

What are biological sexes?

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Abstract

Biological sexes (male, female, hermaphrodite) are defined by different gametic strategies for reproduction. Sexes are regions of phenotypic space which implement those gametic reproductive strategies. Individual organisms pass in and out of these regions – sexes – one or more times during their lives. Importantly, sexes are life-history stages rather than applying to organisms over their entire lifespan. This fact has been obscured by concentrating on humans, and ignoring species which regularly change sex, as well as those with non-genetic or facultatively genetic sex determination systems. But the general point applies equally to humans. Assigning sexes to pre-reproductive life-history stages involves ‘prospective narration’ – classifying the present in terms of its anticipated future. Assigning sexes to adult stages of non-reproductive castes or non-reproductive individuals is a complex matter whose biological meaning differs from case to case. The chromosomal and phenotypic ‘definitions’ of biological sex that are contested in philosophical discussions of sex are actually operational definitions which track gametic sex more or less effectively in some species or group of species. Neither ‘definition’ can be stated for species in general except by defining them in terms of gametic sex. The gametic definition of sex also features in widely accepted models which explain why two biological sexes – either in separate individuals or combined in hermaphroditic individuals – are almost universal in multicellular species. Finally, the fact that a species has only two biological sexes does not imply that every member of the species is either male, female or hermaphroditic, or that the sex of every individual organism is clear and determinate. The idea of biological sex is critical for understanding the diversity of life, but ill-suited to the job of determining the social or legal status of human beings as men or women.

1. Introduction: So what are biological sexes?

Biological sexes (male, female, hermaphrodite) are regions of phenotypic space that individual organisms pass in and out of one or more times during their lives (Figure 1). In some species organisms develop one sex and retain it until they die. In other species individuals change sex during their lifetimes. In some species the sex an individual will later develop is predicted by their sex chromosomes. Other species do not have sex chromosomes. Still others have sex chromosomes but can override them when it is advantageous to develop into the other sex, as I will discuss in detail below.

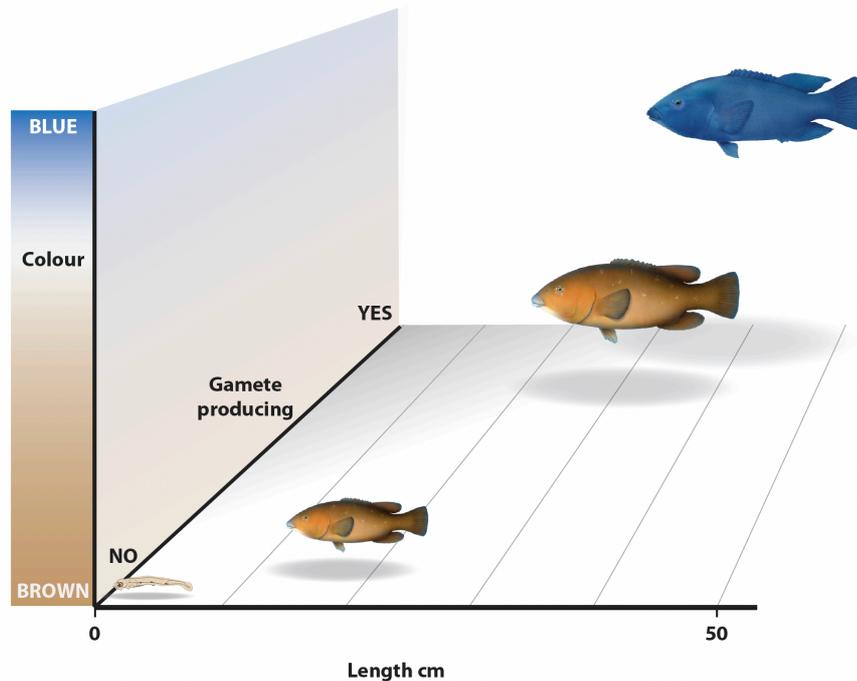


Figure 1. Three dimensions of phenotypic space for the sequential hermaphrodite species the Eastern Blue Groper (*Achoerodus viridis*) – colour, length and the ability to produce gametes. At any one time an individual fish occupies a point in phenotypic space. The lifecycle of an individual fish is a trajectory through phenotypic space. Typical life-history stages, such as the embryonic stage or the male stage, are regions in phenotypic space. This species become reproductively mature as a female at 20-30cm and transforms into a male at around 50cm (Gillanders 1995). See text for explanation. Groper images © State of New South Wales through NSW Department of Industry; Larval groper image illustrated by J.M. Leis, inked by S. Bullock. © Australian Museum.

These biological sexes (regions) are defined by different reproductive strategies. In sexual species reproduction occurs when two gametes fuse to form a zygote. Gametes are the sex cells which contain all or part of the DNA of one parent. They unite with a gamete from another parent to give rise to a new individual. In the human case, the gametes are our sperm and eggs and each contains half of the parent's DNA. In honeybees, in contrast, the male gamete contains all of the male parent's DNA because male honeybees have only half as many chromosomes as females. Male phenotypes evolved as part of a reproductive strategy focused on the production of large numbers of small gametes, such as human sperm. Female phenotypes evolved as part of a reproductive strategy focused on the production of smaller numbers of larger, highly-provisioned gametes, such as human eggs. As well as differing in size male and female gametes are structurally very different. Female gametes are similar in structure to the gametes of asexual species, gametes which develop into a new individual without fusing with a male gamete. Hermaphroditic phenotypes evolved as part of a mixed reproductive strategy in which a single organism has two kinds of reproductive organ, one producing small gametes (sperm) and the other producing large gametes (eggs). The Mangrove Rivulus (*Kryptolebias marmoratus*), for example, is a species

with two sexual forms, male and hermaphrodite, and individual fish can switch between these two forms (Kelley et al 2016). 'Simultaneous hermaphrodites' like the Mangrove Rivulus in which an individual can simultaneously contribute both kinds of gametes to sexual reproduction must be distinguished from 'sequential hermaphrodites' like the Blue Groper (Figure 1) which produce males gametes for part of their lifecycle and female gametes for another part of that lifecycle, usually with many other, related phenotypic changes.

In some species several, distinct regions of phenotypic space have evolved as ways to pursue one gametic strategy. The Ruff, a common wading bird, has three strikingly different male forms (Figure 2). 'Independent' males are large birds with costly ornamental plumage which they display to attract mates. Independents defend small territories on the 'lek', the area where displays are made. 'Faeder' males are smaller and have the same plumage as females. They invest their energy in larger testicles and increased sperm production. 'Satellite' males have a different colour of display plumage and do not defend territories. All three male morphs of the Ruff are pursuing a reproductive strategy focused on the production of large numbers of small gametes, but using different tactics to do so. So three distinct regions of Ruff phenotypic space are ways of being male. The morphs of male Ruff are caused by genetic variation in a section of chromosome 11. In other species with multiple male morphs, such as dung beetles (*Onthofagus spp.*) the morph of an individual male is determined by environmental factors (Emlen 1997).

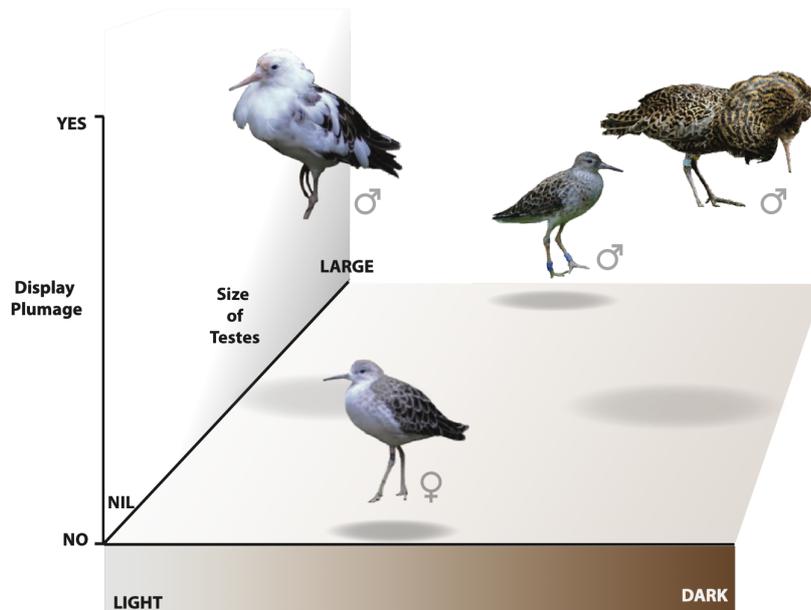


Figure 2. The female and the three male male morphs of the Ruff (*Philomachus pugnax*) represented as regions in a phenotypic space with three dimensions: colour (dark to light), has display plumage (Yes/No), size of testes (small-large). See text for explanation. Ruff images copyright © 2013, Farrell et al.; licensee BioMed Central Ltd.

This understanding of sexes as gametic reproductive strategies can be seen in the way they are commonly defined when biologists discuss the origins, diversity, and evolutionary and ecological impact of sexes (Box 1). Throughout this article ‘biological sex’ refers to this definition: males make small gametes and females make large gametes. Philosophers will have three immediate questions about this definition: what is so important about ‘large’ and ‘small’ gametes?; what about organisms who produce medium-sized gametes?; and what about organisms that do not produce gametes? Rather than identifying problems with the definition these questions point to key features of how and why sexes evolved. The first two questions are answered in Section 3 and the third in Section 6.

Box 1. How biologists distinguish between biologically male and female organisms

“To a biologist, “male” means making small gametes, and “female” means making large gametes. Period!” (Roughgarden 2013, 23)

“A sex is thus an adult phenotype defined in terms of the size of (haploid) gamete it produces: in an anisogamous population, males produce microgametes and females produce macrogametes. A simultaneous hermaphrodite is thus both male and female simultaneously, and a sequential hermaphrodite transforms sequentially from male to female (or vice versa)” (Parker 2011)

“Anisogamy: a form of sexual reproduction in which the fusing gametes are of markedly unequal size. The sexes are defined according to anisogamy; the sex with the smaller gametes is defined as male. In the absence of anisogamy (isogamy), one speaks of mating types rather than separate sexes” (Lehtonen, Jennions, and Kokko 2012)

Philosophers who have discussed biological sex, whether they seek to vindicate the idea (Byrne 2020) or critique it (Dembroff 2020), have not defined it in the way biologists do. The definitions of male and female they do consider are non-starters as general criteria to distinguish male and female organisms. The Stanford Encyclopedia of Philosophy notes that work on the sex/gender distinction in philosophy starts with the idea that, “sex ’denotes human females and males depending on *biological* features (chromosomes, sex organs, hormones and other physical features)” (Mikkola 2017, emphasis in original). But no general definition of sexes can rely on these features because, as Roughgarden puts it, “the criteria for classifying an organism as male or female have to work with worms to whales, with red seaweed to redwood trees.” (Roughgarden 2013, 23). Biological sex certainly cannot be defined by chromosomes. Many species, such as crocodiles, have no sex chromosomes, because their sex is not determined genetically. Chromosomal definitions also fail for species that change sex during their lifecycle, since their chromosomes, of course, remain unchanged. Chromosomal definitions do not work even when restricted to species with genetic sex determination and no sex-switching. In humans and most other mammals males have two different sex chromosomes (XY) and females have two identical sex chromosomes (XX). But in birds it is the other way around: males have two identical and females two different chromosomes. Biologists know which chromosome pairs are ‘male ’ or ‘female ’

because they know which animals are male or female, using the gametic definition (Box 1). These and other examples are discussed in more detail in Section 5.

The same problem defeats any attempt to define sex in terms of phenotypic characters. For a single species we can describe male, female or hermaphroditic phenotypes, as seen in Figures 1 and 3. But phenotypes that are 'male' in one species can be 'female' in others, and vice-versa. Something gets to be a 'male' or 'female' characteristic in a particular species because it is common in males or females in that species: sexual characteristics are defined by sexes, not the other way around. Like chromosomal definitions of sex, phenotypic definitions are not really 'definitions' – they are operational criteria for sex determination underpinned by the gametic definition of sex and valid only for one species or group of species.

As I will describe in Section 3, evolutionary biologists have devoted a great deal of effort to explaining why there are no complex multi-cellular organisms with more than two sexes. This will strike many philosophers as surprising, since they will have read that humans have many sexes. Fausto-Sterling (1993) counted five and many other philosophers argue that there is no determinate number of sexes or that there is a continuum of sexes (see Mikkola 2017 for a review). These authors mean something quite different by 'sexes', as I discuss in Section 2, and their definitions of sexes are not applicable to most sexual species. That makes them unhelpful answers to the question 'what are biological sexes'? In contrast, the gametic definition of sexes (Box 1) allows biologists to address the basic topic in the biology of sex - the many ways in which different species use DNA to create offspring. There are many reproductive systems which do not involve two biological sexes, but systems which can be described as having three or more sexes or a continuum of sexes are found only in a few species at the borderline between single-celled organisms and multi-cellular organisms. As I will explain in Section 3 there is a fairly solid scientific consensus about why this is so. Moreover, the theory of how the gametic reproductive strategies of the two sexes influence evolution under varying ecological conditions makes a major contribution to explaining the diversity of life on earth.

The claim that a species has only two biological sexes is commonly misunderstood as the claim that there are only two kinds of individual in that species. But as I will explain in Section 7, this is completely mistaken. We have already seen that there can be several, very different ways of being the same sex (Figure 2). More importantly, the regions of phenotypic space corresponding to sexes do not have sharp boundaries (Figure 4), so individuals can be atypical of their sex and the sex of some individuals may be completely unclear. Finally, individuals need not pass through *any* of the regions of phenotypic space corresponding to a sex during their lives. Developing a sex is not a requirement for biological viability in most species, and individuals which do not develop a sex play important roles in the biology of some species.

Before proceeding it is important to be clear that I assume the conventional Darwinian view of species, which is an anti-essentialist view (Hull 1986; Sober 1980). A species is a collection of genetically and phenotypically diverse individuals united in a pattern of ancestry and descent. Whether an organism is a member of a species and whether it is typical or representative of that species are completely separate questions. Any bird whose

parents are Ruffs is a Ruff and any animal whose parents are human beings is as much a member of the human species as any other.

2. Why should evolutionary biology get to define biological sexes?

We can question whether biological sex should be defined by the biological sciences and we can question whether that definition should come from evolutionary biology in particular. I argue that it should. The evolutionary biology of sex tries to explain the diversity of ways in which organisms use DNA to make offspring.¹ Many philosophers and gender theorists will protest at making the creation of offspring foundational to how we define sex or distinguish different sexes (see Mikkola 2017). Sex and sexes as aspects of human life and human society are about much more than the production of offspring. That is a good reason to reject an exclusively biological understanding of sex in the human and social sciences. But the use of DNA to make offspring is a central topic in biology and understanding and explaining the diversity of reproductive systems in living organisms is an important scientific task. It is here that the biological understanding of sex and sexes does its work.

Many authors have argued that biological sex simply cannot be disentangled from cultural norms of gender: “sex cannot operate as a sort of material base to the superstructure of gender. Gender is always already implicated within the attempts to define sex.” (Hood-Williams 1996, 13; for a review, see Mikkola 2017). But ‘sex’ here should not be thought to refer to the biological definition of sex (Box 1). Biological sex is an idea applicable to all sexual species, not only to humans. Many of these species do not have anything that can reasonably be compared to human gender roles or gender identities. Trying to apply critiques of the sex/gender distinction to those species is not helpful because the issues that motivated the critiques simply do not arise. Earthworms, for example, are good at swallowing earth but hopeless at having encultured attitudes to worm bodies and worm behavior. In critiques of the sex/gender distinction ‘sex’ can refer to certain anatomical characteristics of human beings, or to human characteristics that are allegedly independent of culture. But whether ‘sex’ in this sense can be separated from gender is simply not relevant to the biological sex of earthworms, which are simultaneous hermaphrodites, where each individual produces both sperm and eggs and where two individuals can fertilise one another.

The real message of these critiques is that the human practices which assign human beings social or legal status as men or women cannot be reduced to establishing their biological sex. In fact, as we will see in Sections 6 and 7, the biological understanding of sexes is even less well-suited to this job than these critics suppose. The biological understanding of sexes has been shaped for the comparative study of reproductive systems across the diversity of life, not for making decisions about the social or legal status of human beings.

We can apply the biological understanding of sexes to humans just as we can to other sexual

¹ A wide range of genetic, epigenetic and exogenetic pathways connect parents and offspring, (see Griffiths and Stotz 2013; Stotz and Griffiths 2017). The evolutionary models to be discussed in Section 3 focus on genetic heredity as I will do throughout this paper, since my focus is the understanding of sexes found in orthodox contemporary accounts of the evolution of sex.

species. It is important not to conflate this with other understandings of sexes, but biologists are not out of order when they seek to understand the distinctive way in which humans use DNA to make offspring. There are systematic differences in how human beings, Chimpanzees, Blue Groper, Ruffs and so forth reproduce. Unlike Blue Groper, but like Ruffs and Chimpanzees, humans do not change from female to male when they reach a certain size. Unlike Chimpanzees and Ruffs, human females have a reproductive period much shorter than their natural lifespan (menopause). Unlike Ruffs, but like chimpanzees, humans produce biologically male and female offspring in a roughly 50/50 ratio. These and a myriad of other findings are organised into patterns across the diversity of life, and those patterns explained, using the idea of biological sex. We will encounter some of these explanations in later sections. It may be that biological sex is of little social or ethical importance, but it is essential for understanding the evolution of the human reproductive system and why it differs from that of other species.

Other philosophers will protest at focusing on evolutionary biology as opposed to various biomedical fields which study sex, such as IVF research or sexology. Surely these medical scientists are also 'biologists'? They are, but it is evolutionary biologists who address basic questions such as 'why does sex exist?', 'why do some species have separate sexes?', and 'why do some species have sex chromosomes?' Biomedical scientists do not address these questions and if they are interested in them they look for answers in evolutionary biology. Research on the origin, variation and distribution of sexes uses the definition above (Box 1). Moreover, as I have briefly sketched above, the operational definitions of sexes used in biomedical fields all rely on the more fundamental definition that comes from evolutionary biology. We will return to this fact and its consequences in Section 5.

A final objection to looking to the biological sciences to define biological sex might be that those sciences themselves are merely reflections of the societies that produced them. Social relations inscribed into nature are read back onto human beings as something natural and inevitable. Numerous studies by historians of science have documented this effect in the study of sex across a wide range of fields, including evolutionary biology (e.g. Milam 2011; Richardson 2013; Richards 2017). However, attending to these concerns does not undermine the common biological definition of the sexes, and if anything seem to reinforce it. As we will see in Sections 5-7, that definition makes clear how and why the biological understanding of sex is unsuited to defining the social and legal status of human beings. It reveals that it is often biologically meaningless to assign a sex to individual organisms or parts of organisms, and that chromosomal definitions of sex rely on a scientifically indefensible genetic essentialism. Joan Roughgarden is one of the most important dissenters from the orthodox theory of the evolution of sexes which is outlined in the next section (Roughgarden 2013). Her development of alternative models of the evolution of sex and sex-associated phenotypes is in part motivated by the concern that orthodox models, with their emphasis on competition over collaboration, are interpreting nature in the light of society and distorting it in the process. Nevertheless, she sees the conventional definition of the sexes as undermining rather than reinforcing the projection of cultural norms of gender onto biology. Like Roughgarden, I think the biological definition of sex is part of the solution, not part of the problem.

3. The evolution of sex and the evolution of sexes

Why sexual reproduction evolved and why it remains so widespread is one of the harder questions in evolutionary biology. The vast majority of organisms – microorganisms – reproduce asexually. Evolutionary biologist John Maynard-Smith used the catchphrase ‘the twofold cost of sex’ to make the point that a lineage of sexual organisms will be only half as productive as a lineage of asexual organisms, since in the asexual lineage 100% of organisms produce offspring rather than 50% (Maynard Smith 1978). This ultra-simple model, which assumes amongst other things that males contribute nothing but genes to offspring and that females invest 50% of their resources in making males, has long been superseded by more complex and realistic models. Nevertheless, even with more realistic measures of cost, it remains puzzling that sexual reproduction is so widespread (Lehtonen, Jennions, and Kokko 2012). Fortunately, for the purposes of this article we can confine ourselves to why, in lineages that are committed to sexual reproduction, two distinct forms of gamete should evolve.

Sexually reproducing organisms produce gametes which fuse to form a new individual. In many unicellular sexual species these two gametes are identical. Many species of yeast, for example, make new individuals from two identical gametes. They reproduce sexually, but they have no sexes, or, if you prefer, they have only one sex. But in almost all multi-cellular organisms gametes come in two, very different forms and one of each kind is needed to form a new individual. The question, then, is why ‘anisogamy’ (not-equal-gametes) evolved from ‘isogamy’ (equal gametes) and why once it evolved it remains so evolutionarily stable. Nothing in molecular or cell biology prevents organisms making three or more different kinds of gamete, or gametes that vary continuously, just as people vary continuously in height. These forms of reproduction can, in fact, be found in some algae. They are found in a group of species at the boundary between unicellular and multi-cellular life, with closely related species being either uni- or multi-cellular. Current evidence suggests that anisogamy evolved several times, not merely once, and that its evolution is strongly associated with the transition from unicellular to multi-cellular life.

The most widely accepted model of the origin of anisogamy was proposed in the 1970s by evolutionary biologist Geoffrey Parker and collaborators (Parker et al 1972, Parker 2011). They assumed that anisogamy evolved in a species with external fertilization, where both gametes are released into a medium and must find one another to fuse, as is seen today in corals and many other marine organisms. This was a reasonable assumption, given that anisogamy evolved very early in the history of multicellular life. There are two goals that these gametes must achieve if they are to reproduce successfully. The first is finding and fusing with another gamete. The second is producing a new individual with enough resources to survive. Because no organism has infinite resources, organisms can either produce many small gametes, making it more likely that some of them will find a partner, or produce fewer but larger gametes, making it more likely that the new individual will have what it needs to survive and thrive. In models of the transition from isogamy to anisogamy, as mutations introduce differences in gamete size, two winning strategies emerge (Figure 3). One is to produce a large number of small gametes – too small to create viable offspring unless they recombine with a larger, well-provisioned gamete. The other winning strategy is to produce a few, large, well-resourced gametes which can create viable offspring, no

matter how small the other gamete they fuse with. Intermediate approaches, such as producing a moderate number of moderately well-provisioned gametes, or a mixture of differently sized gametes don't do as well. Organisms that try to follow these 'middle ways' leave less offspring than their competitors and the population evolves to the two extremes - small gamete makers and large gamete makers. When these two successful and complementary strategies have evolved, fresh evolutionary pressures make the gametes even more distinct from one another. For example, it can be advantageous for the small gametes to become more mobile, or for the large, immobile gametes to emit signals of their presence. The anisogamous gametes we observe today have evolved to be not merely different sizes but fundamentally different kinds of cell.

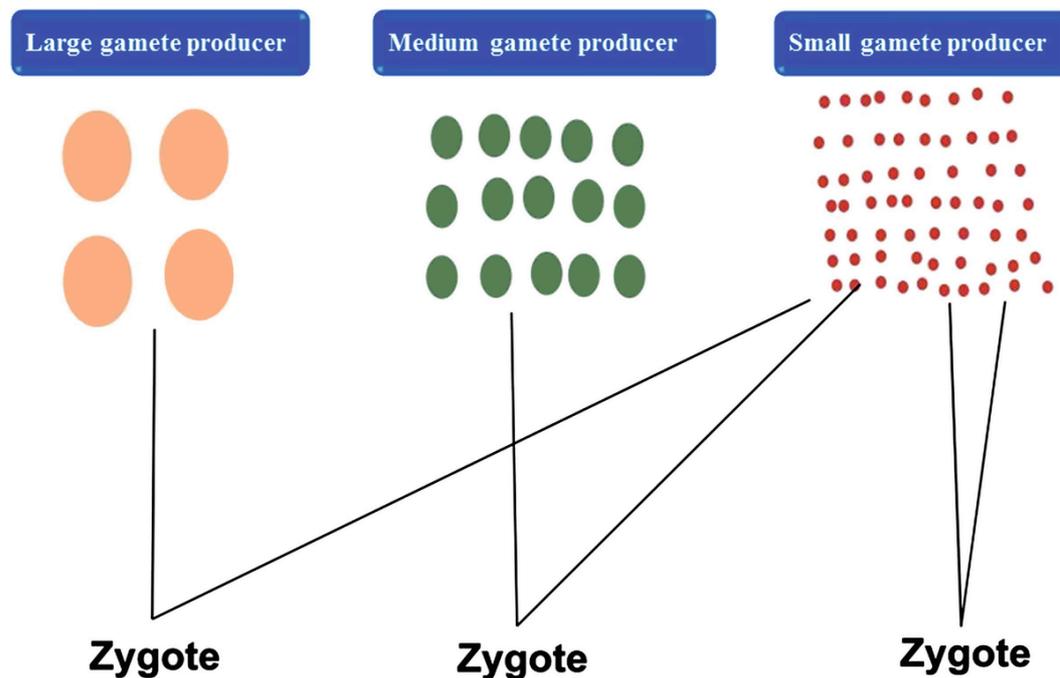


Figure 3. Gamete competition. Small gametes, which are more numerous and may be more mobile, have a higher probability of fusing with another gamete. But if a zygote needs high provisioning, then only gametes which fuse with a large gamete will produce viable offspring. As a result, small and large gamete producers will outcompete medium gamete producers. See text for details. (Kumar et al 2019, 4)

Later work in this research tradition combined this insight about gametic competition with an older suggestion that a *population* of organisms faces the same trade-off between producing more small gametes to achieve more fusions or less, better provisioned gametes to achieve more viability (Lehtonen and Parker 2014). The population is most productive if it produces two different classes of gamete, one well-provisioned and one produced in large numbers. This combination will result in a greatest number of viable fertilisations. Current models combine both these processes, the former known as 'gamete competition' and the later as 'gamete limitation'. These models have also been extended to apply to situations

where one partner retains their gametes internally (Lehtonen and Parker 2019). The current orthodox view of the evolution of sexes is that there is selection for anisogamy in sexual species whenever differences in provisioning are important for the viability of offspring. That condition will usually be met when a lineage becomes multicellular, since multicellular organisms need initial provisioning to build the body with which they can begin to make their own way in the world.

This approach to the evolution of sexes is very widely accepted in contemporary biology. That does not mean that it is the final word, but it does mean that a philosopher who wants to dismiss it as a mass of error had better have some powerful arguments. The best developed alternative account which departs substantially from the theoretical traditional I have sketched here is that of Roughgarden (2013). However, as noted above, Roughgarden uses the same gametic definition of sexes so I will not present her alternative theory here.

Once anisogamy has evolved, it shapes many other aspects of reproductive biology. Most species of limpet - shellfish that you see on rocks at the beach - are sequential hermaphrodites (Borges et al 2016). When young and small they are male, and when mature and large they become female. This is believed to be because small limpets don't have sufficient resources to produce large female gametes, but they're capable of producing the smaller male ones. In some species of limpet, successful males can arrest their growth and remain small (and male) for their entire life.

Sequential hermaphroditism occurs in the opposite direction too. Australian snorkelers love to spot the large blue males of the Eastern Blue Groper (Figure 1), but it's rare to see more than one at a time. Most groper are smaller, brown females. Groper become sexually mature as females when they are twenty or thirty centimetres in length. At around fifty centimetres, they change sex and acquire other male characteristics, such as being blue. In contrast to the limpet, the main problem facing a male groper is controlling a territory on the reef, so becoming male when you are still small is a losing strategy.

This relationship between size and sex-switching is one of many examples where the phenotypic differences between sexes fall into recognisable patterns that can be observed across the diversity of life. These patterns are explained by how the two basic reproductive strategies play out under different ecological conditions.

4. Mating types, self-incompatibility and other complexities

In this section I outline some phenomena in microorganisms and in plants which complicate the picture presented in the previous sections.

Many cultures take male and female to be a universal dichotomy. All sorts of non-biological phenomena, like the sun and moon, are labelled male and female. But the distinction between biological males and females is not like this. It does not even apply to all living things. Sexes are a biological phenomenon that evolved in some species and not in others. The biological definition of sex, like other definitions in the natural sciences, is designed to group phenomena into categories about which we can gather a large body of reliable

knowledge, and to distinguish these categories from one another so that we do not overgeneralise our discoveries. So rather than trying to apply the idea of male and female widely as possible, biologists try to distinguish this very specific way of using DNA to make offspring from other things that organisms do with DNA.

For example, microorganisms which reproduce asexually by division, as bacteria do when one cell splits into two, nevertheless have ways of sharing DNA. But the ways in which genetic material flows between individuals in bacterial populations are fundamentally different from sexual reproduction. Bacterial transfection is one such process and is analogous to a human being collecting some fragments of tiger DNA from a living tiger on a visit to the zoo, and incorporating it into their genome so they can immediately get some useful tiger characteristic. Antibiotic resistance can pass between bacteria of the same or different species in this manner. When bacteria share DNA like this there is no sense in asking which one is male and which is female.

Many single-celled and very simple multi-cellular sexually reproducing organisms have evolved 'mating types'. Mating types exist when gametes are identical in size and structure, but the genome of each gamete contains genetic markers which affect which other gametes it can combine with. Typically, gametes with the same genetic marker can't combine with one another and one function of mating types is to prevent genetically similar individuals from mating, which can have deleterious genetic effects. Some species have many hundreds of mating types, and newspapers often report research into this phenomenon under headlines like: 'Scientists discover species with hundreds of sexes!' But most biologists refer to these as 'mating types' and reserve the term 'sexes' for gametes that are different in size and structure ('anisogamy' - see Box 1).

Why distinguish between these two phenomena? One reason is that the evolution of anisogamy – gametes that differ in size and structure – explains the later evolution of sex chromosomes, sex-associated physical characteristics and much more. Mating types do not have these dramatic knock-on evolutionary effects. Another reason is that they evolve by different evolutionary processes. Mating types often evolve to prevent excessive inbreeding, whilst anisogamy evolves by the competitive dynamic described in the previous section. One theory is that anisogamy can evolve when mating-type genome markers become linked to genes that control the size of the gamete, or mutate in some way that affects gamete size. These differences in gamete size would then kick start the evolution of sexes.

The categories of sexes (anisogamous gametes) and mating types (gametes with genetic incompatibility markers) need to be kept apart because some species have both. To see what that means, imagine that humans had mating types. Successful fertilisation would require not only a male and a female gamete, but also that the two parents had different genes for eye colour or different genes for hair colour or something like that. Matings between two parents with the same genes at these loci would not produce viable offspring. Of course, this does not really happen in humans, but it does happen in some anisogamous fungi (Nieuwenhuis & Aanen 2012). To describe sexual reproduction in these species we need to distinguish between the sexes and the mating types. For example, if there are two sexes and four mating types we cannot simply divide the species into four kinds of sexually

reproducing individuals, since whether any two individuals can reproduce will depend on whether they are male and female, as well as whether they differ in mating type. Whatever names we use for them, two distinctions are needed and not one.

Biologists do sometimes refer to mating types as ‘sexes’ (Aanen et al 2016), but that does not mean that they reject the ideas sketched in Section 3. If the term ‘sexes’ is used more generally, to refer to both forms of gametic diversity, these everything said above is simply rephrased in terms of ‘anisogamous sexes’. The distinction between male and female would be a distinction between anisogamous sexes and the fact that all anisogamous species have only two sexes would remain an important observation that needs to be explained.

Self-incompatibility in plants is another phenomenon that might appear to undermine the distinction between the two biological sexes. Diverse genetic and cellular mechanisms have evolved in flowering plants to prevent ovules (female gametes) being fertilised by pollen (male gametes) from the same plant. It might be argued that, since not all male gametes can fertilise all female gametes, the division of gametes into male and female is mistaken. But the fact remains that every successful fertilisation event involves ovule and pollen - the two sexes. It is noteworthy that some plants, unlike animals, can survive polyspermy, where a female gamete (ovule) is accidentally fertilised by more than one male gamete (pollen grain). This can lead to the spontaneous origin of a new species with a different number for chromosomes from the parent species (Toda and Okamoto 2020). Sex in plants is different from sex in animals in this and other important ways, but the basic evolutionary rationale for anisogamy applies to both.

Across the diversity of life there are many ways to use DNA to create offspring. The biological definition of sexes captures an important way of doing this found in most animal species, many plant species, and some fungal species. Some groups at the boundary between unicellular and multicellular life, such as some volvocine algae, can be seen as representing transitional states in the evolution of distinct biological sexes (Umen and Coelho 2019). But for other groups, including the vast majority of the microorganisms which make up most of life on earth, the distinction between biological males and females is as inapplicable as it is to the sun and the moon.

5. Sex chromosomes and sex-associated phenotypes

Chromosomal definitions of sex are widely used in medicine. The USA’s National Institutes of Health tell interested laypeople that,

‘Sex is biological. It’s based on your genetic makeup. Males have one X and one Y chromosome in every cell of the body. Females have two X chromosomes in every cell.’

NIH News in Health (NIH 2016)

This is the definition targeted by many critics of the idea that there are two discrete biological sexes. For example, Dembroff critiques the idea that there is a stable definition of ‘biological female’ by correctly documenting the failure of “sex hormones and sex

chromosomes” to do the job (2020, 999-100). Another article, entitled ‘Quantum Sex: Intersex and the Molecular Deconstruction Of Sex’, argues that:

“Molecular genetics is likely to require a shift from binary sex to quantum sex, with a dozen or more genes each conferring a small percentage likelihood of male or female sex that is still further dependent on micro- and macroenvironmental interactions.” (Rosario 2009, 279)

But no new discoveries in molecular genetics are needed to reject the chromosomal definition of biological sexes. High school biology is quite sufficient. Many species have males and females but no sex chromosomes. The Australian saltwater crocodile (*Crocodylus porosus*) lays eggs that develop into gigantic, highly territorial males if incubated between 30 and 33 degrees Celsius. At higher or lower temperatures genetically identical eggs develop into females. Like many other reptiles, the crocodile uses incubation temperature and not chromosomes to switch eggs into male or female pathways of development (Lang and Andrews 1994). I mentioned above that birds are ‘reverse heterogametic’, meaning that it is males who have two identical chromosomes (ZZ) and females who have two different chromosomes (ZW). So the NIH definition does not apply to birds. Nor does it apply to all mammals. There are a small number of mammalian species that do not have a Y chromosome, but this does not impact their ability to produce males (Mulugeta et al 2016).

The relationship of sex chromosomes to the definition of sex is perhaps clearest in organisms with facultative genetic sex determination. The Eastern Three-lined Skink (*Bassiana duperreyi*) is an Australian lizard with sex chromosomes. Under some circumstances XY skinks become male and XX skinks become female, just as in humans. But in cold nests, every skink becomes male - whatever chromosomes they have they switch into a male developmental pathway. This effect of temperature on sex is not surprising, as many reptile species use incubation temperature to determine sex. What is more surprising is that varying the size of the egg yolk in this species of skink can produce both sexes with the ‘wrong’ sex chromosomes: XX males and XY females (Radder et al 2009). The skink seems to have three mechanisms for determining sex – chromosomes, temperature, and hormones in the yolk. It is likely that this skink is one of the many species that actively control the sex of their offspring, responding to environmental cues that predict whether male or female offspring have better chances of surviving and reproducing.

If more species were like the skink we would probably not label sex chromosomes as ‘male’ or ‘female’. After all, we don’t think of extreme nest temperatures as ‘male’ and intermediate temperatures as ‘female’, merely because they produce male and female crocodiles or male and female geckos. We think of sex chromosomes as male or female because we focus on species such as humans with simpler genetic sex determination systems. In these species sex chromosomes are quite reliably associated with development into biological males or biological females. Nevertheless, even in these species sex chromosomes play the same role in sex determination as nest temperatures and hormones in the skink. They are mechanisms that turn genes on and off in offspring so that they develop a biological sex. The other changes the body undergoes as it becomes male, female or hermaphroditic implement the reproductive tactics which that species has evolved for its sexes.

Medical definitions of sex in terms of chromosomes are not definitions of biological sex, they are at best operational definitions of biological sex in humans. However, philosophers and gender studies scholars like Dembroff and Rosario cited above are not primarily concerned with whether sex chromosomes are an adequate operational definition of biological sex. Their concern is with whether sex chromosomes are an adequate criterion for determining the social or legal status of human beings as men or women. This is, obviously, a very different question from whether sex chromosomes reliably indicate biological sex and is outside the scope of this paper.

Some medical definitions of sex attempt to remedy the defects of chromosomal definitions by adding in sex-associated phenotypic characteristics:

“Sex” refers to biological differences between females and males, including chromosomes, sex organs, and endogenous hormonal profiles.’
NIH Policy on Sex as a Biological Variable (NIH 2016)

This does nothing to make the chromosomal definition a better definition of biological sex. It merely lists extra clues for identifying biological sex in humans. Like chromosomes, the phenotypic characteristics of an organism can only be labelled as ‘male’ or ‘female’ if there is *already* a definition of sex. There is nothing particularly ‘male’ about being blue as opposed to brown, but colour is a good way to judge sex in Blue Groper. Incubating the egg is a reliable criterion for identifying biologically female primates. But in pipefish and seahorse species the male incubates the eggs in his brood pouch (Vincent et al 1992). Gender studies scholars and philosophers have noticed this logical discrepancy, and have argued that sex is covertly defined in terms of gender: “they must already know what it is to be a man before they can confirm it genetically. The work is circular. It seeks to ground in sex what has already been defined in gender.” (Hood-Williams 1996, 10-11). Similarly, Dembroff asks “what explains why some traits but not others are understood as male or female traits?” and suggests that relevant factors are “Cultural beliefs about gender, technology, and medical practices” (2020, 100). This may be a well-founded critique of medical practices, with certain genes or phenotypes chosen as criteria for categories like ‘man’ because they are associated with male gender. But when phenotypic criteria are used to detect biological sex they are chosen for their association with gametic sex, as size and colour are in Blue Groper (Figure 1).

The shortcomings of chromosomal and phenotypic definitions of biological sex also explain why so many philosophers think that biological sexes form a continuum (see Mikkola 2017 for a review). Many individuals do not have the prototypical chromosomes or phenotypes of one sex. If we represented these individuals in phenotypic space (Figure 4) they would be either at the periphery of a region of phenotypic space that represents a sex, or simply outside any of those regions. But that does not create a continuum of sexes. Consider one such individual, a Blue Groper that is in the process of turning from female into male. It may have a combination of characters associated with one biological sex and characters associated with the other biological sex. But that does not create a continuum of biological sexes. A fish that cannot produce male gametes and cannot produce female gametes is not half male and half female. Producing both kinds of gametes at the same time –

simultaneous hermaphroditism – can be an effective reproductive strategy. But this fish is not a simultaneous hermaphrodite - it is a sequential hermaphrodite in the process of turning from exclusively female to exclusively male. It is no longer implementing a female reproductive strategy and it is not yet implementing a male reproductive strategy. It is not implementing both strategies 'a bit'.

The difficulty of translating these straightforward biological facts into intuitively satisfying statements about the sex of the fish is something that will become familiar in the next two sections as we try to apply the idea of biological sex to individual organisms. The biological understanding of sexes is an effective tool for studying the diversity of reproductive systems across species. It has not been developed to assign every individual organism to a sex and it often fails to do that. This reflects biological reality.

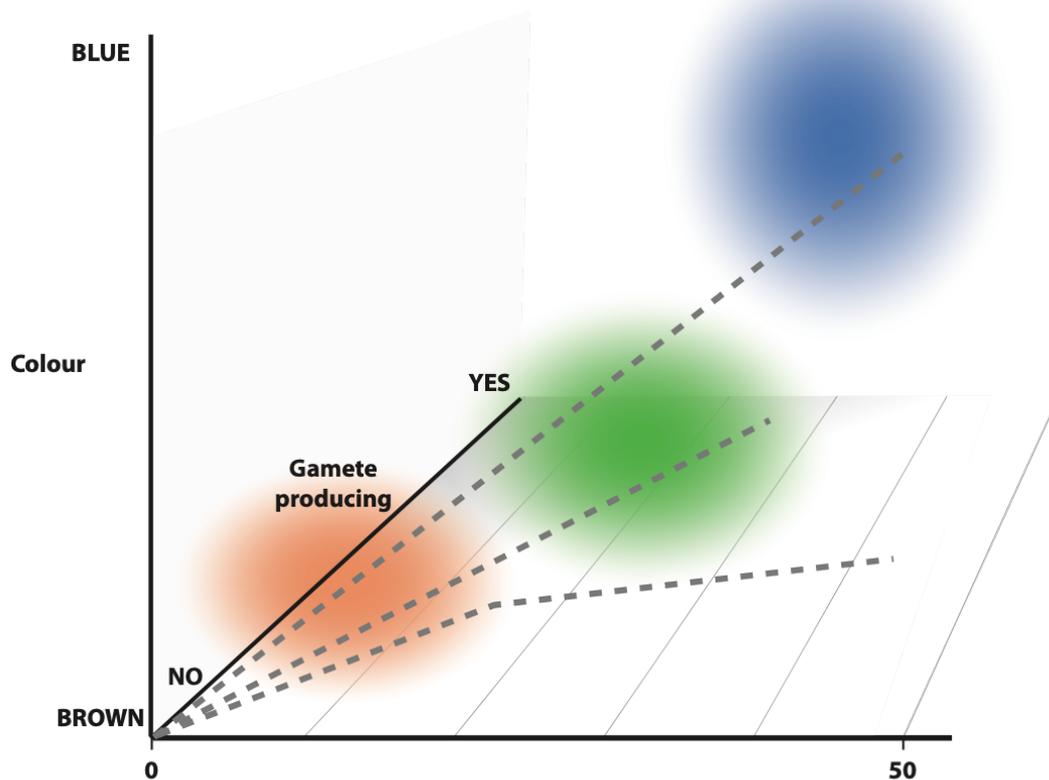


Figure 4. Sexes, and other life-history stages such as juveniles, or adult non-reproductive castes, are regions of phenotypic space. These regions do not have sharp boundaries, as different individuals may implement a gametic reproductive strategy more or less successfully, or just differently. Three dimensions of Blue Groper phenotypic space are drawn with regions representing juveniles (red), females (green) and males (blue). The lifecycle of an individual organism is a trajectory through this space (dotted lines). See Section 6 for discussion.

6. Individual organisms - sex as a process²

It is not the whole organism that is male, female or hermaphroditic but a life-history stage of that organism. This is obvious in species like the Blue Groper where individuals regularly change sex. Figure four shows the normal life-cycle of this species as a trajectory through phenotypic space (top dotted line). It begins as a tiny larvae, develops into a brown female and eventually transforms into a larger, blue male. Not all organisms complete the full life-cycle. The middle dotted line represents an individual that dies before transforming into a male.

² For a general account of organisms as developmental processes, see (Griffiths and Stotz 2018) and for the application of this processual view to 'human nature' see (Stotz and Griffiths 2018).

In this species it is obvious that being male or female is a life-history stage. It is less obvious but equally true for other species. In a sense all complex multicellular organisms 'change sex' because they do not have a sex at conception and must develop one as they grow to reproductive maturity. Once again, this is obvious with the Groper - it makes no sense to label embryonic Groper 'male' or 'female' because they are not currently either and in future they will be both. It is also obvious that species with environmental sex determination do not have a sex at conception. It makes no sense to label a newly laid crocodile egg 'male' or 'female' because it may become either, depending on the temperatures it is exposed to over the coming days. The most we can say is that given how deeply it is buried in the ground and the current weather forecast we predict that it will become either male or female. If we label the egg 'male' or 'female' we are engaging in 'prospective narration', labelling a current event by the future events that we predict will follow (Danto 1982, O'Hara 1988).

The crocodile egg does not have a sex at conception, but at a certain point in development we can say that the egg has begun to develop into a reproductively competent adult, either male or female. These individuals are not actually reproductively competent, however, they are on a developmental trajectory that leads there. So while we can justifiably engage in prospective narration and use terms like 'male embryo' these embryos are not male in the same sense as a reproductively competent adult. Once again, the Blue Groper helps to make this clear. Like these crocodile embryos, a healthy female Groper that has just reached the critical size is on a developmental pathway that leads to becoming male. We could justifiably label it an 'incipient male', but it is not yet male, in fact it is currently still female, and soon it will be neither male or female for a time. When we assign a sex to an organism not yet reproductively competent we are engaging in prospective narration.

This processual nature of sexual identity also applies to organisms with genetic sex determination. This is less obvious because genetic essentialism gives us a misleading picture of the causal role of genes in development. The skink described in Section 5 is a useful example to dispel these essentialist intuitions. Skink embryos with an XX chromosome complement are quite reasonably labelled as 'female'. But, as described above, a number of triggers can send these 'female' embryos down a male developmental pathway. These triggers are thought to have evolved so the skink can respond to environmental cues and give eggs a better chance of surviving and reproducing. What the skink and other species with facultative genetic sex determination make clear is that sex chromosomes are not fundamentally different from nest temperatures. Both are switches that initiate a cascade of gene expression that leads to development as either male or female. It is obvious in the case of the skink that an organism with 'female' genes which actually develops as male is in no sense 'really' female or 'meant to be' female. These genetic essentialist intuitions are the result of thinking of genes as instructions or programs rather than as physical causes (Griffiths 2006; Griffiths and Stotz 2013, Lynch et al 2018).

Juveniles with 'male' sex chromosomes can reasonably assigned male sex for two reasons. First, if we can predict with reasonable accuracy that they will develop into the male region of phenotypic space. Secondly, because they possess a mechanism designed by evolution to switch them into a male developmental pathway (in most but not all mammals this is the

SRY region of the Y chromosome). The same goes, of course, for genetic female and hermaphrodite sex determination.

Juveniles are only one of several cases where an organism cannot produce viable gametes. Eusocial insects such as ants, bees and wasps have a genetic sex-determination system. Some individuals with the 'female' genotype develop into egg-laying queens. But most individuals with that genotype develop into non-reproductive workers. In ant species with complex caste structures individuals with the 'female' genotype can develop down several different developmental pathways, becoming queens, soldiers or different kinds of worker.

The developmental system of social insects has evolved to respond to chemical cues early in development which initiate a cascade of gene expression that produces the appropriate caste. I'll call these 'evolved non-reproductive life-cycles'. For example, the developmental system of honeybees has evolved to allow pheromonal signals from the queen to interrupt the development of ovaries in worker bees and the development of gametes in those reduced ovaries through programmed cell-death. Other pheromones emitted by the developing brood of larvae also act to interrupt ovary and gamete development in workers (Ronai et al 2016). Many other aspects of the worker life cycle have evolved to fit the worker role. For example, workers change their behaviour and take on different tasks in the economy of the hive as they age.

Worker honeybees are 'female' in the sense that their developmental trajectory is an evolutionary modification of the developmental trajectory of their straightforwardly female ancestors (Table 1). I'm not criticising this usage, but I do want to draw attention to the fact that these non-reproductives are not 'female' in the same sense as female reproductives. A Queen ant is female in the standard, gametic strategy sense. The non-reproductive castes, however, have abandoned the production of gametes and adopted a strategy based on transferring resources to relatives who share their genes.

In the eusocial insects all non-reproductive castes have evolved from female forms. But this is just a quirk - the eusocial mammal the Naked Mole Rat (*Heterocephalus glaber*) has non-reproductive workers of both sexes, both of which implement the same reproductive strategy of transferring resources to relatives who share their genes (Jarvis and Sherman 2002). This is the best strategy available to the non-reproductive individuals to maximise their genetic representation in future generations, but it is not a distinctively male or female strategy. The reproductive strategy of the non-reproductive individuals does not centre on the production of one of the two kinds of gametes, and the body of theory about the evolution of male and female strategies does not apply to them. For example, females normally have lower variance in fitness than males, but this important generalisation cannot be straightforwardly applied to organisms that are 'females' in the extended sense that their non-reproductive form is a modification of an ancestral female form.

Case	Meaning
Juveniles	The individual is on a developmental pathway that leads to a reproductively competent male / female / hermaphroditic form
Evolved non-reproductive life-cycle	This life-cycle evolved through the evolutionary modification of a male / female / hermaphroditic life-cycle
Occasional* non-reproductive life-cycle	This individual's development is a modification of a male / female / hermaphroditic life-cycle

Table 1. What does it mean to assign a sex defined by a gametic reproductive strategy to a (life history stage of an) organism which cannot produce gametes? See text for details. *See Section 7 for definition of 'occasional'.

In this section we have seen that it is not the whole organism that is male, female or hermaphroditic but a life-history stage of that organism. Sexes are fundamentally the reproductive stages of life cycles, and assigning a sex to a reproductively competent individual is straightforward. Juveniles, however, are assigned their predicted future sex and these predictions may be more or less reliable. Non-reproductives are assigned sexes because their non-reproductive developmental trajectory is a modification of one of the reproductive forms (Table 1). I do not suggest that this is an exhaustive list of the reasons a life history stage of an individual might be assigned a biological sex, and that, in fact, is an important take-home message from this discussion.

The idea of biological sex when applied to a species is unequivocal - biological sexes are regions of phenotypic space that implement gametic reproductive strategies. But when applied to individual organisms this idea becomes more complex. Individual organisms, and specific life-history stages of those organisms, can stand in various different relations to the gametic reproductive strategies that define sexes. These various relations each provide

good, but different, reasons to assign a life history stage of an individual to a sex. In the following section I will draw out some of the implications of this point.

7. Must every individual have a (biological) sex?

No. We have already met some individuals that it makes no biological sense to assign a sex: embryos in species that switch sex as adults, early embryos in species with environmental sex determination, and individuals who are in the middle of switching from one sex to another.

More generally, in the previous section we saw that once we move away from the core case of individuals who can produce gametes, the sex of an individual is not a simple biological fact but a defensible interpretation of a complex biological reality. For example, there are a number of meaningful places to draw a line around the 'female' organisms. In the naked mole rat it is primarily reproductive behaviour that is repressed in workers, with only limited and reversible morphological differences between workers and breeders. Worker honeybees have their reproductive morphology repressed, but this mechanism sometimes breaks down, allowing them to function as reproductives to some extent (they can lay unfertilised eggs which develop into males). Workers in other bee species lack even this capacity (Gloag et al 2007). There can be a good scientific reasons to draw a line when answering a particular scientific question, but asking which of these organisms is 'really' female is asking for something that is not there.

This reveals something very important about the biological understanding of sexes. I have repeatedly emphasised that the payoff for this way of thinking about sexes is that it helps to explain the evolution of reproductive systems and how they differ across the diversity of life. To this end it is not necessary to assign every individual a sex and in some cases there is no biologically meaningful way to do so. The same applies to kinds of individual - like castes or morphs - not every kind of difference is sexual difference. Calling the non-reproductive castes of social insect additional 'sexes' alongside male, female and hermaphrodite makes no biological sense. Conversely, there are four fundamentally different kinds of Ruff (Figure 2), but three of these are male.

Things seem to be the opposite with the human practice of assigning people a sex as a social and legal status. There is a great reluctance to leave people outside the system of classification and one way to avoid that is by adding new categories. There are obvious reasons why human beings hanker for an all-inclusive system in which every person has a clear social and legal status. But these are not reasons that apply in the study of the evolution of reproductive systems. I will return to the contrast between these two domains at the end of this paper.

Throughout this essay I have used a simple representational device - phenotypic space. The life-history stages of an organism (juveniles, males, females) and other biological phenomena such as castes and morphs can be represented as regions in phenotypic space. The life cycle of an individual organism is a trajectory through this space, passing through one or more of these regions. For evolutionary biology the most important trajectories are

those that occurred regularly in ancestral populations and which played an important role in the evolution of the species. Unusual trajectories are interesting if they provide models for things that used to happen but no longer do. For example the study of 'anarchy' mutants in honeybees, which lay their own eggs and do not contribute to the collective, can tell us something about the evolution of eusocial behaviour in bees (Ronai et al 2016).

But many individual developmental trajectories are just that - individual. I am introducing the term 'occasional' to denote life-cycles that the developmental system did not evolve to produce (Table 1), using that term in its philosophical sense of 'resulting from a particular cause'. Development is a complex process and there are innumerable ways in which genetic and environmental variation can cause it to diverge from its usual paths. For example, in the formation of sex cells (meiosis) there is a weakness in the mechanism which means that homologous chromosomes can fail to separate and some sex cells receive the wrong chromosome complement. The results are often fatal, but in one form they produce the XO chromosome complement (Turner's syndrome). XO individuals can live long and fulfilling lives but cannot produce viable gametes. This is an 'occasional non-reproductive life-cycle' (Table 1). People with this genotype are normally assigned female sex for social and legal purposes, a process outside the scope of the present discussion. They are also commonly regarded as biologically female because their developmental trajectory is a modified version of the typical female developmental trajectory (Table 1). From a medical point of view it is not important whether this developmental trajectory is evolved or occasional. What matters in medicine is how to maximise quality of life for people with the XO chromosome complement. But this is a significant distinction if we want to understand the evolution of the human reproductive system. In this particular case, it is overwhelmingly likely that Turner's syndrome is not an evolved developmental trajectory. It is simply a mechanical consequence of the mechanism of meiosis. The bottom dotted line in Figure 4 shows what the life-cycle of a Blue Groper would be like if it were modified in some of the ways in which the XO genotype modifies the human life cycle - reduced stature, premature ageing and infertility.

Inevitably, the occasional developmental trajectories that are studied in biology and medicine are those like Turner's syndrome that occur frequently and have a reasonably regular course, so that data can be accumulated about them. But the lives of individuals depart from what is usual in their species in all sorts of more idiosyncratic ways. As any biologist who works with natural populations can attest, strange things can happen in development. If we encounter a fish that has been exposed to sex-hormone mimicking molecules from decaying plastic, why would anyone expect to be able to assign it clearly to one biological sex?

Nothing in the evolutionary biology of sex implies that every individual must belong to a sex. There are stages in the evolved life cycle of some species that it is biologically meaningless to assign a sex. Moreover, many individuals have life cycles that depart more or less substantially from the common pattern(s) in their species. There is no biological reason why these individuals should have a determinate sex at every life stage or indeed at any life stage.

8. Conclusions and implications

The primary lesson of this article is that philosophical disputes about ‘biological sexes’ are not about the distinction between male and female organisms as it figures in biology. In a high-profile recent article philosopher Byrne defended the view that ‘human female’ is a biological category, where “Biological categories are categories proprietary to biology.” (2020, 3784). He did not expand on what he means by ‘biology’ but nothing in his article suggests any acquaintance with the literature reviewed here. Criticism of Byrne’s claim assumed that what is at issue is the adequacy of a chromosomal or phenotypic definition of sex in humans. Critics cited scholarship in philosophy, gender and cultural studies, and history of science documenting the inadequacies of such definitions when judged against the criteria of assigning all human individuals to one of two sexes or identifying some measurable characteristics that all males or all females share: “Given this litany of failed attempts to locate a “single, definitive biological indicator” of binary sex classification, why do people continue to look for this indicator, or to insist that sex is universal and fixed?” (Dembroff 2020, 100; see Mikkola 2017 for a broader review).

But biologists do not distinguish male and female organisms using a definition of this kind. As we saw in Section 5, chromosomal definitions are, at best, operational definitions of sex for species with simple genetic sex determination systems. Moreover, when biologists say there are two sexes in the human species this does not imply that every human being is one of those two sexes or that every human individual has a determinate biological sex. It is a statement about the structure of the human reproductive system and its evolution. The biological definition of sex does not imply that there is any genetic or phenotypic character that is shared by all members of a sex in a species. If sexes are gametic reproductive strategies then by definition all reproductively competent adults will produce male or female gametes (or both), but juveniles and the many other kinds of organism who can be regarded as male or female or both will not have even this shared character. And finally, biological sex is not fixed - many organisms regularly change sex and they do so in ways that can be explained using the biological definition of sex.

Philosophers are primarily concerned with the adequacy of the chromosomal and hormonal definitions of sex, operational definitions of sex in humans widely used in medicine. They are not concerned about whether these are adequate operationalisations of biological sex, but about whether they are adequate criteria for assigning social and legal status to human beings as men and women. I hope this essay has made clear that if that is the real issue it will not be settled by digging more deeply into the biology of self-fertilising hermaphroditic fish.

Once the very different things under discussion in these two literatures are distinguished we can distinguish three separate questions that people have in mind when they dispute whether there are two ‘biological sexes’:

1. Are sex chromosomes, or some longer list of sex-associated characters, an adequate criterion for assigning human beings social and legal status as men or women?

This question is completely outside the scope of this essay and has nothing to do with whether the human species has two sexes in the sense intended in biology.

2. Are sex chromosomes, or some longer list of sex-associated characters, an adequate operational definition of biological sex in humans?

The chromosomal criterion is not completely hopeless for humans, but it is far from perfect. There is a large literature on the strengths and weakness of this operational criterion and on its historical use and misuse (a good starting point is Richardson 2013).

3. Are there any species with more than two biological sexes and is the human species one of them?

The short answer is that there are some species at the boundary between unicellular and multicellular life, such as some volvocine algae, which can be seen as representing transitional states in the evolution of distinct biological sexes and might be described as having more than two sexes. They produce slightly anisogamous gametes and in a range of sizes rather than two discrete types. But in complex multi-cellular organisms like plants and animals we find two very different kinds of gamete, each associated with a fundamentally different reproductive strategy, and so two biological sexes. Sometimes these two biological sexes exist in discrete individuals, sometimes they are combined in hermaphroditic individuals, either simultaneous or sequential.

These two domains in which 'biological sexes' are discussed have very different goals and criteria of success. One domain is evolutionary biology, where biologists seek to understand the diversity of reproductive systems and their evolution. The other domain is in philosophy, gender studies and related fields, which seek to both understand and challenge the assignment of people to categories like 'man' and 'woman'. The demands of these two domains are so different that it seems unlikely a common understanding of the sexes could serve both purposes. The biological understanding of sex as I have described it in this essay seems intrinsically unsuited to the role of determining the social and legal status of individual human beings. In some cases there is no biologically meaningful way to assign a sex. In other cases there are sound biological reasons for assigning a biological sex, but they are not compelling reasons for assigning any particular social or legal status to a human being.

My experience in presenting this material is that many philosophers can't see why anyone would be interested in the biology of sex except to draw (problematic) lessons for human society. My motive in writing this essay must, somehow, be to enforce my view of human diversity and they only have to figure out what that is to find out where I have gone wrong. But the truth is that biologists are primarily interested in biology, and often exclusively interested in that. Like them, I find the material presented here fascinating for its own sake and the theory used to explain these phenomena intellectually beautiful. The ability to explain so much about the diversity of life is more than enough justification for continuing to use the common definition of biological sexes in biological research.

There is one way in which discussions of sex and gender should pay *less* attention to how

biologists actually understand sex. That is to stop looking for unusual biological phenomenon, drawing an analogy with sex as a social and legal category, and pointing to this in support of some preferred set of social arrangements. It is true that many organisms change sex, but the fact that Blue Groper have a genetic mechanism that turns them blue and male when they reach fifty centimetres in length contains no lessons whatever for the complex experience of human beings who do not identify with the gender role they have occupied since birth. The claim that there are two sexes in humans, in whatever sense, is not refuted by the fact that slime moulds sometimes derive nuclear DNA from two parent organisms but mitochondria from a third 'parent' (Bloomfield et al 2019). Biology is amazing and it's a good bet that anything you can imagine happens somewhere. But these amazing phenomena will not tell us how best to organise human society.

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