physical traits can seem softer, which is associated with the female body and based on fat-to-muscle ratios. It is still unknown what part of the syndrome causes cognitive issues, although it has been localized to be more severe in 2 specific molecular markers. Hormone therapy for Klinefelter's syndrome focuses on the gendered presentation of the body and behavioral components that are considered masculine, such as high energy, assertiveness, and high sex drive. The hormone therapy does not affect the person's gender identity or sexual orientation, but many individuals say it makes them "feel more like themselves."

The expectations of what a female body and a male body are supposed to do and feel like are based on concepts that adapt social gender roles to biological material. Hormone therapy in the male body continues to be targeted at sex drive and energy, a tradition related to Brown-Sequard's self-experiments. The object of hormone therapy in the female body ranges from reproductive activity to "chemically induced" mood swings. These expectations of what hormones should do for the biological body are placed on the social body, in a manner that disregards the variety of biological gendered components. Rarely will a woman be advised to take hormone therapy to increase her sex drive, because a high sex drive is not considered a desirable component of femaleness. For example, a common effect of taking the birth control pill is reduced sex drive [24], but this is often not mentioned.

Sociologist and science studies researcher Celia Roberts states that hormones came to be seen as messengers of sex, active components that shaped the gendered body. The message attached to this concept is that these hormones also shape gendered behavior, identity, and sexual orientation. This may be true in fetal development, but as we have seen, it is not true in the course of one's life. Oudshoorn points out that this presumed link between reproduction and gendered identity in turn causes people to think of hormones as having a sex, belonging to either the male or female body. Hormones regulate reproduction and influence secondary sex characteristics. However, hormones also perform many important tasks, such as cardiac and metabolic regulation, regardless of the body's gender.

3.3 Conclusion

In this chapter, I link the discussion of myths of chromosomal sex to hormonal sex primarily because of the observed link in medical practice. In DSD syndromes, the body is explained and treated according to a picture that sees chromosomes, genes, and hormones as overlapping causal agents that create the gendered biological components of the body. Genetic material and hormone levels are analyzed along with the material of the body to diagnose and decide on treatment. Sometimes the hormonal treatment is intended to pulling the body in line with gendered expectations of esthetics and performance. Sometimes it is intended to remedy the health effects of the removal of otherwise healthy gonads. The right hormone therapy will also help regulate other important non-gendered biological systems.

The myths surrounding chromosomes and hormones link the biological to the social. Chromosomes move the body toward a certain developmental path, which contains many variants. Some of these variants are considered pathological, or part of a disease category, because they are not as common and they disrupt an image of pure maleness and femaleness. However, the symptoms of these variations are related to assumptions surrounding the gendered body, not actual functional problems. Many people who are considered within the norm will still have a varied gendered body, behavior, and identity.

Hormones help regulate gendered components in the reproductive system, but do not have a sex themselves, nor do they only act on the sexual system. Much is left to be discovered about these regulatory systems and what they imply for our overall health. The idea that there are sex differences in hormones, for example, can block a potential therapy from being used. The gendered body is created through a complex network of interactions, and it will only be when we eliminate all of our assumptions about what maleness and femaleness are that we will be able to see how it all really works.

References

1. Butler, J. (2004). *Undoing gender*. New York: Routledge.
2. Fausto-Sterling, A. (2000). *Sexing the body*. New York: Basic Books, 51–53.
3. Reis, E. (2009). *Bodies in doubt*. Baltimore: John Hopkins Press.
4. Laqueur, T. (1990). *Making sex: Body and gender from the Greeks to Freud*. Cambridge, MA: Harvard University Press, 161.
5. Painter, T. S. (1923). Studies in mammalian spermatogenesis II. The spermatogenesis of man. *Journal of Experimental Zoology, 37*, 291–336.

6. Miller, F. A. (2006, September). 'Your true and proper gender': The Barr body as a good enough science of sex. *Studies in History and Philosophy of Biological and Biomedical Science, 37*, 459–483.
7. Reis, E. (2009). *Epilogue divergence or didorder? The politicis of naming intersex* (p. 153).
8. Roberts, C. (2007). *Messengers of sex*. New York: Cambridge University Press, 33.
9. Thomas, D. (2006). *Wolffian and Mullerian structures*. Rome: Promoarch Eventi.
10. Butler, J. (1990). *Gender trouble feminism and the subversion of identity*. London: Routledge.
11. Holme, I. (2007). *Genetic sex: "A symbolic struggle against reality?"*. University of Exeter Doctoral thesis.
12. Nef, V. (2009). Complementary pathways in mammalian female sex determination. *Journal of Biology, 8*, 74.
13. Biason-Lauber, A. (2006). *Role of WNT4 gene in gonadal differentiation*. Rome: Promoarch Eventi.
14. Jabolonka, E., & Lamb, M. (2005). *Evolution in four dimensions*. Cambridge, MA: MIT Press, 28–113.
15. Dreger, A. D. (1999). *Intersex in the age of ethics*. Hagerstown: University Publishing Group, 42.
16. Caffaratto, M. T. (1963). *L'ermafroditismo umano. Storia-clinica-medicina legale*. Roma: Minerva Medica, 32.
17. Temple, R. (2007). *The genius of China: 3,000 years of science, discovery, and invention*. Rochester: Inner Traditions.
18. Sengoopta, C. (2006). *The most secret quintessence of life: Sex, glands, and hormones, 1850–1950*. Chicago: University of Chicago Press, 33.
19. Sengoopta, C. (2000). The modern ovary: Constructions, meanings, uses. *History of Science, xxxviii*, 425.
20. Oudshoorn, N. (1994). *Beyond the natural body*. London: Routledge, 18–108.
21. Rechtor, J. (1997). *'The Glands of Destiny': A history of popular, medical, and scientific views of the sex hormones in the 1920s America*. Doctoral thesis, University of California, Berkeley.
22. Dreger, A. D. (1998). *Hermaphrodites and the medical invention of sex*. Cambridge, MA: Harvard University Press.
23. Callard, P. R. (1978). Conversion of androgen to estrogen and other steroids in the vertebrate brain. *American Zoologist, 18*(3), 511–523.
24. Panzer, et al. (2006). Original research—Women's sexual dysfunction: Impact of oral contraceptives on sex hormone-binding globulin and androgen levels: A retrospective study in women with sexual dysfunction. *The Journal of Sexual Medicine, 3*, 104–113.

Chapter 4
Sexual Conflict and the Dilemma of Stereotyping the Sexes

Josefin A. Madjidian, Kristina Karlsson Green, and Åsa Lankinen

In a world bursting with information, an important human capacity is the ability to stereotype. Stereotyping enables us to quickly draw conclusions and is in many cases more beneficial than a time-consuming evaluation. As an example, we may consider snakes to be dangerous and avoid them, although careful evaluation would lead to the more correct conclusion that some snakes in fact are harmless. Although an important ability, stereotyping can also be an obstacle in other societal circumstances as well as in scientific research.

Some of Western society's most common stereotypes regard gender, ethnicity, and age. The issue of stereotyping these groups has been discussed, for example, with respect to job interviews. Research in social psychology has shown that an interviewing employer tends to draw stereotyped conclusions about the job seeker, which may reduce the possibility of finding the most suitable employee. Over the past 50 years, gender equity questions have been extensively discussed in Western societies. Massive criticism has been raised concerning how men and women are expected to behave and organize their lives in accordance with a traditional, and stereotypic, pattern. Although society is changing regarding gender issues, most of us still have a learned view of gender roles established since early childhood, and we may find it difficult to become aware of this stereotype.

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Among the general public, there is a stereotyped view of biology and what is "natural" male and female behavior. For instance, it is regarded as "natural" for women to stay at home with their children. Yet such statements rarely find support in biological science. Nature is too diverse and multifaceted to draw any simplified conclusions about what is "natural" in all cases, it simply depends on the circumstances. Besides, what is present in nature is certainly not always inherently good or something we wish to establish in our society.

Due to our capacity for stereotyping and because of the gender stereotypes present in our society, we believe that human stereotypic gender roles are also used in biological research, which not only affects the research but also reinforces the societal stereotypic view of biology as a science. In biological science, studies of mating behavior and reproduction are well established. Deeper knowledge in this area is crucial to answering central and complex questions in biology, such as how ecological and evolutionary processes influence living organisms. These processes may lead to evolution of new traits and eventually to speciation, explaining why we see so many different life forms in nature. It is often particularly important to examine differences between the sexes and their interactions. Here, the problem of stereotyping the sexes becomes obvious. Therefore, it is important both to elucidate this problem and to consider how the sexes are conceptualized in research.

Here, we address how gender stereotypes may affect research on the biological sexes, and also how a constrained view of biological science may reinforce sex stereotypes in society. First, we will give a short introduction to evolutionary biology, and more precisely sexual selection and sexual conflict, because we believe a basic understanding of evolution is a prerequisite for following our line of reasoning. Then, we will highlight how culturally gendered stereotypes are transmitted to biological studies related to the sexes. Finally, we will suggest how to avoid stereotyping in our research field and discuss what both the research itself and society can gain from increased open-mindedness and a broader perspective.

4.1 What Is Evolution?

Theories of sexual selection and sexual conflict are part of evolutionary theory, which Charles Darwin presented in 1859 [1]. The recognition of evolution and how it affects all life forms enlightened the biological sciences and provided a general theory that is useful for investigating diversity in nature. In essence, evolution means that a population, a restricted group of individuals, changes genetically over time. The evolutionary process is thus based on variation among individuals that is genetically heritable. Individuals that are more successful (with respect to surviving and producing offspring) – and thus better adapted – will pass on their variation to a larger extent and their genes will be represented to a higher degree in the next generation. Evolution leads to continuous changes within populations without any predestined direction or endpoint. It is truly impossible to know what species will still be around 1,000 years from now.

The main driver of evolution is natural selection. Natural selection concerns the capacity of an individual to survive and to reproduce. Examples of what may affect survival are a well-working immune system or advanced food-finding skills. Selection regarding reproduction, such as the ability of individuals to attract and acquire mates, is referred to as sexual selection [2]. Here, selection operates on characters or abilities that directly result in reproductive advantages.

4.1.1 Sexual Selection: How Traits That Affect Mating Success Will Change with Time

Sexual selection has shaped many of the elaborate traits we see among animals and plants in nature [3]. Two main features of the theory are mate choice and within-sex competition. Within-sex competition may include various means of dominance, for example, fighting, competition for territory, or singing the most attractive song. Mate choice is characterized by individuals of one sex choosing a partner based on certain traits, for example, the colorful plumages and long tails of birds. In the context of mate choice, it is important to realize that choosing a partner does not necessarily involve any cognitive ability. As long as a particular individual is preferred more often than others for whatever reason, this individual will give rise to more offspring. Thus, the genes coding for the trait in question, for example, a colorful plumage, will increase within the population generation by generation.

The sex that predominantly does the choosing or competing depends on the ecology and the demography, and indeed each sex could do both. However, only during the past decade have researchers acknowledged a similarity in male and female sexual strategies. The standard view was that females always choose and males always compete, which indicates that traditional sex roles in human society may have had an impact on biological science. This view does not consider the possibility of flexibility in sexual strategies, which may depend on ecological circumstances; it is more of a fixed rule. As a result, important information regarding *how* sexual selection operates is omitted [4]. Today, we not only know that both sexes are indeed capable of choosing and competing but also that these behaviors may shift during a lifetime. One example in fish is the two-spotted goby, *Gobiusculus flavescens*, where male and female behavior shift over the season depending on the abundance of either sex [5]. Initially males are more competitive while females choose, but as the number of males decreases over the season, the sexual strategies are reversed.

4.1.2 Sexual Conflict Between Males and Females in Relation to Mating

A relatively new research field within evolutionary biology is sexual conflict. This field is centered on the conflicting interests of the sexes in relation to mating. Although the sexes have a common interest in producing viable young, they may still use different ways of optimizing their own mating success. In a sexual conflict, one sex typically gains an advantage at the expense of the other, such that one sex more successfully mates, while the other is harmed in the process and suffers a mating cost. One example is the bumblebee, where males insert mating plugs in female genitalia, securing paternity of offspring, while the female is prevented from gaining the advantage of remating and producing higher-quality offspring [6].

The theory of sexual conflict was founded in the late 1970s by Geoff Parker [7]. Sexual conflict is not the same as sexual selection; it is rather described as an evolutionary conflict that can generate selection. Sexual selection may lead to sexual conflict, but other selective processes can also create the conflict [8]. As the field differs in major respects from the previously dominating sexual selection theory, several scientists regard sexual conflict as representing a paradigm shift in evolutionary biology [9]. For example, one important difference is the greater emphasis on the differing evolutionary interests of the sexes and also on the physical damage the sexes may impose on each other during their interactions.

Sexual conflict theory has helped to explain some unexpected behavior. One example is in bedbugs. Male bedbugs penetrate females with their penises anywhere on the female [10]. This behavior leads to higher mating success for the male and injury or risk of infection for the female. Another peculiar behavior that makes sense in the light of sexual conflict is exhibited in the penduline tit. In this bird, both males and females may desert the nest, although this will be detrimental to the present offspring [11]. Each sex will benefit if the other sex invests most in feeding the offspring, and more importantly, deserting behavior makes it possible to invest more in future offspring.

The theory of sexual conflict is broad and can be applied to all sexually reproducing organisms, as well as to plants and hermaphrodites (in which both male and female organs co-occur in the same individual), as the conflict always will arise when genomes from two individuals are necessary for producing offspring [12].

4.2 Active Males and Reactive Females: Gender Stereotypes in Sexual Conflict Research

Almost since the time Darwin [2] first presented his theory of sexual selection, it has been questioned and debated from a gender perspective. For instance, Darwin's theory has been criticized for focusing primarily on male reproductive success, as it often has been the variation among males and male traits that has been investigated, while females have been considered as a "limiting resource" for male mating [13]. The theory has also been criticized for describing male roles in active terms and female roles in passive terms [14]; traditionally the focus has been on female mate choice and male-male competition. That is, males have been active and operative, while females observed and chose them. Moreover, the terminology has been criticized because many terms describing the sexes' behavior have had human stereotyped and provocative connotations [13–15]. Females have often been described, for example, as "coy," and "rape" has been used to refer to forced copulation in animals, although rape in human society has numerous implications – social, psychological, and legal – that may not be present in nature [15]. Sexual selection research has become less stereotyped as a result of this criticism and perhaps also due to scientific progress and deeper understandings of the subject. For example, male mate choice and female-female competition have been detected in an increasing number of species and the terminology has improved.

However, the important gender discussion in sexual selection research, as outlined above, has not yet been incorporated into the research field of sexual conflict. Indeed, sexual conflict research has produced a more neutral view of the sexes, highlighting that each sex is evolutionary favored by increasing its own reproductive success despite the cost to the partner [16]. Nevertheless, each sex is still described with sex-specific terminology and assigned sex-specific characters. Even though a conflict trait always confers negative effects on the other sex, male behavior is described using active and offensive terms (harassment, manipulation, persistence), while female behavior is described using reactive and defensive terms (resistance, avoidance, reluctance) [17], (see Table 4.1).

Table 4.1 Terminology used to describe behavior in scientific articles on sexual conflict, which sex the term was for and its value connotation. The summary is based on the 30 most cited sexual conflict articles (in 2009) and the connotation of terms is classified by two independent researchers [17]

Terminology	Sex	Connotation
Adaptation	Both	Neutral
Counteradaptation	Both	Reactive
Resistance	Females	Reactive
Avoidance	Females	Reactive
Reluctance	Females	Reactive
Accept	Females	Reactive
Defense	Females	Reactive
Refusal	Females	Reactive
Response	Females	Reactive
Decreased mating rate	Females	*
Reduction	Females	*
Delay	Females	*
Intimidation	Males	Active
Manipulation	Males	Active
Coercion	Males	Active
Enticement	Males	Active
Exploitation	Males	Active
Force	Males	Active
Forced copulation	Males	Active
Harassment	Males	Active
Intimidation	Males	Active
Persuasion	Males	Active

(continued)

Table 4.1 (continued)

Terminology	Sex	Connotation
Seduction	Males	Active
Stimulation	Males	Active
Imposed cost	Males	Neutral
Persistence	Males	*
Increased mating rate	Males	*
Enforcement	Males	*
Harm	Males	*

* denotes terms that the evaluating researchers classified differently

A similar pattern of active males and reactive females is found in mathematical models, that is, important mathematical investigations of the theory conducted to generate testable hypotheses. Here, it is generally more common for females than for males to be assigned costs, that is, negative effects [17]. Presumably as a consequence of this bias, the experimental research has focused much more on female costs than on male costs. Male mating costs, however, can be found in nature. One example of males obviously suffering a cost comes from spider behavior, where females typically cannibalize males in connection with mating. Instead of reproducing, the male may be eaten – indeed a cost for the male. As an adaptation to this cannibalistic behavior, males have developed conflict traits allowing them to escape from the female, such as long legs, agility, and vigilance [16]. Another example of a negative male mating cost is in the African topi antelope, where females enhance their probability of mating with favored males through aggression toward mating pairs. This behavior causes the male to counterattack and resist the mating attempt, at the cost of losing energy (i.e., suffering an energetic cost) [18]. Few empirical studies on sexual conflict have considered the costs to both sexes in the same study. However, Holland and Rice [19] examined how both sexes were affected by a conflict over mating rate. Interestingly, though the authors find that there is a cost of sexual conflict to both sexes, male traits are still referred to as "harmful," while female traits are referred to as "resistance." Recalling that sexual conflict theory states that either sex will strive to increase its own mating success at a cost to the opposite sex, this antagonism ought to be reflected both in the subjects investigated and in the language used. As this is not the case, it seems as if sexual conflict research, too, has adopted sex stereotypes and a traditionally gendered terminology.

The terminology used for describing behavior and traits may further affect the choice of study species. Thus far, only a few studies have investigated sexual conflicts in organisms outside the group of animal species with separate sexes. This is unfortunate, as a general theory should not be based on only a few examples. Active actions, such as force, may be difficult to envisage in plants and hermaphroditic animals, and the gendered terminology may limit the choice of research organism. That is, sex-stereotypic terms, such as harass and resist, certainly give a picture of one male and one female engaged in reproduction, excluding sexual systems not easily associated with such terms. If we exclusively select study species to which sex-stereotypic terms are easily applied, then sex stereotypes will be reinforced – not because they are general but because the selection of study species is biased and they are the only alternatives investigated.

4.3 Stereotyping in Sexual Conflict Research: Problems for Science and Society

The dilemma of generalizing and stereotyping is a never-ending story. As much as we are aware of the problems it can cause, we still need to categorize information. In this process, many mistakes of stereotyping will be made. Here, we have focused on the use of stereotypic portrayals of sexual strategies in biological research. Researchers, like everyone else, are influenced by societal norms. It is not that difficult to find parallels between stereotypic views of women and men and the ways in which females and males have been described in the sexual selection research. This has been noted in the field of sexual selection. However, when sexual selection theory developed into the new field of sexual conflict, the discussion on gendered terminology was somehow lost. Instead, this new theory created its own sex stereotypes, involving active males and reactive females.

The gendered terminology of sexual conflict may in fact have affected the development of the theory of sexual conflict, especially regarding how the cost of mating is assumed to influence either sex. Apparently, costs are imposed by active traits (of males) on an individual (female) possessing conflict traits or behavior that has a more vulnerable resonance (e.g., resistance). Thus, only active terminology implies that a trait should infer costs. In this case, the scientific language used could be an important factor in shaping the gender bias as regards costs. In turn, this could strongly affect which experiments are conducted and thus which research results are available to consider. What would the sexual conflict research look like today if neutral terminology had been used? Perhaps we would know more about the male costs of mating, reproduction in hermaphrodites and in plants, and perhaps “new” behaviors in males and females would have been discovered. More importantly, we would probably have a better general knowledge base in the area of sexual conflict. Our research to date has shown that stereotyping may indeed have limited the research questions, leading to a constrained view of sexual selection/sexual conflicts in nature. We argue that the continued use of stereotypic terminology and a narrow interpretation of the theory should be avoided as far as possible.

4.3.1 How Can Researchers Avoid Using Sex-Stereotypic Terminology?

The next question will then be how we can avoid using sex-stereotypic terminology in research. One first step for researchers is to be aware of their own most common generalizations. We suggest that one way to start thinking about these issues is to reflect on them more regularly, and not only on specific occasions. It would then be easier to reach a level of awareness where neutral terms and open-mindedness about what sex implies are the norm, and gender stereotyping is acknowledged as a problem. If this problem is not acknowledged, it will be difficult to publish critique both because such critique will not be regarded as important and because the content will be misunderstood. As a result, we will not be able to reach other scientists to discuss these issues. Ultimately, the scientific bias caused by stereotypic gender conceptions should be treated in the same way as scientists treat other confounding factors. This is particularly important because scientific theories are continuously changing, as is the case of sexual selection theory, and awareness of gender issues will increase the quality of theory development.

Indeed, sexual conflict theory has a great potential to explain biological diversity. By avoiding stereotypic thinking, sexual conflict researchers may make important discoveries that can improve sexual conflict theory. One way to minimize our prenotions about sexual strategies is to ask the same question for both sexes or to conduct the same experiments on both sexes [20]. This method would allow us to explore how each sex evolves but in a neutral fashion. However, for practical reasons this is not possible in all species. We suggest that hermaphrodites may be particularly appropriate subjects for conducting symmetrical experiments and challenging stereotypic reasoning in sexual conflict research.

4.3.2 Improved Communication and Possibilities to Kill Myths

What effect does the use of sex-stereotypic terminology in biological research have outside the scientific community? One problem is that the general public might assume that stereotypic descriptions of males and females are “natural,” especially when new knowledge is unintentionally framed in terminology referring to coy females and competitive males. The risk is that this kind of stereotyping will reinforce gender stereotypes. If older stereotypes are to fade away, researchers must not only perform unbiased research but also be more active in *correctly* communicating up-to-date research to the public. It may not always be possible to change gender-stereotypic views and what is perceived as natural through information about new research results, as many of our gender preconceptions are affected by strong feelings related to learned values. Even so, scientific research is expected to provide the public with scientific knowledge that can be utilized when needed, such as for challenging myths.

Biology is sometimes stressed as an argument for explaining and justifying patterns we see in society, for example, traditional human sex roles. This is based on an inaccurate and limited view of what biological sex actually entails. Recall the penduline tit, a bird species in which both parents may desert the nest. This kind of information has the capacity to kill myths. In nature, it may be very "unnatural" for females to assume greater responsibility for parental care, as in fishes where males commonly provide unipaternal care.

If anything, biology and evolutionary science can help explain the fact that flexibility and adjustment to ecological circumstances are important capacities, and that individuals, in a wide array of species, do change their sexual strategies. Biological research does indeed confirm that nature is much more flexible than what is typically described.

References

1. Darwin, C. (1859). *On the origin of species by means of natural selection*. London: John Murray.
2. Darwin, C. (1871). *Descent of man, and selection in relation to sex*. London: John Murray.
3. Andersson, M. (1994). *Sexual selection*. Princeton: Princeton University Press.
4. Clutton-Brock, T. H. (2007). Sexual selection in males and females. *Science, 318*, 1882–1885.
5. Forsgren, E., Amundsen, T., Borg, Å. A., & Bjelvenmark, J. (2004). Unusually dynamic sex roles in a fish. *Nature, 429*, 551–554.
6. Baer, B., Morgan, D. E., & Schmid-Hempel, P. (2001). A nonspecific fatty acid within the bumblebee mating plug prevents females from remating. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 3926–3928.
7. Parker, G. A. (1979). Sexual selection and sexual conflict. In M. S. Blum & N. A. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 123–166). London: Academic.
8. Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society B, 361*, 235–259.
9. Tregenza, T., Wedell, N., & Chapman, T. (2006). Sexual conflict: A new paradigm? *Philosophical Transactions of the Royal Society B, 361*, 229–234.
10. Stutt, A. D., & Siva-Jothy, M. T. (2001). Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius*. *Proceedings of the National Academy of Sciences of the United States of America, 10*, 5683–5687.
11. Szentirmai, I., Székely, T., & Komdeur, J. (2007). Sexual conflict over care: Antagonistic effects of clutch desertion on reproductive success of male and female penduline tits. *Journal of Evolutionary Biology, 20*, 1739–1744.
12. Bedhomme, S., Bernasconi, G., Koene, J. M., Lankinen, Å., Arathi, H. S., Michiels, N. K., & Anthes, N. (2009). How does breeding system variation modulate sexual antagonism? *Biology Letters, 5*, 717–720.
13. Hrdy, S. B. (1999). *The woman that never evolved*. Cambridge, MA: Harvard University Press.
14. Martin, E. (1991). The egg and the sperm: How science has constructed a romance based on stereotypical male-female roles. *Signs, 16*, 485–501.
15. Gowaty, P. A. (1982). Sexual terms in sociobiology emotionally evocative and paradoxically jargon. *Animal Behaviour, 30*, 630–631.
16. Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton: Princeton University Press.
17. Karlsson Green, K., & Madjidian, J. A. (2010). Active males, reactive females – Stereotypic sex roles in sexual conflict research? *Animal Behaviour, 81*, 901–907.

18. Bro-Jørgensen, J. (2007). Reversed sexual conflict in a promiscuous antelope. *Current Biology, 17*, 2157–2161.
19. Holland, B., & Rice, W. R. (1999). Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proceedings of the National Academy of Sciences of the United States of America, 96*, 5083–5088.
20. Gowaty, P. A., Steinichen, R., & Anderson, W. W. (2003). Indiscriminate females and choosy males: Within- and between-species variation in *Drosophila*. *Evolution, 57*, 2037–2045.

Chapter 5
Sex, Gender, and Evolution Beyond Genes

Jonathan P. Drury

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

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[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

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[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.

References

1. Hartman, M. (2010). *"A gene for entrepreneurship?" Marketplace, American Public Media*. http://marketplace.publicradio.org/display/web/2010/03/03/pm-entrepreneur-gene/. Posted 3 March 2010, accessed 17 Sept 2010.
2. Dawkins, R. (1989 [1976]). The selfish gene (2nd edn.). Oxford: Oxford University Press.
3. Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions*. Cambridge, MA: MIT Press.
4. Burt, A., & Trivers, R. (2006). *Genes in conflict: The biology of selfish genetic elements*. Cambridge, MA: Harvard University Press.
5. Bilkó, Á., Altbäcker, V., & Hudson, R. (1994). Transmission of food preference in the rabbit: The means of information transfer. *Physiology & Behavior, 56*, 907–912.
6. de Waal, F. B. M. (1995). Bonobo sex and society. *Scientific American*, March 1995 issue, pp. 82–88.
7. Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: Fitness consequences of social partner choice in female house mice. *Animal Behaviour, 75*, 801–808.
8. West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
9. Waddington, C. H. (1956). Genetic assimilation of the bithorax phenotype. *Evolution, 10*, 1–13.
10. Webster, M. S., Varian, C. W., & Karubian, J. (2008). Plumage color and reproduction in the red-backed fairy-wren: Why be a dull breeder? *Behavioral Ecology, 19*, 517–524.
11. Karubian, J. (2008). Changes in breeding status are associated with rapid bill darkening in male red-backed fairy-wrens Malurus melanocephalus. *Journal of Avian Biology, 39*, 81–86.
12. Gowaty, P. A. (2008). Reproductive compensation. *Journal of Evolutionary Biology, 21*, 1189–1200.
13. Gowaty, P. A., et al. (2007). The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. *Proceedings of the National Academy of Sciences , 104*, 15023–15027.
14. Young, A., et al. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences , 103*, 12005–12010.
15. French, J., Abbott, D., & Snowdon, C. (1984). The effect of social environment on estrogen excretion, scent marking, and sociosexual behavior in tamarins (Saguinus oedipus). *American Journal of Primatology, 6*, 155–167.
16. Hrdy, S. B. (1999). *Mother nature*. New York: Ballantine Books.
17. Janzen, F. J., & Paukstis, G. L. (1991). A preliminary test of the adaptive significance of environmental sex determination in reptiles. *Evolution, 45*, 435–440.
18. Janzen, F. J., & Paukstis, G. L. (1991). Environmental sex determination in reptiles: Ecology, evolution, and experimental design. *Quarterly Review of Biology, 66*, 149–179.

19. Ah-King, M., & Nylin, S. (2010). Sex in an evolutionary perspective: Just another reaction norm. *Evolutionary Biology, 37*, 234–246.
20. Waage, J., & Gowaty, P. (1997). Myths of genetic determinism. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology: Boundaries, intersections, and frontiers*. New York: Chapman & Hall.

Chapter 6
Beyond Coy Females and Eager Males: The Evolution of Darwin's Sexual Selection

Thierry Hoquet

To a biologist, the meaning of sex is complex. In a general sense, "sex" designates any process of genetic recombination [1]. This broad definition also applies to lateral transfer of genes in bacteria and viruses and is not restricted to reproduction. A narrower definition of biological sex for vertebrate animals is directly linked to reproduction. A third meaning is associated with sex as reproduction: it signifies a distinction between "two sexes": "males" and "females". But what are the "sexes", and on what grounds should they be distinguished: merely morphological (males and females differing in their internal and external appearance), gonadic (i.e. based on the possession of testes or ovaries), or genetic (males and females being endowed with two different sets of chromosomes)? Sex as reproduction and sex as the sexes are two different concepts, but they are closely related in the biological scheme, as the most general (and minimal) criterion that biologists use to define the sexes is that "males" make small gametes while "females" make larger gametes—both gametes being involved in sexual reproduction. But a definition invoking production of gametes is conventional and there are exceptions (especially among non-vertebrate living beings) [2]. According to this technical definition, in vertebrate animals the two sexes are equated with two types of gametes or reproductive cells: "the smaller of the two gametes is called a sperm and the larger an egg", which does not mean that "sperm" come cheap [3].

Sexual selection is the concept that Darwin devised to account both for human racial divergence and for sexual dimorphism or the difference of aspect between individuals of the two sexes, males and females. Darwin was struck by the fact that some traits could not have been shaped by natural selection, as they were likely to be detrimental to the survival of their bearers, being wasteful in terms of resources and energy and making their bearers more conspicuous or vulnerable to predators: brightly coloured plumages in birds or exuberant singing in frogs may attract

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predators as well as potential mates. Sexual selection argues that what an individual loses in terms of lower probability of survival may be more than compensated by increased probability of having more couplings or attracting better mates. In modern understandings of biological processes, there is no essential reason to distinguish sexual selection sharply from natural selection: sexual selection is part of natural selection, both contributing to the fitness of the individual and leading to a greater transmission of its hereditary units (genes).

This paper starts with an analysis of Darwin's argument and seeks to understand how sexual selection has suggested different models for the behaviours of males and females, following what I call the "two-sex" hypothesis: the idea that the study of animal behaviour should follow a divide between two different strategies. The two-sex hypothesis suggests that males and females have different strategies, namely, that (1) all males act in the same way (promiscuously) and (2) all females act in the same manner (choosiness). This applies to all males (or females), both within one species and in any species considered. The alleged universality of sexual selection theory is clearly evinced in a milestone paper by A.J. Bateman, where he states that, in non-hermaphrodite organisms, "there is nearly always a combination of an undiscriminating eagerness in the males and a discriminating passivity in the females", a statement that is said to apply to drosophilae and to "derived monogamous species (e.g. man)" [4].

More recently, theoretical attempts have been made to overcome the two-sex hypothesis. Whether or not one agrees that there are two sexes in nature (i.e. two types of gametes), one may challenge the idea that all sperm-producers or all-egg producers, whatever their species, should behave according to the same patterns. This paper shows how sexual selection theories developed away from the two-sex hypothesis to more gender-neutral models: where the analysis of reproductive tactics pays more attention to interspecific and intraspecific differences in behaviour; and where success is increasingly explained not by mating strategies but by taking into account time allocation and random encounters between individuals.

Starting with Darwin's theory, this paper emphasises its male-centred biases, often explained away by the fact that his views were obscured by the prejudices of the Victorian era. In contrast, other social contexts, like the sexual liberation and sex equality movement of the 1970s, triggered strong criticism of male chauvinism in biological theory and paved the way for new models and observations. Accordingly, this paper focuses on the development of sexual selection theory, especially by showing how feminist biologists in the 1970s–1980s have led sexual selection away from stereotypic sex notions, such as "eager" males and "coy" or "monogamous" females.

6.1 Darwin's Sexual Selection

The concept of sexual selection has always been a powerful vector for myths of sex and gender, based on the assumption of a two-sex dichotomy. On the basis of Charles Darwin's work, two mechanisms were put forth under this heading: male competition and female choice. Both can be seen as components of a single mechanism: one being *intrasexual* (within one sex) and the other *intersexual* (between the sexes). This framework stresses competition between males for sexual access to females, engendering more or less pronounced sexual dimorphism and the development of armaments and ornaments in males.

Darwin proposed the concept of sexual selection to account for the differences in instincts and anatomy between male and female organisms. In principle, sexual selection applies to both males and females: it "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction" [5]. But in fact, Darwin makes very clear that the special features of females (organs for the nourishment or protection of the young) are not his concern (they "do not here concern us", vol. I, p. 254). Therefore, sexual selection can be described as a theoretical device mostly focusing on the evolution of males: the hypothesis that certain features of some males (not all) have been transmitted to their male offspring, as their bearers had gained an advantage over their rivals in accessing potential mates, fertilising eggs and leaving progeny. Darwin clearly states his concern: "Our difficulty in regard to sexual selection lies in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of offspring to inherit their superiority than the beaten and less attractive males. Unless this result followed, the traits which gave to certain males an advantage over others could not be perfected and augmented through sexual selection" [5]. If sexual selection today designates differential reproduction due to mate competition [6], without any particular reference to males, it is nonetheless clear that females were mostly left out of Darwin's picture, as was noted by the Unitarian minister Antoinette Blackwell as early as 1875 [7].

In the *Origin of Species* [8] (1859, pp. 87–90), the features attributed to sexual selection are of two sorts: weapons of the males, useful in fights with their rivals; ornaments of the males, such as beautiful feathers or songs, which may be preferred by females. Male–male competition explains such features as the antlers of deers, the horns of antelopes and of many beetles—any feature that supports males in their competition with other males of the same species, allowing winners access to the greatest number of females. But Darwin argued that traits such as the peacock's tail, with no visible utility in intrasexual competition, must be selected by another type of factor. In Darwin's words, "the peacock with his long train appears more like a dandy than a warrior, but he sometimes engages in fierce contests" [8] (1871, vol. II, p. 46). Darwin argued that females have a sense of beauty and are excited and charmed by the extravagant ornaments and displays of the best males. It seems that male–male competition was easily accepted by Darwin's contemporaries, but that many (like A.R. Wallace) refused to accept the idea of female choice: How could a sense of beauty possibly be found among female deers and birds, let alone insects? The question had long been of concern to Darwin, who wrote in his notebooks: "How does hen determine which most beautiful cock, which best singer?" [9].

Darwin's 1871 book *The Descent of Man and Selection in Relation to Sex* devotes two thirds of its content to sexual selection and goes more into detail.

Sexual selection can account for (1) sense organs, which may help in locating a potential partner; (2) locomotion organs, which may help in reaching the partner; and (3) prehensile organs, which can help in holding the partner while mating. In such cases, it is very difficult to differentiate between natural and sexual selection. In other cases, natural and sexual selection seem to contradict each other. Apparently, sexual selection primarily concerns extreme nonadaptive features such as the cumbersome train of the peacock. Understood from the peacock's perspective, sexual selection has to account for the evolution of extravagant "secondary sexual characters"—those "which are not directly connected with the act of reproduction" [8] (1871, vol. I, p. 253). Where utilitarian natural selection is ineffective, sexual selection will do the job. But it would be wrong to assume that sexual selection accounts for all sexual differences. Darwin clearly acknowledges that, in many instances, "it is scarcely possible to distinguish between the effects of natural and sexual selection" (vol. I, p. 257): for instance, prehensile organs may be helpful in grabbing food or in holding the sexual partner while mating.

Besides, the power of sexual selection is not limited to morphological traits: it also extends to habits and behaviours. In Darwin's text, the males are described as enterprising and not very discriminating, for instance male birds: "In all ordinary cases the male is so eager that he will accept any female, and does not, as far as we can judge, prefer one to the other" (vol. II, p. 121); or with insects and crustaceans, "the male is the more active member in the courtship of the sexes" (t. I, p. 272). On the other hand, females are depicted as shy, reticent or "coy": "The female, on the other hand, with the rarest exception, is less eager than the male. As the illustrious Hunter[1] long ago observed, she generally "requires to be courted"; she is coy, and may often be seen endeavouring for a long time to escape from the male" (vol. I, p. 273).

Darwin is willing to acknowledge the existence of exceptions to the above depictions[2]; still he thinks they encompass a general pattern, and that the exceptions are few. The cited sentences have been widely quoted and criticised as projecting Darwin's Victorian prejudices on the behaviours of animals.

As early as 1875, Antoinette Blackwell (1825–1921) noted that both male competition *and* female choice aim at explaining how *male* traits evolved by conferring a benefit to their bearer in situations of fight or seduction [7]. The Darwinian mechanisms aim to explain how evolution adds to the features of males, while female traits are considered to be basic. Neither intra- nor intersexual selections provide an explanation for female traits.

Besides, Darwin's distinction between coyness and eagerness had an important legacy regarding the ways in which sexual dimorphism was conceived of at the end of the nineteenth century. Two biologists based in Scotland, Patrick Geddes (1854–1932) and John A. Thomson (1861–1933), suggested that the features

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[1] John Hunter (1728–1793), whose *Observations on certain parts of the animal oeconomy* (1786) were republished in 1840, with annotations by Richard Owen.

[2] Darwin did not think males were necessarily more "evolved" than females in the sense of possessing a "higher" degree of organisation. See, for instance, Darwin's analysis of rudimentary males in barnacles ([5], t. I, p. 255).

analysed by Darwin reveal what could be called the metaphysical essences of males and females: *maleness* and *femaleness* are interpreted as the manifestation of two kinds of energetic processes called *katabolic-disruptive* and *anabolic-accumulative*, respectively. Darwin had already stated that the "male is more liable to vary than the female", and that "variations are more apt to occur in the male than in the female sex" (1871, t. I, p. 275, t. II, p. 128). Greater variational tendencies in males were used to equate males with a *progressive* element, a belief hastily taken up in Geddes and Thomson's book *The Evolution of Sex* (1889) [10]. For them, many species clearly evince that, "*on an average*", "the females incline to passivity, the males to activity". This contrast may be less visible among "superior" organisms, but it seems to the authors that "even in the human species the contrast is recognised. Everyone will admit that strenuous spasmodic bursts of activity characterise men, especially in youth, and among the less civilised races; while patient continuance, with less violent expenditure of energy, is as generally associated with the work of women" [10] (1889, p. 18).

Geddes and Thomson even find this contrast among gametes, between the active male sperm and the seemingly awaiting female egg. They explain that males are stronger, more beautiful and more emotional than females, not because of sexual selection on their ancestors, but "simply because they are males—*i.e.* of more active physiological habit than their mates" [10] (1889, p. 24). Finally, they reinterpret the *eagerness* that Darwin attributed to males as a series of disruptive processes, while the alleged female *coyness* is understood as mere passivity: males live at a loss, while females live at a profit, the former being katabolic (consuming energy), the latter anabolic (accumulating energy). As a result, their book often figures prominently in the feminist collection of howlers, as the iconic example of male-centred prejudice. But Darwin's view of eager males and coy females was still to thrive for many years.

6.2 Bateman's Hardening of Sexual Dichotomies

In an influential paper published in *Heredity* in 1948, Angus J. Bateman endeavoured to search for "a fundamental cause of intramasculine[3] selection, independent of mating system and probably inherent in the mechanics of sexual reproduction" [4] (p. 352).

Bateman wanted to understand why it seems "a general law" in nature "that the male is eager for any female, without discrimination, whereas the female chooses the male" (p. 352).

The conclusion of his genetic study of fruit flies, *Drosophila melanogaster*, was that males are "inherently subject to stronger selection than females". This means

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[3] "Intramasculine" designates a selection that occurs between males, as opposed to "female selection" or choice of mates on the part of the female.

that their contribution to the next generation is more variable than that of females (p. 367). All females have approximately the same success in mating, while the fertility and reproductive success of males is strongly dependent on their frequency of insemination. This difference of variance between the reproductive success of males and females entails what Bateman calls “undiscriminating eagerness in males and discriminating passivity in females” (p. 362).

In Bateman’s own words (1948, p. 365): “there is competition between male *gametes* for the fertilisation of the female *gametes*”. Because females produce many fewer gametes than males do, Bateman claimed that their fertility is much more limited than the fertility of the male. On the contrary, in the male, “fertility is seldom likely to be limited by sperm production”, and depends rather on their frequency of insemination (p. 364). Implicit in Bateman’s argument is the idea that sperm are less expensive to produce than eggs are.

Bateman’s paper was understood as evidence for the fact that “female multiple mating was unlikely to be very common as it was unlikely to enhance female fitness” [11].

Many critiques have been raised against Bateman’s conclusions. Above all, while being very forthcoming about polygamous tendencies in males, he did not actually monitor the courtship and promiscuous behaviour of fruit flies, nor did he directly measure the actual number of inseminations. Instead, he was using dominant marker genes and simply counting the carriers of the genes in the progeny. In other words, he only took into account inseminations that led to identifiable offspring [12, 13]. And even so, Bateman acknowledged that full identification was not always possible for about one fourth of the progeny (flies carrying two marker genes; 1948, p. 355).

Snyder and Gowaty also pointed out statistical mistakes and biased reporting in Bateman’s paper, concluding both that Bateman’s results are unreliable and that Bateman’s paper “retains its place as the single most important empirical observation in sexual selection” [14] (2007, p. 2457).

6.3 Expanding Bateman’s Paradigm

The problem with Darwin–Bateman’s opposition of male eagerness and female coyness is that it tends to associate a particular behaviour with each sex. The behaviour of individuals depends on the type of gametes they produce. Bateman’s paper strongly suggests that there are some genetic correlates to what Geddes and Thomson called “maleness” and “femaleness”. But it is not true that throughout nature, all males behave in the very same way, while all females behave in another—also unique—way.

Although selection might create a marked dimorphism in some species (the all-too-famous peacock), other cases exist in nature, cases revealing either little sexual dimorphism (magpies) or “sex-role reversal”, that is, species where the traditional Darwinian account of eager males and coy females is exactly the reverse: females are gaudy and pugnacious, larger and more brightly coloured than males, pursuing them and aggressively competing for nesting territory, while males are drab and are in charge of incubation and care for the young. A genus of shore birds, the phalaropes (sea snipes), illustrates this.

Such cases can be taken into account by the concept of “parental investment”, which explains why certain individuals have more reproductive success than others. Robert L. Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence its reproductive success) at the cost of the parent’s ability to invest in other offspring” [15]. Elaborating among others on the work of Bateman on drosophilae and on William Hamilton’s study of the genetic evolution of social behaviour, Trivers’ 1972 paper perpetuates the idea that “the parental investment pattern that today governs the operation of sexual selection apparently resulted from an evolutionarily very early differentiation into relatively immobile sex cells (eggs) fertilized by mobile ones (spermatozoa)” [15]. Mobile sperm and immobile eggs are decisive elements in parental investment. The paper, no doubt, also bears heavily on the stereotypes of indiscriminate males and sexually restrained females: “the cost of the copulation itself is always trivial to the male, and in theory the male need not invest anything else in order to copulate” [15]. Any precopulatory contribution the male will make (like territory defence) seems usually “small compared to the cost of the eggs” [15]. This intrinsic difference in parental care investment between males and females is understood as leading to important consequences, making desertion and multiple mating (including extra-pair copulation) common features in the animal world. Trivers’ final words are the following: “Throughout, I emphasize that sexual selection favours different male and female reproductive strategies and that even when ostensibly cooperating in a joint task male and female interests are rarely identical” [15].

Trivers contends that the sex that invests the least in raising the young (*usually* but not *necessarily* the males) displays the greatest amount of variation in reproductive success, while the sex that invests the most becomes limiting for the other sex. Although Trivers has been abundantly cited in support of the “fact” of male aggressiveness and female passivity, the concept of “parental investment” enables one to understand that it is not the biological sex that determines the intensity of sexual selection and, consequently, the extent or modalities of sexual dimorphism. If there are circumstances in which males invest more and females become sexually competitive, they clearly challenge the focus on gametes as the sole or main estimate of parental investment.

6.4 Anisogamy and the Feminist Challenge to Sexual Selection

Trivers’ concept of parental investment makes clear that female choosiness and male promiscuity are conceived of as based on “anisogamy”, a word coming from the Greek (*an*, not; *iso*, the same), which means that the gametes of the males and the gametes of the females are not the same and especially not of the same size or cost. Thus understood, the difference between males and females means only one thing: the two-sex divide and the division between "coyness" and "eagerness" are supposed to be the mere behavioural equivalent of those gametic "facts": females with costly eggs are depicted as careful investors, while males with cheap sperm seem readier to mate. In fact, these assumptions are flawed in many different ways.

First, it should be noted that anisogamy is not a necessity in nature. In some species, sexual reproduction occurs in cases of isogamy (with gametes of the same size). More importantly, most of the literature on anisogamy has focused on the idea that sperm are cheap. But is this so? In the fruit fly *Drosophila bifurca*, the sperm is twenty times longer than the size of the male who made it. It is so expensive that males conserve their sperm and it leads to a one-to-one gamete ratio. Such sperm don't come "cheap", and males take twice as long to mature as females. As to anisogamic species, it is a fallacy to compare the cost of one egg with the cost of one sperm, because an ejaculate consists of millions of sperm and other glandular secretions. In many species (cockroaches, butterflies), male sperm is accompanied by various nutrients in addition to the genetic material. The possibility of sperm depletion has to be taken into account: sperm undeniably has a cost. Far from being a limitless resource, it is subject to caution allocation, a fact that entails the existence of male mate choice, contrary to narratives of indiscriminate male behaviours. The traditional account of anisogamy should be taken with caution, even though gamete production undeniably has a cost. Female/feminist biologists like primatologist Sarah B. Hrdy have both criticised the idea that males produce "cheap" gametes and the "American supermarket mentality" built into the anisogamy argument that tends to forget that resources can be scarce [16]: gamete production has a cost, which should not be overlooked. The real issue is to determine what cost assessment must take into account.

The traditional "anisogamy" account is also flawed in that "coyness" is not a fact. In the 1970s, several women primatologists were focused on what female animals were actually doing [16, 17]: they were trying to remind their colleagues that females are also actors and described the modes of competition or collaboration among them. Hrdy's study on langurs shows how females, far from being "coy", actively seek coitus, a behaviour that can be used to sow doubt as to the identity of the father and so have the effect of lowering the rate of infanticide [17]. The literature on polyandry as a common female mating strategy has expanded during recent decades. It is now well known that females in many bird species solicit from other males and actively engage in extra-pair copulations (EPCs)—contrary to the common assumption that EPCs were systematically initiated by male intruders.

Moreover, feminist biologists have made clear that Darwin's two-sex model of sexual selection was clearly biased in favour of the male sex, leading to what Hrdy called, after Antoinette Blackwell, "the woman that never evolved" [16]. Whereas the Darwinian paradigm of sexual selection wrongly concentrated on two factors (male–male competition and female choice), evolutionary biologist Patricia Gowaty has extended the list of selective forces and factors of success in reproduction: female competition for resources; female choice of partners; male behaviours opposing female choice, like sexual coercion; female resistance to this coercive control; male competition for coercive access to females; competition between males and females for control of resources essential to reproduction; and male competition for resources [18]. Others have emphasised the importance of non-reproductive behaviours in nature, particularly sexual dynamics other than male-female [2, 19].

In spite of those critics, the anisogamy thesis is supported by the fact that gametes often come only in two forms, small and large: gamete size is not a continuum. Organisms with three or more gamete sizes are exceedingly rare—for instance, the green ciliate *Chlamydomonas euchlora* [3]. As we have seen earlier, this feature is crucial to the standard biological definitions of a "male" (an individual making small gametes) and a "female" (one making large gametes), the smaller of the two gametes being called a *sperm*, the other the *egg*. Gamete size plays a key role in defining both male and female "strategies" (the word "strategy" referring here to "a blind unconscious behaviour program"—Maynard Smith quoted by Dawkins 2006 [20]). According to this gametic definition of sex, there is today a general consensus that, at least in vertebrates, species with a sexual reproduction are divided into two and only two sexes. But there may be, within one sex in a single species, several "morphs" or aspects: for instance, there may be two types of females, those reproducing sexually and those reproducing asexually ("parthenogenetically"); or, in some species of fish, birds or mammals, two types of males, one generally identified as the male sex and the other which is more juvenile or "feminised" in his aspect. The different "morphs" in one sex can be called different "genders".[4] The males who do not match the dominant type are generally neglected (hastily identified as females) or called "sneakers". If sperm-producing individuals come in different morphs, with different behaviours, then doesn't it become impossible to define something like a "typical male behaviour"? Another recent challenge to sexual selection theory deals with the preferences of females: should all females go for the more "masculine" males, and are the others necessarily "sneakers"? Recent studies show that females may prefer the "feminised" males, and that those males may play an important role in assorting pairs [3, 22].

The anisogamy thesis of the difference of the sexes expands on the old metaphysical dichotomy activity/passivity and considers female processes as less worthy than their male counterparts. This tendency towards androcentrism (i.e. male-centredness) might be called "inadvertent machismo" [23]: it pervades not only the evolutionary science of animal behaviour but also conceptualisations of the cell, of the bacterial world or textbooks on reproduction, and it has been strongly criticised in feminist critiques [24–26].

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[4] I follow here Joan Roughgarden's suggestion (2004): "sex" refers to the two individuals producing the two different types of gametes (eggs/sperm, conventionally defining what is a male and what is a female), while "gender" refers to the different morphs in one sex. Matt Ridley [21] makes a different use of the terms: "sex" refers to sexual (vs asexual) reproduction, while "gender" refers to the distinction between "males" and "females", two terms that Ridley understands as defining two different "natures".

6.5 Perspectives: The Search for Gender-Neutral Models

Dissatisfaction with Bateman's paradigm has led several evolutionary biologists to emphasise that variances in lifetime reproductive success between males and females are not necessarily linked to mate choice or male–male competition but that they could be explained by chance effects and both sexes mating randomly.

Important papers by William Sutherland (1985) [27] in the UK, Hubbell and Johnson (1987) [28] in the USA and Michel Veuille in France [29, 30] (1982, 1986) have also suggested that the variance in male mating success presented in Bateman's paper was the value expected under a Poisson law, that is, that corresponding to the variation in mating success resulting from random encounters with unmated females. This idea was further developed by Gowaty and Hubbell [11, 31]: they provided new models to quantify nongenetic factors, such as chance and time, to account for variations in lifetime reproductive success. Their model, called SPT (switch point theorem), considers how "variation in encounters, latencies, survival, and their more complex proxies (relative reproductive rate, the operational sex ratio, and density) favours shifts in mean behaviour of the sexes and as a result more nuanced reports of ecologically induced variation in sex-typical behaviour" [31]. Those new tools allow testing of sex role flexibility in both sexes, instead of assuming the Darwin–Bateman two-sex hypothesis of two defined strategies. The emphasis on time in mating processes suggests a focus on environmental (i.e. nongenetic) constraints of variation and on chance effects on the number of mates.

Such aleatory factors have already been taken into account by classic papers in behavioural ecology (such as Trivers [15]), but their importance was then overshadowed by an extreme gametocentrism (the anisogamy thesis), with essentialist overtones: instead of studying populational or individual behaviours, biologists were haunted by the search for "maleness" and "femaleness". Differences in parental investment between males and females and the existence of anisogamy do not imply that males are necessarily indiscriminate in their matings or that sperm come cheap. Richard Dawkins stated, in a very Geddes-and-Thomson fashion, that "the word *excess* has no meaning for a male" [10]: Does this sentence refer to the profligacy of males, and how does it cover the case of males from several species dying from exhaustion after mating? Two-sex models, in the tradition of the Darwin–Bateman paradigm (coyness vs eagerness), are an exact replica of the metaphysical dichotomy between passivity and activity. Besides, the existence of two sexes, or two types of gametes, does not entail the existence of two (and only two) types of behaviours: one for males, one for females. As already suggested, there might be several "genders" or mating types in one sex.

Given the numerous challenges to the Darwin–Bateman paradigm, Joan Roughgarden and her lab proposed replacing the competitive framework of sexual selection with cooperative game theory models [3]. In species with sexual reproduction, evolutionary success is not only about mating: in order to complete the task of reproduction, individuals have to breed and raise their young until they are sexually mature.[5]

Biologists are facing the challenge of devising new models that avoid gender stereotypes or essentialist assumptions about “males” and “females” and the way they should behave. When tested against the prevailing traditional predictions, these new models may better account for the variation we keep on discovering in nature.

References

1. Margulis, L., & Sagan, D. (2007). *What is sex?* New York: Simon & Schuster.
2. Ah-King, M. (2009). Queer nature, towards a non-normative perspective on biological diversity. In J. Bromseth, L. Folkmarson Käll, & K. Mattsson (Eds.), *Body claims*. Uppsala: Centre for Gender Research, Uppsala University.
3. Roughgarden, J. (2009). *The genial gene*. Berkeley: University of California Press.
4. Bateman, A. J. (1948). Intrasexual selection in Drosophila. *Heredity, 2*, 349–368.
5. Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: J Murray.
6. Shuker, D. M. (2010). Sexual selection: Endless forms or tangled bank? *Animal Behaviour, 79*, e11–e17.
7. Blackwell, A. (1875). *The sexes throughout nature*. New York: GP Putnam’s Sons.
8. Darwin, C. (1859). *On the origin of species*. London: J Murray.
9. Barrett, P. H., et al. (Eds.). (1987). *Charles Darwin’s notebooks 1836–1844*. Ithaca: Cornell University Press.
10. Geddes, P., & Thomson, J. A. (1889). *The evolution of sex*. London: Walter Scott.
11. Gowaty, P. A., & Hubbell, S. P. (2005). Chance, time allocation, and the evolution of adaptively flexible sex role behavior. *Integrative and Comparative Biology, 45*, 931–944.
12. Tang-Martinez, Z., & Ryder, T. B. (2005). The problem with paradigms: Bateman’s worldview as a case study. *Integrative and Comparative Biology, 45*, 821–830.
13. Dewsbury, D. A. (2005). The Darwin-Bateman Paradigm in historical context. *Integrative and Comparative Biology, 45*, 831–837.
14. Snyder, B. F., & Gowaty, P. A. (2007). A reappraisal of Bateman’s classic study of intrasexual selection. *Evolution, 61*, 2457–2468.
15. Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1871*. Chicago: Aldine.
16. Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge: Harvard University Press.
17. Fedigan, L. M. (1982). *Primate paradigms. Sex roles and social bonds*. Montréal: Eden Press.
18. Gowaty, P. A. (1992). Evolutionary biology and feminism. *Human Nature, 3*, 217–249.
19. Bagemihl, B. (1999). *Biological exuberance*. London: Profile Books.
20. Dawkins, R. (2006). *The selfish gene* (30th anniversary ed.). Oxford: Oxford University Press.
21. Ridley, M. (2003). *The Red Queen. Sex and the evolution of human nature*. New York: Harper Perennial (London: Viking, 1993).
22. Watters, J. V. (2005). Can the alternative male tactics “fighter” and “sneaker” be considered “coercer” and “cooperator” in coho salmon? *Animal Behaviour, 70*, 1055–1062.
23. Eberhard, W. G. (1990). Inadvertent machismo? *Trends in Ecology & Evolution, 5*, 263.

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[5] The question then arises as to whether such attempts broaden the theoretical framework of behavioural ecology, renew it completely, or rather but underscore certain possibilities already implicitly present within the existing sexual selection framework.

24. Beldecos, A., et al. (1988). [The biology and gender study group] The importance of feminist critique for contemporary cell biology. *Hypatia, 3*, 61–76.
25. Martin, E. (1991). The egg and the sperm: How science has constructed a romance based on stereotypical male-female roles. *Signs, 16*, 485–501.
26. Zuk, M. (1993). Feminism and the study of animal behavior. *BioScience, 43*(11), 774–778.
27. Sutherland, W. (1985). Chance can produce a sex difference in variance in mating success and account for Bateman's data. *Animal Behaviour, 33*, 1349–1352.
28. Hubbell, S. P., & Johnson, L. K. (1987). Environmental variance in lifetime mating success, mate choice, and sexual selection. *American Naturalist, 130*, 91–112.
29. Veuille, M. (1982). L'évolution des systèmes de reproduction, du dimorphisme sexuel et du comportement sexuel chez *Jaera*. Thèse, Fac. Sci. Paris.
30. Veuille, M., & Mazeau, S. (1986). Variation in sexual behavior and negative assortative mating in *Drosophila melanogaster*. *Behavior Genetics, 16*, 307–317.
31. Gowaty, P. A., & Hubbell, S. P. (2009). Reproductive decisions under ecological constraints: It's about time. *Proceedings of the National Academy of Sciences, 106*, 10017–10024.

Chapter 7
Human Sex Differences in Height: Evolution due to Gender Hierarchy?

Priscille Touraille

Among specialists in the field of evolutionary biology today, some concede that the evolution of sex differences in height (sexual stature dimorphism) in the *Homo* lineage is an "intriguing puzzle" [1]. In textbooks, you find the same hypothesis you already find in Darwin's *Descent of Man*: size dimorphism is the result of an increase in the size of males due to sexual selection occurring via combat between males, as it is for gorillas or elephant seals [2].

My analysis emphasizes the inconclusiveness of existing models for the human species through a transdisciplinary inquiry including evolutionary anthropology, human behavioral ecology, genetics, paleoanthropology, nutritional sciences, obstetrics, biological and cultural anthropology, classical ethnography, and feminist and gender perspectives in the social sciences [3].[1] Confronting blind spots and recent developments in each of the above-mentioned fields results in a new and more realistic hypothesis to explain human sexual stature dimorphism. The previous lack of inclusive investigations such as the present one may actually explain why human sexual height differences are under-theorized compared to the amount of theorizations produced to explain body size differences in other animal species.

The two blind spots I started with are gender theory, on the one hand, and the behavioral ecology paradigm, on the other. In first-wave feminist and gender studies approaches, the way to conceive of the body "is [as] a real, physical entity, unchanging across time and space, and which is, in and of itself, unaffected by culture" [4].[2] The problem with this conception, which remains unchallenged in the social sciences,

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[1] This research was originally a PhD thesis, now published in French. See [3].

[2] For poststructural feminism, as for Judith Bulter (see [5]), the body cannot be apprehended as a "reality" outside any sociohistorical context. This position will be shortly debated in the paper's conclusion.

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is that it promotes the common and false idea of a permanence of similar sexed characteristics among species. It also promotes the equally false idea that human biological characteristics have not been exposed to any microevolutionary change recently, since “culture” took over.

Human behavioral ecology, on its part, postulates that cultural traits necessarily lead to increased survival or reproductive success and that culture in some way replaced natural selection or was not able to contradict it: the question of whether cultures incur decreases in survival or reproduction is put aside.

Animal behavioral ecology has investigated the survival costs of secondary sex characteristics for some decades [17]. Why, then, is behavioral ecology focused on humans incapable of asking about the costs of sexual height differences in our own species? I claim that identifying the costs of human sexual stature dimorphism will lead to the emergence of new insights. Let’s start with the issue of costs.

7.1 The Danger of Giving Birth in Humans

Human females are among the most vulnerable birth givers in the animal kingdom. Considered a divine penalty in biblical mythology, a situation of mortal jeopardy in popular representations, and a failure of human evolution in paleoanthropological science, trouble in human birth giving is still poorly accounted for in the evolutionary sciences.

Many of the well-known difficulties encountered by women in birthing – be it hemorrhage, eclampsia, or obstructed labor in general – are largely considered by-products of the disproportion of the head-to-pelvis ratio, which makes it difficult for the fetus’ head to pass through the pelvic canal. The cephalopelvic disproportion per se affects six million women every year, according to WHO statistics [7]. The costs in terms of women’s suffering and infant and mother mortality are huge. This phenomenon seems a priori to have nothing to do with sex differences in height, but as we will see later in this chapter, these costs could well be linked to women’s height relative to men’s.

7.2 Sex Differences in the Size of Mammals: A Brief Survey

Let’s first remember that sexual size dimorphism is neither systematic nor univocal in nonhuman animals. It is an extremely variable phenomenon [8]. But whenever males are of larger size than females, it is recognized to have recurrent survival costs for males as well as for females [6].

The model explaining bigger sizes among males goes back as far as Darwin [9]. He suggested the hypothesis of an increase in the size of males. This explanation, which is far from being so simplistic, holds for a great number of large mammals in which one-to-one fights between males remain an important factor in determining social status, access to females, reproductive success, and hence the propagation of genes for a large size. According to this by now well-supported hypothesis, large size is the result of a reproductive escalation largely based on selection for fighting behaviors.[3]

An alternative model appeared in the 1980s suggesting that the larger size of males could instead be the result of a decrease in female size or of a simultaneous change in which males get bigger and females smaller [10]. The availability of resources is at the heart of this model. Female mammals tend to consume more nutritious food than males do even if their body size is less than that of the males owing to the specific demands of gestation and lactation put on the body. The classical interpretation derived from this model is that a small size is advantageous for female reproduction. The model implicitly states that it is always more efficient for females to be large [11] in terms of reproduction (as for the males but for different selective reasons). Female small size is thus considered to be a trade-off between antagonistic selections: nutritional selection pressures for a small body, on the one hand, and reproduction pressures for a big body, on the other. But instead of saying that sexual size dimorphism emerged from a selection of small size variants, it would be clearer to say that big size variants were counterselected in cases of low access to nutritious resources. Concerning mammals, only females would really "need" to be big for their own survival in relation to their progeny. The question thus arises as to whether large males' evolution itself wouldn't be a hindrance to females' reproductive interests in the sense that large males' consumption and food appropriation would tend to reduce the availability of resources for females.

7.3 Human Sex Differences in Height

Human populations are characterized by significant variations in average height. In all populations, men are on average taller than women (by 13 cm on average) [12]. There is, nonetheless, significant variation in the degree of sexual stature dimorphism among populations (from 18 cm in the Assyrians to 6 cm in the Mountain Ok of Papua New Guinea, for instance) [12]. The debate is not settled as to whether the observed variability is an effect of environmental conditions (differential nutritional and sanitary conditions) or whether it is also the result of selection for heritable sex-specific variations in size. Both perspectives seem to be partly valid.

One idea, which some evolutionary biologists have defended for some time, is that actual sexual stature dimorphism in *Homo sapiens* is the remnant of the same dimorphism existing in ancestral primate species. This idea is in line with common thinking that sees sex characteristics as somehow homogenous across the animal kingdom: this is perhaps the reason why numerous textbooks retain it. However, the hypothesis of sexual differences as an evolutionary "legacy" goes against the working

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[3] See discussion in [3].

hypothesis in this field of study. The ongoing research currently holds that each species, each population, has its own specific evolutionary pattern of dimorphism [13]. It also postulates that genetic variation is so important for genetic determinants of size that it cannot be "fixed" and can always be suspected to be under selection, if divergent selection pressures on males and females do exist [14].

7.4 Genetics of Height

The height characteristic is said to be influenced by several genes and is recognized to be highly genetically heritable (up to 80 %). Hundreds of genes are now recognized to be implicated in final adult height [15]. Overall, height is not inherited along sex lines: tall people usually have tall children, independent of sex. But it is recognized that boys are on average taller than their sisters. This fact infers that developmental modifier genes control a sex-specific expression of body size [14]. Those modifier genes, heritable along sex lines, would be as sensitive to selection as any other gene. The process is still poorly understood in genetics, but one thing is certain: if selective forces act differently on males and females (whatever these forces may be), those modifier genes can be selected for – they are the genes that permit size dimorphism to emerge.

7.5 The Classical Selective Model: Increase of Male Stature

The hypothesis of increased male size in humans has not been tested until very recently. For years, it was the hypothesis given in the absence of a more convincing one. Sexual stature dimorphism has been used by Alexander and colleagues to suggest that human societies have long had a mating regime in which a man has two or more mates at the same time [16]. The problem with the final – and never questioned – argument in Alexander's paper about height sex difference is that even if some men have several mates, and thereby produce more offspring than others, this cannot in itself explain an increase in male body size. Behavioral ecology has long argued against the automatic character of this type of causality [17]. The first assumption that needs to be investigated is that the men siring more children must also be the tallest in the population. This point recently received some support in relation to European populations [18]. Still, the selective mechanisms are far from resembling males fighting each other with their bare hands! The behaviors that allow us to explain stature selection are not under genetic control; they are now under cultural control. We will evoke this hypothesis at the end of the chapter. In any event, what has never been brought to light is that sex differences in size can emerge without unequal male reproduction, for example, if some selection is directed at decreasing female size.

7.6 The Missing Data in the Classical Explanation

The idea that a big mother is a better mother [11] applies to human females as well as to other female mammals. It has been established in biological anthropology that the reproductive success of women increases with the stature of the mother [19] because a "greater height in women where malnutrition is endemic is associated with enhanced capacity to conceive and to deliver a baby more likely to survive" [20]. In one study in Gambia, Africa, a fall in infant mortality for each additional centimeter of the mother has been recorded [21]. Yet human females have an extra reason to be taller than, or at least as tall as, males that other females in the primate order do not have. Paleoanthropology and obstetrics both help to clarify this reason.

Paleoanthropology shows that, because "female stature and pelvic width are highly correlated" [22], the increased stature of *Homo* females permitted the delivery of children with increasingly wider skulls through a bony canal that had already narrowed considerably owing to permanent bipedalism. According to the fossil record, *Homo ergaster* was as tall as the tallest populations of *Homo sapiens* today. The most widely accepted model today is that the increase in female size was responsible for the increase in *Homo*'s stature, birthing constraints being the dominant factor of selection for tallness [23]. The global increase in stature is interpreted as females reducing the dimorphism already existing in the ancestor lineage. But the idea that hominids had strong sexual stature dimorphism is far from being an obvious fact, as the paleoanthropological practice is to sex fossils on the basis of their size alone and not on the basis of DNA (sex chromosomes diagnosis).[4] Today, the *Homo* lineage is considered closer to chimpanzee lineage based on both molecular similarity and studies of the relationship between species. Common chimpanzees and bonobos have – more or less – the same size differences that modern humans have, casting serious doubt on the notion that the last common ancestor to humans and chimps was at all dimorphic. The fact that *Homo ergaster* (and *sapiens*) females are said to have only caught up to males prevents us, in a certain respect, from posing the theoretical question of why females did not pass males in height. If, on the contrary, we depart from the hypothesis that dimorphism was already weak in the ancestral lineage, then the global and drastic increase in height for obstetric reasons would raise the question of why women are not taller than men in our species. The questioning is also prevented by a false idea shared by common thinking and an old paleoanthropological mode of reasoning: the idea of the adaptation of the female pelvis to parturition. The pelvis is a bony structure whose timing of growth is, like the skull, in some way independent of the timing of growth of long bones. In biology, correlated growth rhythms for different bony structures are called allometry. Morphological differences due to allometry are not considered adaptive (which

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[4] Well-known controversies exist in the discipline on this topic. For instance, important size differences in Australopithecines fossils, first attributed to sex, were then suspected to signify that two different species were actually present.

means that they are not under selection). Males have bigger skulls and pelvises than females in absolute terms, but females' skulls and pelvises are proportionally larger than those of males when compared to height. It is worth noting that no anthropologist has ever tried to use adaptation to explain the relatively bigger size of female brains, though they have systematically tried to use it to explain the relatively larger female pelvis. If the relatively larger size of the pelvis is due to an allometric growth relation, as it is for the brain, then it cannot have been selected for obstetrical reasons, and female pelvises cannot be said to be "adapted to parturition." Stature is a more convincing candidate for that.

The medical literature on birthing began to influence evolutionary biologists only very recently: "Despite increasing evidence that female stature significantly influences obstetric performance, little attention has been devoted to the evolutionary implications of this phenomenon" [19]. Modern obstetrics does indeed support the contention that smaller size in women (regardless of the average stature of the population) results in a higher risk of mortality and obstetric complications. Tall women have bigger pelvises, and it is true that they also have bigger babies than smaller women do. But smaller women have babies that are also proportionally bigger than those of tall women, owing to the fact that baby size is not well correlated, as one can imagine, with the phenotype of the mother but with its own genotype, depending on a number of genes coming from the mother, but not always expressed by her, and a number of genes coming from the father. In these conditions, it is completely logical to assume that the tallest women in a given population will be the women least prone to obstetrical complications, because the size of a tall woman's fetus will be, in any case, better correlated with her pelvis than the size of a small woman's fetus will be with her pelvis in a population composed of individuals of taller mean size.

Hence, considering both paleoanthropological and medical arguments and considering that the latter are of greater significance in places where women have no access to operative delivery, women would be as tall as or even taller than men in our species if birthing selective pressures alone were at work. As already mentioned, this is not what anthropologists observe in extant populations. Taking into account the costs of small stature for women, we are thus forced to assume that, in the course of human history, women must have experienced selective constraints that prevented them from reaching the taller size they should have reached relative to men.

7.7 Hypothesis of Nutritional Constraints on Women's Size Selection

Some authors have stated that nutritional factors are involved in the existence of sexual stature dimorphism, but without being clear about the underlying mechanisms [24]. To my knowledge, the idea that such sex differences in the human species could be the selective result of the limitation of female stature under harsh nutritional conditions was first proposed by paleoanthropologist Margaret Hamilton in her unpublished thesis [22]. The first problem with Hamilton's argument is that it states that it is an "advantage" for women to have a small stature when resources are chronically scarce. As for the primate model, the interpretation is the inverse, and the problem of costs is not settled. The second problem, in some ways related to the first, is that it considers "limitation of resources" without reference to any social context. Above all, the hypothesis omits crucial sociopolitical dimensions.

For the hypothesis of a female size restriction to apply to the whole human species, a scarcity of resources must have been long lasting and recurrent in all human populations. This hardly seems plausible if one adheres to the argument of the global obstetric advantage of tall stature in women. Starting from there, we should expect to find women taller than men in at least some past or present human populations. It is thus necessary to suppose here that the limitation of resources experienced by women is more constant among populations than what would be expected if it resulted from a simple ecological cause.

7.8 Gender Order: A Decisive Piece of the Puzzle?

It is a generally accepted idea that women "need to eat less" than men. Until recently, scientific paradigms followed popular conceptions claiming that men have a greater need for proteins (especially animal protein) than women do. This idea has been challenged by nutritional scientists [25]. Given that proteins are of critical significance for *Homo sapiens* females (as they are for all female mammals), a human behavioral ecology paradigm should predict that cultural traits should, in all cases, promote privileged access to the best foods for women and children over men.

Yet the ethnographical literature is filled with remarks showing the limited access for women and children to what is considered the best food by the society itself – and the most nutritious from a scientific point of view – especially proteins that men control through the gender division of labor [26, 27].[5] Social anthropology does not systematically address the problem of nutritional inequalities. One reason could be that nutrition is not a primary focus area for cultural anthropologists. A second reason may well be that the issue of inequality, especially gender inequality, is in some way taboo in the discipline. Ethnographies nonetheless describe how restrictions very often target the critical period of a woman's reproductive lifetime and how women as a group are supposed to get less food, at least in terms of quality, than men. In hunter-gatherer societies, important prey hunted by men are often tabooed for women [28]. The idea of normally restricted access to protein for women appears to be supported by what has been observed in dramatically different societies. In a recent study, quantitative data are presented on the Hadza of Tanzania. Behavioral

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[5] For a discussion of the arbitrary, nonnatural character of this division, see [27].

ecologist Frank Marlowe, looking at six different camps, quantified men's and women's consumption of different food items over a 1-year period. He observed that meat amounted to as little as 1.2 % of women's diets and to as much as 19.3 % of men's diets [29]. For the majority of societies, these kinds of data are missing, but human behavioral ecologist fieldwork in the area confirms what the representations reported by ethnographic data predict.

From a gender theory point of view, the realistic hypothesis to be made is that this trait did not emerge independently in different cultures but that its existence is highly dependent on the gender categorization itself and its implications. The gender order [30] – a hierarchical order that nearly all cultural anthropologists consider a human universal – is very likely to have appeared in the first human societies as evidenced by its hegemonic presence. Representations of gender inequality represent a strong constraint for cultural variation or change, not counting the various advantages they give to – all or some – members of the male category. This in turn would explain why women, as a subservient category, have been denied access to the best foods. Such a phenomenon has been documented for other subservient categories as well, such as children, peasants, and slaves. Food inequality is thus but one of the many expected consequences of a primary thought construction that gives rise to an overall inequality structure, often strengthened by proscriptions, threats, violence, or deception [31].

From an evolutionary point of view, consistent food disparities between men and women may contribute to smaller stature of women compared to men. Assuming that women with genes for smaller stature would survive lower nutritional levels better than women with genes for tall size, such a consistent dietary inequality may also lead to changes in the gene pool. Thus, genes for tall size in women would be counterselected more than genes for tall size in men, leading to the evolution of size differences. While Alexander and colleagues state that sexual stature dimorphism is the cue for assessing a long-lasting polygyny regime in the human species [16]. I instead suggest, in the same train of thought, that men's taller size may be better interpreted as a cue of a long-lasting, generalized restriction of nutritional access imposed on women by the gender order.

7.9 Mate Choice: Another Hypothesis Linked to Gender

However, nutrition cannot be the whole story. Some work in evolutionary psychology has suggested that sexual stature dimorphism is the product of mate choice whether it is on the female or the male side. In one European population, some evidence actually exists that taller men and smaller-than-average women have more progeny, because men "prefer" women smaller than themselves and women "prefer" men much taller than themselves [18]. Evolutionary psychologists do not consider the fact that natural selection (via obstetrics) favors tall women. Had they considered it, they should have put forward that, in principle, cultures should favor tall women by directing men's preferences in that way, rather than the reverse.[6] They should have acknowledged that cultures actually do not fit this prediction. Data and models about the adaptive significance of tallness for women call their nature/culture paradigm into question: so they ignore it. I recently reinterpreted these data in a gender perspective [32].[7] The idea that a male should normally be taller than his female partner, for whatever reason given, is a gender representation. If this cultural conception makes women choose partners that are suboptimal for their own biological survival and reproductive interest, it might be an example of culture creating opposing selective forces to natural selection. By ignoring this, we confirm popular thinking that envisions men being taller than women as some kind of natural law.

7.10 Conclusion

The present work challenges evolutionary thinking on culture that postulates that the only cultural traits capable of enduring in the long term are those that maximize reproductive success. It also challenges first-wave feminist thinking that sees biology as fixed and neutral and not permeable by social injunctions. Furthermore, creating a dialogue between widely separated fields also challenges the radical constructionist approach put forward by some gender scholars [5] who claim that "sex" is produced by biological discourses and, by virtue of this very fact, that sex is as socially constructed as gender. If, as I argue, gender can produce some sex differences in morphology on the long term, it is a supplementary argument to reaffirm a strong distinction between what is produced by the mind and the artifacts of mind (culture) and what is produced by biological information (DNA). This conceptual distinction is necessary to clarify what it is we are talking about in the social and life sciences so that we can challenge the stereotypical thinking that impedes us all.

References

1. Plavcan, M. J. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology, 44*, 25–53.
2. Diamond, J. (1992). *The third chimpanzee: The evolution and future of the human animal*. New York: Harper & Collins.

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[6] In fact, the taller a man is relative to a woman partner, the more likely it is that childbirth will be difficult. A woman choosing a man taller than herself will perhaps help her daughters be taller, but this choice represents a risk more important to her own survival and thus to the "reproductive success" of the "tall genes."

[7] The whole book has recently been transtated in English, Touraille, P. (forthcoming beginning 2014). Biological costs of a small stature for *Homo sapiens* females: New perspectives on stature sexual dimorphism. In T. Heams, P. Huneman, G. Lecointre, M. Silberstein (Eds.), *Handbook of evolution theory in the sciences*. London: Springer.

3. Touraille, P. (2008). *Hommes grands, femmes petites: une évolution coûteuse. Les régimes de genre comme force sélective de l'adaptation biologique*. Paris: Maison des sciences de l'Homme.
4. Pilcher, J., & Whelehan, I. (2004). *Fifty key concepts in gender studies*. London: Sage.
5. Butler, J. (1993). *Bodies that matter. On the discursive limits of sex*. New York: Routledge.
6. Clutton-Brock, T. (1994). The costs of sex. In R. V. Short & E. Balaban (Eds.), *The differences between the sexes*. Cambridge: Cambridge University Press.
7. Murray, C. J. L., & Lopez, A. D. (1998). *Health dimensions of sex and reproduction. The global burden of sexually transmitted diseases, HIV, maternal conditions, perinatal disorders and congenital anomalies*. Boston: Harvard School of Public Health.
8. Gould, S. J. (1985). *The Flamingo's smile: Reflections in natural history*. New York: Norton & Company.
9. Darwin, C. (1871). *The descent of man, and selection in relation to sex* (1st ed.). London: John Murray.
10. Martin, R. D., Willner, L. A., & Dettling, A. (1994). The evolution of sexual size dimorphism in primates. In R. V. Short & E. Balaban (Eds.), *The differences between the sexes*. Cambridge: Cambridge University Press.
11. Ralls, K. (1976). Mammals in which females are larger than males. *The Quarterly Review of Biology, 51*, 245–276.
12. Gustafsson, A., & Lindenfors, P. (2006). Human size evolution: No evolutionary allometric relationship between male and female stature. *Journal of Human Evolution, 47*, 253–266.
13. Fairbairn, D., Blanckenhorn, W. U., & Székely, T. (Eds.). (2007). *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press.
14. Badyaev, A. V. (2002). Growing apart: An ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology & Evolution, 17*, 369–378.
15. Allen, H. L., et al. (2010). Hundreds of variants clustered in genomic loci and biological pathways affect human height. *Nature, 467*, 832–838.
16. Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., & Sherman, P. W. (1979). Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective*. North Scituate: Duxbury Press.
17. Clutton-Brock, T. (1985). Size, sexual dimorphism, and polygyny in primates. In W. L. Jungers (Ed.), *Size and scaling in primate biology*. New York: Plenum Press.
18. Nettle, D. (2002). Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 269*, 1919–1923.
19. Guégan, J.-F., Teriokhin, A. T., & Thomas, F. (2000). Human fertility variation, size-related obstetrical performance and the evolution of sexual stature dimorphism. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 267*, 2529–2535.
20. Martorell, R., Delgado, H. L., Valverde, V., & Klein, R. E. (1981). Maternal stature, fertility and infant mortality. *Human Biology, 53*, 303–312.
21. Sear, R., Allal, N., & Mace, R. (2004). Height, marriage and reproductive success in Gambian women. *Research in Economic Anthropology, 23*, 203–224.
22. Hamilton, M. E. (1975). *Variation among five groups of Amerindians in the magnitude of sexual dimorphism of skeletal size*. Ph.D. thesis. University of Michigan, Ann Arbor.
23. McHenry, H. (1996). Sexual dimorphism in fossil hominids and its socioecological implications. In J. Steele & S. Shennan (Eds.), *The archaeology of human ancestry. Power, sex and tradition*. New York: Routledge.
24. Wolfe, L. D., & Gray, P. J. (1982). A cross-cultural investigation into the sexual dimorphism of stature. In R. L. Hall (Ed.), *Sexual dimorphism in Homo sapiens. A question of size*. New York: Praeger.
25. Carpenter, K. J. (1994). *Protein and energy. A study of changing ideas in nutrition*. Cambridge: Cambridge University Press.
26. Stanford, C. B. (1999). *The hunting apes. Meat eating and the origin of human behaviour*. Princeton: Princeton University Press.

27. Brightman, R. (1996). The sexual division of foraging labor: Biology, taboo, and gender politics. *Comparative Studies in Society and History, 38*, 687–729.
28. Whitehead, H. (2000). *Food rules. Hunting, sharing and tabooing game in Papua New-Guinea*. Ann Arbor: Michigan University Press.
29. Marlowe, F. (2010). *The Hadza Hunter-gatherers of Tanzania*. Berkeley: University of California Press.
30. Connell, R. (1987). *Gender and power. Society, the person and sexual politics*. Stanford: Stanford University Press.
31. Camporesi, P. (1989). *Bread of dreams: Food and fantasy in early modern Europe*. Chicago: University of Chicago Press.
32. Touraille, P. (2009). Coûts biologiques d'une petite taille pour les *Homo sapiens* femelles: nouvelles perspectives sur le dimorphisme sexuel de stature. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Eds.), *Les Mondes darwiniens. L'évolution de l'évolution*. Paris: Éditions Syllepse.

Chapter 8

How Do Voices Become Gendered? A Critical Examination of Everyday and Medical Constructions of the Relationship Between Voice, Sex, and Gender Identity

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The human voice—those mysterious vibrations that come out of our mouths and enter our and other people's ears when we speak, sing, hum, cry, cough, or clear our throats—is commonly understood as a sound that represents the person who produces it. What appears on a physical level merely as oscillating air molecules is hereby interpreted as providing the listener with intimate information about the individual from whose mouth the voice emerges. Take as an example the everyday situation when someone we do not know calls us and instantaneously an image of the characteristics of the caller appears in front of us as if this image were propelled from the depth of the sounds reaching our ears. According to the popular science book, *The Human Voice: How This Extraordinary Instrument Reveals Essential Clues About Who We Are*, which draws on the results of scientific research, the voice is indeed capable of betraying even those of the speaker's personal characteristics that are normally kept from view:

> [T]he moment we open our mouths and start to speak … our voice is doing something terrifyingly intimate—leaking information about our biological, psychological, and social status. Through it, our size, height, weight, physique, sex, age and occupation, often even sexual orientation, can be detected. The voice is a stethoscope, and transmits information not only about anatomical abnormalities but even illnesses. [1]

How are we to understand these instances of vocal self-expression, in which the voice appears to communicate the details of a person's uniqueness "without even the mediation of articulate speech" [2]? Is it valid to conceptualize the voice as a "stethoscope," that is, as an examination device that is capable of listening in to and transmitting to others "what we are, what we believe and how we feel" [3]? Or are there indications that the relationship between our voice and the biological, psychological,

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and social aspects of our subjectivity is more complex than we spontaneously assume, so that a detailed investigation of this relationship is necessary?

In this chapter, I will take a closer look at one aspect of those personal attributes we tend to perceive as if they were contained in and conveyed by the voice and critically examine the assumption that "voice has a sex" [4] or that it reflects a person's gender [5]. Common sense easily persuades us that when it comes to something like our perception of male-female differences in voice pitch, we must be dealing with a natural phenomenon, something "caused" by basic anatomy and physiology. This understanding of the relationship between notions of voice, sex, and gender[1] is often taken for granted both in everyday life and in the scientific literature, and it forms the basis for medical diagnosis and treatment of people who experience problems with the communication of gender.

In the following, I will subject this conventional perspective to close scrutiny by raising a series of questions: How do voices become gendered? Does the voice have a sex in the sense of a biologically determined attribute? Do speakers and listeners invest voices with gendered meanings in interaction by using their voice organs in particular ways and interpreting certain aspects of the sound they hear as either "male" or "female"? Or is the gendering of voices a transient outcome of meaning-making practices that are regulated by historically and culturally variable stories about bodies, sex, gender, and communication that are beyond individual control? I will conclude by suggesting that an appreciation of different theories about the relationship between voice and gender provides us with an opportunity to become aware of an unheard of diversity of human bodies, identities, and voices and prompts us to reconsider how we habitually explain what we regard as the successful or unsuccessful communication of gender.

8.1 The Commonsense View/Medical Perspective

The commonsense view of sex differences of voices as "caused" by differences in physiology translates into medical practice. Many medical voice specialists, who may be laryngologists, phoniatricians, ENT surgeons or speech-language

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[1] The terms "sex" and "gender" are often used heterogeneously and at times interchangeably. For some scholars, notably those who work in the medical sciences, the notion of "sex" includes the notion of "gender," because they understand not only the sexual characteristics of a person's body but also their "gender identity" (the sense of belonging to one of the two genders) and their gendered behavior as biologically determined. According to other perspectives, however, "gender" as a cultural construct is positioned as distinct from "sex." Following those views, what gender means for a person and how they perform their gender in their behavior is independent of their physical characteristics. Other theorists, again, contest the sex-gender distinction and abandon the term "sex" because for them there is no access to bodies and identities other than through the lens of culture-specific meaning-making practices. In this chapter I use the term "gender" in order to refer to the notions of "sex," "gender identity," and "gendered behavior" taken together. The term "sex" will appear only when I quote from or refer to texts that subscribe to the first view mentioned above.

pathologists, and nonclinical scientists subscribe to a theoretical perspective according to which "the physical distinction between men and women dictates … that a speaker's gender can be easily determined on the basis of voice" [6]. How is this claim of the biological determination of the voice's gender explained in the scientific voice literature?

According to the medical voice literature, on which I will focus my examination, the voice originates from the "voice organ" in the speaker's throat. The voice organ consists of the larynx or voice box, which houses the vocal folds, and of the vocal tract, which comprises the space above the larynx between the vocal folds and lips and includes the throat, mouth, and nasal cavities. Processes of sexual determination are seen as causing the "sexing" of the human body and of the voice organ as one of its components. Sexual determination is understood here as a complex double-tracked development, in which the presence of XX or XY sex chromosomes leads to the formation of female or male internal sex organs that are capable of producing female or male sex hormones, which are responsible for the shaping of female or male voice organs and voices during puberty. As Abitbol and Abitbol put it: "In the girl, estrogen and progesterone secretion will lead to a woman's voice. In the boy, testosterone will yield a man's voice" [7]. Importantly, the notions of a "woman's" and a "man's" voice are here understood to reflect the consonance of a biologically female (or male) body *and* a female (or male) gender identity (a person's sense of being a man or a woman). According to the (mainstream) medical profession, gender identity is regarded as one of the results of the sexual differentiation of the brain and is therefore seen as following from sex. In other words, the link between XX chromosomes and female gender identity and between XY chromosomes and male gender identity is understood to be biologically determined [8].

The claim that the voice has a sex (and gender identity) is based on an understanding according to which the sexual characteristics (or size) of the voice organ determine the gender (or pitch) of the voice as an acoustical event: The bigger "male" voice organ is seen as naturally inclined to produce a lower-pitched "male" voice, whereas the smaller "female" voice organ produces a higher-pitched "female" voice. As Coleman explains:

> Perceptions of a speaker's vocal "pitch," and subsequently the maleness or femaleness of his voice, … result from the combining of the information conveyed by both the speaker's F_0 [=fundamental frequency of vocal fold vibration] and resonances of his vocal tract. [9]

According to this perspective, it is the length and mass of the vocal folds and the dimensions of the vocal tract that are regarded as mainly responsible for the gendering of the voice as sound: As an effect of higher testosterone levels male vocal folds are longer, thicker, and heavier; provide more resistance to being blown apart; vibrate more slowly with a bigger amplitude; and produce lower-pitched sounds than the shorter, thinner, and lighter female vocal folds (see, for instance, [10]). Additionally, male adolescents experience a greater increase in vocal tract volume than females during puberty, which leads to a lowering of vocal tract resonance frequencies, also contributing to the perception of a lower pitch than in females (see, for instance, [11]).

Following the concept of the naturally sexed voice, the sexual characteristics of the voice organ, which are regarded as biologically determined, ensure that the voice is already gendered as it passes through the voice organ and before it emerges from the speaker's mouth. As a consequence, both speakers and listeners are positioned as uninvolved in the gendering of the voice. For irrespective of the speaker's vocal behavior and irrespective of the outcome of listeners' perception and interpretation of what they hear, the fixed anatomical dimensions of larynx and vocal tract are taken to have already determined the voice's gender.

8.2 Challenging the "Natural Binary"

The data used in the medical voice literature to provide evidence about the sex-specific anatomical dimensions of human voice organs are, as a rule, either derived from cadaver studies, computer tomography, or acoustic reflection studies, in which people are asked to remain motionless so that accurate measurements can be taken. In the living human being, however, voice organs are flexible apparatuses that are mostly made up of pliable cartilages, muscles, connective tissues, and mucous membranes and only to a smaller extent of rigid bones. During voice production, we move these structures in order to produce particular speech sounds, pitch levels, and voice qualities. This is to say that, irrespective of whether the voice produces sound in the form of speaking, singing, or other utterances, it is necessarily a production that is not so much shaped by fixed anatomical dimensions of the larynx and vocal tract but rather by the way the speaker or singer moves and shapes his/her voice organ.

When we gesture with our larynx, vocal folds, and vocal tract, we change both the dimensions of our voice organ and the characteristics of the sound waves emanating from our mouth. For instance, we can employ two antagonistic muscles in the larynx to modify the length and mass of the vocal folds, which leads to a change in the fundamental frequency of vocal fold vibration, which, in turn, is perceived by listeners as a change in voice pitch.[2] As Baken and Orlikoff emphasize, "[s]peech is not usually monotonous: the normal speaker uses a range of fundamental frequencies to indicate word and sentence stress, statement form and affective content" [12].

The voice's variability (as an organ and external object of audition) is even more obvious in singing. While average singing ranges for adults have been shown to range from 2 to 3 octaves (see, for instance, [12, 13]), some singers are capable of

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[2] I am referring here on the one hand to the thyroarytenoid or vocalis muscle, whose contraction results in a shortening and thickening of the vocal folds and to a slowing down of vocal fold vibration, which can be measured acoustically as a decrease in average fundamental frequency of vocal fold vibration. On the other hand I am referring to the cricoarytenoid muscle, whose contraction leads to a lengthening and stretching of the vocal folds and an increase in speed of vocal fold vibration, which can be measured as an increase in average fundamental frequency of vocal fold vibration.

extending their vocal range to up to 8 octaves and of reaching pitches far beyond what is considered "normal" for their voice type.[3] These observations suggest that the limitations the anatomical dimensions of the larynx and vocal folds impose on the fundamental frequency range of the human voice can be regarded as negligible. If we consider additionally that the normal singing ranges for men and women overlap considerably[4] and that the average speaking fundamental frequency of 160 Hz, which is used in clinical practice as a "gender-dividing line,"[5] lies well within both of those frequency ranges, the following becomes apparent: The difference in average speaking fundamental frequency, which is regarded in the medical literature as "[t]he most accepted difference between male and female voices" [14], seems to be the result of vocal behavior rather than of biological constriction. Additional evidence that this difference might be the effect of learned behaviors rather than of "biophysical inevitabilities" [15] comes from research showing that the average speaking fundamental frequency values for men and women and the extent of the observed gender difference vary between language groups and cultural contexts. Simpson reports, for instance, on the results of a study about a dialect of Chinese that found an average fundamental frequency of 170 Hz for male speakers and of 187 Hz for female speakers (difference of 1.7 semitones [ST] and notably both above the "gender-dividing line") and on studies that found male and female averages of 127 and 186 Hz, respectively, for English speakers (difference: 6.6 ST) and averages of 118 Hz for men and 207 Hz for women who spoke French (difference: 9.7 ST) [15].

Just as we can actively adapt the length and mass of our vocal folds, we can also modify the dimensions of our vocal tract by moving our larynx up and down in our throat and stretching our lips widely or protruding them. These articulatory activities, which lead to a change in the resonance frequencies of the voice, have been observed, for instance, in preadolescent children who "learn elements of vocal tract gesturing in order to produce gender-typical voices within a short time of beginning to enunciate" [16]. Based on studies showing no differences in the anatomical dimensions of the voice organs of preadolescent girls and boys, we are thus led to assume that children can conform in their voice production to gender models they choose to imitate independent of anatomical possibilities or restrictions. As Delph-Janiurek remarks, these observations taken together point to "the lack of

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[3] See, for instance, the following web page for sound recordings of singers who are capable of producing pitch levels and vocal ranges that exceed the normative ranges for biological males and females: http://www.divadevotee.com/2010/11/female-with-largest-vocal-rangegeorgia.html.

[4] Schultz-Coulon and Asche (1988), for instance, have determined the following lower and upper limits of normal singing ranges for adults: men (87–587 Hz) and women (147–784 Hz). These normative data suggest that every healthy adult speaker, regardless of the size of their voice organ, is assumed to be capable of varying the fundamental frequency of their voice within the range of 147–587 Hz (this is equivalent to a range of 24 semitones or two octaves).

[5] As Oates and Dakakis [14] report, gender attribution experiments have shown that speakers who use a speaking fundamental frequency of below 160 Hz are likely to be judged as male, whereas speakers who use a speaking fundamental frequency of above 160 Hz are likely to be judged as female.

uniform, universal differences between the voices of women and men … [and] suggest that voices themselves are stylized and performed to a far greater degree than is commonly assumed" [16].

Following the view that a voice's gender is the result of a behavior or a *doing* rather than a person's biological characteristic, not only the speaker or singer but also the listener is seen as actively involved in the gendering of the human voice. For if we take a closer look at the processes involved in listening, it becomes apparent that the voice is subject to continuous metamorphosis once it comes out of a person's mouth. Rather than being equipped with a stable existence that could be measured and compared to normative values, the voice appears as a chameleon-like creature. What emerges from our mouths as a clutter of traveling sound waves is at first transformed from an acoustical to an auditory event when it produces a sensation in the listener's ear. These auditory sensations are then put in order with the help of processes of perception: Irregular vibrations are discerned from regular vibrations, high-pitched sounds are distinguished from low-pitched sounds and skilled listeners may differentiate various types of voice quality and speech melody. In further steps, we attach meanings to the perceptual categories we have created and might call pleasant sensations "sound"; unpleasant sensations "noise"; high-pitched, melodious, and gentle sounds "female"; and low-pitched, monotonous, and forceful sounds "male"[6] or follow idiosyncratic interpretation processes.

Several accounts in the research literature indicate that listeners' classifications of voices as female or male are not necessarily predictable from or in agreement with a speaker's sex or gender identity. Hall reports, for instance, on a biologically male phone-sex operator who successfully poses as a female before his customers by imitating several aspects and versions of cultural stereotypes of vocal femininity [17]. Studies of listeners' reactions to voice samples of male-to-female transsexual speakers (see, for instance, [18]) (who are defined as presenting with a "male" voice organ and a "female" gender identity) and female-to-male transsexual speakers (see, for instance, [19]) (who are defined as presenting with a "female" voice organ and a "male" gender identity) provide further evidence that neither the anatomical dimensions of a person's voice organ nor their gender identity determine whether a voice will be classified as female or male.[7] Rather, these and other reports indicate

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[6] While many studies have found that the average fundamental frequency and resonance frequencies of a voice are critical to listener judgments of speaker gender, results from studies that investigated stereotypical expectations about the differences between male and female voices indicate that listeners consider also other vocal characteristics when making these judgments, among them the variability of intonation patterns and various perceptions of voice quality (see [14] for an overview).

[7] Of the 15 male-to-female transsexual speakers included in Gelfer and Schofield's study, listeners identified 6 consistently as male speakers, 4 were identified as male in 90 % or more of listener judgments, 3 were identified as female in 90 % or more of listener judgments, and the voice samples of two speakers received female gender attributions in less than 60 % of listener judgments. Of the 14 female-to-male transsexual speakers included in Scheidt et al.'s [19] study, listeners identified 9 consistently as male speakers and 1 consistently as female. Two speakers were identified as male in more than 90 % of listener judgments and the remaining 2 speakers received male gender attributions in 78 and 54 % of listener judgments, respectively.

that listeners may even have diverging understandings of what constitutes vocal masculinity or femininity and therefore don't necessarily agree on how they attribute gender to voices (e.g., [20]).

What this suggests is that once the voice has left the confines of the voice organ, its meanings are no longer controllable by the speaker's anatomy, identity, behavior, or intentions but are reconstructed by sensation, perception, and interpretation processes taking place in the listener, who may draw on conventional or unconventional understandings of gender. The voice's gender is thus seen as "constituted in interaction" [21] between speaker and listener and appears to be a social accomplishment rather than a natural given. The results of these social doings may prove unproblematic (in case speaker and listener agree in their gender attribution) or entail calls for strategies to repair misunderstandings that occur when speaker and listener diverge in their constructions of the voice's gender.

8.3 How Voices Become "Appropriately" and "Inappropriately" Gendered

Some theorists go even further in their challenge to the concept of the naturally sexed voice and argue that how the sex of our bodies is classified at birth, how we position our identities along gender lines, how we gesture with our voice organs, and how we interpret the sounds we hear are neither governed by biological forces nor under the conscious control of the individuals involved in a conversation but instead formed by stories (or "discourses") about bodies, sex, gender, identity, and communication that are circulated among human beings (see, for instance, [16, 22]). In this view, voices become gendered as a result of meaning-making practices, which are seen as shaped by norms and expectations that are prevalent in the historical and cultural context in which interaction partners find themselves.

Such an understanding of voice and gender as "discursive products" [16] draws attention to the tendency in both common opinion and academic discourses to construct notions of sex, gender, and voice as if they each occurred in two and only two mutually exclusive versions, male or female. This is the case despite research findings showing that deviations from this model have been found not only in relation to other time periods and cultural settings (see, for instance, [23]) but also appear as regular entries in contemporary international medical classification lists [24]. Under the heading "congenital malformations, deformations, and chromosomal abnormalities" one can find, for instance, that sex chromosomes in humans don't come only in two but in several versions (such as X0, XXX, XXY, XYY sex chromosomes), that the adrenal glands of a person with XX chromosomes may produce higher amounts of testosterone than what is normal for a female, that the body of a person with XY chromosomes might not be receptive to the testosterone it produces, and that babies may be born with testes and a vagina or with a vagina and no uterus and ovaries. Moreover, the section entitled "gender identity disorders," listed under "mental and behavioral disorders," indicates that there are children, adolescents, and adults who don't feel comfortable in the confines of the sex category that has been attributed to them at birth and who present with a gender identity that doesn't follow from their biological sex (see, for instance Bockting [25] for a list of varied self-descriptions of gender identity taken from a national survey of the US transgender population).[8]

Accordingly, the possibilities of communication behavior, and the way human beings gesture with their variously shaped bodies in order to perform their diverse gender identities, are not restricted to the two patterns that are commonly taken for granted. While this diversity is excluded from consideration when the "normal" human voice is discussed, it is partly reflected in clinical terms invented to refer to voices that transgress the normative ranges of the biological male or female[9]: People whose vocal folds deviate—due to "sexual hormone imbalances" [26]—from the size that is considered "normal for their sex" are diagnosed with "androglottia" or "gynecoglottia" [27]. Adolescents who persist in producing a high-pitched voice despite the presence of a "normal male voice organ" are diagnosed with "puberphonia," [28] and in cases where, despite "unambiguous genotypical and phenotypical sex determination there is evidence of a mental sense of belonging to the other sex" [29], people are diagnosed with "gender dysphonia" [30], a voice disorder in which the voice's sexual characteristics are at odds with the speaker's gender identity.

The prevalent preconception of sex, gender, and voice as binary oppositions thus produces notions of "appropriately" gendered voices "that cohere with hegemonic, normative prescriptions of gender" [16] and of "inappropriately" gendered voices that deviate from the ideal of the unambiguously male or female voice. If we take a look at textbooks for voice clinicians, we can imagine that the tendency for people to fashion their voice production according to contemporary and local ideals of femininity or masculinity might be compelled by the threat of pathologization that looms as soon as deviations from these norms are detected: As a rule, a "disorder of sexual development" or "intersex condition" is attributed to "women with manly larynx … and men with womanly formed vocal chords and womanly voice production" [27], a "problem of sexual identification" [31] is seen as causing puberphonia in male adolescents and people who don't identify with the sex that has been attributed to them at birth are diagnosed with "transsexualism" or "gender identity disorder," which is regarded as an incurable mental health condition [32]. Another example demonstrating that societies ascribe great importance to communication practices that conform to gender ideals is the vocal coaching of male politicians, which aims at eliminating "effeminate" speech habits and encouraging unambiguously

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[8] Responses in this survey reflected various theoretical positions: while a gender identity described as "female with the genitalia of a male" stays within a binary notion of sex and gender, descriptions such as "transgender," "genderless," "gender fluid," and "genderqueer" indicate positions that transgress conventional categorizations.

[9] Please note that these diagnoses are informed by a binary concept of sex and gender and therefore do not do justice to the situation of people who experience and think about their bodies and identities in alternative terms.

"masculine" forms of vocal self-presentation. As Delph-Janiurek (1999) reports, George Bush is a famous example of a politician who was asked to undergo training for voice masculinization.

According to Hirschauer [33], not only speakers but also listeners have an interest in contributing their share to the unproblematic communication of gender in interaction, for the correct detection and attribution of a speaker's gender is considered an everyday competence of conversation partners and addressing a speaker with the wrong title or pronoun is regarded as embarrassing.[10] However, if we take a look at listening practices, it becomes apparent that we cannot hear "maleness" or "femaleness" when we listen to someone speak or sing but are merely capable of discerning different pitch levels, sound qualities, and speech melodies. It is only due to the commonsense expectation that human beings fall naturally into two mutually exclusive categories and that the voices of the members of one group sound unmistakably different from the voices of the members of the other group that most people habitually conflate the auditory perception of voice characteristics and attributions of a female or male body and identity and create unequivocal categories of "female" and "male" voices.

While scientific findings show no significant differences between the acoustical properties of the utterances of newborn girls and boys [4], voices are perceived as male or female right from the start of our lives, when people hear even a baby's cries as sexed sounds and ask themselves "what does *she* need?" or "is *he* hungry again?" This normative arrangement of bodies, identities, and voices into two groups is repeated over and over again, for instance, by talking to or about children, adolescents, and adults with words that have sex-specific meanings (for instance, "boy," "girl," "he," "she," "Sir," "Madam") and by ticking one of the two gender boxes that are provided on official forms and documents, which are used to gather personal data. These classification practices reenact the medical sex attribution at birth and contribute to an ongoing affirmation of the expectation that gender identity always follows from sex and that both sex and gender occur in only two versions.

According to the discursive perspective, the gendering of voices is theorized as being the result of a habit of performance and interpretation that is suggested and reinforced by a cultural order that acknowledges only biological males and females as "normal" human beings. While this cultural order is produced and maintained by the communication practices of individuals—speakers and listeners alike—it is a system of rules that exceeds an individual lifetime and that is implemented in so many different forms and by so many different people that its effects are regarded as beyond individual control.

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[10] When considering the forms of address and reference to persons that are available to us, it becomes apparent that the restriction of the notion of gender to two mutually exclusive versions is already built into many languages. The lack of linguistic forms, which would signify understandings and experiences of sex and gender that transgress the female-male binary, further increases the difficulty of acknowledging gender diverse voices and identities and contributes in turn to a consolidation of the gender binary perspective.

8.4 Conclusion

Both the theory of doing gender and the perspective that emphasizes the effects of discourses on the production of gender make important contributions to a reconsideration of how the relationship between voice and gender is traditionally conceptualized. These theories, along with empirical findings showing variation in both biology and performance, suggest a move away from the concept of the naturally sexed voice organ and voice toward an understanding of the communication of gender as being performed through complex meaning-making practices to which individual speakers and listeners contribute but which they cannot control. The value of revising the concept of the naturally sexed voice is not restricted to a mere intellectual bauble for academics but extends to the everyday experience of any human being who engages in communication and social interactions.

If, for instance, we took seriously the suggestion that we should understand voices as “auditory combinations of the physiological and the discursive” [16], we would no longer think that an individual speaker’s physical characteristics or behavior patterns or an individual listener’s perception skills can be held responsible for situations in which the communication of gender fails and a conversation partner is addressed as a member of a gender grouping to which he/she feels no belonging. Rather, we would think of such situations—in which the speaker’s and the listener’s contributions to the production of gender in interaction diverge—as the standard outcome of the complex and variable processes that take place when we talk to each other and try to make sense of who we are. If we further acknowledged that deviations from the model of the naturally sexed body and mind can and do occur at all levels of sexual determination and that the structures and processes that make up the various notions of the gendered voice don’t appear only in two kinds and don’t necessarily follow the models of the ideal female and male, we would make room for an unheard of diversity of human bodies, identities, and behavior that demonstrates the multiform ways in which gender can be embodied and emphasizes the various meanings the notion of gender can assume.

I conclude by suggesting that instead of striving for speaking and listening practices that are oriented toward an alignment with the ideals of unambiguous maleness or femaleness, we would be better served by considering the following ideas raised in the forgoing discussion: A continued repetition of the myth of the naturally sexed voice leads not only to the consolidation of a narrow concept of sex and gender but also to a restriction of who we can be and become in human encounters. By learning to think, speak, and write differently about the relationship between voice and gender, however, we contribute to a change of meaning-making practices, which will facilitate the gradual replacement of the distinction between “appropriately” and “inappropriately” gendered voices with an understanding that the notion of “normality” is an ideal that cannot be embodied or secured by anybody.

References

1. Karpf, A. (2006). *The human voice: How this extraordinary instrument reveals essential clues about who we are*. London: Bloomsbury.
2. Cavarero, A. (2005). *For more than one voice: Toward a philosophy of vocal expression*. Stanford: Stanford University Press.
3. Sies, L. F. (1987). *Voice and voice disorders: A handbook for clinicians*. Springfield: Thomas.
4. Abitbol, J. (2006). *Odyssey of the voice*. San Diego/Oxford/Brisbane: Plural Publishing.
5. Rees, M. (Ed.). (2007). *Voice and gender and other contemporary issues in professional voice and speech training*. Bakersfield: Voice & Speech Trainers Association.
6. Ko, S. J., Judd, C. M., & Blair, I. V. (2006). What the voice reveals: Within- and between-category stereotyping on the basis of voice. *Personality and Social Psychology Bulletin, 32*, 806–819.
7. Abitbol, J., & Abitbol, P. (2006). The larynx: A hormonal target. In R. T. Sataloff, J. S. Rubin, & G. S. Korovin (Eds.), *Diagnosis and treatment of voice disorders*. San Diego: Plural Publishing.
8. Gooren, L. J. G. (1995). Closing speech. In Council of Europe (Ed.), *Proceedings XXIIIrd Colloquy of European Law: Transsexualism, medicine and law* (pp. 233–238). Strasbourg: Council of Europe.
9. Coleman, R. O. (1976). A comparison of the contributions of two vocal characteristics to the perception of maleness and femaleness in the voice. *Journal of Speech and Hearing Research, 19*, 168–180.
10. Titze, I. (1989). Physiologic and acoustic differences between male and female voices. *Journal of the Acoustical Society of America, 85*, 1699–1707.
11. Xue, S. A., Cheng, R. W. C., & Ng, L. M. (2010). Vocal tract dimensional development of adolescents: An acoustic reflection study. *International Journal of Pediatric Otorhinolaryngology, 74*, 907–912.
12. Baken, R. J., & Orlikoff, R. F. (2000). *Clinical measurement of speech and voice*. San Diego: Singular Thomson Learning.
13. Schultz-Coulon, H. J., & Asche, S. (1988). Das "Normstimmfeld" – ein Vorschlag. *Sprache – Stimme – Gehör, 12*, 5–8.
14. Oates, J., & Dacakis, G. (1997). Voice change in transsexuals. *Venereology, 10*(3), 178–187.
15. Simpson, A. P. (2009). Phonetic differences between male and female speech. *Language and Linguistics Compass, 3*(2), 621–640.
16. Delph-Janiurek, T. (1999). Sounding gender(ed): Vocal performances in English university teaching spaces. *Gender, Place and Culture, 6*, 137–153.
17. Hall, K. (1995). Lip service on the fantasy lines. In K. Hall & M. Bucholtz (Eds.), *Gender articulated: Language and the socially constructed self*. New York: Routledge.
18. Gelfer, M. P., & Schofield, K. J. (2000). Comparison of acoustic and perceptual measures of voice in male-to-female transsexuals perceived as female versus those perceived as male. *Journal of Voice, 14*, 22–33.
19. Scheidt, D., Kob, M., Neuschaefer-Rube, C. (2003). Zur stimmlichen Situation von sogenannten Frau-zu-Mann-Transsexuellen: Selbstwahrnehmung, Fremdwahrnehmung und akustische Daten zur Geschlechtsdarstellung. In M. Gross, E. Kruse (Eds.), *Aktuelle phoniatrisch-pädaudiologische Aspekte 2003/2004* (pp. 172–177). Niebüll: Verlag Videel. http://www.egms.de/static/en/meetings/dgpp2003/03dgpp005.shtml
20. Andrews, M. L., & Schmidt, C. P. (1997). Gender presentation: Perceptual and acoustical analyses of voice. *Journal of Voice, 11*, 307–313.
21. West, C., & Zimmerman, D. H. (1987). Doing gender. *Gender & Society, 1*(2), 125–151.
22. Rakow, L. F. (1986). Rethinking gender research in communication. *Journal of Communication, 36*, 11–26.
23. Herdt, G. (Ed.). (1994). *Third sex, third gender. Beyond sexual dimorphism in culture and history*. New York: Zone Books.

24. World Health Organization. (2007). *International statistical classification of diseases and related health problems 10th revision*. http://apps.who.int/classifications/apps/icd/icd10online
25. Bockting, W. O. (2008). Psychotherapy and the real-life experience: From gender dichotomy to gender diversity. *Sexologies, 17*, 211–224.
26. Verdolini, K., Rosen, C. A., Branski, R. C. (Eds) (2006) *Classification manual for voice disorders-I*. American Speech-Language-Hearing Association Special Interest Division 3 Voice and Voice Disorders. Mahwah: Lawrence Erlbaum.
27. Hirschfeld, M. (2006). Selections from the transvestites: The erotic drive to cross-dress. In S. Stryker & S. Whittle (Eds.), *The transgender studies reader*. New York: Routledge.
28. Pau, H., & Murty, G. E. (2001). First case of surgically corrected puberphonia. *The Journal of Laryngology & Otology, 115*, 60–61.
29. Neumann, K., & Welzel, C. (2004). The importance of the voice in male-to-female transsexualism. *Journal of Voice, 18*(1), 153–157.
30. De Bruin, M. D., Coerts, M. J., & Greven, A. J. (2000). Speech therapy in the management of male-to-female transsexuals. *Folia Phoniatrica et Logopaedica, 52*(5), 220–227.
31. Aronson, A. E., & Bless, D. M. (2009). *Clinical voice disorders*. New York: Thieme.
32. Benjamin, H. (2006). Transsexualism and transvestism as psycho-somatic and somato-psychic syndromes. In S. Stryker & S. Whittle (Eds.), *The transgender studies reader*. New York: Routledge.
33. Hirschauer, S. (1989). Die interaktive Konstruktion von Geschlechtszugehörigkeit. *Zeitschrift für Soziologie, 18*, 100–118.

Chapter 9

Parenthood in Norway: Between Politics and Science

Ole Jacob Madsen

Gender equality politics is essential to the development of democracy [1]. In the twentieth century, women's rights made considerable advances. Women have increasingly participated in public life, a sphere previously reserved for men. However, childcare is an area in which gender equality lags behind. Although advanced Western liberal governments have aspired politically and legislatively for gender equality over recent decades – by getting more women back into working life earlier and their partners more involved in family life – social changes have been relatively slow. In Norway, when parents are given a free choice, mothers generally take a long leave of absence, while fathers do not [2].

Based on a report on this dilemma concerning the public debate on paternity leave in Norway, I discuss whether this inertia stems from an underlying belief in natural differences and certain roles for men and women with regard to childcare. I explore the arguments of experts and the research they base their arguments on and consider how conceptions of nature and culture influence the debate about parenthood, in this case fatherhood in particular. Parenthood is situated somewhere between politics and science and nature and culture, which stresses the need for a balance between realities and ideals. The debate over whether nature or culture is considered fundamental to caring for children has been prevailing for some time. Donald H. Winnicott, one of the most influential developmental psychologists, considered the child's natural development to be dependent on the mother and upon her ability to perform motherhood in a manner in line with contemporary views on how to be a good mother [3]. Thus, from a historical perspective, developmental psychology has traditionally emphasised the mother's 'natural' role as caregiver. However, developmental psychologist and feminist Nancy J. Chodorow was a pioneer in pointing out the importance of both a mother and a father for a child's

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natural development [4]. Moreover, political ideology in Scandinavia has been progressive in encouraging fathers to take parental leave. The recent media debate over the influence of culture versus biology on the life choices and interests of women and men in contemporary Norway reveals that this subject is still of interest to the general public.

9.1 Scandinavia at the Forefront

One of Scandinavia's internationally acclaimed trademarks is its progressive work and family policy. This policy has been driven by the social democratic welfare state, which has been at the forefront of advances in gender equality since the 1970s [2]. In the 1960s, Scandinavian women's weak position compared to Scandinavian men in the educational system, the labour market and generally in political and public life became a political concern, and improving women's position became an important political goal and societal project of the welfare state, alongside other social rights movements [1].

Although Scandinavian family politics have been progressive and particularly successful in securing parents the welfare and laws that give them the opportunity to stay at home with their child during the first year of life, reforms have been less successful in narrowing gender differences. The gender-neutral parental leave that had been available for fathers since the 1970s did not automatically transform fathers into carers [5]. In fact, by the 1980s fewer than 5 % of fathers in Denmark, Finland and Norway made use of the leave, while Sweden led the field with one in four fathers making some use of the available leave [2]. Both Norwegian and Swedish legislators then strengthened the entitlements to paternity care by earmarking a special period of parental leave for fathers, implementing a 4-week father's quota provided on a use-it-or-lose-it basis. The Norwegian father's quota launched in 1993 was provided to give the opportunity for an early bond between men and their children. The underlying assumption was that, in general, mothers and fathers were equally capable caregivers [5].

By 2005 the majority of employed parents in all Nordic countries were entitled to a paid leave of absence, while at the same time retaining job security in connection with the birth or adoption of a child. The large majority of parents took up some of the paid leave available, but the division of caring is unequally distributed [2]. In stark contrast with the father's quota – used by as many as 70–80 % of eligible fathers in Norway – only approximately 10 % of Norwegian fathers in 2002 utilised the additional parental leave available to both parents. These numbers also apply to Denmark and Finland, while the corresponding figure for Sweden, of around 17 %, gives somewhat more cause for optimism [2]. Nonetheless, the picture is relatively predictable: when the decision about dividing leave is left to the parents, mothers take a long leave, while fathers do not. In other words, the male-breadwinner model prevails: the man provides food for the table, while the woman stays at home. This remains a concern for the Norwegian Government, and in particular the left-wing parties have been instrumental in extending the father's quota as a means of achieving more gender equality. From 2005 until 2011, the Norwegian Labour Party Government (2000–2001) and Norway's Red-Green Coalition Government (2005–2013) extended the father's quota a number of times, from 4 to 5 weeks (2005), 5–6 weeks (2006), 6–10 weeks (2009) and 10–12 weeks starting from 2011 (2010). The present leave for parents in Norway in 2011 is either 47 weeks at 100 % wage compensation or 57 weeks as 80 % wage compensation. Three weeks before and 6 weeks after delivery are reserved for the mother, 12 weeks are reserved for the father (the father's quota), while the rest of the parental leave period is left to parents to divide as they see fit. However, the legislative amendment remains controversial and a topic of debate between both politicians and experts, as we now will further examine.

9.2 Paternity Leave

A new bill proposal for a mandatory father's quota of 11 weeks minimum was put forward in 2008 by the Equal Pay Commission and the Men's Panel, both commissions appointed by the Government. The proposal was welcomed by left-wing and Moderate political parties and special interest groups like feminists and lobbyists seeking to strengthen fathers' rights, but was met with more reserved feelings and resistance by Moderate and Christian conservatives and several professional experts, mainly biologists, psychologists and medical practitioners.

Thus far, gender-neutral parental choice has largely reproduced gender inequality when it comes to caring for young children, leaving the mother as primary carer [2]. The male-breadwinner model dominates over the shared-breadwinner model. Could the reason simply be that, when parents are given free choice in dividing parental leave, the patterns conform to the natural preferences of men and women with regard to caregiving? One article covering the proposal was published in Norway's biggest daily newspaper Aftenposten under the headline: 'Politicians must understand why women resist. – Researchers warn against taking parental leave from the mother and giving it to the father' [6]. In the news story, firefighters in Oslo are interviewed about gender roles and caregiving, and one of the firemen admits: 'I'm not as good a caregiver as my girlfriend. There are considerable differences in how we tackle situations, for instance when our daughter is hurt. I take good care of her, but I believe that women, when it comes down to it, are better caregivers than men. It has to do with biology. […] Our task has always been to hunt and put food on the table. Deep down, we're still designed this way' [7].

Human biologist Terje Bongard gives his expert support to the fireman in question. He argues that women are more caring with their children than men are. That is how we are naturally selected. A political proposal cannot simply reverse that, according to Bongard [7]. His appeal to natural differences is in line with the male-breadwinner model: men are hunters, while women are gathers and more naturally inclined to tend to childcare. Bongard maintains that natural selection during the past hundred thousand years has developed our emotional life this way. For this reason, official pressure on women to make careers can actually reduce their quality of life and cause emotional unrest and resistance.

In the same report, associate professor in psychology Leif Edward Ottesen Kennair, a leading evolutionary psychologist in Norway, interprets the proposal for a nearly equal division of parental leave between the sexes as a breach of the traditional way of organising life, where we lived in small units with close ties between family members [7]. Children were breastfed for several years, slept close to their parents and spent their entire awake time with their mother. During a short period of time all this has changed. Children now sleep in their own room, they are not breastfed for the same period of time, they go to kindergarten earlier, and family ties are weakened. Kennair worries that the proposal is the latest advance in an ongoing social experiment we don't know the result of: 'When we interfere with the biological attachment to the mother, we may create societal or psychological changes' [7]. Kennair suggests we need more research on the possible consequences of the proposal and maintains that the proposal is based on ideology. His underlying concerns are for the 'child's best': 'Why doesn't anybody ask what is in the child's best interest?' [7] Later in a discussion with Aftenposten readers online, Kennair stresses that he is primarily reasoning from the point of view of developmental psychology, not evolutionary psychology: 'Developmental psychologists are worried – look at the research on attachment and infancy. Breastfeeding advocates are worried. I ask politicians to prove that they have examined the relevant research on children's development' [8].

Later the same week, Kennair's colleague, associate professor in clinical child psychology Turid Suzanne Berg-Nielsen, entered into the public debate. A headline in Norway's largest tabloid newspaper VG read: '– Changing caregiver may harm infants' [9]. In the story, Berg-Nielsen expresses her concerns about the proposal: '– My point is that the child has been somewhat forgotten in this ideological debate' [9]. Berg-Nielsen argues that there is currently no scientific evidence to support swapping the mother with the father after 11 weeks and then changing back again after another 11 weeks (which could be an option). On the contrary, frequent changes in the closest caregiver – either the mother or the father – may seriously harm the child's development: 'Research shows that infants less than 12 months are easily stressed' [9]. Berg-Nielsen further adds that among infants the level of cortisol may increase rapidly if bonds to the primary caregiver are interrupted, which is worrying because high levels of the stress hormone may cause permanent brain alterations. The news story doesn't refer to explicit studies, but in Berg-Nielsen's recent work, she explains that these kinds of reactions may have an evolutionary explanation – the infant is 'programmed' to respond with intense stress reactions and high levels of cortisol when the preferred caregiver is absent or doesn't respond to the infant's signals [10]. Berg-Nielsen refers to, among other things, an overview article by Gunnar and Donzella, which reports on previous studies on rodents and primates suggesting that responsivity and regulation of the limbic hypothalamic-pituitary-adrenocortical (L-HPA) system later in life may be formed by social experiences (like caregiving) during early development [11]. Gunnar and Donzella base their argument on a study by Bayart et al. on rhesus monkeys, which reports that, in non-human primates, the presence of the mother serves to buffer L-HPA axis activity [10]. The authors also cite retrospective studies on humans suggesting that adults who suffered emotional loss early in life, like the loss of a parent, or who suffered from maladaptive attachment show dysregulation of the L-HPA axis later in life.

'Infants are naturally inclined to choose a person as a caregiver when afraid, hungry or tired. We believe this psychological closeness is created through breast-feeding and that person is most often the mother', Berg-Nielsen reasons in the news story. She concludes that it is not 'unnatural' per se for the father to play the part of a primary caregiver, especially in cases where the mother is disabled, nonetheless the current proposal is not based on scientific knowledge on attachment and stress levels among young children. Berg-Nielsen receives support from another expert: medical practitioner Gro Nylander, who is the leading advocate of breastfeeding in Norway. Although Nylander values equality strongly, she is concerned that we are – in the name of equality politics – working against the child's best interest [12].

Despite these controversies, a majority in the Norwegian Parliament (the Storting) passed a governmental proposal in the 2009 state budget that expanded the father's quota from 6 to 10 weeks. However, in 2010, the father's quota was again debated after the Conservative Party of Norway decided to oppose the father's right to a 10-week leave of absence and instead campaigned for the old arrangement of free choice between parents. Again professionals let their voices be heard, all of them representing the view of science and research on behalf of the child. Professor in children's diseases Trond Markestad writes in the newspaper Dagbladet that although fathers should participate during parental leave, the common argument that this always is in the child's best interest is repulsive. He opposes the father's quota and uses research to back up his standpoint: 'Recent research underlines the importance of safety, predictability, continuity, and the ability to interpret small children's changing needs' [13]. No ideology should overshadow the consideration of the child, warns Markestad. Markestad's warning appears to be based on the underlying assumption that women are naturally better able to create such an ideal environment for the child.

However, not all professionals were unanimous in opposing the billing proposal. Child psychologist and member of the Norwegian Labour Party Ragnar Kværness wrote an answer to Markestad in support of the proposal, pointing out that his professionalism leads him to the opposite conclusion [14]. Kværness maintains that it is fair enough to fight politically for old family patterns but cautions against what he perceives as Markestad's use of his professional authority to cast doubt on men's caring abilities. Gender researchers Øystein Gullvåg Holter and Jørgen Lorentzen also support the father's quota, claiming that the recent proposal from the Conservative Party to remove the father's quota is more based on ideology than on knowledge [15]. Their perspective is that equality in Norway has created a better life for both women and men over the years and that domestic life today is more harmonious. They also argue that violence towards children has proportionally decreased over the past 50 years as a result of increased equality. A more equal family life and a present and caring father are therefore in the best interest of the child. The research they draw on (although not mentioned in the article) is primarily the report ‘Equality and quality of life’ published by the Work Research Institute (AFI), financed by the Ministry of Children, Equality and Social Inclusion [16]. The report is a survey study and shows, among other things, that younger women and men report having experienced less domestic violence than earlier generations of Norwegians.

9.3 Discussion

9.3.1 The Return of the Mother

Despite overall aims to strengthen fathers as caregivers, motherhood has returned to the forefront in the debates on childcare in Norway, especially over the past 10-year period, mainly through the strong emphasis on breastfeeding [5], in parallel to an even stronger emphasis on individual freedom in the political climate. During the past decade, Norwegian officials have recommended that mothers fully breastfeed until the child is 6 months old and prolong breastfeeding until the age of 1 year. A national survey conducted in 2007 showed that 75 % of infants were breastfed at 7 months, 63 % at 9 months and 46 % at 12 months [17]. Breastfeeding had increased from the previous survey in 1999, when 36 % of mothers reported breastfeeding at 12 months. The emphasis on breastfeeding has brought the medical expertise right into the debate over the father’s quota. Medical professionals have typically stressed women’s superior biological care abilities, and breastfeeding has now become one of the most important arguments against extending the father’s quota. This also has a psychological dimension. The focus is not exclusively on the positive health effects of the breast milk itself but also on the secondary psychological effects of the breastfeeding situation, such as facilitating attachment and reducing stress.

9.3.2 ‘What a Child Needs’

The rationale behind Norwegian parental leave politics is based on a social agenda of increasing equal opportunity and women’s participation in the labour market, but it is predominately formulated in terms of child-oriented interests [5]. Present public debates strongly conform this, and representing ‘the child’s best interest’ seems almost a mandatory position if one is to be taken seriously. The Men’s Panel’s official recommendations for increasing equality among men and women takes the United Nations Convention on the Rights of the Child as its starting point [18]. Sociologists Brandth and Kvande maintain that when leave schemes were gradually extended in the late 1980s and early 1990s, the idea of equal rights continued to be a strong rational for developing parental leave, but at this point an additional rationale emerged – namely, the child's need for a caring father [5]. Strengthening the father's place in a child's life was believed to be of importance to encouraging him to take part in childcare during the first year.

Interestingly, the very same justification – the child's need – is now used both by medical and psychological expertise that casts doubt on the idea of the father being the primary caregiver during part of the child's first year. Hence, advocates both for and against the proposal seem to recognise this 'child centrism' and use it to their advantage. The sceptics and adversaries of the proposal, such as Berg-Nielsen, Kennair and Markestad, frequently express concerns that the child's best interest is being neglected to promote ideological equality politics. This is also the case for professional supporters of the proposal such as Kværness, Holter and Lorentzen – who all maintain that securing fathers' involvement in caregiving is in the child's best interest. The 'child centrism' is now so predominant that one perhaps must view any claim to represent the child with suspicion, not just from politicians or special interest groups, but even from professional experts.

9.3.3 From the Perspective of Knowledge

The gap between biologists, psychologists and medical practitioners, on the one hand, and more progressive-minded psychologists and gender researchers, on the other, is perhaps not so surprising. Health professionals usually take the child into consideration, while social scientists take the family into consideration. Both parties must appeal to research to claim legitimacy in their attempts to represent 'the child's best interests'. 'Research shows' arguments support contradictory positions based on their different emphasis on the influence of nature versus culture. But although young children's stress levels and equality and stableness in families are not irrelevant knowledge, one must still ask critical questions about their relevance to the case in question. Studies on cortisol levels in rhesus monkey babies and retrospective studies on adults are somewhat limited when it comes to their generalisability, although not irrelevant. Whereas the argument that the proposal of extending the father's quota is associated with less violence against children presupposes several causal bonds and third factors not sufficiently accounted for. These examples demonstrate that a meta-reflection on the strength and relevance of scientific knowledge is required.

The fact that conclusions drawn based on research findings are not concurrent when it comes to deciding on the proposal shows that research may support a large variety of political agendas. Research in itself is rarely, if ever, unequivocal and conclusive. How it is taken up and used by politicians, social commentators and even scientists will vary. Political decisions are based on several different sources of information, where research is in fact only one type, people's experiences being another. Different notions of the 'child's best interest' are based on different ideas about the individual's place in society – as political ideology has moved from focusing on equality between the sexes and women partaking in the labour market towards an emphasis on individual freedom, the room for natural and biological explanations has expanded.

Scientific experts with the best intentions wield important power in influencing the public, especially when they confirm ‘common sense’ and appeal to ‘human nature’. Many researchers challenge the assumptions and methods of evolutionary psychology, suggesting that the idea of ‘natural’ female and male sexual differences is a naturalisation of archaic culture turned into a convenient popular myth [19, 20]. In addition, appeals to the Stone Age always seem to be highly selective and seldom reflect ugly phenomena like infanticide and in general most of the things modern, civilised man takes for granted. A frequent rhetorical strategy in public debates is to conveniently describe differences in child rearing as ‘natural’, but to refrain from this when phenomena are abhorrent to our modern sensibility. Of course, there are no rules without exceptions. Biologists Thornhill and Palmer’s controversial book *A Natural History of Rape: Biological Bases for Sexual Coercion* received criticism for giving rapists a ‘genetic excuse’ [21]. Finally, it is easy to forget that part of the reason why countries like Sweden and Norway have led the way in gender equality and women’s rights has historically been a willing disregard for what has been perceived as ‘human nature’ at the time. It was not long ago that common sense held that women were genetically capable of little more than raising children. Hence, over the course of history, the notion of an innate, biological ‘human nature’ has frequently contained political and cultural biases.

Particularly Bongard, in the cited news story, appears to stretch the theory of evolution’s explanatory power when he indirectly claims that women’s feelings make them naturally inclined to stay at home with their children. At least a critical examination of broad scientific explanations of individual behaviour would seem to be necessary. But this is also a problem that politicians and campaigners for equality openly disregard, not just ‘nature’, but also ‘science’ in general that interferes with overall political goals. Bongard and Kennair, who share an evolutionary approach to the question of parental leave, were heavily criticised by parliamentary politicians, primarily it seems because their views didn’t fit with governmental agendas. The leader of the Men’s Panel, Arild Stokkan-Grande, was quoted as saying: ‘That’s so stupid it can only be said by a professor’, while MP Gunn Karin Gjul demanded that scientists devote themselves less to opinions and more to research [22]. This in particular seems rather unjust, as Kennair had called precisely for more research before decisions are made. The strong political condemnation led science journalist Bjørn Vassnes to write an attack on Norwegian politicians’ arrogant attitudes towards research. He explained their hostility in terms of the 1968 movement’s ideological rejection of the natural sciences [23].

On a different level, the question of parenthood in Norway and the dominating relations between mothers, fathers and children demonstrate how certain understanding of what constitute ‘good’, ‘healthy’ or even ‘true’ selves are continually produced and reproduced through government politics, the media and expert knowledge. Sociologist Steph Lawler, in her book *Mothering the Self*, maintains that contemporary Euro-American parenthood rests on motherhood as the foremost guarantor of the liberal democratic order, in which individuals are expected to manage themselves [24]. Fatherhood, it appears, is sometimes a disturbance to the whole arrangement of knowledge power, as it falls outside what is socially imaginable (what, as Lawler claims, often is conceptualised as ‘natural’). Lawler also underlines the inherent ‘child-centred’ discourse of psychologists, other health and social work professionals such as health visitors and social workers – who have a tendency to replace the notion of parental rights with parental responsibilities, generally reiterating the paramountcy of ‘the best interests of the child’ [24]. The present psychology paradigm emphasises individual autonomy, which is expressed in therapeutic language that helps individuals work on, and perfect themselves as free citizens, thus overlooking the social context. Individual freedom means that people want to be free in their choices, despite the fact that they frequently fall into old gender patterns when choosing parental leave. Governmental policies that intrude on what is perceived of as individual freedom, like the father quota, are not only perceived as undesirable because they interfere with the idea of parental choice but because they interfere with the whole truth of ‘natural’ self-governing that permeates the present Euro-American ideology. Nonetheless, Lawler suggests that the answer is not political apathy, but a continuous politicisation of the politics of the self and subjectivity, because both children and adults are too straightforwardly conceptualised into essential, transcendent phenomena [24].

9.4 Conclusion

It is interesting how conceptions of nature and culture have influenced the political debate on parenthood. Emphasising equal opportunity in life and in the labour market, as well as the need for women in the labour market, has resulted in progressive political reforms in Scandinavia over the past several decades, thus stressing a cultural perspective on how caregiving is distributed and performed. At the other end of the continuum, psychology experts base their argument on their conceptions of what is natural. Thus, the different perspectives on individuals – as parts of a social system, or as autonomous and isolated from their social context, which leaves more room for natural and biological explanations – have different impacts on individuals, as well as on society.

The debate about the influence of nature versus culture on women’s and men’s roles is a lively one in contemporary Norway. The current political Euro-American ideology emphasises individual freedom more than the social democratic agenda does – an agenda that pushed the social reforms in Scandinavia. An opinion poll from October 2010 shows that two of three Norwegian voters now back the Conservative Party’s proposal to give parents back their free choice over parental leave [25]. Only 28 % of the people surveyed supported a special father’s quota. The future of the current parental leave arrangement is therefore very uncertain. An abolishment of the father’s quota altogether might occur during the next Storting period. Perhaps when societal changes are perceived as too enforced and therefore ‘unnatural’, political reforms are likely to be rejected. Yet if there is one thing that appears consistent throughout history, it is our ability to adapt to changing requirements, as well as perhaps our habit of falling back into traditional patterns just for the sake of convenience. After all, that is in our nature.

References

1. Ellingsæter, A. L., & Leira, A. (2006). Introduction: politicising parenthood in Scandinavia. In A. L. Ellingsæter & L. Arnlaug (Eds.), *Politicising parenthood in Scandinavia. Gender relations in welfare states* (pp. 1–24). Bristol: The Policy Press.
2. Leira, A. (2006). Parenthood change and policy reform in Scandinavia, 1970s–2000s. In A. L. Ellingsæter & L. Arnlaug (Eds.), *Politicising parenthood in Scandinavia. Gender relations in welfare states* (pp. 27–51). Bristol: The Policy Press.
3. Winnicott, D. W. (1960). The theory of the parent-infant relationship. *The International Journal of Psychoanalysis, 41*, 585–595.
4. Chodorow, N. J. (1978). *The reproduction of mothering: Psychoanalysis and the sociology of gender*. Berkeley: University of California Press.
5. Brandth, B., & Kvande, E. (2009). Norway: The making of the father's quota. In S. B. Kamerman & P. Moss (Eds.), *The politics of parental leave policies* (pp. 191–206). Bristol: The Policy Press.
6. Leira, A. (1998). Caring as social right: Cash for childcare and daddy leave. *Social Politics, 5*, 362–378.
7. Engh, C., & Ruud, S. (2008, March 4). Politikerne må forstå hvorfor kvinner stritter imot [Politicians must understand why women resist]. *Aftenposten*, 4–5.
8. Kennair, L. E. O. (2008, March 4). Nettprat – Advarer mot å ta permisjon fra mor [Internet talk – Cautions against taking permission from the mother]. *Aftenposten.* Retrieved from http://tux1.aftenposten.no/nettprat/kennair2008/
9. Vikøyr, H. (2008, March 7). Omsorg på skift kan skade spedbarn [Changing care giver may harm infants]. *Verdens Gang*, 4–5.
10. Berg-Nielsen, T. S. (2010). Følsom, formbar og uferdig. Epigenetikk, utvikling av hjernen og stressbarhet. In: E. Befring, I. Frønes, & M.-A. Sørlie (Eds.), *Sårbare unge. Nye perspektiver og tilnærminger* [Vulnerable young ones. New perspectives and approaches] (pp. 75–85). Oslo: Gyldendal Akademisk.
11. Gunnar, M. R., & Donzella, B. (2002). Social regulation of the cortisol levels in early human development. *Psychoneuroendocrinology, 27*, 199–220.
12. Vikøyr, H. (2008, March 7). Høres rimelig ut [Sounds reasonable]. *Verdens Gang*, 4–5.
13. Markestad, T. (2010, May 12). Valgfrihet for barnas skyld [Parental choice for the children's sake]. *Dagbladet*, 74.
14. Kværness, R. (2010, May 20). For barnas skyld [For the sake of the children]. *Dagbladet*, 66.
15. Holter, Ø. G., & Lorentzen, J. (2010, November 3). God familiepolitikk [Better family politics]. *Aftenposten*. Retrieved from http://www.aftenposten.no/meninger/debatt/article3885971.ece
16. Holter, Ø. G., Egeland, C., & Svare, H. (2008). *Likestilling og livskvalitet [Equality and quality of life]*. Oslo: Work Research Institute.
17. Norwegian Directorate of Health. (2009). *Spedkost 12 måneder. Landsomfattende kosthold-sundersøkelse blant 12 måneder gamle barn* [Diet for infants. National survey among infants aged 12 month]. Oslo: Norwegian Directorate of Health
18. The Men's Panel. (2008). *Equality and social inclusion Ministry of Children 10*. Oslo: Ministry of Children, Equality and Social Inclusion.
19. Rose, S. (2001). Moving on from old dichotomies: Beyond nature-nurture towards a lifeline perspective. *The British Journal of Psychiatry, 178*, 3–7. doi:10.1192/bjp.178.40.s3.

20. Fausto-Sterling, A., Gowaty, P. A., & Zuk, M. (1997). Evolutionary psychology and Darwinian feminism. *Feminist Studies, 23*, 402–417.
21. Thornhill, R., & Palmer, C. (2000). *A natural history of rape biological bases of sexual coercion.* Cambridge, MA: MIT Press.
22. Ertzeid, H. (2008, March 4). Dette er så dumt at det bare kunne være sagt av en professor [This is so stupid it can only come from the mouth of a professor]. *Aftenposten*. Retrieved from http://www.aftenposten.no/nyheter/iriks/politikk/article2292562.ece
23. Vassnes, B. (2008, March 6). Det man ikke vet… [What we don't know…]. *Dagbladet*, 48.
24. Lawler, S. (2000). *Mothering the self. Mothers, daughters, subjects*. London: Routledge.
25. Tjernshaugen, K. (2010, October 17) To av tre spurte sier nei til pappakvote [Two out of three say no to father's quota]. *Aftenposten*. Retrieved from http://www.aftenposten.no/nyheter/iriks/article3860173.ece

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My scientific career started in genomics at the University of Ottawa where I earned a B.Sc. Hon. degree in biopharmaceutical sciences followed by an M.Sc. in biology at Carleton University, studying evolutionary theory, especially evolution of subcellular processes. Specifically, I study evolution of processes involved in the formation of new individuals, such as the coming together of nuclei from one or two parents. I am interested in the variation of these processes in almost all life forms and how that variation informs evolutionary notions of sex. I am also interested in the role sexual selection might play on levels that are normally overlooked by biologists, such as within the microcosm of an egg.

As a student of science, I am dedicated to understanding how the legacy of male domination of the natural sciences has shaped biological ideas. The impact of male bias sets in motion many of the ideas raised in this chapter. I am thrilled to be able to contribute to such a body of work and look forward to the discussions it will surely raise.

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Lindsay Jackson Derraugh is a Ph.D. student at Carleton University, Canada.

I earned B.Sc. Hon. and M.Sc. degrees in biology from Carleton University. My research focuses on evolutionary theory, specifically the evolution of unconventional modes of reproduction such as gynogenesis (fertilized egg tosses out all sperm nuclei), androgenesis (fertilized egg tosses out all egg nuclei!), and parthenogenesis (zygote formation without sperm), as well as interactions between egg and sperm nuclei when multiple sperm nuclei fertilize an egg. As a theoretical biologist, I strive to develop new hypotheses and test them whenever possible by accumulating evidence from past and present literature. The oddities of nature drive my curiosity and research. Hopefully our chapter can encourage biologists, and individuals of all disciplines, to define the sexes only when absolutely necessary and be cognizant of the fact that the dichotomies we create are hardly ever universal.

Jonathan P. Drury is a Ph.D. candidate in the Department of Ecology and Evolutionary Biology at UCLA. He is interested in mate choice, the evolution of showy traits, and tropical biology. He has worked as a research assistant on several projects at the Smithsonian Tropical Research Institute, including a project on the community ecology of tropical trees. Currently, he is working on an investigation of the reproductive behavior of damselflies in the genus *Hetaerina* and a comparative study of showiness in bird plumage.

Root Gorelick is an associate professor in biology, mathematics, and interdisciplinary studies at Carleton University, Canada.

I am an evolutionary theorist, who was previously an economist and physicist. Our lab works on evolution of sex, evolutionary genetics of asexuality, chromosomal evolution, evolution of diversity, and mathematics of quantifying diversity and division of labor. I teach evolution of sex, introductory botany, evolutionary concepts, and population genetics. Once, during a single frenetic year, I had the pleasure of co-teaching a course in women and the law, as well as teaching mathematics, economics, experimental statistics, and biology.

My studies of sex began by asking how plants are pollinated and fertilized. I then asked how signals on top of DNA determine sex of individuals and drove evolution of sex chromosomes. This grew into studying how heritable non-DNA signals influence evolution of gamete production and fertilization. This work cast doubts on differences between females and males and seems to debunk most remaining sexual division of labor. I am trying to infuse more feminist, queer, and trans theory into my biological research, hoping to eventually repay the favor by making my work accessible across all these disciplines.

Kristina Karlsson Green has a Ph.D. in biology from Lund University, Sweden. Her thesis involved research on mating strategies and sexual conflicts in aquatic spineless animals. She is interested in evolutionary ecology, with a special focus on coevolution and sexual selection. She has continued her research with a postdoctoral period at the University of Helsinki, Finland.

Thierry Hoquet is a professor of science history and philosophy at the Faculté de Philosophie, Université de Lyon (Jean-Moulin), France.

I am the scientific editor of the website www.cnrs.buffon.fr and a member of the boards of several journals (*Critique*, *Corpus, Bionomina-International Journal for Biological Nomenclature and Terminology*).

My current research focuses on three different topics: (1) eighteenth-century natural history (mostly Buffon and Linnaeus); (2) Darwin and the history of Darwinism, with a special interest in the question of variations; and (3) the history of the concept of sex in biology, especially with regard to the history of the concept of sexual selection.

As a historian and a philosopher of science, I was primarily interested in the great books in science and how major texts shaped our understanding of nature. Working on the concept of sex, my interest in gender issues is now growing, and I am especially interested in the paradoxical figure of the "feminist biologist," with a dual commitment to both feminist theory and biological research. Female researchers like Sarah B. Hrdy, Patricia Gowaty, Marlene Zuk, and Joan Roughgarden are good examples of this research tradition.

Åsa Lankinen is an associate professor in plant ecology at the Swedish Agricultural University (SLU), Sweden. Her research interest is in the interface between evolutionary biology, genetics, and plant ecology in both cultivated and wild plants. She has been doing research on sexual selection and sexual conflict for the past 15 years, in which her main focus has been on developing and experimentally testing how sexual selection could function in plants.

Josefin A. Madjidian has a Ph.D. in plant ecology and systematics from Lund University, Sweden. In her thesis she examined sexual conflict over stigma receptivity in a hermaphroditic herb. Apart from an interest in gender perspectives on biology, she has also been working with the mutualistic interaction between pollinators and plants.

Ole Jacob Madsen is a clinical psychologist and a philosopher. He recently defended his Ph.D. thesis at the Centre for the Study of the Sciences and the Humanities at the University of Bergen, Norway. Madsen is examining how the therapeutic culture is currently unfolding in Norwegian society, and he argues that these cultural changes present psychologists with new societal ethical dilemmas. Of particular interest is the validity of the traditional critique claiming that psychology causes ideological dissimulation and transforms societal and political issues into individual, psychological, and biological problems.

Priscille Touraille is a social anthropologist, CNRS researcher in the multidisciplinary lab "Éco-anthropologie & ethnobiologie" (research team of human population genetics) of the National Museum of Natural History, Paris, France. Her research interests include the anthropology of gender, namely, how gender thinking establishes itself cross-culturally and the possibility that gender regimes could have had influenced biological characteristics, as, for instance, the sexual dimorphism of stature or of hairiness. She is currently working on epistemological issues regarding the use of sex and gender concepts in the social and life sciences.