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The Animal Sexes as Historical Explanatory Kinds

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Though biologists identify individuals as ‘male’ or ‘female’ across a broad range of animal species, the particular traits exhibited by males and females can vary tremendously. This diversity has led some to conclude that cross-animal sexes (males, or females, of whatever animal species) have “little or no explanatory power” (Dupré 1986: 447) and, thus, are not *natural kinds* in any traditional sense. This essay will explore considerations for and against this conclusion, ultimately arguing that the animal sexes, properly understood, are “historical explanatory kinds”: groupings that can be scientifically significant even while their members differ radically in their current properties and particular histories. Whether this makes them full-fledged natural kinds is a question I take up at the very end.

1—The Animal Sexes and Natural Kinds

Almost everything about sex is controversial. But, among biologists at least, one thing is not: that males and females differ invariably and fundamentally in the relative size of the gametes they produce. Even Joan Roughgarden—as ardent a critic of traditional sex and gender binaries as any—underscores that “‘male’ means making small gametes, and ‘female’ means making large gametes. Period!” (2013: 23). This simple criterion for biological sex may be applied to any anisogamous species, i.e., any in which sexual reproduction involves the fusion of differently sized gametes (e.g., egg and sperm), each normally containing a half-complement of chromosomes. Anisogamy itself has evolved repeatedly across life’s tree and is ubiquitous, though not strictly universal, among sexual organisms (Lehtonen and Parker 2014).

Of course, that male and female differ in this way does not mean that every living thing is either male or female. In some species—commonly in plants, and frequently in fish—hermaphroditism is the rule, with each organism capable of producing gametes both large and small. Asexual species, the mostly single-celled isogamous lineages in which gametes are uniformly sized, and the rare protozoan group (e.g., *Chlamydomonas eukhloria*) whose gametes come in more than two size variants, also lack distinct male and female sexes.

Yet in the “vast majority of animal species,” from humans to horseshoe crabs, from bustards to beetles, almost all organisms are either male or female, but not both, a system known as gonochory

(Fairbairn 2013: 9).¹ Of course, differences between male and female often extend well beyond the reproductive cells, with the sexes varying in mass, anatomy, and behavior besides. The male blanket octopus, for instance, not only transfers sperm to its mate using a sex-specific detachable delivery arm called a hectocotylus, but he is also comparatively puny—40,000 times less massive than the female. The female *Anopheles* mosquito likewise varies from conspecific males: she possesses special mouthparts that permit her to collect blood meals used to provision developing eggs.

The sex differences just mentioned are species-specific. But biologists as far back as Darwin have also identified coarser-grained patterns in the traits typical of males and females across the animal world. Male animals, it seems, are often more competitive in seeking mates, and sport the ornaments and armaments that aid in such competition.² Females, on the other hand, are commonly more discriminating in mating, and more commonly provide the bulk of species-typical parental care (Janicke et al. 2016). Theorists try to account for these and other trends by tracing them, in one way or another, to a difference of gamete size—just the difference that, biologists submit, defines the sexes themselves (Fromhage and Jennions 2016; Lehtonen et al. 2016; Schärer et al. 2012).

That there exists a scientific consensus on this universal standard of *what it is* to be male or female, and that this difference is widely (though not universally) thought to be “the basis for other differences between males and females” (Hall and Haliday 1998: 219), may appear to indicate that the *cross-animal sexes*—groups consisting of *all male animals*, and of *all female animals*—are deep and important ones that any student of the living world should recognize, that they are, in other words, *natural kinds*.

What are natural kinds? Many ways we group things simply reflect our own priorities. Pests, for example, is a category encompassing the many rather different animals that humans regard as a nuisance, from cane toads to termites and feral cats. However, to think that there are natural kinds—in the view of many philosophers, at least—is to think that some special ways of grouping things trace “the structure of the natural world rather than the interests and actions of human beings” (Bird and

¹ Even in gonochoric species, some organisms may produce both (or neither) large and small gametes, but these individuals are rare, and this property is not typically understood as an adaptation. This contrasts with species in which hermaphroditism is species-typical, as is the case for about 5% of animal species (Jarne and Auld 2006).

² There are just a few known animal species in which females possess more extensive armaments than males, among them the polyandrous Northern Jacana, whose females are equipped with wing spurs, and a few varieties of dung beetle, whose females have larger horns used in female-female contests for resources. By contrast, there are countless species, across many phyla, in which the males alone are weaponized. See Emlen (2014) for an accessible survey.

Tobin 2017). Scientists, it would seem, aim to uncover the contours of these kinds and represent them in their classifications, as Mendeleev did with his periodic table of elements.

What exactly is it about natural kinds that sets them apart? The most discussed proposal is *kind essentialism*. On this view, natural kinds alone have an *intrinsic essence*: properties possessed internally by each kind-member that (1) are necessary and sufficient for membership and (2) account, at least in part, for other kind-typical features (for discussion, see Reydon 2012: 219). For instance, all and only gold atoms have nuclei with 79 protons, which is responsible—in concert with the physical laws—for the characteristic conductivity, reflectivity, and boiling and melting points of all pure samples of gold.

If having an intrinsic essence is the mark of a natural kind, do the cross-animal sexes qualify? In a rare discussion of the question, John Dupré concludes in the negative, arguing that, though gamete size may provide a suitably strict standard for sex membership (thus satisfying condition (1) above), it is not appropriately *explanatory* of other sex-typical features (as required by (2) above) (Dupré 1986, 1995). The essence of gold—having 79 protons—underpins, at least in part, the metal’s attractive yellow luster; due to this nuclear constitution, free electrons form an ‘electron sea’ that readily reflects much of the visible spectrum, blue light aside. But that female orangutans make large gametes does not, in the same way, bring about their sex-typical parental behavior. Instead, gamete size and extended care for young (i.e., nursing through age 8 in orangutans) are, in the view of many biologists, products of a common cause: the female orangutan’s genetic constitution. Nevertheless, the genetic constitution of the orangutan cannot be understood as the essence of female *animals*, the kind at issue here. While sex in orangutans and other mammals is set by the familiar X and Y chromosomes—with XX normally putting mammals on the path to becoming female, and XY on the path to developing as males—this sex determination system is parochial; no gene, chromosome, or combination thereof brings about female (or male) characteristics across the whole animal kingdom.

This explanatory shortcoming in sex’s purported defining characteristic promises to illuminate another notable feature of the cross-animal sexes, one that arguably also distinguishes them from kinds like *gold*: that there are no substantive generalizations true of all—or even of nearly all—males, nor of females. For instance, though females more often provide parental care than do males across the animal kingdom, among bony fish in particular the pattern reverses: sole male care is more common than either sole female care or joint care. And though males are generally the more decorated sex, among some shorebirds the female is the more brightly plumed. Dupré suggests that this variability should be unexceptional, given the explanatory failure of gamete size. After all, on the essentialist picture, generalizations across kind-members were expected precisely because a kind’s defining

property brought about—and thereby explained—sundry other features of the individuals possessing them. When this relation is lacking, it is no surprise that strong generalizations are likewise absent.³

But if the cross-animal sexes are not essentialist kinds, what are they? After all, even if they don't satisfy essentialism's strictures, they seem rather unlike the purely conventional, human interest-based groupings, such as pests, with which natural kinds are often contrasted. This paper attempts to answer that question by presenting a novel account of the animal sexes according to which they are historical kinds. I hope to show that by understanding the animal sexes in the way that I propose, we can make sense of the genuinely explanatory calling that the cross-animal sexes have in evolutionary biology, while at the same time appreciating the mesmeric diversity in male and female characteristics evident across the animal world.

My discussion proceeds as follows. First, section 2 emphasizes known diversity in animal sex characteristics, a diversity that section 3 argues is still consistent with the existence of genuine *trends* in the characteristics of male and female animals. After reviewing the best explanation for these trends in section 4, section 5 presents the paper's central theoretical claim: that to be a male (or female) animal is to be one whose reproductive developmental process originates—in a way I will spell out—in that animal's earliest small (or large) gamete-producing animal ancestors. After arguing in its favor, I conclude by considering whether the animal sexes—so understood—are not merely *explanatory* but also genuinely *natural* kinds.

2—Diversity in the Cross-animal Sexes

A first important fact about the cross-animal sexes—one apparent even when considering just those species in which the sexes are separate—is how heterogeneous each are. In particular, males differ from fellow males, and females from fellow females, not just in their species-typical characteristics (e.g., the male rainbow trout has fins, while the male mountain wren has wings) but also in the traits that are distinctive, within a given species, of males, or of females. The penis can illustrate. The possession of a penis may initially seem a promising candidate for a distinctively male

³ I have reviewed just one strand in Dupré's complex reasoning on the sex categories, and two further features of his view warrant note. First, having rejected both essentialism and the suggestion that the cross-animal sexes have any significant *explanatory* calling, Dupré does not conclude that they entirely lack a *scientific* role—though exploring any such role has not been his focus. Second, irrespective of their scientific interest, Dupré will remain content to consider the sexes *natural kinds*, though for him this means little; on his extremely permissive account, natural kinds extend well beyond the categories of science to Pontiacs, puff pastries, and much else besides.

attribute, one possessed by males, whatever their species, and absent in females. Yet not only are penile structures themselves extremely diverse—inflatable or stiffened by bone; single or paired; helical, boomerang, or forked—but males of many species, including most fish, birds, and amphibians, lack them entirely. And, in some cases, it is the female who is so endowed; in *Neotrogla*, a genus of Brazilian cave-dwelling bark lice, the female inserts her “penis” into the male’s “vagina” to harvest his sperm (Yoshizawa et al. 2014).⁴

Male and female diversity is even more evident in behavioral traits, such as in reproductive and parenting activities. For instance, though some may presume that it is the female’s exclusive role to care for young, sole female care is but one pattern of many—in fact, an uncommon one, given that, in most species, juveniles are left to fend for themselves. Even focusing on just those groups that do aid their offspring—by providing defense, nutrition, or instruction—single-handed caretaking can be found among males, as well as among females. In giant water bugs, for example, the female lays newly fertilized eggs atop the male’s back, which he goes on to carry, protect, and aerate until hatching. Similarly, solicitous males are found among seahorses, who gestate embryos in a special-purpose abdominal patch or pouch, as well as among amphibians like the Darwin frog, whose male ferries his metamorphosing brood within his vocal sac.

Diversity even extends to the very factors that lead embryos to develop into males, or into females, in the first place. As mentioned above, no particular gene or chromosome triggers the development of either male or female phenotypes across animals. And in some cases the environment is the determining factor. The green spoonworm’s sex, for instance, depends on features of its social environment: larvae develop as female if they settle on unoccupied ocean floor, but as male if they settle near a conspecific female.⁵

Given such examples, just what is it that animal males, and females, always have in common? That is, knowing nothing about a creature—except that it is an animal male, or an animal female—what can we infer about it, beyond one feature of its gametes? Perhaps *nothing*, as it turns out (Gorelick et al. 2016). From a creature’s anatomy, to its behavior and genetics, biologists have uncovered no

⁴ See Schilthuizen (2015) for a recent overview of genital diversity and evolution, and Eberhard (1985) for the classic treatise on the topic.

⁵ See Bachtrog et al. (2016) for a review of sex determination mechanisms across animals. From a more philosophical point of view, my [2015] explores a rationale for the scientific practice of holding that sex is ‘determined’ or ‘caused’ *either* by the environment *or* by genetics, given that appropriate genetic and environmental conditions are always jointly required for normal development.

feature—save gamete size—perfectly distinctive of either sex. In fact, when it comes to how non-gametic sex traits are distributed between males and females, almost *anything is possible*.

3—From Diversity to Trends

And yet, that anything is possible does not mean that all possibilities are equally probable. In this case in particular, that stronger conclusion is almost certainly false: for a variety of anatomical and behavioral traits, some are much more common among males than among females; for others, the reverse.

Let's return to the penis, understood broadly as any structure used to transfer gametes from one sex partner to another prior to fertilization. Though this apparatus has evolved repeatedly and independently across animals—derived, developmentally, from the anal fins of some fish, the limb pathway of amniotes, and the sensory organs of spiders (Brennan 2016)—it is almost invariably, Brazilian cave-dwelling bark lice notwithstanding, a feature of the male animal alone (Yoshizawa et al. 2014: 1001). An equally strong trend, to be expected given that male and female genitals coevolved, concerns females: that they are much more likely than males to possess receptive genitals—from the ovipore of the insect to the triple vagina of the kangaroo—that collect, and regulate the use of, gametes of the other sex. Females are also more often the sex that gestates offspring, a pattern so striking that some accounts of pregnancy restrict it to females *by definition*, a constraint recently disputed by those studying the rare species in which males become gravid (Stölting and Wilson 2007: 884).

A second class of sex-correlated traits comes from the more complex study of behavior. For instance, among animals, it is common for males to engage in more within-sex competition than conspecific females, including in direct contests between adults for access to mates (Andersson 1994, Clutton-Brock 2017). Females, on the other hand, are commonly more reproductively discriminating, that is, less likely than conspecific males to mate with available members of the other sex. A weaker—but still apparently real—sex-linked trend concerns parenting behavior: females, more often than do males, provide the majority of parental care (Clutton-Brock 1991).

For a third type of sex-correlated trait, consider the developmental systems that build male and female phenotypes. Though what biologists call the *primary* sex-determination mechanisms—of which the mammalian XY/XX scheme is an instance—vary substantially across animals, aspects of the causal process activated by these mechanisms (like that causing gonadal differentiation) are similar across many animal species. In particular, the DM (*Doublesex* and *Mab-3*) family of transcription factors “appears to be directly involved in sexual development in all major animal groups” (Herpin and Schartl

2015: 1265). The proteins produced by these genes contribute to the development or maintenance of male gonads in particular—and, by way of this, other aspects of male phenotype—in animals from flatworm to chicken, from mouse to flea. This regularity in the process of sex differentiation—in contrast with radical diversity in primary sex determination—has inspired the slogan “[m]asters change, [but] slaves remain” (Graham et al. 2003).

4—Explaining Trends

With a variety of sex-linked trends now in view, we can ask: what explains them? In particular, given that it is possible for animal males and females to differ so radically among themselves—as illustrated by section 2—why are there *any* patterns in male and female traits? After all, most biologists hold that members of each cross-animal sex must—as a matter of definition—have just a *single* feature in common: large gametes for females, small gametes for males. But why should an organism’s gamete size mean *anything at all* for its other features?

Before exploring possible answers, it is worth considering an important, and potentially debunking, reply: that bias—most notably, our tendency to see the natural world through the lens of normative gender roles—has significantly distorted the study of sex differences and, to some degree, the conclusions drawn within it (Ah-King and Nylin 2010: 234; Gowaty 1997; Tang-Martínez 2016). For instance, Darwin’s (1871) description of male animals as generally “courageous and pugnacious” (ibid: 516) and females as “with rarest exceptions...coy” (ibid: 222) seems to have been shaped by a Victorian model of behavior (Dewsbury 2005: 835; Richards 2017). More recently, phenomena contrary to our own social expectations—e.g., promiscuous females (Hrdy 1980) and discriminating males (Edward and Chapman 2011)—appear to have been recognized by the research community only very late in the course of inquiry and only after contentious debate (Hrdy 1986).⁶ And even presuming that these particular errors have been remedied (often following attention from feminists, e.g., Haraway 1991, Gowaty 2003), other aspects of our total picture of animal sex differences may well remain misshapen due to their prejudicial origins.

Granting the justice of these concerns, what bearing should they have on our understanding of the trends in male and female traits described in section 3? Ought they, perhaps, be discarded along with Darwin’s anthropomorphic language of the ‘coy’ and ‘pugnacious’? Though caution is indeed

⁶ There are even stronger grounds for concluding that research into *human* sex difference in particular—an important topic beyond the scope of this paper—has been influenced by intellectual and social preconceptions (for discussion, see Fausto-Sterling 2000 and Fine 2010).

called for, even those critics who are most attentive to the role of sex and gender bias in science do not generally go so far as this. Rather than questioning the *existence* of such trends, critics more often emphasize a cluster of problems with the way behavioral trends in particular have sometimes been understood or described. For instance, Ah-King and Ahnesjo (2013) argue against the common practice of grouping individual reproductive behaviors into broader “sex roles,” with the “male sex role” involving heightened reproductive competition, minimal reproductive discrimination and parental care, and the “female sex role,” the reverse (as in Barlow 2005; Williams 1966). Among other issues, such usage may indicate that sex characteristics come in just two cohesive packages, when the reality—as we’ve seen—is more complex. A second and related problem lies with the occasional suggestion that trends in sex differences might actually be *laws* (e.g., in Bateman 1948: 352), language that could mislead us into thinking that the generalizations have few, if any, exceptions. Along the same lines, critics take issue with claims that sex differences were generated “inevitably” by certain evolutionary processes or transitions, or that certain trends follow as a matter of “logic” (e.g., in Avise 2013; Parker 2014). Even if there is reason to think that these trends are not mere accidents, claims of “inevitability” are belied both by the intra-sex diversity already reviewed, and by our current understanding of the process that gave rise to animal sex differences in the first place.⁷

And just what is that process? This question brings us to the main task of this section: to explore explanations for trends in male and female traits across animals. At the heart of virtually all accounts is that males produce comparatively small gametes, and females large.⁸ Of course, as reviewed above, gamete size does not do its work in the way the essentialist would envision, that is, via an immediate influence of gamete size, in each particular organism, on that organism’s other traits.

⁷ Neither the work just cited actually maintains that sex differences are generated in a fully inevitable way; their claims, instead, are that a regular pattern of difference evolve *when certain other conditions are fulfilled*. In this way, it is the *language* of inevitability that is the subject of possible critique.

⁸ The one possible exception to the consensus about the importance of gamete size in the explanation of sex differences is the ‘time-in/time-out’ explanation articulated Gowaty and Hubbell (2005), according to which mean behavioral differences between animal males and females result from universal behavioral dispositions—i.e., those present in both males and females—activated differently due to the different circumstances that particular organisms experience. Space does not permit me to explore this view here, but a few comments are in order. First, it is notable that this proposal is directed exclusively at accounting for sex-linked behavioral differences. Given this, anisogamy would still need to be called on to account for anatomical patterns of sex difference. Second, it remains uncertain if the account’s explanations of *behavioral* differences isn’t still committed—albeit in a special way—to an explanatory role for anisogamy. After all, the systematic difference in circumstances between males and females—which are then said to activate different particular behaviors—will *itself* need an explanation. For elaboration of this second point, see Schärer et al. (2012).

Instead, going explanations are uniformly evolutionary, with theorists positing that ancestral organisms with smaller gametes experienced different selection pressures than those with larger gametes, with current patterns of sex difference the eventual result.

Yet two subtly, but importantly, different sorts of evolutionary explanations have been suggested, which I will call the ‘direct anisogamy’ and the ‘original anisogamy’ accounts. And though theorists seem to increasingly advocate a version of the original anisogamy story, it is worth describing the direct account first, both given its continuing influence and for the sake of contrast.

In particular, in a paper foundational to the modern discussion of the evolution of sex difference, Bateman suggested that widespread differences in male and female mating behaviors could be explained by the fact “that females produce much fewer gametes than males” (1948: 364-5), a difference that he said follows from the fact that smaller gametes are energetically cheaper than larger ones. The resulting mismatch in gamete number, as Bateman saw it, had the consequence that reproductive success is, for males, roughly proportional to their number of mating partners, but not so for females. After all, all of a female’s gametes can be fertilized by a single male, while a male will have sperm enough for the eggs of many females. Bateman argued that, given this difference, it pays, from an evolutionary point of view, for males to vie for access to as many females as possible. This has led males to develop, among other traits, an “undiscriminating eagerness,” and females—to maximize the quality of their more strictly limited offspring—a “discriminating passivity” (ibid 365).

I have labelled this explanation ‘direct’ based on the role that gametic differences play in the selective story told. In particular, according to the explanation, a difference in gamete number between the sexes—thought to be a close consequence of anisogamy—*itself* makes a difference to which mating behaviors are most adaptive in extant organisms (and in their recent ancestors), thereby accounting, at least in part, for which behaviors are observed today.

Is this explanation cogent? And can it account, not only for the mating strategies found in particular populations (e.g., in the fruit flies that Bateman himself studied) but also for such behaviors across animal species—and thus for trends in such behaviors? Though it may succeed with the former, it appears to founder with the latter. The main problem is not the existence of so many species in which the small gamete producer, i.e., the male, lacks the traits that the direct explanation seems to predict. This fact *is* important, since it indicates that gametic differences can, at best, have particular selective consequences *given certain background conditions*. But the direct account’s principal shortcoming is that it is not the correct evolutionary explanation of mating behaviors in so many of the species that *do* instantiate the focal trend, e.g., in which males *are* more reproductively competitive than females.

Rather than gamete size, or gamete number, *parental investment* is more often taken to be the explanatory linchpin in accounting for sex differences in mating behaviors within species.⁹ As influentially defined by Trivers, parental investment is “investment by the parent in an individual offspring that increases the offspring’s chance of surviving ... at the cost of the parent’s ability to invest in other offspring” (1972: 55). It includes the costs of gestation, offspring feeding, and guarding, as well as gamete production itself, though this last is sometimes but a small contributor that makes no difference to the overall balance of investment between males and females. For instance, though Mandrill females do indeed invest more in making each of their larger gametes (i.e., eggs) than do males in their smaller gametes (i.e., sperm), this difference is trivial in comparison with the orders-of-magnitude-larger commitment of female Mandrills via gestation and lactation.

Why is it that overall parental investment—or, more specifically, sex differences in parental investment—matters so much? To mention just one of many paths of influence: because members of the more investing sex are more often occupied with preparing for or assisting offspring, they are underrepresented among breeding-ready adults. As a result, it is comparatively easy for members of the more investing sex to find mates, and comparatively difficult for members of the less-investing sex. In such a situation, each member of the less-investing sex stands to gain more, reproductively, from devoting resources to traits that increase the chances of mate acquisition, thereby explaining the emergence—over evolutionary time—of such traits in members of that sex.¹⁰

Yet can the parental investment theory, as just sketched, account for trends in sex differences across animal species? Needless to say, it promises only to address behavioral variation between the sexes, leaving aside the other types of sex difference surveyed above. Even so restricted, parental investment theory is not equipped to explain behavioral differences on its own, for the simple reason that it says nothing about *which sex*, male or female, typically invests more. And facts about parental

⁹ Even Bateman recognized, in passing, the importance of pregnancy and other forms investment, though the strict letter of his proposed explanation is in the gametic terms that I rehearsed. Of importance here is not Bateman exegesis but rather having these two contrasting explanations before us, both of which have had currency among theorists.

¹⁰ Though I describe parental investment theory as the successor to the direct account, it too is an oversimplification. To account for the evolution of sexually competitive traits in particular species, biologists often appeal to two population-level features that are *influenced* by differences in parental investment but are distinct from it: the ratio of breeding-ready males to females (or a property closely related to this), and the Bateman Gradient (the slope of the relationship between reproductive success and mating success). For details, see Kokko et al. 2012.

investment cannot be extracted from the presence of anisogamy itself, even presuming that gametic investment is generally proportional to gamete size.¹¹

This limitation brings us finally to the ‘original anisogamy’ account, a label I use for a family of emerging explanations according to which sex differences across animals—in mating behaviors as well as in many other traits—are “ultimately rooted in anisogamy, [... but] not directly due to anisogamy” (Fromhage and Jennions 2016:5; see also Avise 2013, Lehtonen and Parker 2014, Lehtonen et al. 2016). Very schematically, these accounts 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 described above.¹²

How might ancient gametic sex differences have such interesting explanatory potential? By a process recently dubbed the ‘sexual cascade.’ This can be envisioned as a series of evolutionary transitions in which an earlier sex difference—in the first instance, a gamete size difference itself—“precedes and creates the selective pressure for the next” (Parker 2014: 7), a process that is then iterated. For instance, heightened male reproductive competitiveness in a contemporary group might be immediately explained by increasingly female-biased parental investment that evolved at an earlier time, which is itself explained—at least in part—by the evolution of female viviparity, and so on, back to the sex differences in gamete size that, according to biologists, define the sexes themselves.

To illustrate part of the process in more detail, consider the advent of internal fertilization, a reproductive system in which gametes fuse while inside the body of the male or female parent. This common adaptation has emerged in widely divergent animal lineages, in many cases from ancestral conditions in which male gametes joined with female gametes near—but still outside—the parents. Importantly, internal fertilization has not evolved to occur in males and females with equal frequency; it is vastly more common in females. And why? Here is one plausible account: though internal fertilization, in itself, can benefit both parents, as it gives resulting zygotes some protection from

¹¹ It is not at all clear that differences in *gametic investment* between the sexes do directly track differences in investment in individual male and female gametes, given that males of most species produce a vastly larger number of gametes than do females, both over their reproductive lives and per offspring embryo generated.

¹² Though based on an evident difference between the two kinds of explanations that biologists offer, the explicit contrast between direct and original explanatory accounts is my own. As an aside, some presentations of (what I call) the original anisogamy account (i.e., Fromhage and Jennions 2016) are advertised as *vindicating* Bateman’s original insight, by showing in a more complex way how anisogamy might have generated other sex differences.

predation, *female* internal fertilization emerged more often because it is comparatively evolutionarily accessible; i.e., given the other sex differences preceding it, female internal fertilization can arise via a much more modest, and more probable, novel variation. In particular, prior to the evolution of internal fertilization, the male's, but not the female's, gametes were already actively mobile, a difference largely maintained to this day. Given this pre-existing fact about gamete mobility, a simple change—say, the female's withholding of her gametes at the exit of the reproductive tract—might have been enough to bring about the target trait. After all, even with the female's gametes at a slightly greater remove, the male's gametes may still have been able to reach them under their own steam. But the converse process, in which a female's gametes were somehow transported to within the male, would have required a more complex set of innovations, and partly for this reason, arose in only a handful of cases.¹³

From the transition just described, we can trace this sexual cascade both backwards and forwards in time. Going backwards, the active mobility of male—but not female—gametes is usually explained by selective forces resulting from anisogamy itself (Lessells et al. 2009). Going forwards, female internal fertilization has been used to account, at least partly, for quite a number of the sex differences mentioned in section 3, including the comparative frequency and complexity of the male intromittent organs (Eberhard 1985), an increased uncertainty of male paternity (important because it can make male parental care less likely, see Queller 1997), and the higher rates of female internal gestation and viviparity (Kalinka 2015). And given that gestation often shifts the balance of parental investment strongly towards the gestator, the stage is then also set—via parental investment theory—to explain the heightened male reproductive competition found in many extant species (Avisé 2013).

Needless to say, just because this sequence unfolded countless times, in separate lineages, it does not follow that it unfolded in all lineages. Many present-day external fertilizers, for example, took a more direct path from differences in gametic investment to sex differences in reproductive behavior. Other lineages deviated from the cascade at a late point, leading to different suites of reproductive traits. For instance, females in some species evolved to prefer males who contributed hard-to-find resources, putting males in comparatively high demand and bringing about what is controversially called a “sex role reversal”; in other cases, ecological conditions have favored substantial—sometimes

¹³ In contrast to the account just given, it may be that internal fertilization, even in its initial stages, was actually more fitness-enhancing for females than for males, or that there were additional dynamics at work (see Lehtonen and Parker 2019). What matters for my purposes is not that the explanation given, an elaboration of one that Darwin himself offered, be fully correct, but instead that the correct explanation take the same overall form

equal—investment by both parents.¹⁴ That animal populations have taken variable paths, sometimes to other destinations, is only to be expected, and not just because a stochastic element exists in all evolutionary processes. More important for explaining the diversity we see today is that no trait is fitness-enhancing in itself, but only relative to an organism’s other endowments and its environment—including the environment provided by the other sex. Because these have varied over the history of animal life, evolutionary outcomes have differed likewise.

And yet, without denying this diversity, the original anisogamy account suggests that animal lineages have traversed certain kinds of paths more commonly than others, a bias thought to be no accident: it resulted from the fact that the simple gamete size difference in the distant past of all animals increased the probability of certain further sex differences in a large range of background conditions (Fromhage and Jennions 2016; Lehtonen et al. 2016). These differences, in turn, increased the probability of other differences still.

As I’ve reconstructed the original anisogamy account, gametic differences play a qualitatively different explanatory part than they did in the direct account. In particular, the original anisogamy explanation recognizes that sex differences in gamete size do not, at least in many cases, *currently* make a difference to the adaptiveness of alternative male and female behaviors.¹⁵ What does make a difference are other sex differences that evolved in later parts of the cascade.¹⁶ And yet because these

¹⁴ For reasons of space, I cannot pursue the place of our own species among these options, perhaps a foolish pursuit given the evident *variability* in reproductive behaviors across human populations. Still, given the substantial *paternal* care evident in so many human groups, and the presence of seemingly sexually selected traits of *female* humans (e.g., permanent breasts, absent in all non-human primates), it seems safe to say that we have not followed what we might call the ‘simple cascade’ trajectory, one leading to exclusively male sexual competition, and substantial parental investment only among females. And why have humans gone, at least somewhat, off-cascade? No doubt the answer is complex, but the explanation many well involve our long, and demanding, juvenile period. In particular, though our mammalian lineage bestowed upon us female internal fertilization, and substantially obligates female parental investment via gestation and nursing, the long-term dependency of human young, and the demands of raising such juveniles to be reproduction-ready adults, may have selected for substantial paternal care alongside maternal care, resulting in the complex situation we see before us: in which some level of sexual competition, and non-trivial parental investment, is typical of human males *and* females both.

¹⁵ This isn’t to deny cases in which current gamete size differences *do* make a difference to behavioral strategies—for instance, those bird species in which the female’s egg is orders of magnitude larger than each of a male’s individual sperm, and in which there are but minor further differences in parental investment between the sexes.

¹⁶ Just what does it mean for gametic differences to *not make a difference* in this way? For heuristic purpose, think of this as follows: in the counterfactual scenario in which gametic investment between the sexes was equalized—while all else about male and female physiology stayed the same—there

further differences did not *replace* gamete size variation but were tacked on top of them, the original anisogamy view still promises to explain the trends in animal sex differences that are observed today.

5—The Animal Sexes as Historical Kinds

The original anisogamy approach is still under active development and is not universally accepted. The ancient origins of animal evolution remain shrouded in mystery, after all, and the sexual cascade picture is incomplete. But presuming its general contours are correct, what might this mean for the nature of the animal sexes themselves?

It suggests that the animal sexes may be rather different than the biologist’s simple “definition” suggests, as I now aim to show. In particular, though an animal’s sex can generally be *identified* by the size of its gametes, such differences—I submit—are *indicators only*, and fallible ones at that. Rather than being grounded in any shared current properties, I propose that the animal sexes be understood as *historical kinds*, and, in particular, as developmental historical kinds that tie an animal’s sex to the origins of the developmental process by which its reproductive traits are formed. This historical feature, it turns out, is closely tied to—if not identical with—what explains trends in sex differences across animals. Consequently, if this proposal is right, the animal sexes will turn out to be explanatory kinds, though of a somewhat queer sort.

Individual species are the sorts of things most often understood as historical kinds in biology. But the species model cannot simply be applied to the animal sexes: we cannot say, for instance, that male animals are members of different *reproductive lineages* than female animals, a difference in virtue of which they constitute different historical kinds. Naturally, males and females are jointly required for reproduction, and thus males and females in any population collectively possess the same causal and genealogical antecedents; in the case of different-sexed full siblings, they have fully identical ancestors.

Given this obvious fact, in what sense could ‘animal male’ and ‘animal female’ be historical kinds—i.e., those grounded in shared relationships to the *past*, rather than in shared *current* properties? To see, start by conceiving of the sexes, within a species, as alternative developmental outcomes of the same basic biological resources—of largely identical and “fundamentally bipotent” genomes (Beukeboom and Perrin 2014: 37).¹⁷ Though different species exploit different “switches” to direct

would, in many species, be *no* change in the overall parental investment difference between the sexes, and no qualitative change in selection pressures on male and female reproductive behaviors.

¹⁷ Partly for this reason, Richardson suggests that the sexes be understood as “dynamic dyadic kinds” (2014: 196-199). This interesting proposal, which I believe is compatible with my own, is aimed at characterizing the sexes *within* a species, rather than across species.

individuals down one or the other of these developmental paths, animals with separate sexes appear to enjoy the same two-sex system, in the following sense: this system derives from a common evolutionary source, the mechanisms that underpinned bipotency in the common ancestors of all animals.¹⁸ Those ancestors, it turns out, were already anisogamous, and able to develop into two reproductive variants (Cunningham et al. 2017). And this capacity, it seems, has persisted to this day, through locally gradual—and ultimately radical—change in its molecular underpinnings.

Not only does the bipotent system have a common origin across animals, but so do the particular settings of that system—the particular developmental paths that generate the adults we call ‘male’ and ‘female.’ The best evidence for this is the existence of a few conserved features of animal male and female reproductive developmental systems, particularly in the genetic networks critical for gonadal differentiation.¹⁹ Still, such conservation is not required for male-specific developmental systems, and female-specific systems, to share such origins. What *is* required, as I conceive of it, is that a *sex development lineage* links reproductive developmental processes—those that bring about traits of specific relevance to reproduction, from gonads to genitals to mating behaviors—activated in present-day males, and females, to those in males and females (respectively), in the founding animal population.

To grasp the idea of a sex development lineage, consider the two reproductive types—one producing smaller gametes, the other larger—in that earliest animal population, a group of coral-like organisms living about 700 million years ago. At that early point, sex differences were likely very minor, with males and females (characterized by gamete size) differing only in gametic features, and perhaps in the particulars of the gonadal tissues that produced them. As this population evolved, and repeatedly split, sex-specific traits—and the developmental processes that generate them—gradually changed. Yet through such change, parents and their same-sex descendants would have exploited reproductive developmental systems similar enough to be considered variants of the *same system*. The sex developmental lineage is defined as the extension of these local relationships in reproductive developmental systems from generation to generation. Based on the presence of a few conserved features across animal males and animal females—most notably, in the process of gonadal differentiation itself—it appears that such lineages link the developmental systems found in the earliest

¹⁸ Though both hermaphroditic species, and those with alternative reproductive tactics, can be fit into this picture, the details are too complex to pursue here.

¹⁹ See section 3 and Beukeboom and Perrin (2014), chapter 3.

large- or small-gamete-producing animal ancestors, with processes instantiated in male and female animals today.

In making the case for a common origin in animal male and female reproductive developmental systems, I just implied that an animal's sex is set by some intrinsic feature—presumably the size of its gametes—which the sex developmental lineage happens to track. But what if we kick away the gametic ladder that we climbed to get here, and understand an animal's sex *in terms of* the history of the developmental system that produced it? This, in effect, is my positive proposal. An animal's sex, I want to suggest, is set by its reproductive developmental system, and in particular by whether that system is a variant—as determined by its sex developmental lineage—of the developmental process at work in its earliest male, or female, animal ancestors.²⁰ Putting things somewhat more carefully, my idea is this: 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.

To illustrate, consider two male animals: a Rhinoceros beetle sporting offensive armaments, and a Titi monkey gently ferrying newborns on his back. In virtue of what are they both male animals? The orthodox, gamete-based answer, is that they are male just because they produce comparatively small gametes. My alternative historical proposal is this: they are male in virtue of the fact that the developmental processes that brought about their reproductive traits are variants of the developmental processes activated in each of their earliest small-gamete-producing animal ancestors. And to be a variant of such an early process is to be part of the same sex developmental lineage.

²⁰ This is closely related to the fact that the actual animal sexes—or, more narrowly, some of their gonadal and gametic traits—seem to be homologies, such that two animals are jointly male in the same way that our forearm bone, and one of the bat's wing bones, are both *humerus bones*. Though this may be correct as a point about the actual animal sexes, my account actually does not require a relationship so strong. In particular, for two animals to be male I do not require that their developmental system's actually originate in the *same* small- or large-gamete-producing ancestors; it would be sufficient if they traced to distinct early anisogamous animal populations. This feature of my proposal is not one I can motivate here, except to say that it is tied to the likely repeatability of the sexual cascade: even had there been distinct origins of anisogamy in different animal populations—or, even had anisogamy (along with other preconditions for the full cascade, such as mobility) evolved elsewhere in the universe—sexual cascade theory suggests that we should nevertheless expect the same series of intermediate and ultimate adaptations, and thus it would be worth categorizing such diverse creatures together. Given this, my actual view is that the animal sexes are what I call “type-historical kinds,” but I leave this complication aside here.

This historical account can make better sense of biological categorization and explanatory practices, I believe, than can the orthodox view (i.e., the view on which males are just those organisms that produce comparatively small gametes, and females comparatively large ones). But in making this case, let me acknowledge some of the theoretical presuppositions on which I rely, not all of which I can defend here. Moreover, the viability of the entire picture depends on the empirical claims discussed above being in the main accurate. Given this, my primary aim can only be to make the historical approach a live option, rather than to close the case in its favor.

A first consideration supporting the historical account of the sexes is the simplest: that, like other historical accounts of kinds, such as the now-popular genealogical approach to species, it makes immediate sense of *diversity* in the current characteristics of kind-members—in this case, in male and female traits across the animal kingdom. Capturing such diversity is something that any historical account can do very naturally, in virtue of the scope that an extended causal chain gives to the play of course-changing contingencies, yielding kind-members with radically different characteristics. In the case of the sexes in particular, much time—perhaps as much as 700 million years—has passed since the developmental origin that all females (and males) appear to share.

My proposal's developmental element also contributes, in a different way, to its openness to intra-*species* diversity in male traits, and in female traits. For example, consider an individual who has, in the main, come to be via the 'female' developmental pathway. (This pathway, of course, will be female in virtue of its history, albeit a history that will be largely the same across members of the species.) And yet, for various reasons—say, due to a congenital anomaly or inherited condition that interfered narrowly with gamete production—such an individual might not produce sex-typical gametes. Yet, on the view under consideration, this will not undermine that animal's status as a full-fledged *female*, in contrast to the orthodox anisogamy account with its singularly gametic focus.²¹²²

Consider, next, the flip side of the coin: coarse-grained trends in sex differences—and in male and female traits—across the animal kingdom. In accounting for such trends, I submit that the

²¹ One might wonder what happens, on my view, if an individual's development goes by way of an intermediate developmental pathway, one perhaps resembling those in its male and female parent equally. On my view, an individual with a genuinely intermediate developmental origin would be neither male nor female, but this presents no problem for the overall account. After all, as Khalidi (this volume) explains, the presence of intermediate or vague cases need not, in and of itself, undermine a kind's status as *natural*.

²² It is worth noting that the anisogamy standard can also be given a developmental gloss, making it more open to this particular kind of intra-species diversity in reproductive characteristics. See Byrne (2018) for details.

historical account has a direct explanatory payoff. To see this, first recall the original anisogamy explanation from section 4: that though current gamete size does not directly explain trends in male and female traits, the presence of ancient gamete size differences in animal ancestors does, via the sexual cascade. On my construal, this explanation has three claims at its heart: (1) that ancient animals were anisogamous, and thus came in small-gamete- and large-gamete-producing variants, variants that differed by having activated sex-specific developmental pathways; (2) that this two-variant system persisted through change; and (3) that—as described by the sexual cascade—selection pressures biased evolutionary change in the underpinning of sex-specific developmental pathways towards some patterns of sex difference and not others.

As the reader may note, I've just made explicit a critical part of the full original anisogamy explanation, one that I earlier left unstated: that differences between male and female animals are invariably underpinned by sex-specific developmental pathways. Not only is this feature central to our present understanding of the evolutionary process—a point emphasized by recent work in 'evo-devo,' the evolutionary study of development—but it is also the key to how the historical account of the sexes works its explanatory magic. Let me explain.

To be a female (or male) animal, I've proposed, is to be one whose reproductive traits are the product of a developmental pathway that is a variant of, and successor to, the pathway activated in early large-gamete producers (or small). What this proposal does, in effect, is to pack into the 'key property' of animal males, and of animal females, two key elements of the original anisogamy explanation—sex-limited versions of (1) and (2) above. By requiring, for an animal to be one sex or the other, that these states of affairs hold, an animal's sex promises to explain, via the sexual cascade, the likelihood that it possess other sex-linked traits, such as those described in section 3. For instance, partly by virtue of the origin of its developmental system, an animal female will have a relatively low probability of reproductive ornaments and armaments but a higher probability of having receptive genitals. Such probabilities, it is worth noting, are explanatory, and not merely predictive: given the key property of female animals, the sexual cascade explains their likelihood of having certain traits; it does not simply predict that they likely will. In consequence, I submit that, if the animal sexes are as I propose, they are explanatory kinds.²³

²³ Some may object to the standard for *explanatory kinds* to which I am appealing, along the lines suggested by Devitt (2008). In particular, he maintains that no historical relation can be explanatory of the intrinsic properties of individual kind-members, nor, presumably, trends in those characteristics. To some degree, I think this is a matter of labeling, as even Devitt would want to distinguish between historical kinds with 'explanatory potential,' that is, whose key historical property made reference to

We come now to a final consideration in favor of my proposal. On the orthodox account, it is true “by definition” that to be male is to produce small gametes, and to be female, to produce large ones. This, I said, is the one uncontroversial element of the biologist’s understanding of sex. Yet, ironically, it is just this idea that I have rejected. Is this not fatal to my analysis? After all, are not biologists the experts on the contents of their categories?

Though I see the results of the biological sciences as nearly definitive in revealing the kinds pertaining to life, the explicit definitions that biologists offer of the sexes are not definitive in themselves. When trying to understand the nature of a kind, the philosopher of science should look to the role that a kind plays in the work of scientists and in the world itself.²⁴ It is when we take this more general view that we find reasons to favor my account. Still, it would be awkward if such a project revealed kinds radically different from those that scientists describe. But my proposal does not do this, due to the fact that, not long after anisogamy evolved, gamete size became an entrenched output of the developmental processes associated with each sex, even as other aspects of that process varied. In consequence, the kinds defined by the biologist’s more straightforward criterion, and the animal sexes as understood on my view, tend to extensionally overlap.

But this may not always be true, and when the orthodox and historical accounts threaten to come apart, it arguably puts the historical account in the better light. Consider sex categorization in *Drosophila bifurca*, a fruit fly with giant (6-cm-long!) sperm. Though *D. bifurca* eggs are still, by mass, larger than sperm, by other measures, length included, such sperm exceed the female’s eggs in size, and are nearly equinumerous with them. Nonetheless, biologists seem not to have given the least thought to questioning whether the sperm-producers are ‘male’ and the egg-producers, ‘female,’ though this would be something to consider on the orthodox account of sex.²⁵ By contrast, leaving this unquestioned, as biologists do, is just what one would expect on the account I favor. After all, giant sperm have been produced via a gradual evolutionary process, continuous with the

genuinely explanatory prior causes, and those that did not. All I need, in these terms, is that the animal sexes satisfy the former standard. Yet, since space doesn’t permit me to pursue such niceties here, let me simply note that the main line of thinking in philosophy of biology is consistent with the label I use. Consider, for instance, Khalidi’s (this volume) discussion of what it takes for a kind to be explanatory, both in the case of species and the sexes themselves. Thanks to Michael Strevens for pressing this objection.

²⁴ This is consistent, for instance, with inquiries into the nature of ‘fitness,’ where philosophers of biology have often endorsed a dispositional view even when biologists themselves often ‘define’ fitness in terms of actual reproductive output, a choice plainly useful on practical grounds but which leaves fitness without an explanatory role.

²⁵ See, for instance, Lupold et al. 2016.

developmental process at play in the small-gamete-producing ancestors throughout the whole animal kingdom.

Of course, since even the *Drosophila*'s giant sperm remain smaller than eggs *by mass*—arguably the size comparison that matters most—this observation is hardly definitive. More telling would be a study of the categorization practices of biologists, one that asked researchers how they would sex-categorize *D. bifurca*—as well as other animal groups already enjoying ‘giant sperm’ (Vielle et al. 2016)—in the counterfactual scenario in which sperm evolved to be more massive than eggs. For this, though, we must wait for another day.

6—The Animal Sexes as Natural Kinds?

If the animal sexes are indeed explanatory kinds, and if their nature is as I describe, does this mean they are *natural kinds* as well? The answer is not straightforward, due partly to persisting controversy over what it takes for a kind to be *natural*. Given the wide range of traits possessed by males and females, the sexes will certainly not be natural kinds according to any strict view like traditional essentialism. On the other hand, they may qualify if you accept a highly permissive view, like Dupré's (1995) own “promiscuous realism,” on which any discontinuity in nature, however fleeting or trivial, may be enough for this status. But these views, each motivated by certain metaphysical concerns, are positioned at the extremes. What would an account say whose aim was not to apply some prior metaphysical criterion to science but to reconstruct the principles driving scientists' *own* division between the natural kinds—those, roughly speaking, of central and lasting scientific significance—and more adventitious groupings?

In prior work, I present one such view. On the Categorical Bottleneck Account (Franklin-Hall 2015a), the natural kinds are those categories that well-serve both our actual epistemic purposes—such as those of prediction and explanation—and those of a large range of inquirers relatively like us. Kinds may be capable of doing this in a variety of ways, two of which are particularly straightforward. First, they might possess a set of relatively fine-grained properties that invariably run in tandem, a trait that makes them predictively useful for myriad purposes. Second, they might have broad explanatory potential (something distinct from—though often associated with—having a predictive role).

How do the animal sexes perform by such a measure? On the one hand, despite real trends in inter-sex differences, the animal sexes remain—in many if not most respects—highly heterogeneous. This significantly limits their predictive usefulness. It is for their explanatory calling that the animal sexes are, I think, of greatest interest. Still, on the Categorical Bottleneck view, what's critical to natural

kind status isn't just having *some* actual explanatory or predictive use for us, whatever our idiosyncratic interests happen to be, but to have such use for many inquirers relatively like us. Among other virtues this sets apart as widely important kinds (e.g., the chemical elements, and the biological species) from more special-purpose, though still scientifically respectable, groupings (e.g., benthic organisms). With this more demanding standard in mind, the case that the animal sexes are natural kinds seems, to my mind, uncertain. After all, though an inquirer aiming to account for broad and loose trends in sex characteristics will be well-served by the animal sex categories, an inquirer captivated only by sex *diversity*—in making sense of the fascinatingly unique combination of sex characteristics found in each of the world's 2 million animal species—may find that the cross-animal sexes serve no live predictive or explanatory ends. If so, we would end up with a rather interesting result: animal sexes as explanatory, but not natural, kinds.

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