

From Sex to Gender

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Abstract

Why are we not hermaphrodites? This paper argues that while hermaphroditism is an efficient means by which genes may propagate themselves, inherent tendencies towards polygyny undermine its stability. Understanding the forces that have established a segregation of sex functions between male and female individuals provides insight into the concept of gender.

1 Introduction

As Trivers (1985) noted, reproduction is an inherently social activity. At a minimum it involves one organism begetting another. By that metric alone, sexual reproduction (henceforth, sex) merits its own mention. Sex requires sexes, and apparently two will do nicely. Although this might appear the *raison d'être* for males and females (gonochorism), that is not so.¹ To understand the triumph of gonochorism, fault must be found with hermaphroditism, for if the benefits of sexual reproduction lie in the recombination of genes alone, then this recombination can be achieved more cost effectively than through the separation of male and female reproductive functions in different individuals.

One reason to raise this issue is that the social organization of a society of hermaphrodites would arguably be very different from that of gonochorists. For instance, gender roles as we know them are largely predicated on not only sex but on each individual being of one sex only. Moreover, and perhaps more central to hermaphroditism's undoing, we will argue, is that hermaphroditism is likely to be unstable in the face of polygyny – and polygyny is likely to be both individually and collectively opportune. Put another way, had our ancestors been strictly monogamous, we would have an altogether different concept of gender.

But first, let us consider the case against gonochorism. How can we claim that hermaphroditism is a viable alternative? After all, the hermaphrodite needs to maintain two reproductive functions [Charnov 1979]. Certainly, but from the genes' perspective, the organism may be considered the fixed cost – and the hermaphrodite's genes economize on the organism. An hermaphrodite

¹Our analysis assumes anisogamy (sex cells being of different size) as opposed to isogamy (sex cells of equal size).

can be thought of as a car with two seats. Although the hermaphrodite incurs the fixed costs of both male and female functions (two seats), it is less expensive to build one two-seater than two one-seaters (gonochorism).

Another way to see that gonochorism is costly, consider a population of N individuals. If hermaphroditic, the next generation will consist of cN individuals, where c is the average number of offspring to the female function (and in this case, individual). If gonochoric, however, the next generation will consist of $cN(1 - m) < cN$ individuals, where $m \in (0, 1)$ is the fraction who are males, since males do not bear children.

The cost of dedicating an entire organism to the male function is one of the main disadvantages of gonochorism, see Maynard Smith [1978] – a disadvantage that could be overcome by hermaphroditism. But if hermaphroditism is so economical, then why are we not hermaphrodites? If inbreeding were the culprit, this could be solved through self-incompatibility (a handy feature of snails and worms).² Understanding where hermaphroditism breaks down is a more subtle exercise.

Before diving into possible reasons why we are not hermaphrodites, to appreciate the importance of that question, we may want to consider what hermaphroditism would do to our concept of gender. Would it even be meaningful? For some dimensions, yes. For instance, say if males are more aggressive than females, it is conceivable that the individual could let the male side dominate in some instances and the female in other instances. But toggling between the male and female “sides” has its limitations. For instance, it is difficult to imagine how sexual dimorphism could be maintained in hermaphrodites. Instead, the evolutionary forces favoring a large male might be mitigated by the fact that only part of the individual’s reproductive capacity is through the male function, e.g., Greeff and Michiels [1999a]. The moderating effect would be even greater if the feature that might favor the male function is deleterious to the female function. For instance, gaudy coloration or risk taking may favor the male (but not the female) function at the expense of raised mortality – which affects the organism and therefore the male and female functions equally. The inherent internal conflict between male and female functions severely limits the scope for secondary sexual differentiation.

²But not, for instance, the freshwater mussel *Utterbackia imbecillis*.

2 Hermaphrodite Sex

So far, we have argued that hermaphroditism could be advantageous. We have also argued that our concept of gender is rooted in the segregation of male and female organisms. How then did we arrive at the gonochorism that underpins our notion of gender?

Let us turn to the social organization of hermaphroditic mating and our proposed reason for why hermaphroditism might be unstable. Consider two sex functions, male and female. An organism that houses both would be an hermaphrodite. Each sex function produces corresponding sex cells and there is a fixed cost involved in building and maintaining each. Moreover, there is a variable cost associated with the production of sex cells that differs between male and female sex cells. The biological definition of male and female is that the sex with the larger sex cell is female. To fix ideas, let us assume that the male sex cell is so small that it can be produced at negligible, say zero, marginal cost. The female sex cell, on the other hand, must carry enough energy to initiate the process of cell division, and thus is costly. This variable cost means that the number of female sex cells produced is finite.

Limited female fecundity may be one reason for the male and female function to favor different reproduction strategies, as argued by Trivers [1972]. To the male function, any mating opportunity carries an upside at little opportunity cost. The female function, however, should favor quality over quantity. How is this tension resolved in a population of hermaphrodites?

Let us assume that each female function only produces one sex cell, so that each hermaphrodite carries one female sex cell and an infinite number of male sex cells. Moreover, we start by assuming that all individuals are of equal quality. For a successful mating, both a male and a female sex cell is required. Thus an important question in every encounter must be whether the prospective partner will offer its female sex cell for mating. Say hermaphrodite A is considering mating with hermaphrodite B, whose female sex cell is not available (e.g., from already being mated). In this case, the only mating possibility that remains between A and B is for A to offer its female sex cell for mating with B. If A agrees, it will obtain an offspring through its female function, but will not have mated its male function. In this situation, will A ever obtain offspring through its male function? For that, A will need to find a partner willing to offer its egg although A's egg is no longer available. Let us assume there is a probability p that there will be such a partner, then the expected payoff from this strategy is:

$$1 + p.$$

An alternative scenario would be for A to decline mating with B in the hope that in a future encounter, with say C, C's female sex cell will be available. That would be advantageous since A would then be guaranteed offspring through both its male and female functions. In total A would obtain two offspring.³ Of course, this strategy hinges on indeed meeting C, and if we denote that probability by q , then the expected payoff in terms of offspring is:

$$q(1 + 1).$$

Clearly, insisting on reciprocal mating is likely to yield a higher payoff than agreeing to non-reciprocal mating the lower the search cost (higher q) and the lower the probability of finding someone else who is willing to mate its female function without reciprocal access (lower p). In this particular example reciprocal mating results if:

$$q > \frac{1 + p}{2}.$$

Also note that p depends on the equilibrium strategies. In an equilibrium where everybody insists on reciprocal mating, $p = 0$.

The upshot of this thought exercise is that unless the probability of meeting another partner is small, no one will get away with only mating its male function without also giving the partner reciprocal access to its own female function.⁴

A direct implication of reciprocity is that each individual can mate reproductively only once. Certainly, there are male sex cells to go around for further matings, but all female sex cells will be taken, thus rendering further mating purely recreational. Also note that the described mating is strictly monogamous.

The above scenario implicitly assumed no quality differences between individuals. The extent to which this is true among slugs and snails can only be speculated, but it is manifestly not the case among more evolved species. As

³As sperm abound, hermaphrodite A could try to find additional partners with available eggs. But this opportunity exists in the first case as well, and can therefore be ignored in the example at hand.

⁴High search cost is a notable feature of many hermaphroditic animal species, either from low motility or population density, see Ghiselin [1969].

is well known from the matching literature, heterogeneity can undo a monogamous equilibrium, see e.g., Becker [1991].⁵ To see this, let us return to A's encounter with B. Again, let us assume B does not give A access to its egg (either from its prior fertilization, or B's saving it for another partner). Is it possible that A would agree to mate non-reciprocally (i.e., A's egg is fertilized by B's sperm)? Hermaphrodite A would risk not being able to use its male function, but if B is of sufficiently high quality (relative to others), the quantity-quality trade-off may be justified. In this case, heterogeneity may undo reciprocity and, as a consequence, monogamy.

We can now ask the next question: would A in this scenario want to be an hermaphrodite? After all, A only made use of its female function. The fixed cost associated with the male function could be put to better use if dedicated to producing more eggs.

In fact, in a heterogeneous population, low quality individuals might do better as purely female. While this is not enough to undo the existence of hermaphrodites in equilibrium, it is a start. For high quality individuals to gain fitness by being purely male there must be some gain to the male reproductive success from so doing. If the resources dedicated to the female function could be used to boost reproductive success through the male function (e.g., by building a bigger body), high quality individuals may want to shed their female function and be all male. Thus, hermaphroditism may be individually suboptimal and thus unstable, formal conditions for which we derive in Edlund and Korn [????].

3 Gender

Men and women both look and behave differently, and these differences are central to the concept of gender. We conclude by a brief discussion of gender and how it relates to gonochorism.

Darwin introduced the notion of secondary sexual differentiation (SSD). It pertains to features that increase the ability to attract partners and/or compete with rivals but are otherwise of little value or potentially deleterious. The peacock's tail is the classic example. Size dimorphism is another example closer to home.⁶ While greater size may be useful for foraging or fighting

⁵Polygamy arises if one side is more heterogeneous than the other. One reason for why that would be the case is the limited female fecundity.

⁶Darwin noted that secondary sexual differentiation tends to be more pronounced among

off predators, intra-male competition is likely to be an important reason why males are typically larger and more muscular than females in a number of species. Size dimorphism is obviously only possible among gonochorists. A link to gender may be that men’s greater body size and strength has been a rationale for occupational segregation of men and women, an important dimension along which social realities and expectations are different for men and women.

Male SSD may also offer an explanation to why the process towards gonochorism appears irreversible: an hermaphrodite may not be competitive against a pure male (and therefore better off either as a pure male or female).⁷ Let us stick with the example of dimorphism, and, for the sake of argument, assume that “females” prefer taller partners. Pure males can be taller than hermaphrodites since they do not need to maintain a female function. Consider a population of females, males and hermaphrodites. The hermaphrodites are not as tall as the males and may therefore effectively only be able to mate as females. In other words, SSD may render a biologically functional hermaphrodite all female for practical purposes – its male function losing out in the competition with pure males – and not a very good female at that, since he/she is hamstrung by the burden of maintaining a male function. Thus, SSD can drive out hermaphroditism (and may be a *sine qua non* for the existence of pure males).

Behavior Although less hard wired, SSD may also apply to behavior, and the scope for behavior to be “gendered” may be radically different among hermaphrodites. We will concentrate on three aspects: violence, promiscuity and mating systems.

Violence: Male violence is a form of SSD of particular interest. Like the peacock’s tail, it is likely to reduce longevity but may help in the competition for mates. For instance, a non-negligible fraction of homicides is male on male and often motivated by a common love interest. War is another example where lethal violence can be largely described as intra-male, since women are disproportionately, if not entirely, spared. Would such violence make any sense in a population of hermaphrodites, where each male comes bundled

males. In our framework, the reason females do not invest in SSD is that females can invest in more sex cells while males cannot (recall, sperm are produced at zero marginal cost).

⁷Hermaphroditism in animals is not only rare, it is also, phylogenetically in decline, mainly relegated to invertebrates.

with a female? Does violence even exist among hermaphrodites? Among marine slugs, mating is unilateral, and they compete to mate in the male role, resulting in something that has been termed “penis fencing.” The successful slug injects sperm through the skin of the partner [Michiels and Newman 1998]. Bodily harm is substantial but not lethal, which makes sense since little would be gained if it were the latter. Thus, rather than being lethal and male-to-male, slug violence is non-lethal and male-to-female. In other words, hermaphroditism seems to preclude war but not rape.

Promiscuity: That eggs are expensive and sperm cheap underly female choosiness. For humans (and other gonochores) it predicts that heterosexual matings would be less promiscuous than male homosexual matings because the female side is limiting. A hermaphrodite is both male and female – will the female side still be limiting? In principle, it could be. In practise, however, hermaphroditic mating is remarkably promiscuous by our standards, and the sharing of an organism by male and female functions may be key to understanding why that is. A hermaphrodite gains fitness through both its male and female functions. The male function can gain from promiscuity. To obtain a partner for the male function, the hermaphrodite can offer access to its own female function. The female function can thus aid the organism’s reproductive success by being promiscuous (or rather, as promiscuous as the male function).⁸ Of course, once the eggs are fertilized, female access is an empty promise. But if the state of the eggs can be dissimulated, as is the case when fertilization is internal, it may work.

Still, the female function is quantity restricted and should aim for quality. Promiscuity makes that difficult, but not impossible. In many animal species, copulation does not guarantee egg access. Instead, sperm is collected in the female reproductive tract for further triage before fertilization. Thus, a second round of cryptic female choice allows the female function to mate repeatedly *and* remain selective. While not restricted to hermaphroditic species, it holds particular promise for them since it allows the individual to not only mate promiscuously in the female function (which may have recreational value) but also in the male function. In other words, everybody could seemingly offer access to eggs in order to gain reciprocal access.

This form of female cheating has not gone unchallenged however. Charnov

⁸Alternatively formulated, the female function can gain reproductive success through the male function since, genetically, an egg is as related to another egg as it is to another sperm (of the same hermaphrodite).

[1979] pointed to sperm competition as a male counter strategy, and sperm competition is indeed both common and resource demanding among hermaphrodites [Greeff and Michiels 1999b]. Other counter strategies include love darts and hypodermic insemination: In snails, insemination is accompanied by the affixion of “love darts” that prod ovulation in the partner. These darts are visible to others, and interestingly, snails that carry these are avoided as partners [Haase and Karlsson 2004]. Among the above discussed marine slugs, insemination is hypodermic, thus circumventing protective measures in the reproductive tracts shielding the eggs from fertilization. In the end, however, there are only so many eggs to go around.

Thus, female chastity, in practise and as a cultural ideal, may be the preserve of gonochorism.

Mating systems: Darwin distinguished between natural and sexual selection. Natural selection referred to the selective pressure of the environment, whereas sexual selection referred to improvements to inclusive fitness that stemmed from reproducing more successfully than the population average. This greater reproductive success could be achieved in a strictly monogamous setting through greater ability to attract a partner whose qualities helped in the offspring’s survival and partnering. However, reproductive success can also be had through the familiar extensive margin: more partners. The extensive margin is likely to be more important for males than females because of the latter’s limited fecundity. Thus, sexual selection through the extensive margin relies on effective (as opposed to formal) polygyny.

Polygyny characterizes the vast majority of gonochoric species, including our own. While formal monogamy characterizes some human societies, the remarriage rates of divorced or widowed men (as well as the number of extramarital relations) exceed those of women in such societies, thus resulting in *effective* polygyny.⁹ Hermaphroditism may preclude polygyny and thus reduces the scope for sexual selection. That is, hermaphroditism prevents the disproportionate propagation of genes that enhance attractiveness, be it our good looks or common senses.

⁹Even if women also remarry, if men remarry at a higher rate than women, we would consider that on net, men remarry more, and therefore there is effective polygyny. Moreover, if women remarried/repartnered as much as men, we would consider that effective monogamy (everybody mates once, scaled by a factor n). Thus note that promiscuity, $n > 1$, is consistent with effective monogamy.

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