

# Why anisogamy drives ancestral sex roles

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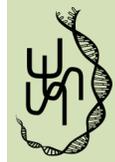
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There is a clear tendency in nature for males to compete more strongly for fertilizations than females, yet the ultimate reasons for this are still unclear. Many researchers—dating back to Darwin and Bateman—have argued that the difference is ultimately driven by the fact that males (by definition) produce smaller and more numerous gametes than females. However, this view has recently been challenged, and a formal validation of the link between anisogamy and sex roles has been lacking. Here, we develop mathematical models that validate the intuition of Darwin and Bateman, showing that there is a very simple and general reason why unequal gamete numbers result in unequal investment in sexually competitive traits. This asymmetry does not require multiple mating by either sex, and covers traits such as mate searching, where the male bias has been difficult to explain. Furthermore, our models show males and females are predicted to diverge more strongly when the fertilization probability of each female gamete is high. Sex roles thus ultimately trace back to anisogamy and the resulting consequences for the fertilization process.

**KEY WORDS:** Anisogamy, female, isogamy, male, sex roles, sexual selection.

Males and females often clearly differ beyond the definitional dimorphism in gamete size and number, and in particular, males tend to be more competitive over fertilization opportunities (e.g., Parker and Pizzari 2015). While the ultimate reasons behind this asymmetry are still being debated, anisogamy is widely held to be the ultimate driving factor (Bateman 1948; Parker et al. 1972; Trivers 1972; Schärer et al. 2012; Parker 2014; Parker and Pizzari 2015). This view has recently been challenged by some researchers (Gowaty and Hubbell 2005; Gowaty and Hubbell 2009; Ah-King 2013) who argue that sex roles instead arise by chance, or from sex differences in environment-driven “habits of life,” such as encounter rates, mortality schedules and remating rates. Differences in these life habits are assumed to be extrinsic, arising from an individual’s or species’ ecological setting, rather than being an intrinsic consequence of anisogamy (reviewed in Schärer et al. 2012). Anisogamy itself has evolved independently several times; the selective forces that are thought to generate it have been extensively analyzed, and it seems unlikely that it has evolved by chance (see e.g., Parker et al. 1972; Lessells et al. 2009; Togashi and Cox 2011; Lehtonen and Parker 2014).

Although it has been argued that explanations based on chance cannot explain why a given sex is more likely to exhibit a characteristic sex role (Schärer et al. 2012), to our knowledge, no mathematical models exist that explicitly explore why an asymmetry at the gamete level (anisogamy) should tend to generate a stereotypical asymmetry in the sex roles at the organism level (“classical” sex roles). Here we confirm the intuition of Bateman (1948) by developing mathematical models that—despite assuming no initial asymmetry between the sexes other than anisogamy—show how typical sex roles arise as a simple, general, and almost inevitable consequence of gamete dimorphism. In particular, we focus on sexually competitive traits, and show that such traits tend to be more strongly selected for in the sex producing the smaller gametes (i.e., the male sex, by definition) as a consequence of gamete dimorphism. This asymmetry, based on simple principles of resource allocation does not require multiple mating, nor any preexisting asymmetry except a difference in gamete sizes. It applies to a wide range of traits, such as mate searching. Models are derived first for the simple scenario where all female gametes are



fertilized, and they are subsequently generalized to sperm-limited scenarios.

## Models

### A SIMPLE, INTUITIVE MODEL

We begin by analyzing a simple and intuitive general model. A focal individual's fitness ( $w$ ) is modeled as the number ( $n$ ) of gametes it produces, times the probability ( $p$ ) of each of its gametes being fertilized (i.e.,  $w = np$ , the total number of successful fertilizations). A fraction  $r$  of an individual's fixed resources for reproduction is allocated to a sexually competitive trait that can influence  $p$ ;  $r$  trades off against the resource for gametes, so that both  $n$  and  $p$  are functions of  $r$ . We assume here and throughout this article that, regardless of the gamete size ratio, two mating types exist and that gametes of the two types fuse disassortatively (this was the likely ancestral state before the evolution of anisogamy; see Wiese et al. 1979; Maynard Smith 1982; Hoekstra 1987; Lessells et al. 2009). Disassortative fusion of gamete types, in turn, leads to the so-called "Fisher condition" (Houston and McNamara 2005), and selection for an even sex ratio (Düsing 1884; Fisher 1930), at least under commonly made assumptions (Charnov 1982). Using (arbitrarily) subscripts  $x$  for females (producing the larger and less numerous gamete type) and  $y$  for males (producing the smaller and more numerous gamete type), the fitnesses of each sex are

$$\begin{cases} w_x(r_x) = n_x(r_x)p_x(r_x) \\ w_y(r_y) = n_y(r_y)p_y(r_y) \end{cases} \quad (1)$$

The corresponding selection differentials (Taylor 1996) are proportional to

$$\begin{cases} \frac{w'_x(r_x)}{w_x} = \frac{n'_x(r_x)}{n_x(r_x)} + \frac{p'_x(r_x)}{p_x(r_x)} \\ \frac{w'_y(r_y)}{w_y} = \frac{n'_y(r_y)}{n_y(r_y)} + \frac{p'_y(r_y)}{p_y(r_y)} \end{cases} \quad (2)$$

Note that a 1:1 sex ratio necessarily implies that male gametes outnumber female gametes. If we now make the common (Lehtonen 2015) simplifying assumption that all female gametes are fertilized, then  $p_x(r_x) = 1$  and  $p'_x(r_x) = 0$  (note that we relax this assumption below). The female selection differential thus simplifies to  $n'(r_x)/n(r_x)$ , which is necessarily negative, maintaining female investment in any putative alternative trait at  $r = 0$ . To clarify, we can also make the common assumption (e.g., Lessells et al. 2009; Togashi and Cox 2011; Lehtonen and Parker 2014) that  $n = (1 - r)/m$  (where  $m$  is gamete size). The  $1-r$  resource units available for gamete production are simply split into  $m$ -sized pieces so that gamete number is inversely proportional to gamete size. Thus (2) becomes

$$\begin{cases} \frac{w'_x(r_x)}{w_x} = -\frac{1}{(1-r_x)} + 0 \\ \frac{w'_y(r_y)}{w_y} = -\frac{1}{(1-r_y)} + \frac{p'_y(r_y)}{p_y(r_y)} \end{cases} \quad (3)$$

If everything is identical except for gamete size, then the first terms on the right hand side are necessarily equal (and negative), and the second term is necessarily zero for females while it can take many values for males. So while females are selected to invest reproductive resources only into gametes,  $p'(r_y)$  can be positive, permitting males to invest into sexually competitive traits at the expense of gamete number. In evolutionary time such traits could, for example, involve preejaculatory traits linked with the evolution of mobility and behavioral complexity, following Darwin's original insight (Darwin 1871; Parker 2014), or they could be postejaculatory traits (e.g., Parker and Pizzari 2015). Gamete number itself is often regarded as a sexually selected trait (e.g., in sperm competition: Parker and Pizzari 2010), and changes in gamete number will also affect  $p$  (namely, if sperm number increases without changing the number of fertilized eggs, then the *per-sperm* probability of fertilization will necessarily decrease). The model can therefore also be viewed as describing a trade-off between allocating  $1-r$  into sexually selected gamete number and  $r$  into another sexually competitive trait.

By eliminating any a priori assumptions about differences between males and females—other than gamete size—this very general model shows how asymmetric selection can arise despite the problem's underlying symmetry. However, this approach becomes difficult to apply if not all female gametes are fertilized. Such gamete limitation is not uncommon in nature, particularly in external fertilizers (Levitan and Petersen 1995; Yund 2000; Levitan 2010), in which anisogamy likely originally evolved from isogamy (Lessells et al. 2009; Togashi and Cox 2011; Lehtonen and Parker 2014). Yet, even under gamete limitation the fertilization probability of the more numerous gamete type must necessarily be lower than that of the opposite type, so intuition suggests that the selection asymmetry outlined above should still hold under a 1:1 adult sex ratio. We explore this more formally in the following.

### AN EXPANDED MODEL

To investigate gamete limitation effects (and better incorporate existing literature), we next use an alternative fitness formulation that explicitly includes the fertilization process. Fitness gains arise through three fitness components in both sexes:

1. Finding a mating partner or spawning group: gains arise through resource allocation to a mate search function (Hammerstein and Parker 1987; Puurtinen and Kaitala 2002;

Fromhage et al. 2016) *s*, involving traits like active movement and search behavior.

2. Reducing competition by same-sex gametes for opposite-sex gametes: The process is modeled via two functions: an “exclusion function” *g*, which reduces the number of competing gametes, which in turn influences a gamete competition function *c* (see below and supporting information for details). Exclusion traits could correspond to elimination of competing gametes, mate guarding, or mate monopolization.
3. The fertilization process: a fertilization function (Schwartz et al. 1981; Vogel et al. 1982; Styan 1998; Mesterton-Gibbons 1999; Lehtonen 2015) *f* describes the number of successful fertilizations as a function of total numbers of each gamete type in a given fertilization environment, and gametes can originate from one or several individuals of each sex. This component can be used to model gamete limitation effects.

All three fitness components combine to give total, individual-level fitness, and together can cover a wide range of sexually competitive traits. Now let  $r_{x1}, r_{y1}$  denote allocation into the mate search trait, and  $r_{x2}, r_{y2}$  into the exclusion trait (note that the exclusion function *g* modulates *c*, so that *g* is implicit in the equations below). These trade off with allocation to gametes, which in turn influences the fertilization function *f*. Denoting mutant strategies with a hat (^), the mutant fitness functions are

$$\begin{cases} \hat{w}_x = \hat{s}_x \hat{c}_x \hat{f} \\ \hat{w}_y = \hat{s}_y \hat{c}_y \hat{f} \end{cases} \quad (4)$$

For simplicity, the *r*-variables are excluded from equation (4), but note that (e.g., for females)  $\hat{s}_x = s(\hat{r}_{x1}, r_{y1})$ ,  $\hat{c}_x = c(\hat{r}_{x2}, r_{x2})$  and  $\hat{f}$  (which is equivalent for both sexes: Houston and McNamara 2005; Lehtonen 2015) depends on *all* four *r*-variables for a given sex. This is because fitness gains through (i) mate encounter rate depends on the *r*-value of both the (mutant) focal individual, and that of the (resident) members of the opposite sex; (ii) gamete competition depends on the *r*-value of the focal, and other individuals of the same sex; and (iii) fertilization depends on total gamete numbers of both sexes, which depend on the *r*-values of all individuals whose gametes are present in that environment.

Equation (4) is essentially the same model as equation (1). It is simply a different breakdown of the same process that permits analysis of specific biological traits (see S1 in the supporting information for demonstration of this equivalence).

For selection on allocation to mate search in females, equation (4) yields

$$\frac{w'_x(\hat{r}_{x1})}{w_x} \Big|_{\hat{r}_{x1}=r_{x1}} = \left[ \frac{s'(\hat{r}_{x1})}{s(\hat{r}_{x1})} + \frac{f'(\hat{r}_{x1})}{f(\hat{r}_{x1})} \right] \Big|_{\hat{r}_{x1}=r_{x1}} \quad (5)$$

and for exclusion traits

$$\frac{w'_x(\hat{r}_{x2})}{w_x} \Big|_{\hat{r}_{x2}=r_{x2}} = \left[ \frac{c'(\hat{r}_{x2})}{c(\hat{r}_{x2})} + \frac{f'(\hat{r}_{x2})}{f(\hat{r}_{x2})} \right] \Big|_{\hat{r}_{x2}=r_{x2}} \quad (6)$$

and analogous equations for males by exchanging the indices.

Our next aim is then to identify components in equations (5) and (6) that consistently generate sex-specific asymmetries. There is no reason for selection on mate searching *s'* to differ between the sexes when sexes are assumed to be initially similar in all respects except gamete size and number. In S2 we show why, under fairly general conditions, selection on *c'* does not systematically differ either. The most obvious candidate for sex-differential selection then is *f'*, which appears in both equations (5) and (6). Although the total number of fertilizations must be equal for males and females (the Fisher condition: Houston and McNamara 2005), the marginal costs of resource allocation via *f* (i.e., *f'*) could differ significantly when gamete numbers differ. This is easiest to see by first again assuming that all female gametes are fertilized. This implies that  $f'(\hat{r}_y) = 0$ , whereas  $f'(\hat{r}_x) < 0$  because any reallocation in females directly trades off with gametes that would be fertilized. This can then be generalized to any level of gamete limitation: in S3 we examine the mathematical properties of several published fertilization functions (Schwartz et al. 1981; Vogel et al. 1982; Styan 1998; Mesterton-Gibbons 1999; Lehtonen 2015) and show that when starting from conditions that are symmetrical apart from gamete size and number, marginal costs (*f'*) are higher for females than males under a wide range of biological scenarios.

As we have shown above and in the supporting information, selection for sexually competitive traits is systematically stronger in males than females when investment patterns in the two sexes are equal ( $r_x = r_y$ ) and the sex ratio is 1:1. To see the implications of this, consider the following thought experiment: assume that male investment is at its evolutionarily stable strategy (ESS: Maynard Smith 1982), so that  $r_y = r_y^*$ , and that female investment is also at the male ESS, that is  $r_x = r_y = r_y^*$ . But if  $r_y^*$  is the male ESS, then selection on males must be 0, and therefore selection on females must be negative because we have shown that under very general conditions, it must be lower than selection on males. So if an ESS exists at which males invest  $r_y^*$  resource units into the sexually competitive trait, then the female investment ESS must be lower than that of the male. Anisogamy, via its effects on gamete numbers and fertilization therefore provides a very general reason why sexually competitive traits tend to evolve more readily and extensively in males.

Strictly, for approximating the selection differential (e.g., in eqs. (5) and (6)), the equations should be multiplied by the variance in *r* (Taylor 1996). However, there is no a priori reason to assume a sex difference in *r*-variance. Furthermore, multiplying by the variance does not affect the value of *r* at which the selection

differential equals zero—in other words, it does not change the ESS, nor the argument presented in the previous paragraph.

### EVOLUTIONARILY STABLE STRATEGIES

To make the implications of equations (5–6) more concrete, and to illustrate effects of gamete limitation, we compute actual ESSs for two specific scenarios. To isolate the effect of anisogamy, both scenarios are chosen so that they are entirely symmetrical in the sense that both sexes have exactly the same evolutionary options available to them, the only assumed difference between the sexes being gamete size and number.

In the first scenario, individuals can increase fertilization probability by investing in mate searching. It is assumed that all individuals mate once or not at all, which might occur if the population is so sparse that the probability of finding two or more mates is negligible. This has two important and useful implications: there is no gamete competition (or, more generally, no within-group, within-sex competition), and there is also no difference in the Bateman gradients (Bateman 1948) between the sexes (both sexes get zero fitness if they do not mate and the same fitness gains if they do mate—hence gains per mating are equal). Therefore the results cannot be driven by these processes. ESS expenditures can be determined by setting equation (5) to zero after substituting explicit functions for  $s$  and  $f$  (see Fig. 1 legend and S4 for details on the model, and S6 for how evolutionary stability was assessed), and the results (Fig. 1, left side) indicate that males always invest more into mate searching than females. Moreover, this asymmetry increases with the anisogamy ratio and decreases with increasing gamete limitation.

Now consider a second hypothetical scenario. Fertilization is external, everyone always finds a mate, and individuals meet in spawning groups of two males and two females. There is potential for competition for fertilization opportunities, within each sex, within groups. We examine the evolution of an exclusion trait: an individual of either sex can decrease the number of gametes of the competing same-sex individual within the group. This could, for example, correspond to monopolizing mates, preventing the competitor from releasing all of its gametes, chemically killing or even eating its gametes. This is modeled with function  $g(r)$ , which decreases with  $r$  and has limits  $0 < g(r) < 1$ . For example, if one  $x$  individual allocates  $r_x$  to this exclusion trait and  $(1 - r_x)$  to gametes, and the other allocates  $\hat{r}_x$  to the exclusion trait and  $(1 - \hat{r}_x)$  to gametes, then the number of gametes from each individual that enter the fertilization process is  $n_x g(\hat{r}_x) = \frac{1-r_x}{m_x} g(\hat{r}_x)$  and  $\hat{n}_x g(r_x) = \frac{1-\hat{r}_x}{m_x} g(r_x)$ , respectively (S5). We obtain the candidate ESS by setting equation (6) equal to zero and find that females do not invest in the competitive trait (Fig. 1, right side), whereas males can invest notably under low gamete limitation. Under high gamete limitation, neither sex invests in the exclusion trait.

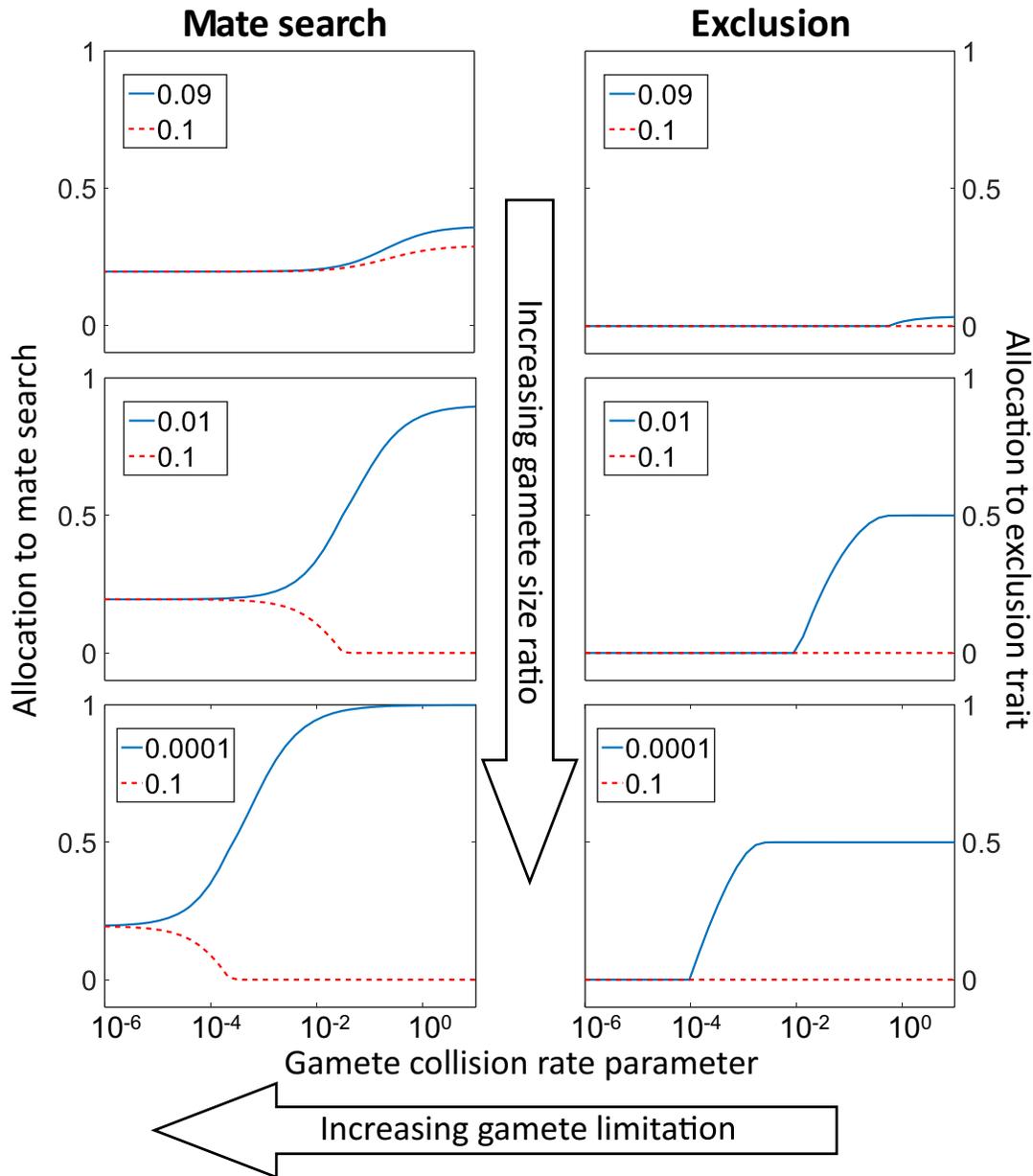
### Discussion

Our results demonstrate that—with no assumptions of initial asymmetry between the sexes other than anisogamy—typical sex roles arise as a simple, general, and almost inevitable consequence of gamete dimorphism. In particular, we have focused on sexually competitive traits, showing that such traits are more strongly selected for in the sex producing the smaller gametes.

The fundamental logic of the models is not reliant on any particular level of sperm competition (most clearly seen in eqs. (1–3), which is why we have not varied the strength of sperm competition in our main results (e.g., via spawning group size). Although low sperm competition—or equivalently, high local sperm competition—often makes the evolution of sexually competitive traits more likely (Parker 1982; Schärer and Pen 2013), the main point of our models is that if a sexually competitive trait appears, it is far more likely to evolve in males, regardless of whether this happens under low or high sperm competition. Existing theory predicts that allocation to sexually selected traits in males often (e.g., Parker 1982), but not always (e.g., Parker 1993), decreases with increasing sperm competition, and this is true also with the present model. In S7 we present examples illustrating this, confirming that male-biased selection for sexually competitive traits is a general phenomenon, not reliant on particular spawning group sizes.

We have presented theoretical reasons for a consistent link between anisogamy and sex roles, but what of the proposed environment driven “habits of life”? One aspect of the model that could, in principle, affect the results is an unequal adult sex ratio (ASR) arising, for example, through sex differences in mortality rates. This is clearest in equation (3), where selection on the producer of the less numerous gamete type is always negative. Should the ASR become so female-biased that male gametes became less numerous than female gametes, selection could reverse. Although theoretically possible, we consider this scenario to be unlikely for the following reasons. First, it is only plausible under very low anisogamy ratios; otherwise the ASR would have to be extremely female-biased for gamete numbers to reverse. Second, the most natural way for a consistent bias in the ASR to arise is as a consequence of the sexually competitive trait itself. However, an increasingly female-biased ASR would reduce the payoffs for investing in this trait as gamete numbers approach equality, making a reversal in the directions of selection unlikely.

Our models do not cover variation in offspring reproductive value, which would be linked to the evolution of traits such as parental care or mate choice. Parental care is, however, best seen as a secondary adaptation arising through specific socio-ecological circumstances (Parker 2014; Parker and Pizzari 2015) and its evolution can under some conditions result in a reversal of the primary sex roles established by anisogamy (Andersson 1994; Clutton-Brock 2007). Importantly, soon after the evolution



**Figure 1.** ESS allocation to two different traits (calculated numerically: see S4–S6 for details). The left column depicts allocation to a mate search trait, while the right column shows allocation to an exclusion trait.

The anisogamy ratio increases from top to bottom, as indicated by the gamete sizes displayed in the small panels. For both traits, increasing anisogamy is clearly linked to diverging sex roles, and furthermore, the producer of the smaller (and by definition, male) gametes invests more in the competitive trait. The models are entirely symmetrical, with no a priori assumptions about the sexes, except for gamete size; if gamete sizes are reversed for a given panel, the competitive allocations also reverse. Within each panel, sex role divergence increases with decreasing gamete limitation. The fertilization function used here is  $f(n_x, n_y) = n_x n_y \frac{e^{un_x} - e^{un_y}}{n_x e^{un_x} - n_y e^{un_y}}$  where  $n_x$  and  $n_y$  are total egg and sperm numbers, respectively (Lehtonen 2015). Increasing the gamete collision rate parameter ( $u$ : see S4–S5) increases the rate of gamete fusions, and therefore decreases gamete limitation. Gamete numbers trade off with  $r$  following the common  $n = (1 - r)/m$  assumption (e.g., Lessells et al. 2009; Togashi and Cox 2011; Lehtonen and Parker 2014).

In the left column, each individual mates once or not at all, so there is no gamete competition and equation (5) is used. The probability of finding a mate is  $s = 1 - e^{-0.1\sqrt{r_x+r_y}}$  (derived from (Puurtinen and Kaitala 2002); see S4), but other mate search functions yield similar results (data not shown).

In the right column, reproduction takes place in groups of two males and two females, implying gamete competition, and equation (6) is used. We have used the exclusion function  $g(r) = e^{-2r}$  (where  $0 \leq r \leq 1$ ), but again, other competitive functions produce similar results (data not shown).

of anisogamy during the transition to multicellularity, both sexes were probably sessile or weakly mobile and released gametes into sea water (i.e., broadcast spawning by both sexes). The simplest change from this ancestral condition to parental care would be one in which the female retains her eggs close to her body for brooding (termed sperm casting: Bishop and Pemberton 2006), as found in many marine invertebrates. The alternative strategy (“egg casting”: Henshaw et al. 2014) where the male retains the sperm and broods the resulting zygotes has to date never been found, and there are good theoretical reasons why such a strategy is unstable (Henshaw et al. 2014). While an early hypothesis (Trivers 1972) predicted a direct link between gametic investment and parental care (and indeed paternal care is much rarer than maternal care in most taxa) modern theory on the evolution of parental care does not demonstrate an obvious association (Dawkins and Carlisle 1976; Queller 1997; Kokko and Jennions 2008), and no such link was found in a recent study on birds (Liker et al. 2015). For the evolution of parental care in vertebrates much will depend on reproductive mode; in mammals with long periods of gestation, males are unlikely to be present when offspring are released while in fish and birds the opportunity for male care is much more evident, and found much more commonly (Dawkins and Carlisle 1976). It is therefore clear that parental care is quite a separate question from the one studied here.

Nevertheless, the asymmetry demonstrated by equations (1–6) is very general. Together these models cover most forms of competition over fertilizations, and show that it is almost inevitable that sexually competitive traits evolve more readily in males than females when gamete size and number is the only initial difference. This formally validates Darwin’s (1871) and Bateman’s (1948) view that the evolution of anisogamy was the seed for the spectacular diversity of reproductive biology we observe in nature today.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- S1.** Why the fitness function in equation (4) is a special case of equation (1).
- S2.** Properties of the gamete competition function — why selection for gamete resources via gamete competition *does not differ* between the sexes.
- S3.** Properties of fertilization functions — why selection for gamete resources via fertilization kinetics *does differ* between the sexes.
- S4.** The mate search model.
- S5.** The within-group competition model.
- S6.** Numerical methods and stability.
- S7.** Examples showing that the strength of sperm competition can, but does not always, affect sex role divergence.