

Supplementary material for “Why anisogamy drives ancestral sex roles” by Jussi

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Mathematical methods and details on the models (S1-S7).

All numerical calculations were done with MATLAB (Mathworks Inc. 2015) and The Multiprecision Computing Toolbox for MATLAB (Advanpix LLC 2015) ; the latter is required due to very large exponents in the computations. MATLAB code is available from the authors on request.

S1. Why the fitness function in equation (4) is a special case of equation (1)

Equations (1) and (4) in the main text have slightly different purposes, but they are, in fact, two different breakdowns of the same fitness function. While equation (1) is slightly more general, equation (4) is less abstract and more clearly tied to the published literature. To see this equivalence, we use a standard sperm competition (Parker and Pizzari 2010) equation:

$$\hat{c}_x = \frac{\hat{n}_x}{\hat{n}_x + (k-1)n_x}$$
 where k is group size, \hat{n}_x is the number of gametes produced by the focal

(mutant) individual, and n_x is the wild-type number of gametes (presented here for type x ; the same of course applies to type y). Plugging this into equation (4) yields

$$\hat{w}_x = \hat{s}_x \hat{c}_x \hat{f} = \hat{s}_x \frac{\hat{n}_x}{\hat{n}_x + (k-1)n_x} \hat{f}$$
 which can be rearranged to $\hat{w}_x = \hat{n}_x \hat{s}_x \frac{\hat{f}}{\hat{n}_x + (k-1)n_x}$. Now the

connection to equation (1) becomes clear. \hat{f} is the total number of fertilizations within a

fertilization environment, and therefore $\frac{\hat{f}}{\hat{n}_x + (k-1)n_x}$ is the probability of a random x -gamete

being fertilized in that environment. Multiplying this by the probability of finding a mating

partner or group (i.e. finding a fertilization environment where the fertilization process takes

place) (\hat{s}_x) gives the total probability of fertilization for a random gamete from the focal

individual.

$$\text{In other words, } \hat{w}_x = \hat{s}_x \hat{c}_x \hat{f} = \hat{s}_x \frac{\hat{n}_x}{\hat{n}_x + (k-1)n_x} \hat{f} = \hat{n}_x \hat{s}_x \frac{\hat{f}}{\hat{n}_x + (k-1)n_x} = \hat{n}_x \hat{p}_x.$$

S2. Properties of the gamete competition function – why selection for gamete resources via gamete competition *does not differ* between the sexes

At its simplest, the gamete competition component of equation (4) is of the form

$$\hat{c}_x = \frac{\hat{n}_x}{\hat{n}_x + (k-1)n_x} \text{ (or similar for } y\text{)}. \text{ Because we are working with a resource allocation model,}$$

$$\hat{n}_x = \frac{1-\hat{r}_x}{h(m_x)}, \text{ where } h(m_x) \text{ is the cost of producing a gamete of size } m_x \text{ (e.g. a simple linear}$$

$$\text{relationship like } h(m_x) = m_x\text{)}. \text{ Therefore } \hat{c}_x = \frac{\frac{1-\hat{r}_x}{h(m_x)}}{\frac{1-\hat{r}_x}{h(m_x)} + (k-1)\frac{1-r_x}{h(m_x)}} = \frac{1-\hat{r}_x}{1-\hat{r}_x + (k-1)(1-r_x)}. \text{ In other}$$

words, because we are dealing with changes in resources, not direct changes in gamete numbers, gamete size cancels out from c , and c is therefore of similar form for the two sexes. (This assumes that there is no within-sex variation in the trade-off between gamete size and number—if the cost of producing a gamete varies within a sex, then h may not cancel out in the above equation).

S3. Properties of fertilization functions – why selection for gamete resources via fertilization kinetics *does differ* between the sexes

Fertilization functions can be expressed in terms of gamete numbers or density in a given fertilization environment (external or internal). They can define either the total number of successful fertilizations, or the proportion of fertilized eggs – the latter is usually used in fertilization functions for clearly diverged eggs and sperm. Here, we transform all functions of the latter type into a form where the output is absolute number of successful fertilizations, simply by multiplying the proportion of fertilized eggs by the total number of eggs. For simplicity, for a given fertilization environment, we here denote total egg numbers by X and total sperm numbers by Y , so that the fertilization function, $f(X,Y)$, denotes the number of successful fertilizations.

We are interested in the marginal costs via f when resources are reallocated away from gamete production, and in particular whether these marginal costs differ for the two sexes.

We must first consider exactly which mathematical property of the functions we need to examine. Denote female gamete size (arbitrarily) by m_x and male gamete size by m_y , and the corresponding gamete production costs by $h(m_x)$ and $h(m_y)$ as in S2. If total resources are 1 for both sexes (i.e. the total resource budget is the unit of measurement), and r_x resource units are allocated to a sexually selected trait in females and r_y in males, gamete numbers per

individual are $\frac{1-r_x}{h(m_x)}$ and $\frac{1-r_y}{h(m_y)}$. However, a mating or spawning group can consist of several

individuals: namely $(k-1)$ ‘resident’ individuals and 1 mutant individual, and this applies for each sex (we assume rare mutants as is standard in the ESS approach, so that a mutant never appears simultaneously in both sexes in the models). If mutants are denoted by a ‘hat’ ($\hat{}$),

then in each fertilization environment the total gamete numbers are $X = (k_x - 1) \frac{1-r_x}{h(m_x)} +$

$\frac{1-\hat{r}_x}{h(m_x)}$ and $Y = k_y \frac{1-r_y}{h(m_y)}$ when a mutant x -individual appears, and similarly $X = k_x \frac{1-r_x}{h(m_x)}$ and

$Y = (k_y - 1) \frac{1-r_y}{h(m_y)} + \frac{1-\hat{r}_y}{h(m_y)}$ when a mutant y -individual appears.

The marginal costs due to the fertilization process are then $\frac{df}{d\hat{r}_x} = \frac{dX}{d\hat{r}_x} \frac{df}{dX} = -\frac{1}{h(m_x)} \frac{df}{dX}$ and

$\frac{df}{d\hat{r}_y} = \frac{dY}{d\hat{r}_y} \frac{df}{dY} = -\frac{1}{h(m_y)} \frac{df}{dY}$ evaluated at $\hat{r}_x = r_x = r$ and $\hat{r}_y = r_y = r$ (because we want to

examine how a symmetrical situation with $r_x = r_y$ results in asymmetrical selection on r).

Therefore in order for males to be under stronger selection to invest in a sexually competitive

trait, our aim is to show that $\frac{1}{h(m_x)} \frac{df}{dX} > \frac{1}{h(m_y)} \frac{df}{dY}$ (evaluated as above) for a selection of

fertilization functions f that cover a wide range of biological scenarios. If we furthermore

assume (again, due to our need to examine a symmetrical starting point) that $k_x = k_y = k$,

then both sides can be multiplied by $k(1-r)$, yielding $\frac{k(1-r)}{h(m_x)} \frac{df}{dX} > \frac{k(1-r)}{h(m_y)} \frac{df}{dY}$ which is equivalent to $X \frac{df}{dX} > Y \frac{df}{dY}$. This final form simplifies our work, as it transforms the resource allocation problem into a function of gamete numbers. This is helpful because fertilization functions are typically stated as a function of gamete numbers or density.

Note that in making this comparison, we are not comparing marginal effects on the full fitness function, but on one component (f). However, if we can demonstrate a general asymmetrical marginal effect in one component of fitness, this results in asymmetry in marginal costs on total fitness. Since $m_y < m_x$, and hence $Y > X$, note that $X \frac{df}{dX} > Y \frac{df}{dY}$ is a more strict requirement than $\frac{df}{dX} > \frac{df}{dY}$, and it is not obvious that it should always be fulfilled.

To summarize: if we can show that the condition $X \frac{df}{dX} > Y \frac{df}{dY}$ holds generally for many fertilization functions f , then we have found a seemingly general and robust link between anisogamy and sexual selection. Note that $X \frac{df}{dX}$ is in fact the derivative $\frac{df}{d \ln(X)}$, which is what one must generally use when dealing with relative, rather than absolute changes in the trait of interest.

S3.1 A general analytical proof for a class of simple fertilization functions

We begin by demonstrating the generality of the inequality $X \frac{df}{dX} > Y \frac{df}{dY}$ analytically for a certain class of fertilization functions. These are of the form $f(X, Y) = \alpha X \varphi(Y)$, where α is a constant, and φ is a saturating function of Y . Examples include functions of the form

$$f(X, Y) = \alpha X (1 - e^{-uY}) \text{ (Schwartz et al. 1981; Vogel et al. 1982), and } f(X, Y) = \alpha X \frac{Y}{u+Y}$$

(Mesterton-Gibbons 1999; Ball and Parker 2007). The negative exponential function, for

example, arises from the simple assumption that the number of efficacious spermatozoa follows a Poisson distribution (Schwartz et al. 1981).

Now, $\frac{df}{dX} = \alpha\varphi(Y)$ and $\frac{df}{dY} = \alpha X\varphi'(Y)$, so we need to show that $\alpha X\varphi(Y) > \alpha XY\varphi'(Y)$, or $\frac{\varphi(Y)}{Y} > \varphi'(Y)$. Because $\varphi(0) = 0$ (no sperm \rightarrow no fertilizations), this can be further rewritten as $\frac{\varphi(Y)-\varphi(0)}{Y-0} > \varphi'(Y)$. Now, according to the mean value theorem (Larson and Edwards 2013) there exists a point β in the open interval $]0, Y[$ where $\varphi'(\beta) = \frac{\varphi(Y)-\varphi(0)}{Y-0}$. Therefore the inequality $\frac{\varphi(Y)-\varphi(0)}{Y-0} > \varphi'(Y)$ is equivalent to $\varphi'(\beta) > \varphi'(Y)$, where $0 < \beta < Y$. But because φ is saturating, $\beta < Y$ implies that $\varphi'(\beta) = \frac{\varphi(Y)-\varphi(0)}{Y-0} > \varphi'(Y)$, and we have the required proof for all fertilization functions of this form. This already covers the types of fertilization functions most commonly used in evolutionary models (e.g. Mesterton-Gibbons 1999; Ball and Parker 2007; Parker and Lehtonen 2014; Abe and Kamimura 2015).

S3.2 Numerical proofs for more complex fertilization functions

Other fertilization functions are generally more complicated than the class investigated above. Analytical comparison of the marginal costs becomes difficult or impossible, and numerical methods are used instead. The method we use is simple in principle: we randomly draw one million parameter combinations from a plausible range for each function, and for each parameter combination compare the marginal costs, checking that the inequality $X \frac{df}{dX} > Y \frac{df}{dY}$ holds. Though not a rigorous mathematical proof, it is entirely sufficient for the purposes of an evolutionary model. The MATLAB code (including the derivatives) is available from the authors. Here, we describe the fertilization functions tested, with brief descriptions of the biological scenarios that they cover.

1) ‘Polyspermy block’ model (Styan 1998). This function allows for multiple sperm sticking to an egg, as well as an imperfect (delayed by time t_b) polyspermy block. It is a generalization of the so-called ‘Don Ottavio’ model (Vogel et al. 1982), which assumes that the polyspermy block is perfect (immediate); this is covered by the polyspermy block model as a special case. The number of successful fertilizations in the polyspermy block model is given by

$$f = X[1 - e^{-z} - (1 - e^{-z} - ze^{-z})(1 - e^{-b})], \text{ where } z = F_e \frac{Y}{X}(1 - e^{-\beta_0 X t}) \text{ and}$$

$$b = F_e \frac{Y}{X}(1 - e^{-\beta_0 X t_b}). \text{ Note that } F_e \text{ is a parameter that defines the fraction of sperm-egg}$$

contacts that are potentially fertilizing. In other words, on average, contact with $\frac{1}{F_e}$ sperm

are required to fertilize one egg, making the product $F_e Y$ a kind of ‘effective sperm

number’. Therefore the condition $X \frac{df}{dX} > Y \frac{df}{dY}$ is expected to hold when $Y > X$ and

$F_e Y > X$, but not necessarily if $Y > X$ and $F_e Y < X$. Note that the notation used by the

original author is slightly different from the one used here (e.g. X has a different meaning;

see Styan (1998) for details).

Initially, the parameters were picked as follows: $1 < X < 1001$; $10X < Y < 110X$

(because the model is intended for systems with strong anisogamy); $0 < F_e < 1$;

$0 < \beta_0 < 10$; $0 < t < 100$; $0 < t_b < 10$. This resulted in the inequality condition failing

for approximately 1.5% of the million trials. When the parameter range was restricted so

that $0.1 < F_e < 1$ (implying that $F_e Y > 0.1 * 10X = X$, i.e. the ‘effective sperm number’

is larger than the number of eggs), the condition $X \frac{df}{dX} > Y \frac{df}{dY}$ was fulfilled for each one of

the million trials. In summary, for these functions, the necessary condition was fulfilled as

long as the effective sperm number $F_e Y$ was larger than the number of eggs.

2) *Symmetric models that apply to any anisogamy ratio* (Lehtonen 2015). These models are symmetric in the sense that they do not specify which gamete type is the egg and which is the sperm (which the above models do), although mating types are assumed. Thus, the effects of any numerical imbalance arise from the models, and are not assumed. Such models are particularly relevant for the early stages of the evolution of anisogamy, where male and female gametes may have been very close to each other in size and number (i.e. conditions with low anisogamy ratios).

We tested the two symmetrical functions $f = XY \frac{e^{aTX} - e^{aTY}}{Xe^{aTX} - Ye^{aTY}}$ and $f = \frac{\mu}{a} \ln \frac{X - Y}{Xe^{-\frac{a}{\mu}Y} - Ye^{-\frac{a}{\mu}X}}$.

Here, a is a gamete collision rate parameter, T is gamete longevity, and μ is gamete mortality. However, for our purposes, we can replace aT and $\frac{\mu}{a}$ with a single parameter u controlling the level of gamete limitation.

Gamete numbers X and Y were now both randomly picked from the range of 1-1000, so that either one could arbitrarily be the more abundant type. u was picked from the range of 0-10. For both the above functions, the marginal costs were higher for the less

abundant type ('female') in each one of the million trials (i.e. $X \frac{df}{dX} > Y \frac{df}{dY}$ if $X < Y$, and

$X \frac{df}{dX} < Y \frac{df}{dY}$ if $X > Y$).

S4. The mate search model

For the mate search model we used three different mate search efficiency functions which define the probability of mating as $s(r_x, r_y) = 1 - e^{-\Phi}$, where either $\Phi =$ (i) $\alpha(r_x + r_y)$, (ii)

$\alpha r_x r_y$ or (iii) $\alpha \sqrt{r_x + r_y}$. Note that (i) and (ii) are from Fromhage et al. (2016), and (iii) is

equivalent to the mate encounter function used in Puurtinen and Kaitala (2002) if we assume

the link $v = \sqrt{r}$ between velocity and resource allocation, which plausibly implies that costs escalate with increasing search velocity. The results in Fig. 1 were computed with encounter rate (iii) with $\alpha=0.1$; the alternatives yield qualitatively similar results, where males always invest more into the search trait. The α -parameter has a very minor effect on the results. The probability of not encountering any mates is $e^{-\Phi}$; we assume that the probability of encountering two or more mates is negligible, so the probability of mating is then $1 - e^{-\Phi}$. It is then relatively straightforward (if tedious) to differentiate the fitness function sf as needed for the selection differential (equation 5, main text), which is then used for finding the ESSs. For our results, we used the symmetrical fertilization function $f = XY \frac{e^{aTX} - e^{aTY}}{Xe^{aTX} - Ye^{aTY}}$ (Lehtonen 2015), which permits the analysis of the effect at very low anisogamy ratios.

S5. The within-group competition model

For the second model, individuals reproduce in groups of 2 males and 2 females, allowing scope for competition between individuals of the same sex within a spawning group (the model can be expanded to k individuals of each sex). The competitive interaction is defined by an exclusion function $g(r)$ (see main text); $g(r)$ acts to reduce the number or effectiveness of competing gametes of the same sex. We shall assume that the cost of each gamete is equal to its size, so that gamete number = $(1 - r)/m$. If one x individual allocates the resident strategy r_x to this competitive trait, and the remainder to gamete production, and the other (a mutant) allocates \hat{r}_x to the competitive trait, and the remainder to gamete production, then the actual number of gametes from the resident that make it into the fertilization process is

$$n_x g(\hat{r}_x) = \frac{1-r_x}{m_x} g(\hat{r}_x) \text{ and that from the mutant is } \hat{n}_x g(r_x) = \frac{1-\hat{r}_x}{m_x} g(r_x).$$

Therefore the gamete competition component for the mutant is $\hat{c}_x = \frac{(1-\hat{r}_x)g(r_x)}{(1-\hat{r}_x)g(r_x)+(1-r_x)g(\hat{r}_x)}$,

and the total number of fertilized gametes is $f\left(\frac{1-\hat{r}_x}{m_x}g(r_x) + \frac{1-r_x}{m_x}g(\hat{r}_x), 2\frac{1-r_y}{m_y}g(r_y)\right)$; the

same applies for y by exchanging the indices. Note that f is a function of total gamete numbers of both sexes in the group, and we assume that only one sex at a time includes a mutant individual (i.e. mutations are rare, a standard assumption of ESS models). The fitness function for both sexes is the product of these two components, $w=cf$, and the selection differentials are as in equation (6) from the main text. By substituting a suitable competitive function and fertilization function (we used the same function as in the mate search example), selection differentials and ESSs can be calculated (the latter numerically).

For Fig. 1 we used the competitive function $g(r) = e^{-2r}$. Other functions with similar properties (e.g. $\frac{1}{(1+r)^2}$) yield qualitatively similar results.

S6. Numerical methods and stability

ESS values were computed numerically by the following iteration:

$$\begin{pmatrix} r_{x_{i+1}} \\ r_{y_{i+1}} \end{pmatrix} = \begin{pmatrix} r_{x_i} \\ r_{y_i} \end{pmatrix} + \begin{pmatrix} \left. \frac{d\hat{w}_x}{d\hat{r}_x} \right|_{\hat{r}_x=r_x=r_{x_i}} \\ \left. \frac{d\hat{w}_y}{d\hat{r}_y} \right|_{\hat{r}_y=r_y=r_{y_i}} \end{pmatrix} \delta$$

where δ is a sufficiently small number and i is one round in the iteration.

To ensure that the numerical solutions were both convergence stable and evolutionarily stable strategies, we started the iteration from 10 randomly picked pairs of initial values for r_x and r_y from the range of $0 < r < 1$. A numerical solution was only accepted as a stable strategy if all ten initial values converged to the same result; this was the case with all results shown in the figures.

This numerical process ensures that 1) selection drives the evolution of the trait towards this value (convergence stability (Otto and Day 2007)) and 2) once an allele coding for this value has reached fixation, no other mutant allele can increase in number (evolutionary stability (Otto and Day 2007)).

S7. Examples showing that the strength of sperm competition can, but does not always, affect sex role divergence

First, we present a simple example where sex roles diverge regardless of the level of sperm competition: a loaded raffle (Parker 1993; Parker 1998) with k individuals competing for fertilizations. Here, allocation to gametes trades off with a trait that increases the competitive weight of the focal individual's gametes (Parker 1993; Parker 1998; Schärer and Pen 2013).

To simplify the analysis, we assume that there is no gamete limitation. Then, equations (1-3) in the main text show that females should maintain allocation to gametes, and not invest in the competitive trait. However, males may benefit from investing into such a trait. The fitness function for a mutant in a group of k males is

$$\hat{w}_y = \hat{c}_y \hat{f} = \left[\frac{\frac{1-\hat{r}_y}{m_y} h(\hat{r}_y)}{\frac{1-\hat{r}_y}{m_y} h(\hat{r}_y) + (k-1) \frac{1-r_y}{m_y} h(r_y)} \right] \hat{f} = \left[\frac{(1-\hat{r}_y) h(\hat{r}_y)}{(1-\hat{r}_y) h(\hat{r}_y) + (k-1)(1-r_y) h(r_y)} \right] \hat{f}, \text{ and}$$

$$\left. \frac{d\hat{w}_y}{d\hat{r}_y} \right|_{\hat{r}_y=r_y} = \left[\frac{(1-k)(h(r_y) - (1-r_y)h'(r_y))}{k^2(1-r_y)h(r_y)} \right] \hat{f}.$$

Note that the assumption of no gamete limitation means that \hat{f} is unaffected by male

allocation, implying $\hat{f}' = 0$. Now, if there is an ESS, it will be at $h(r_y) - (1 - r_y)h'(r_y) =$

0, or

$r_y = 1 - \frac{h(r_y)}{h'(r_y)}$. This does not depend on k , and therefore is independent of the strength of sperm competition. For example, the loading function $h(r) = e^{br}$ yields $r_y = 1 - \frac{h(r_y)}{h'(r_y)} = 1 - \frac{e^{br}}{be^{br}} = 1 - \frac{1}{b}$. Therefore in this scenario, sex roles should diverge regardless of the strength of sperm competition. The proportion of resources devoted to the sexually selected trait depends only on the ‘efficiency’ of the trait, b .

A similar result can be found for the within group ‘exclusion’ model (S5) with varying group size, if we assume that the competitive effect is multiplicative and there is no gamete limitation.

For an example where group size does have an effect on sex role divergence, consider the exclusion competition model (S5) with additive competitive effects, for groups of k males and k females (note that assuming whether the effect is additive or multiplicative is irrelevant for pairwise interactions, i.e. when $k=2$, but becomes important when $k > 2$). Then, if residents devote r resource units to the competitive trait, and the mutant \hat{r}_x resource units, the total gamete number for that sex (here, males) is

$$\begin{aligned}
 Y &= \frac{(1-\hat{r}_y)(k-1)g(r_y)}{m_y(k-1)} + (k-1)\frac{(1-r_y)}{m_y} \left[\frac{g(\hat{r}_y) + (k-2)g(r_y)}{(k-1)} \right] \\
 &= \frac{(1-\hat{r}_y)}{m_y} g(r_y) + \frac{(1-r_y)}{m_y} [g(\hat{r}_y) + (k-2)g(r_y)].
 \end{aligned}$$

The first term arises because there are $k-1$ residents who affect the focal individual, but this effect is split between the focal and $k-2$ other individuals (summing to $k-1$; hence the term $(k-1)/(k-1)$). The second term arises because there are $k-1$ residents, and they are each affected by the mutant and $k-2$ other residents, and this total effect is split between all $k-1$ residents. This total number of gametes gives rise to the gamete competition function

$$\hat{c}_y = \frac{\frac{1-\hat{r}_y}{m_y}g(r_y)}{\frac{(1-\hat{r}_y)}{m_y}g(r_y) + \frac{(1-r_y)}{m_y}[g(\hat{r}_y) + (k-2)g(r_y)]} = \frac{(1-\hat{r}_y)g(r_y)}{(1-\hat{r}_y)g(r_y) + (1-r_y)[g(\hat{r}_y) + (k-2)g(r_y)]}.$$

The fitness function for the y-focal individual is then $w_y = \hat{c}_y \hat{f} =$

$$\frac{(1-\hat{r}_y)g(r_y)}{(1-\hat{r}_y)g(r_y) + (1-r_y)[g(\hat{r}_y) + (k-2)g(r_y)]} \hat{f}, \text{ and}$$

$$\left. \frac{d\hat{w}_y}{d\hat{r}_y} \right|_{\hat{r}_y=r_y} = \left[\frac{(1-k)g(r_y) - (1-r_y)g'(r_y)}{k^2(1-r_y)g(r_y)} \right] \hat{f}.$$

Now, if there is an ESS, it will be at $(1-k)g(r_y) - (1-r_y)g'(r_y) = 0$, or

$$r_y = 1 + (k-1) \frac{g(r_y)}{g'(r_y)}.$$

In this case, the ESS clearly depends on k , and therefore on the strength of sperm competition. For example, the competitive function $g(r) = e^{-br}$ yields

$$r_y = 1 + (k-1) \frac{g(r_y)}{g'(r_y)} = 1 + (k-1) \frac{e^{-br}}{-be^{-br}} = 1 - \frac{k-1}{b}.$$

Therefore males invest most in this competitive trait when gamete competition is low (small k). Again, equations (1-3) in the main text tell us that in the absence of gamete limitation, females should maintain investment in gametes. Therefore in this scenario, sex roles diverge more strongly when sperm competition is low (i.e. when local sperm competition is high: Schärer and Pen 2013).

The results in Fig. 1 (main text) are computed with $k=2$ and $b=2$, and therefore allocation approaches a maximum value of $1 - \frac{k-1}{b} = 1 - \frac{2-1}{2} = \frac{1}{2}$ as sperm limitation decreases.

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