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What Do Sexes Have to Do with (Models of) Sexual Selection?

Aya Evron^{1,2} 

¹Department of Philosophy, The Hebrew University of Jerusalem, Jerusalem, Israel and ²The Cohn Institute for History and Philosophy of Science and Ideas, Tel Aviv University, Tel Aviv, Israel
Email: ayaevron@gmail.com

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Abstract

Sexes are normally taken to be fundamental categories in biology—many sexually reproducing organisms fall under the categories of female/male. Much research aims at explaining differences between sexes. Sexual selection forms a central framework for explaining “typical” distributions of traits among sexes and explicating circumstances leading to “reversal.” I claim that sexual selection models need not make use of sexes and that sexes lack explanatory significance in such models. I offer a framework of reproductive dimorphism and argue that it is better than that of sexes because it (1) is more compatible with explanations of sexual selection and (2) allows for their greater applicability.

1. Introduction

Darwin (1860) famously felt uncomfortable every time he saw a peacock’s tail: “the sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick.” The reason for his discomfort was that he was baffled by some traits found quite commonly in nature that seemed to be in tension with his theory of natural selection. Accounting for traits like the peacock’s tail doesn’t seem feasible in the framework of natural selection alone. Such extravagant phenotypes don’t seem to be adaptive, and even worse, they seem to lower fitness. This is because these are costly traits: they can attract predators, parasites, and so on. So how is it that such traits are found quite regularly in nature?

Darwin came up with the idea of sexual selection, thus providing a possible conceptual account of such traits. According to Darwin, sexual selection was driven primarily by two forces: male–male competition and female choice. Through male–male competition—males competing with one another over access to females—males could end up with weapons, with armaments. Through female choice—females choosing between males that vary in the ways a trait is manifested—males could end up with ornamentation. Both ornaments and armaments may provide males with

better chances of mating with females, and so such traits can be selected for and reinforced, as long as these don't become too costly for the bearer.

R. A. Fisher (1930) provided a possible mechanism for such a process, known as the *runaway process*. Fisher's model assumes that there is a genetic variation in a given trait of males in a population and that differences in the trait are accompanied by differences in survival. Also, the model assumes that females choose males based on their trait and vary in their preferences. Thus females that prefer the fitter trait manifestation will have sons with higher fitness and daughters that prefer fitter males. Alleles for trait and preference become associated in the offspring. This association spreads initially for survival advantages but eventually also, and possibly more so, due to higher mating success. This preference–trait feedback loop may continue and select for more and more extravagant manifestations of the trait until it carries a significant fitness cost.

Fisher's verbally framed runaway process was later mathematized and modeled. Important contributors to this effort were Lande (1981) and Kirkpatrick (1982). Such models became central in the study of sexual selection. Theory of sexual selection nowadays deals with the evolution of an array of traits exhibited by either females or males. The focus is traits that aren't directly connected to the act of reproduction, also known as *secondary sexual traits*; these include dimorphic behavioral, morphological, physiological, and psychological traits. To account for these, additional parameters have been introduced into models besides trait and preference, parameters aimed at measuring the differences between the sexes in availability to mate.

In light of all this, it may seem that the categories of male and female are indispensable and central to sexual selection theory. Nonetheless, this article argues to the contrary. My argument hinges on a distinction between sexes and reproductive dimorphism. Reproductive dimorphism means (1) that a species contains (at least) two, distinct types of individuals and (2) that reproduction occurs between these two types. Such a nonrandom pattern of mating is called *disassortative mating*. If we have dimorphism that grounds disassortative mating in a species, there is no need to further add the sex categories into our framework. Turning now to sexes, this framework entails that in addition to there being two forms in a species, each of these forms in all similarly dimorphic species constitutes a significant biological category. In other words, the notion of sexes cuts across various taxa to join each resulting group together into a category. In the reproductive dimorphism framework, on the other hand, each of these taxa has two forms, yet no further step is made to achieve cross-taxon categorization; that is, the framework avoids placing, a priori, members of different taxa under the same (sexual) category. So, if a correlation is found between a trait and females/males in a given species, no expectation arises regarding this trait and females/males of other species.

Once the distinction is made clear, I show that the framework of reproductive dimorphism better fits ongoing explanations of sexual selection. Having established this, I argue that reproductive dimorphism is a better framework for explanations of sexual selection.

Before continuing, let me clarify what is at stake. If my argument is accepted, it means that within a central field of biology that appears to revolve around sexes, that of sexual selection, sexes aren't actually significant categories. This raises the worry that studying differences between the sexes might include false generalizations

derived from implicit false assumptions. Because the classification into sexes is taken as a general characteristic of sexually reproductive organisms, when a trait is found in a given species and is attributed to sex differences, it may then be too readily extrapolated to other species. A further implication, which exceeds the field of biology, is that many arguments—social, cultural, political—based on the theory of sexual selection may need reassessment.

I proceed as follows. Section 2 describes the biological definition of sexes and their significance. Section 3 motivates the focus on sexual selection theory. Then, in section 4, I distinguish between a framework of sexes and that of reproductive dimorphism. With this in place, section 5 analyzes models of sexual selection, showing how, appearances to the contrary, they rely on reproductive dimorphism rather than sexes. Section 6 discusses the Darwin–Bateman paradigm: it does rely on sexes but suffers from empirical and theoretical problems. I conclude that the reproductive dimorphism framework is a better fit for sexual selection theory, reflecting more accurately its theoretical content and empirical import.

2. What are sexes?

Most discussions of sex categories in philosophy focus on how biological textbook definitions of sexes are used in social, political, and medical contexts. On this background, several alternative definitions of sexes have been offered to replace the textbook ones. Aja Watkins and Marina Dimarco (2023) and Paul E. Griffiths (2021) are two recent and somewhat opposing examples of how the problematic aspects of the textbook definitions may be dealt with. In this article, I don't offer an alternative definition of sexes but rather analyze how the textbook biological definitions are used within models of sexual selection.

Standard definitions of sexes in biology are based on the difference between sex cells (gametes, i.e., the egg and the sperm) and proceed as follows:

Male 1. Denoting the gamete (sex cell) that, during sexual reproduction, fuses with a female gamete in the process of fertilization. Male gametes are generally smaller than the female gametes and are usually motile 2. (Denoting) an individual whose reproductive organs produce only male gametes. (Hine 2019)

Female 1. Denoting the gamete (sex cell) that, during sexual reproduction, fuses with a male gamete in the process of fertilization. Female gametes are generally larger than the male gametes and are usually immotile 2. (Denoting) an individual organism whose reproductive organs produce only female gametes. (Hine 2019)

Such gamete difference is called *anisogamy* and is contrasted with *isogamy*, which denotes sexually reproductive organisms whose gametes are morphologically similar.

Importantly, while this gametic criterion allows a stipulative definition of sexes, which as such is unimpeachable, anisogamy isn't the only dimorphism associated with being a "male" or a "female." A host of additional traits are taken to correspond to the distinction between sexes. It is widely held that the genetic, chromosomal, physiological, morphological, and behavioral traits of organisms differ according to their sex. Thus on one side is a gametic dimorphism that defines sexes; on the other

side are many other traits that are taken to be dimorphic and presumed to correlate with sexes. But, importantly, without knowing of which taxon we are speaking, and given solely the sexual categorization of a given organism, an attempt to make a prediction regarding any other sexual trait will likely fail.

Even characteristics found in a relatively wide range of taxa are nevertheless taxa-specific. Other than the gametic differences as defined earlier (and maybe not even gametic differences; see Gorelick, Carpinone, and Derraugh 2013, 2017), none of the characteristics found in males or females of a given taxon are generalizable to all other taxa. Any trait that has been so far identified as, say, female-specific in one species has been found to be male-specific in another or lacking altogether. This is true of traits at all levels—molecular, physiological, behavioral, and psychological. This variety offers an initial motivation for questioning the sex categories as biologically significant. This is shown in the following examples.

The first example is at the chromosomal level. In some species, sex is mostly determined genetically. This is the case in most mammals, birds, and insects. Yet in mammals, the mechanism underlying the female morph is homogametic, that is, having two of the same kind of chromosome (tagged XX), while the mechanism for the male is heterogametic, typically consisting of two different kinds of sex chromosomes (XY). In comparison, in birds and many insects, the females are heterogametic (ZW), while the males are homogametic (ZZ). On the other hand, in some taxa, including many tortoises and crocodiles, sex determination mechanisms aren't genetic at all. Alternative sex determination systems rely on environmental factors, such as temperature or social cues (see Bachtrog et al. 2014).

At the genetic level, there is a family of genes known throughout all Metazoa called the DM-domain. The most conserved developmental function of which they are part is organizing the sexual fate of cells, organs, or individuals. However, the specific parts they play in different sexual cascades of organisms are varied and involve many other factors. For example, they vary in different organisms in their position along the sex determination hierarchy, and they have different molecular functions in different taxa and different regulatory regimes. Moreover, though it was once thought that there would be sex-specific genes, many mechanisms are discovered to be part of a threshold mechanism, where no gene is restricted only to males or to females; rather, the abundance and influence of a whole group of genes are involved in determining the sex outcome, and none of these are responsible for it by themselves or are characteristic of one sex and absent in the other (see Beukeboom and Perrin 2014).

Morphologically, in some species, males are bigger than females. In others, females are bigger than males. Yet in others, there is no systematic difference in size between the sexes. At the behavioral level, postcopulatory parental care, a hot topic in sexual selection, is taken to be usually performed by the female. The phenomenon where males and/or females of a given species act or appear opposite of what is expected of them is called *sex role reversal* and was traditionally taken to be an exception. This expectation, as far as it still prevails, is essentially based solely on the different gametes each morph produces. In fact, there are diverse strategies of parental care across the animal kingdom. These include female uniparental care, biparental care, and male uniparental care, while different strategies are sometimes found in closely related species (see Dulac, O'Connell, and Wu 2014). Furthermore, many taxa of organisms lay eggs and don't have any contact with their offspring afterward.

Let me stress that the preceding examples of diversity in parental care shouldn't be taken as outliers. Here are examples of the distribution of parental care among the sexes in highly studied taxa: in mammals, parental care is found in all species, and males rarely participate; among fish, only 30 percent of species have parental care, of which 50 to 80 percent is male-only care; more than 80 percent of amphibians abandon their eggs after laying them, and all forms of parental care (male only, female only, biparental) are found in the remaining 20 percent; among reptiles, more than 95 percent exhibit no parental care following egg laying; and last, 90 to 95 percent of avians provide biparental care (Zilkha, Scott, and Kimchi 2017). This shows that “typical” sex roles aren't as typical as commonly assumed.¹ In short, sex role “reversals,” or monomorphism, aren't rare and aren't restricted to esoteric taxa.²

This section shows that gametic dimorphism doesn't consistently correspond to other dimorphisms. This diversity isn't confined to minor exceptions. Generally, and strictly, knowledge that an organism falls under “female” or “male,” that is, that they produce bigger or smaller gametes, is largely uninformative regarding secondary sexual traits.

Sexes may be part of both the explanandum and the explanans. The diversity discussed in this section can be used to argue that the sexes are not a significant part of the phenomena to be explained or that differences in phenotypes among organisms should not be studied primarily along sexual lines. I will not decide nor even discuss this in detail here. It seems reasonable to characterize the mainstream of the sexual selection program as holding fixed the explanandum—as asking why it is that males and females differ, while not worrying much about the existence of differences between males and females and their basis. This mainstream framework is what I target in this article. So, in what follows, I bracket questions about the (characterization and stability of the) explanandum. Put differently, my analysis and conclusions can be prefaced with the clause “to the extent that there are differences between the sexes, what explains them is . . .”

3. Why sexual selection?

Biological research to which the sex categories may seem indispensable is extremely wide and varied. Coarsely, one can identify three general, overlapping, and nonexclusive research orientations relevant to the study of sexes: developmental, mechanistic, and evolutionary. These push research to focus on different aspects of sexual differences. So, a study may be conducted to discover the developmental mechanism underlying a phenotypic difference between the sexes of a given taxon. An evolutionary goal, in turn, may push the study to consider the evolutionary, specifically selective, basis for a correlation between gamete size and some phenotypic feature.

Formally, a typical mechanistic study accounts for the differences between the sexes as follows. A correlation between a sex (defined by gamete production) and a

¹ For social influences on what is considered “typical,” see Tang-Martinez (2016, and references therein).

² A similar meta-analysis of the other monomorphic/dimorphic traits mentioned is hard to find. But examples of both “typical” sex roles and sex role “reversals” abound, especially when the animal kingdom is considered in its entirety.

certain genotype/phenotype is known/found in the studied taxon/taxa. The correlation is explored to reveal a mechanism that connects the sex-specific traits of the taxa studied (be it chromosomes, genes, hormones, or neural circuits) to other sex-specific traits targeted, including “higher-level” traits (e.g., behavioral). This involves pinpointing key factors that are manipulable, or are different in closely related organisms, such that when they are lacking, silenced, ablated, or artificially introduced, the trait in question is affected as well. Importantly, part of this mechanistic process also (typically) results in the production of smaller versus bigger gametes. For when any phenotype is said to be observed in females/males, it is effectively because it is correlated with bigger versus smaller gamete production.

When focusing on a given species or taxon, taxa-specific phenotypes correlated with gamete production may be taken as a given male/female phenotype. So, for example, being a male and the chromosomes involved in the mechanism of becoming a male become somewhat of an interchangeable idea; these may be operational definitions of biological sex (Watkins and Dimarco 2023; Griffiths 2021; Richardson 2022). But remember, looking at the variety of animals captured by the categories of “male” and “female,” other than the gametes produced, no further phenotypes are always either male or female. So any such bundling together of phenotypes in a given study in fact narrows its conclusions; it applies to a group of organisms much smaller than the groups captured by the categories of male and female.

Does this mean that the sexes are significant explanatorily when considering specific taxa? I cannot conclusively show this here, but I think the answer is no. Generally, although mechanistically oriented studies reveal how a correlation between smaller/bigger gamete production unfolds and is upheld, they aren’t meant to answer what it is about smaller versus bigger gametes that explains such correlations. Sexual selection models, on the other hand, are addressed primarily at such differences, with gametic differences taken to be of explanatory significance. Here it is explicitly asked what may make (a mechanism maintaining) a correlation between smaller gamete production and a given phenotype more evolutionarily resilient than (a mechanism that maintains) a correlation between smaller gamete production and another set of phenotypes or a correlation between the same phenotypes, but with the production of bigger gametes.

In what follows, I ask how the sex categories are used in sexual selection theory to account for other dimorphic traits. I argue that, appearances to the contrary, on a closer look, the sex categories play no explanatory role in models of sexual selection. But first, I elaborate on the distinction between two frameworks—sexes and reproductive dimorphism.

4. Sexes versus reproductive dimorphism

Beyond the descriptive fact that the male and female categories don’t allow the clean mapping of any secondary sexual trait onto the animal kingdom, I also suggest that these categories aren’t essential to explaining differences between the sexes where they exist. My argument hinges on a distinction between sexes and reproductive dimorphism. Once the distinction is clear and in place, analyzing models of sexual selection shows that what is needed, and in fact operative, in explanations of the differences between the sexes isn’t the sex categories but rather reproductive

dimorphism. On the basis of this analysis, I claim that the notion of reproductive dimorphism provides a better framework than that of sexual categories for accounting for the differences in traits that sexual selection theory aims to explain. This is because (1) reproductive dimorphism is more compatible with the difference makers in sexual selection explanations and (2) explanations formulated in terms of reproductive dimorphism have a broader scope.

Generally speaking, I ask whether gametic dimorphism grounds two significant biological categories—males and females—or whether it is a basis of two³ morphs in species, neither forming a cross-taxa significant category. By sexes as significant categories, I mean that the evolution of two different gametes continues to further be accompanied with a split in a cluster of other properties.⁴ If this is the case, then knowledge of the gamete size produced by an organism would allow us to infer what other phenotypes it has. In comparison, by mere “reproductive dimorphism,” I mean that gametic differences aren’t consistently accompanied by other dimorphic properties so that by knowing the gamete size of an organism, there is no anticipating its other phenotypes.

The significance of anisogamy in the case of sexes, I claim, is that each member of a species can mate only with part of the members of the species, that is, those that carry a complementary gamete—members of the other morph. With two complementary gametes in place, the way for different selection pressures to act on each morph is open. This can indeed result in further differences between the morphs. However, if no consistent selection pressures are acting on organisms because they have smaller rather than bigger gametes (or vice versa), then grouping together organisms based on gametic differences seems unwarranted. Reproductive dimorphism, then, is a weaker notion than sexes.

The reproductive dimorphism framework takes sexual reproduction by combination of dimorphic gametes as only one possible way to get reproductive dimorphism. Let me clarify the question I am posing with the following thought experiment. Say that reproductive dimorphism was instantiated another way so that there were no differences in gamete size but there still existed two morphs that mate with one another. Would accepted explanations of sexual selection need to be adjusted in any way? Answering this question will enable us to adjudicate between the two alternative frameworks—reproductive dimorphism versus sexes.

I now turn to examining models of sexual selection. I ask what models of sexual selection use to explain differences between the sexes. In other words, I am looking to find what the difference makers in such models are. If the models do depend on gamete differences, the sex categories would be the better framework for accounting for further dimorphic traits. If examining the models shows that they don’t in fact depend on differences in gamete size but rather on “mere” dimorphic parameters, the framework of reproductive dimorphism should be preferred over that of sexes.

³ The framework is not restricted only to two morphs; see the conclusions.

⁴ Khalidi (2021) explores accounting for sexes as cluster kinds. As clusters, the sex categories are reduced to subordinate taxa-specific categories and so don’t correspond to the biological categories of male/female that apply to most anisogamous sexually reproducing organisms. This point, together with consideration of the models used to account for sexually dimorphic traits, I find pushes us to favor a framework of reproductive dimorphism.

5. Sex categories and sexual selection models

My aim in this section is to see whether sexual selection models accounting for sexual dimorphic traits rely on sexes or mere reproductive dimorphism. That is, do the explanations depend on the categories of “male” and “female”? Could the explanations work based on there being two morphs whose gametes are unspecified? These are questions that need to be addressed to appreciate whether the sex categories play a crucial role in accounting for sexually selected traits.

The first type of model I consider is based on Fisher’s verbal mechanism presented in the introduction, the runaway process. The typical parameters in such models are a trait carried by one morph and a preference for it carried by the other morph. The frequencies of both the trait and the preference in a population are then used to show when their frequency in the population will rise, become stable, take over, or disappear (Andersson 1994; Kuijper, Pen, and Weissing 2012).

A textbook example is Lande’s (1981) model. The model tracks correlated changes in mean ornament size (t) in one morph and a preference (p) for it in the other morph.⁵ The changes in t and p depend on two factors: the total force of directional selection acting on the ornament and either the additive genetic variance of the ornament or the additive genetic covariance between trait and preference. Lande assumes that there is positive covariance between trait and preference that leads to their correlated evolution. Under certain conditions, we see a stable equilibrium (figure 1; Lande 1981; Kuijper, Pen, and Weissing 2012).

Put more simply, the model shows the dynamics between selection acting on an ornament carried by one morph, say, making a peacock’s tail bigger (or more colorful or complex, whatever peacocks seem to prefer), and the preference of the other morph for the size (or color or complexity) of that ornament. With the assumption that the trait and the preference coevolve, the model shows how different starting points may lead to different stable means of both ornament size and preference for it in the population.

Notice that in the runaway process, the factors that account for the frequency of phenotypes relate to reproductive dimorphism and not sexes. One morph has a preference for a trait found in the other, and there is a correlation between the preference and the trait. Indeed, in the version of Lande’s model just discussed, none of the parameters refer to gametes. It is irrelevant to this model which is the morph producing bigger gametes and which is the morph producing smaller gametes; this makes no difference for predicting the outcome. Regardless of which morph exhibits the trait and which exhibits the preference for it, the dynamics of the model proceed in the same manner—depending on the starting points of both trait and preference, a stable mean of both will be achieved. Hence this sort of model is applicable both for cases of “typical” sex roles and for cases of sex role reversal.

The gametes are related to the model only insofar as they are part of the mechanism that in fact generates reproductive dimorphism, and so further dimorphisms may be correlated with gametic dimorphism for many sexually reproducing species. But the model does not assume that gamete size generates

⁵ Lande originally attributed the t to males and the p to females, but more recent versions allow for their reversal.

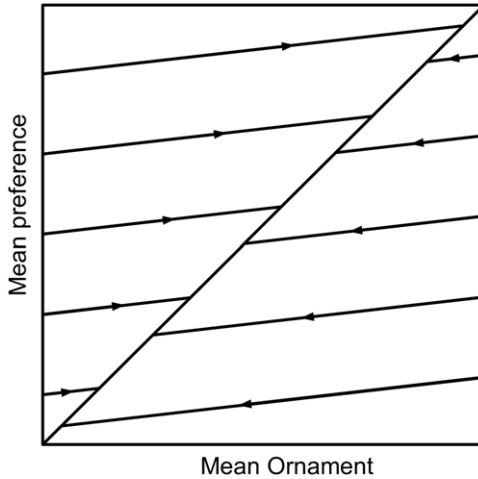


Figure 1. Illustration of the correlated evolution of ornament size and preference in two morphs, based on Lande's (1981) model. The diagonal line is the equilibria line. Arrows indicate evolutionary trajectories for both parameters.

dimorphism; it relies on reproductive dimorphism however it may be grounded in reality.

Importantly, adding gametes to such a model by fixing which sex carries the ornament and which carries a preference for it would restrict its application. The models are more general when they assume one morph with heritable variation in ornaments, another with heritable variation in preference for it, and a positive covariance between these two phenotypes. Reproductive dimorphism is the basis needed for these models to work, and the sex categories are irrelevant. Sex-free models are thus more general and may be applied to a wider variety of taxa.

Besides a trait and a preference, additional measures have been introduced into the theory of sexual selection that refer to the availability of males and females to mate. The most widely used measures are relative parental investment, operational sex ratio, and potential rates of reproduction. Considering which sex is more limited in its availability to mate is used to predict which sex will take on which role—which will be choosier; which will show courtship behavior; which will be more ornamented, more combative, and so on (Andersson 1994). I want to look at an example of such a model in the context of a recent paper arguing for the explanatory significance of sexual kinds, so I first present this account and then examine the example in light of it.

I have argued so far that the sexes aren't significant in models of sexual selection because the sex categories aren't difference makers in such models. One might agree with my analysis and yet argue that although sexes don't play a role in such explanations today (or in the recent past), they are still important because we can trace them back to the evolution of anisogamy. A sophisticated version of this idea was presented recently by Laura Franklin-Hall (2020), who argues that the sexes play a historical explanatory role.

Franklin-Hall (2020) offers an account of sexes as "historical explanatory kinds," in which sexes promise to be explanatory categories precisely because they provide a

link between anisogamy and other dimorphic traits, as follows. Individuals of the anisogamous male and female ancestors were able to develop into two reproductive variants, resulting in the production of either smaller gametes or bigger gametes. Each of these developmental paths formed the foundation of a sex developmental lineage. Within and alongside the branching of familiar species-oriented evolutionary trees, each of these developmental options was accompanied by different evolutionary pressures and gradually accumulated its own traits. This process was dubbed the *sexual cascade* (Parker 2014).

In agreement with this picture, Franklin-Hall (2020, 16) offers the following refined definitions for sexes:

an animal is *male* (or *female*) just in case its reproductive traits came about by way of developmental processes linked via a sex development lineage to the developmental processes responsible for reproductive features in that animal's earliest *small-gamete* (or *large-gamete*)-producing animal ancestors. It is only those earliest ancestors whose sex, male or female, was set by gamete size directly. (emphasis original)

It is important to note, as Franklin-Hall does, that her account is mostly congruent with the simple biological gamete-based definitions. Her inspiration for her account of sexes is partly based on what she characterizes as a “family of emerging explanations” that “very schematically . . . suggest that sex differences in gamete size in ancient animal ancestors can explain contemporary sex differences by having brought about a series of intermediate evolutionary innovations, innovations that themselves more directly account for the constellation of current sex differences” (11).

I shall now examine one of these works, by Fromhage and Jennions (2016), which Franklin-Hall cites as filling in at least part of the gap between anisogamy and other sexual traits. I choose it because it indeed *seems* to do so, and it is cited also by others suggesting that it does so (e.g., Long and Weissing 2020; Parker 2020). Nonetheless, I show that the model presented is based on Fisherian principles that are sex-neutral.⁶

Fromhage and Jennions (2016) offer mathematical models of the evolution of male and female parental care. The models depict the relation between the variables of adult sex ratio, mature sex ratio, operational sex ratio (OSR), duration of parental care, number of mates, and competition. They examine how these affect one another to bring about different outcomes of the distribution of care between the sexes. They show that uniparental care is the expected outcome in cases where lower sexual selection pressures are acting on one sex and/or more individuals of one sex are involved per breeding attempt. These dynamics are demonstrated in the graphs of figure 2, drawn from their paper.

Male care and female care are measured in terms of the duration of parental care. The parameters presented here that shift the distribution of care to uniparental care are k and n ; k stands for sexual selection pressures—it measures the proportion of

⁶ Another work cited by Franklin-Hall (Lehtonen, Parker, and Schärer 2016) is aimed at giving a formal validation of the Darwin–Bateman paradigm. I won't discuss it here, for I argue against sex-specific versions of the paradigm altogether in the last section.

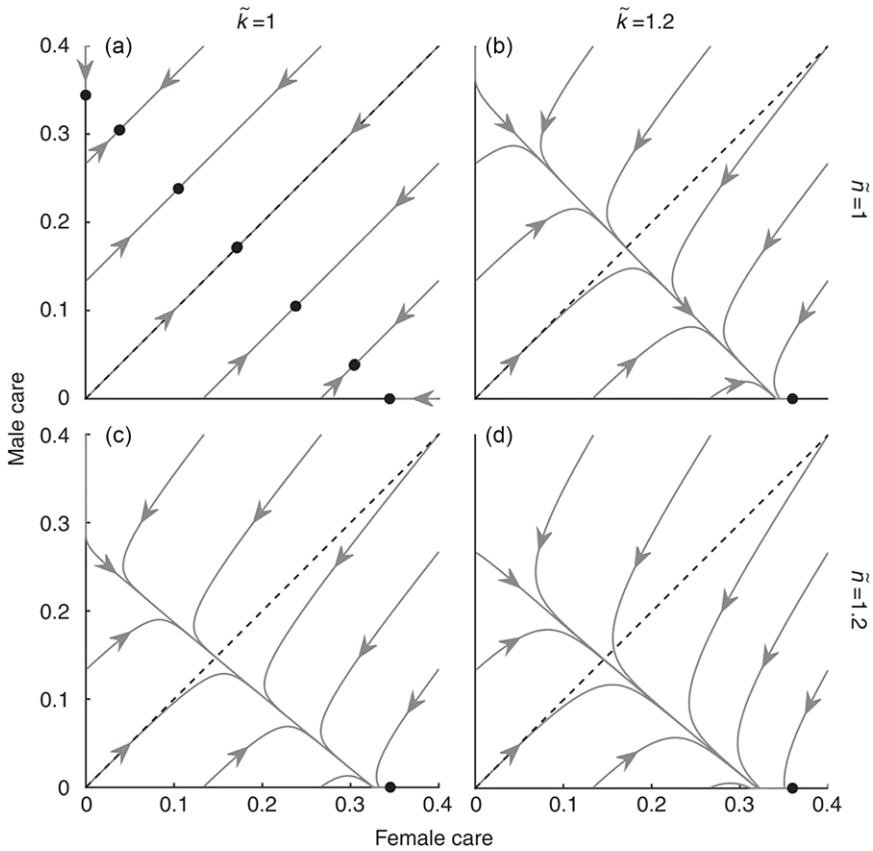


Figure 2. Evolutionary trajectories of parental care (arrows). Dashed lines mark equal caring by both sexes. Black dots mark stable end points.

members of a sex ready to mate and compares it with that of the other sex. Here in the graphs, when k is higher than 1, the selection pressure is higher on males than it is on females. In the graphs, n represents the social mating system. When the same number of males and females is involved in each breeding attempt (monogamy), n equals 1; when, as presented in the graphs, more males than females are involved in a breeding attempt, n is higher than 1. As the dynamics in the graphs show, whenever there is higher selection pressure on one sex (here males) or more individuals participating in a breeding attempt, or both, parental care ends up being uniparental and given by the sex under lower selection pressure (here females) or less involved in breeding attempts, or both.

The authors write that their model shows “that a positive feedback can drive sex role divergence and select for greater investment into caring by the sex that cares more initially” (Lehtonen, Parker, and Schärer 2016, 3). One can easily point out that “the sex that cares more initially” is almost by definition the female. For if every offspring is a result of a fusion between two gametes—one small and one big, and

bigger gametes are a higher investment than smaller gametes—the females invest more as a straight result of anisogamy. This difference in investment is part of what is termed *precopulatory parental care*. So there seems to be a close connection between precopulatory parental care and postcopulatory parental care. But let us take a closer look at what the model tells us and what this logical move requires of us.

First, notice that the model doesn't restrict the initial difference in care to be biased one way or the other. All the possibilities are open in the model—higher initial care by either sex. Granted, one may add to the model the assumption that there is an initial bias toward female care because they invest more into gametes. This brings me to the second point. Any bias in the initial differences in care only makes a difference when both sexual pressure and number of mates are equal between the morphs/sexes (figure 2, top left). When these factors aren't equal, any initial bias in care doesn't make a difference—it will end up being uniparental care no matter what distribution of care we started with.

To reiterate, models of sexual selection account for dimorphic morphological and behavioral traits without using the sex categories. The models use variables that aren't inherently male or female. The variables can be set to be either male biased or female biased (or unbiased), depending on the biology of the species. Additionally, in a given species, often what determines the bias isn't strictly the gamete differences. Thus there seems to be no need to fix, by fiat, which morph corresponds to which sex; that is, there is no need to assume that, for example, females carry the preference or that the OSR is male biased. Doing so would only restrict the applicability and generality of the theory. For example, it would make it unsuitable for cases of sex role reversals. Notably, sex identity, that is, gamete size, isn't a difference maker here. Therefore I conclude that models of sexual selection are based on reproductive dimorphism and disassortative mating, not on sexes per se.

One might again agree with my analysis of the models and still reply that there is good reason to associate bias in care with gametic differences, namely, the Darwin–Bateman paradigm. I will discuss the paradigm in the following section, review works showing that it is very poorly supported empirically, and argue that a sex-free hypothesis of sexual selection would still be preferable even if the paradigm were empirically solid. To sum up for now, models of sexual selection do just fine without invoking sexes. The phenomena they aim to explain are well explained without sexual categories, and adding the sex categories to them would only do them harm—most clearly, such a move would limit their scope of applicability.

6. The Darwin–Bateman paradigm

Previous sections have made the following points: (1) gamete size isn't a difference maker in explanations of other dimorphic traits; (2) these dimorphic traits are, rather, explained by disassortative mating; and (3) reproductive dimorphism is a better framework than sexes. I now consider the Darwin–Bateman paradigm, which may appear to undermine these three conclusions.

Darwin implies that the differences between smaller gametes (“male element”) and bigger gametes (“female element”) may be related to the evolution of certain behavioral differences between males and females. According to this hypothesis, because smaller gametes are easier to move around, it could have had more logistical

sense for males of “lowly organized” animals to approach and seek females than the other way around. This, in turn, could explain why their “more highly developed male descendants” have evolved to have stronger “passions” and are more “eager” as compared with females, which are instead “coy,” and may also account for why males more commonly develop secondary sexual traits (Darwin 1981, 1:273–74; Dewsbury 2005; for different readings of Darwin, see Milam et al. 2011).

Inspired by Darwin’s work, Bateman sought to give a causal explanation for the differences in sex roles. He suggested that differences relating to gamete production cost are key to explaining the differences in selection strength for courting behaviors in males and females. Like Darwin, he took sexual selection to act more strongly on males than on females. Bateman came to believe that female reproductive success was limited by their number of eggs, whereas for males, sperm production was rarely a limiting factor; rather, males were limited by the number of females they managed to inseminate. Trivers, a key figure in making Bateman’s study rise to the status of a paradigm, saw the differences in relative parental investment of the sexes, among these food reserves of the male and female gametes, as the important catalyzers of selection pressure differences between the sexes (Hoquet 2020a).

This line of thought has come to be known as the Darwin–Bateman paradigm (Dewsbury 2005). Dewsbury summarized the paradigm as follows:

- a. Male reproductive success is more variable than that of females.
- b. Males gain more in reproductive success from multiple matings than do females.
- c. Therefore males are generally eager to mate and relatively indiscriminate, whereas females are more discriminating and less eager.

These principles are taken to rise out of the gametic differences between the sexes. The crux of this hypothesis is that because sperm cells significantly outnumber egg cells, males compete for females, but not the other way around. Hence reproductive success for females is essentially guaranteed, whereas males compete with each other to reproduce. Owing to this fundamental asymmetry, sexual selection leads to the behavioral and morphological differences between males and females. For example, males may evolutionarily end up with traits that aid them in outrivaling one another for access to females, such as developing armaments and ornaments, whereas females allocate their energy differently, for example, to parental care.

The Darwin–Bateman paradigm is different from the sexual selection models discussed earlier: unlike the other cases, this hypothesis does straightforwardly endow sexes with explanatory significance. Under the Darwin–Bateman paradigm, gamete size is responsible for differences in sexual selection strength and thus accounts for further dimorphism in behavior, morphology, and so on. That said, as I review next, the paradigm in its sex-based form remains very poorly supported empirically; therefore it cannot be used to advocate for sexes as significant categories. The paradigm’s later versions, which seem to be supported empirically to some extent, are sex-free versions. All in all, we find that the hypothesis that assigns explanatory weight to sexes is uncorroborated empirically, whereas the general, better-supported alternatives aren’t based on sexes.

6.1. Bateman's experiment

The Darwin–Bateman paradigm was consolidated based on Bateman's extensive experiment on *Drosophila*, published in 1948. For decades, this experiment pretty much single-handedly constituted the (alleged) empirical support for the paradigm and was key in driving and holding up its status as a paradigm. The experiment was purported to neatly support Bateman's principles, but as I review here, this interpretation is questionable. Bateman set out to examine the relationship between sex, mating success, and number of mates. To that end, he conducted a series of trials on populations of *Drosophila*, estimating the numbers of matings and reproductive success of approximately four hundred individual flies (Hoquet 2020a).

Bateman predicted that the variance in fertility of males will be higher and more strongly correlated with variance in the number of mates in comparison to females. Indeed, he claimed to have found that the variance in reproductive success was greater for males than for females. Moreover, his results reported a linear relationship between the number of mates and the number of offspring for males, and likewise, but to a lesser extent, for females. This work thus seems to elegantly support Bateman's hypothesis and to vindicate the importance of gametic differences for sexual selection. Nonetheless, although Bateman's experimental work has been taken to establish a link between anisogamy and behavioral dimorphism between males and females, it is both riddled with methodological and conceptual flaws in its original formulation and has been grossly misquoted and misrepresented since it was published.

First, Bateman's method was based exclusively on phenotypic markers. By comparing the phenotypic markers of parental and offspring generations, he estimated the numbers of matings and the reproductive success of males and of females. Bateman made no systematic behavioral observations directly counting mating events. Nonetheless, some authors stated that Bateman observed certain behaviors that he never examined or reported. As an influential example, Trivers stated that Bateman observed that females who failed to copulate were courted like others and that the males who failed to reproduce showed no disinterest in trying to copulate. Such behaviors would strengthen Darwin's notion of males being eager to mate, and here even regardless of individual female disinterest and of individual male reproductive success. But in fact, no such behavioral observations were actually made or reported (Hoquet 2020a).

Second, and quite strikingly, for sixty-five years, this paradigmatic experiment hadn't been replicated. In 2012, Gowaty, Kim, and Anderson took on the challenge. Their experiment produced evidence of an unavoidable observational bias in Bateman's method owing to lethal effects of double mutation on offspring survival. Bateman's method could count only mating events that resulted in viable offspring. Thus, for example, if a female mated with no progeny, it would escape detection and be wrongly counted as having zero copulations. All in all, Gowaty, Kim, and Anderson concluded that Bateman's methodology mismeasured fitness variances that are the key variables of sexual selection, and their repetition produced no evidence of sexual selection. Thus, although Bateman is often said to have provided evidence for a relationship between mating success (number of copulation partners) and reproductive success (offspring production), what he actually studied is the

relationship between reproductive success and the number of partners with which individuals produced progeny. The difference may be subtle, but it is significant for the current discussion. If males actually mated more times than progeny indicates, this may *weaken* the positive relation reported between number of matings and reproductive success. As for females, if more matings have occurred than were actually counted, a *positive* relation may have been overlooked.

Indeed, Hoquet, Bridges, and Gowaty (2020) went back to Bateman's original data to reanalyze them and assess whether they are consistent with his principles. Following the insights from Gowaty, Kim, and Anderson's (2012) replication attempt, they selected the populations that were reliable for evaluating predictions regarding the relation between number of mates and reproductive success. After cleaning the data and analyzing them, Hoquet, Bridges, and Gowaty (2020) showed that the relevant populations fail to support Bateman's paradigmatic predictions of sexual selection. Namely, statistically significant greater variance in reproductive success among males than females was rare, few populations showed statistically significant sex differences in variance concerning number of mates, none of these populations had statistically significant sex differences in the slopes of reproductive success on number of mates, and the correlations between variance in number of mates and variance in reproductive success were significantly positive both for females and for males (Hoquet, Bridges, and Gowaty 2020).

Finally, the validity of making inferences regarding sexual selection from the kind of results Bateman got, even were they to be well established empirically, has been called into question. Many possible alternative explanations fit his results. In fact, Bateman himself didn't take his own account to be the only possible one. For example, Bateman assumed without evidence that fertility is heritable. He didn't consider the possibility that differences in fertility are random (Snyder and Gowaty 2007). And further factors could affect the behavior of either sex, for example, physiological mechanisms of sexual conflict or naturally occurring schedules between copulations (Hoquet, Bridges, and Gowaty 2020).

6.2. Bateman's updated principles

As discussed earlier, monomorphism and sex role reversals, for example, in parental care, exist—indeed, they are fairly widespread. This means that the Darwin–Bateman paradigm, in its earlier forms, can at most be seen as setting a *ceteris paribus* condition, along the following lines: were nothing to interfere with the outcomes toward which the gametic difference alone would push, the “typical” sex roles would have been exhibited by most species, and monomorphism and sex role reversal would be very rare. In other words, all else equal, the effects that gametic dimorphism has on the differential selection strength between males and females would result in substantial behavioral and morphological differences between the sexes. Also, the differences would be such that males would be the ornamented and armed, females would be more invested in care, and so on. But this leaves the explanation of all the cases of sex role reversals and the less discussed cases of monomorphism (and also species for which there is no single role for each sex but rather a multiplicity of possible roles; see Roughgarden 2013) incomplete. We need to provide additional factors to account for cases that don't obey the rule.

Following this shortcoming, the models of sexual selection discussed in previous sections can be advocated based on their being more generally applicable. And as a reminder, their generality is in virtue of their being not about sexes. In fact, many modern versions of Bateman's principles have come to be sex-neutral as well and thus similarly more generally applicable. The principles are summarized, for example, as follows:

- a. There is higher variance in offspring production in the sex experiencing stronger sexual selection.
- b. There is higher variance in the number of mates in the sex experiencing stronger sexual selection.
- c. The relationship of the regression of offspring on the number of mates is often steeper in the sex experiencing stronger sexual selection (Morimoto 2020).

Here the same logic as in Bateman's original predictions applies for the relations between sexual selection strength and the following parameters: variance in reproductive success (a), variance in mating success (b), and the correlation between variance in reproductive success with variance in mating success (c). But, unlike the original formulation, no principle is limited to either sex. Thus stronger sexual selection could be acting on either males or females, and accordingly, higher variance in offspring production and number of mates can be exhibited by either sex. The sex experiencing stronger sexual selection would generally be expected to take on the "eager to mate" role. This sex-neutral version of Bateman's principles is, arguably, empirically supported. Though there may be disagreement whether specific experiments do actually support the principles (see the exchange between Hoquet 2020b and Morimoto 2020), it seems that the version that is now usually used to explain either "typical" or "reversed" behaviors of males and females is a sex-neutral version of the principles (Fritzsche et al. 2021; Jones et al. 2005).

Like the models discussed in previous sections, here, too, the neutral version of the principles promises to be more general than the original Darwin–Bateman paradigm. This is because sexes aren't difference makers in it. Here, too, whereas anisogamy is evolutionarily relevant for reproductive dimorphism, the gametic difference itself (difference in size, number, or energy) plays no explanatory role in predicting which sex will take on which role, and so it covers both "typical" role distribution and sex role reversals and may also account for monomorphism if there are no substantial differences between the sexes in factors that are difference makers, namely, sexual selection strength and variance in reproductive and mating success. Couched within the reproductive dimorphism framework, once disassortative mating is in place, if members of one morph are subjected to stronger sexual selection than the members of the other in a given species, the former would generally be expected to take on the "eager to mate" role.

To sum up, in this section, I focused on the Darwin–Bateman paradigm, for unlike the other models discussed previously, it is a hypothesis in which the sex categories play a significant role. This appears to undermine my conclusions in previous sections. But looking at the modern versions of the hypothesis and empirical studies used to support it, clinging to the sex-specific Darwin–Bateman paradigm seems unreasonable. The Darwin–Bateman paradigm in its earlier form both is ill supported

empirically and offers a limited scope of applicability compared with later versions and other models of sexual selection. In light of these shortcomings and the sexual models available that aren't based on sexes, I find that the paradigm isn't a convincing hypothesis to use to advocate the sex categories.

7. Conclusion

In this article, I examined the relation between models of sexual selection and sexes. Earlier models based on the sex-specific Darwin–Bateman paradigm, I argued, are ill motivated, for the paradigm lacks empirical support and is much more limited in scope compared with its alternatives. Analyzing alternative models of sexual selection showed that, despite appearances to the contrary, sexes aren't difference makers in them. Moreover, adding sexes to such models would make them less general and would limit the range of phenomena to which they may be applied. I offered a distinction between reproductive dimorphism and sexes and argued that thinking in terms of reproductive dimorphism is preferable to a sexual framework because it is more compatible with ongoing explanations of differences between sexes and allows for greater applicability of such explanations.

Sexual selection theory is widely seen as assigning sex categories a central explanatory role. Finding that within this field the sex categories are insignificant can be taken to motivate a revisionist attitude toward sex (see Watkins and Dimarco 2023); although I am sympathetic toward such a move, the issue is complex, and I don't aim to settle it here. However, within the context of sexual selection, I find that replacing the concept of sexes with that of reproductive dimorphism would be valuable. In addition to the aforementioned theoretical considerations, and although I have presented reproductive dimorphism mainly as reflecting two morphs in a species, the framework does not require that a species only have one pair of such reproductive morphs or that any such pair in a species will be an exclusive reproductive pair. This also fits the models considered here: nothing in them seems to prevent their application to species that may have more than two reproductive morphs. Indeed, some work can be found considering sexual selection in species in which the gametic sexual categories do not apply, such as fungi (Nieuwenhuis and Aanen 2012) and bacteria (Vos, Buckling, and Kuijper 2019). The framework of reproductive dimorphism welcomes such use of explanations from sexual selection also in organisms where they would not seem as readily applicable in the framework of sexes.

Finally, the classification into sexes encompasses a wide range of sexually reproductive organisms, and if one assumes that it forms significant biological categories, one is in danger of making false extrapolations. My argument shows that when a trait is found in either sex in a given species and it is attributed to sex differences, sexual selection theory does not support an expectation that it will be exhibited by either males or females in other taxa based solely on belonging to the same sex. Also, sexual selection theory, read in the reproductive dimorphism framework, does not support arguments for the “naturalness” of any behavior exhibited by either sex in a given species, based solely on comparing it to individuals of other species that share its sexual affinity.

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