

Gametic Selection, Meiotic Drive, Sex Ratio Bias, and Transitions Between Sex Determination Systems

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Contributions:

Abstract

2 Sex determination systems are remarkably dynamic; many studied taxa
display transitions of sex-determining genes between chromosomes or the
4 evolution of entirely new sex-determining systems. Predominant theories in
which new sex-determining systems are favoured by selection involve sex ra-
6 tio selection or sex-specific selection (e.g., sexually antagonistic selection).
Here, we utilize population genetic models to study the spread of novel sex-
8 determiners when there is a period of sex-specific haploid selection. Many
loci experience selection on their haploid genotypes during gametic competi-
10 tion (e.g., pollen/sperm competition) or meiosis (i.e., meiotic drive). Haploid
selected loci typically experience a form of sex-specific selection because
12 meiotic drive and/or gametic competition occurs predominantly in one sex
or the other. In addition, haploid selection can cause the zygotic sex ratio
14 to become biased because sex ratios are determined by the fertilization suc-
cess of X- versus Y-bearing pollen/sperm. Notably, we find that the spread
16 of new genetic sex determination systems is not affected by sex ratio biases
that are caused by haploid selection. In addition, we find that, with haploid
18 selection, transitions between male and female heterogamety (XY to ZW or
ZW to XY) can occur despite breaking up favourable associations the be-
20 tween ancestral sex-determining locus and selected loci. These transitions
occur because an unlinked neo-Y (neo-W) can have higher fitness in males
22 (females), even if the population mean fitness is reduced. Such transitions
are not possible with diploid selection alone, in which case tighter linkage
24 increases the fitness of both males and females. Furthermore, a period of
selection among haploids can favour the stable maintenance of polymorphic
26 sex determination systems. Thus, our models offer several new insights to
be explored as information about sex determination in non-model taxa accu-
28 mulates.

Introduction

30 Animals and angiosperms exhibit extremely diverse sex determination systems (re-
viewed in Bull 1983, Charlesworth and Mank 2010, Beukeboom and Perrin 2014,
32 Bachtrog et al. 2014). Among species with genetic sex determination of diploid
sexes, some taxa have heterogametic males (XY) and homogametic females (XX),
34 including mammals and most dioecious plants (Ming et al. 2011); whereas other
taxa have homogametic males (ZZ) and heterogametic females (ZW), including
36 Lepidoptera and birds. Within several taxa, the chromosome that harbours the
master sex-determining region changes. For example, transitions of the master
38 sex-determining gene between chromosomes or the evolution of new master sex-
determining genes have occurred in Salmonids (Li et al. 2011, Yano et al. 2012),
40 Diptera (Vicoso and Bachtrog 2015), and *Oryzias* (Myosho et al. 2012). In ad-
dition, many gonochoric/dioecious clades with genetic sex determination exhibit
42 transitions between male (XY) and female (ZW) heterogamety, including lizards
(Ezaz et al. 2009), eight of 26 teleost fish families (Mank et al. 2006), true fruit
44 flies (Tephritids, Vicoso and Bachtrog 2015), amphibians (Hillis and Green 1990),
the angiosperm genus *Silene* (Slancarova et al. 2013), Coleoptera and Hemiptera
46 (Beukeboom and Perrin 2014, plate 2). Indeed, in some cases, both male and fe-
male heterogametic sex determination systems can be found in the same species,
48 as exhibited by some cichlid species (Ser et al. 2010) and *Rana rugosa* (Ogata
et al. 2007). In addition, multiple transitions have occurred between genetic and
50 environmental sex determination systems, e.g., in reptiles and fishes (Conover and
Heins 1987, Mank et al. 2006, Pokorná and Kratochvíl 2009, Ezaz et al. 2009, Pen
52 et al. 2010, Holleley et al. 2015).

Predominant theories in which new sex determination systems are favoured by
54 selection involve fitness differences between sexes (e.g., sexually antagonistic se-
lection) or sex ratio selection. van Doorn and Kirkpatrick (2007; 2010) show that
56 new sex determination loci can be favoured if they arise in close linkage with a
locus that experiences sexual antagonism. For example, linkage allows favourable
58 associations to build up between a male-beneficial allele and a neo-Y chromo-

some. Such associations can favour a new master sex-determining gene on a new
60 chromosome (van Doorn and Kirkpatrick 2007) and can also favour a transition
between male and female heterogamety (e.g., a ZW to XY transition, van Doorn
62 and Kirkpatrick 2010). However, any sexually-antagonistic loci that are linked to
the ancestral sex-determination locus will develop similar, favourable associations
64 and select against the spread of a new sex-determination system.

It has been suggested that sex ratio selection could be a particularly impor-
66 tant force driving transitions between sex-determining systems (Beukeboom and
Perrin 2014, Chapter 7). For example, flexible sex determination systems may be
68 favoured in order to exploit local environmental conditions that are optimal for
males or females, which creates locally biased sex ratios (Charnov and Bull 1977,
70 Werren and Taylor 1984, Pen et al. 2010). In addition, feminizing mutations may
invade when female biased sex ratios are favoured due to selection among demes
72 (Wilson and Colwell 1981, Vuilleumier et al. 2007). In other situations, sex ratio
selection may favour transitions in order to restore equal sex ratios. For example,
74 Kozielska et al. (2010) consider systems in which the ancestral sex chromosomes
experience meiotic drive (e.g., where driving X or Y chromosomes are inherited
76 disproportionately often), which causes sex ratios to become biased (Hamilton
1967). They find that new, unlinked sex-determining loci (masculinizing or femi-
78 nizing mutations, i.e., neo-Y or neo-W loci) can then spread, restoring an even sex
ratio.

80 Here, we use mathematical models to find the conditions under which new
sex determination systems are favoured when loci experience haploid selection.
82 Haploid genotypes at many loci experience selection during gamete competition
and/or meiotic drive (Mulcahy et al. 1996, Joseph and Kirkpatrick 2004). Com-
84 petition among gametes/gametophytes (e.g., sperm/pollen competition) is distinct
from meiotic drive because drive only occurs among heterozygotes whereas ga-
86 metes from homozygous parents can participate in gamete competition. We use
the term ‘haploid selection’ to encompass both processes. Meiotic drive refers to the
88 biased (non-mendelian) segregation of genotypes during gamete production and is

almost always sex-specific, e.g., occurring either during the production of male or
 90 female gametes only (Ubeda and Haig, 2005; Lindholm et al. 2016). Because
 there are typically more pollen/sperm than required for fertilization, haploid com-
 92 petition is also typically sex specific, occurring primarily among male gametes.
 Haploid competition may be particularly common in plants, in which 60-70% of
 94 all genes are expressed in the male gametophyte and these genes exhibit stronger
 signatures of selection than random genes (Borg et al. 2009, Arunkumar et al. 2013,
 96 Gossmann et al. 2014). In addition, artificial selection pressures applied to male
 gametophytes cause the frequency of resistant alleles to increase (e.g., Hormaza
 98 and Herrero 1996, Ravikumar et al. 2003, Hedhly et al. 2004, Clarke et al. 2004).
 A smaller (but non-negligible) proportion of genes are thought to be expressed and
 100 selected during competition in animal sperm, although precise estimates are un-
 certain (Zheng et al. 2001, Joseph and Kirkpatrick 2004, Vibranovski et al. 2010).
 102 There are various ways in which a period of haploid selection could influence
 transitions between sex determination systems. Firstly, if we assume that haploid
 104 selection at any particular locus predominantly occurs in one sex (e.g., meiotic
 drive during spermatogenesis or pollen/sperm competition), then such loci experi-
 106 ence a form of sex-specific selection. In this respect, we might expect that haploid
 selection might affect transitions between sex determination systems in a similar
 108 manner to sex-specific diploid selection (as explored by van Doorn and Kirkpatrick
 2007; 2010). That is, new masculinizing mutations (neo-Y chromosomes) could be
 110 favoured via linkage associations with alleles that are beneficial in the male hap-
 loid stage. However, sex ratios can also become biased by linkage between the
 112 sex-determining region and a locus that harbours genetic variation in haploid fit-
 ness. For example, there are several known cases of sex ratio bias caused by sex-
 114 linked meiotic drive alleles (?, , Chapter 3) or selection among X- and Y-bearing
 pollen (Lloyd 1974, Conn and Blum 1981, Stehlik and Barrett 2005; 2006, Field
 116 et al. 2012; 2013). It is not immediately clear how the spread of new sex deter-
 mination systems would be influenced by the combination of sex ratio biases and
 118 associations between haploid selected loci and sex-determining regions.

Surprisingly, our models show that haploid selection influences the evolution
of new sex determination systems in a way that is distinct from both diploid sex-
specific selection and sex ratio selection. We find that new genetic sex determina-
tion systems are not affected by any sex ratio biases caused by associations between
sex-determining regions and haploid selected loci. In addition, we find that asso-
ciations that build up between an ancestral sex-determining locus and a haploid-
selected locus can favour transitions between male and female heterogamety (e.g.,
a neo-W allele arising at a previously autosomal locus spreads in an ancestrally
XY system), despite the fact that these ancestral associations were built up by se-
lection. This does not occur in models that do not include haploid selection.

Model

We consider the transition between an ancestral and novel sex determination sys-
tems using a three locus model. Locus **X** is the ancestral sex-determining region,
with alleles X and Y (or Z and W). Locus **A** is a locus under selection, with al-
leles A and a . Locus **M** is a novel sex-determining region, at which the null allele
(M) is initially fixed in the population such that sex of zygotes is determined by
the genotype at the ancestral sex-determining region, **X** (XX become females and
 XY become males, or ZW become females and ZZ become males). To eval-
uate the evolution of new sex-determination systems, we consider the invasion,
fixation, maintenance, and/or loss of novel sex-determining alleles (m) at the **M**
locus. We assume that the **M** locus is dominant over the **X** locus such that zygotes
with at least one m allele develop as females with probability k and as males with
probability $1 - k$, regardless of the **X** locus genotype. With $k = 0$, the m allele
is a masculinizer (i.e., a neo-Y) and with $k = 1$ the m allele is a feminizer (i.e., a
neo-W). With intermediate k , the m allele confers environmental sex determina-
tion such that zygotes develop as females in a proportion (k) of the environments
they experience. Finally, we also analyze a model of maternally-controlled en-
vironmental sex-determination (ESD), where mothers with at least one m allele

produce daughters with probability k .

148 In each generation, we census the genotype frequencies in male and female
gametes/gametophytes (hereafter gametes) before haploid competition (see Sup.
150 Mat. for recursion equations). First, competition occurs among male gametes
(sperm/pollen competition) and among female gametes (egg/ovule competition)
152 separately. Selection during haploid competition depends on the **A** locus geno-
type, relative fitnesses are given by w_A^{\varnothing} and w_a^{\varnothing} ($\varnothing \in \{\varnothing, \sigma\}$; see table 1). Ran-
154 dom mating then occurs between male and female gametes. The resulting zygotes
develop as males or females, depending on their genotypes at the **X** and **M** loci
156 (and the **M** genotype of their mother in the case of maternal control) as described
above. Diploid males and females then experience selection, relative fitnesses are
158 given by w_g^{σ} in males and w_g^{\varnothing} in females, where g is the diploid genotype at the
A locus ($g \in \{AA, Aa, aa\}$). The next generation of gametes are then produced
160 by meiosis, during which recombination and sex-specific meiotic drive can occur.
Recombination occurs between loci **X** and **A** with probability r , between loci **A** and
162 **M** with probability R , and between loci **X** and **M** with probability χ . Therefore,
any order of the loci can be modelled with appropriate choices of r , R , and χ (see
164 Table S.1). Males/females that are heterozygous at the **A** locus experience meiotic
drive; Aa heterozgotes of sex \varnothing produce gametes bearing allele A with probability
166 α^{\varnothing} . Thus, the **A** locus can experience sex-specific haploid competition, diploid
selection and/or meiotic drive.

168 Results

The only asymmetry between males and females in our model is that, under the
170 ancestral sex determination system, males develop with genotype XY (or ZZ) and
females with genotype XX (or ZW). Therefore, without loss of generality, we
172 primarily present results for ancestral XY sex determination. Ancestral ZW sex
determination can be considered by changing the notation such that X becomes Z ,
174 Y becomes W and the labelling of male and female selection terms are reversed.

Table 1: Relative fitness of different genotypes in sex $\phi \in \{\text{♀}, \text{♂}\}$

Genotype	Relative fitness during haploid competition
A	$w_A^\phi = 1 + t^\phi$
a	$w_a^\phi = 1$
Genotype	Relative fitness during diploid selection
AA	$w_{AA}^\phi = 1 + s^\phi$
Aa	$w_{Aa}^\phi = 1 + h^\phi s^\phi$
aa	$w_{aa}^\phi = 1$
Genotype	Transmission during meiosis in <i>Aa</i> heterozygotes
A	$\alpha^\phi = 1/2 + \alpha_\Delta^\phi/2$
a	$(1 - \alpha^\phi) = 1/2 - \alpha_\Delta^\phi/2$

Resident equilibrium and stability

176 In the resident population (allele M fixed), we follow the frequency of A in female
gametes (eggs) from an XX female, $p_X^\text{♀}$, and in X-bearing, $p_X^\text{♂}$, and Y-bearing,
178 $p_Y^\text{♂}$, male gametes (sperm). We also track the total frequency of Y-bearing male
gametes, q , which may deviate from $1/2$ due to meiotic drive in males.

180 Various forms of selection can maintain a polymorphism at the **A** locus, includ-
ing sexually antagonistic selection, overdominance and conflicts between diploid
182 selection and selection upon haploid genotypes (ploiddally antagonistic selection,
Immler et al. 2012) or a combination of these selective regimes. Here, we assume
184 that selection and meiotic drive are weak relative to recombination ($s^\phi, t^\phi, \alpha_\Delta^\phi$ of
order ϵ). The maintenance of a polymorphism at the **A** locus then requires that

$$\begin{aligned}
 0 &< -((1 - h^\text{♀})s^\text{♀} + (1 - h^\text{♂})s^\text{♂} + t^\text{♀} + t^\text{♂} + \alpha_\Delta^\text{♀} + \alpha_\Delta^\text{♂}) \\
 0 &< (h^\text{♀}s^\text{♀} + h^\text{♂}s^\text{♂} + t^\text{♀} + t^\text{♂} + \alpha_\Delta^\text{♀} + \alpha_\Delta^\text{♂}).
 \end{aligned} \tag{1}$$

186 which indicates that a polymorphism is maintained under various selective regimes.

In particular special cases, e.g., no sex-differences in selection or meiotic drive
 188 ($s^\delta = s^\varphi$, $h^\delta = h^\varphi$, and $\alpha^\delta = \alpha^\varphi = 1/2$), the equilibrium allele frequency and
 stability can be calculated analytically without assuming weak selection. How-
 190 ever, here, we focus on weak selection in order to make fewer assumptions about
 fitnesses.

192 Given that a polymorphism is maintained at the **A** locus by selection, with
 weak selection and drive, to leading order, the frequencies of *A* in each type of
 194 gamete are the same ($\hat{p}_X^\varphi = \hat{p}_X^\delta = \hat{p}_Y^\delta = \bar{p}$) and given by

$$\bar{p} = \frac{h^\varphi s^\varphi + h^\delta s^\delta + t^\varphi + t^\delta + \alpha_\Delta^\varphi + \alpha_\Delta^\delta}{(2h^\varphi - 1)s^\varphi + (2h^\delta - 1)s^\delta} + O(\epsilon). \quad (2)$$

Differences in frequency between gamete types are of order ϵ to leading order and
 196 given by

$$\begin{aligned} \hat{p}_X^\delta - \hat{p}_X^\varphi &= V_A(D^\delta - D^\varphi + \alpha_\Delta^\delta - \alpha_\Delta^\varphi) + O(\epsilon^2) \\ \hat{p}_Y^\delta - \hat{p}_X^\varphi &= V_A(D^\delta - D^\varphi + \alpha_\Delta^\delta - \alpha_\Delta^\varphi + (1 - 2r)(t^\delta - t^\varphi))/2r + O(\epsilon^2) \\ \hat{p}_Y^\delta - \hat{p}_X^\delta &= V_A(D^\delta - D^\varphi + \alpha_\Delta^\delta - \alpha_\Delta^\varphi + t^\delta - t^\varphi)(1 - 2r)/2r + O(\epsilon^2) \end{aligned} \quad (3)$$

where $V_A = \bar{p}(1 - \bar{p})$ is the variance in the frequency of *A* and $D^\varphi = (\bar{p}s^\varphi +$
 198 $(1 - \bar{p})h^\varphi s^\varphi) - (\bar{p}h^\varphi s^\varphi + (1 - \bar{p}))$ corresponds to the difference in fitness between
A and *a* alleles in diploids of sex $\varphi \in \{\varphi, \delta\}$ (\bar{p} is the leading-order probability
 200 of mating with an *A*-bearing gamete from the opposite sex). The frequency of *Y*
 among male gametes depends upon the difference in *A* allele frequency on X- and
 202 Y-bearing male gametes and the strength of meiotic drive in favour of the *A* allele
 in males, $q = 1/2 + \alpha_\Delta^\delta(\hat{p}_Y^\delta - \hat{p}_X^\delta)/2 + O(\epsilon^3)$. Without haploid competition or drive
 204 ($\alpha_\Delta^\varphi = t^\varphi = 0$), these results reduce to those of van Doorn and Kirkpatrick (2007).

Turnover between sex-determination systems

206 The evolution of a new sex determination system requires that a rare mutant allele, m , at the novel sex-determining locus increases in frequency when rare. The
 208 spread of a rare mutant m at the **M** locus is determined by the leading eigenvalue, λ , of the system described by the next generation frequency of eggs and sperm
 210 carrying the mutation, (S.1c), (S.1d), (S.1g), (S.1h), which is an eight equation system. Dominant neo-Y (when $k = 0$) or neo-W alleles (when $k = 1$) are only
 212 found in male diploids (neo-Y) or female diploids (neo-W) such that their growth rate ultimately depends only on the change in frequency of m -bearing gametes
 214 produced by males (for a neo-Y) or by females (for a neo-W). Furthermore, if the m allele is fully dominant over the ancestral sex-determining system, phenotypes
 216 are not affected by the genotype at the ancestral sex-determining region (**X** locus). Therefore, the invasion of rare mutant neo-Y or neo-W alleles can be simplified and
 218 given by the largest eigenvalue that solves the quadratic characteristic polynomial

$$\lambda^2 + b\lambda + c = 0 \quad (4)$$

where b is the average of the growth rates of the two haplotypes that carry the
 220 m allele (mA and ma), $b = (\lambda_{mA} + \lambda_{ma})/2$, and c also involves the fitness of m alleles when they recombine onto the other **A** background in a heterozygote, $c =$
 222 $\lambda_{mA}\lambda_{ma} + \rho_{mA}\rho_{ma}$ (see table 2).

Table 2: Parameters determining invasion (equation 4) for neo-Y or neo-W alleles

neo-Y ($k = 0$)
$\lambda_{mA} = \{p_X^\varnothing w_A^\varnothing w_A^\delta w_{AA}^\delta + (1 - p_X^\varnothing) w_a^\varnothing w_A^\delta w_{Aa}^\delta \alpha^\delta (1 - R)\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\delta\}$ $\lambda_{ma} = \{(1 - p_X^\varnothing) w_a^\varnothing w_a^\delta w_{aa}^\delta + p_X^\varnothing w_A^\varnothing w_a^\delta w_{Aa}^\delta (1 - \alpha^\delta) (1 - R)\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\delta\}$ $\rho_{mA} = R(1 - p_X^\varnothing) w_a^\varnothing w_A^\delta w_{Aa}^\delta (1 - \alpha^\delta) / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\delta\}$ $\rho_{ma} = R p_X^\varnothing w_A^\varnothing w_a^\delta w_{Aa}^\delta \alpha^\delta / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\delta\}$
neo-W ($k = 1$)
$\lambda_{mA} = \{\bar{p}^\delta w_A^\delta w_A^\varnothing w_{AA}^\varnothing + (1 - \bar{p}^\delta) w_a^\delta w_A^\varnothing w_{Aa}^\varnothing \alpha^\varnothing (1 - R)\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\varnothing\}$ $\lambda_{ma} = \{(1 - \bar{p}^\delta) w_a^\delta w_a^\varnothing w_{aa}^\varnothing + \bar{p}^\delta w_A^\delta w_a^\varnothing w_{Aa}^\varnothing (1 - \alpha^\varnothing) (1 - R)\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\varnothing\}$ $\rho_{mA} = R(1 - \bar{p}^\delta) w_a^\delta w_A^\varnothing w_{Aa}^\varnothing (1 - \alpha^\varnothing) / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\varnothing\}$ $\rho_{ma} = R \bar{p}^\delta w_A^\delta w_a^\varnothing w_{Aa}^\varnothing \alpha^\varnothing / \{\bar{w}_H^\varnothing \bar{w}_H^\delta \bar{w}^\varnothing\}$

$\bar{p}^\delta = p_Y^\delta q + p_X^\delta (1 - q)$ is the average frequency of the A allele among X- and Y-bearing male gametes

$\bar{w}_H^\varnothing = p_X^\varnothing w_A^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing$ is the mean fitness of female gametes during haploid competition

$\bar{w}_H^\delta = \bar{p}^\delta w_A^\delta + (1 - \bar{p}^\delta) w_a^\delta$ is the mean fitness of male gametes during haploid competition

$\bar{w}^\varnothing = \{p_X^\varnothing w_A^\varnothing (1 - q) p_X^\delta w_A^\delta w_{AA}^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing (1 - q) p_X^\delta w_A^\delta w_{Aa}^\varnothing + p_X^\varnothing w_A^\varnothing (1 - q) (1 - p_X^\delta) w_a^\delta w_{Aa}^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing (1 - q) (1 - p_X^\delta) w_a^\delta w_{aa}^\varnothing\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta\}$ is the mean fitness of females during diploid competition

$\bar{w}^\delta = \{p_X^\varnothing w_A^\varnothing q p_Y^\delta w_A^\delta w_{AA}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q p_Y^\delta w_A^\delta w_{Aa}^\delta + p_X^\varnothing w_A^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{Aa}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{aa}^\delta\} / \{\bar{w}_H^\varnothing \bar{w}_H^\delta\}$ is the mean fitness of males during diploid competition

Equation (4) and table 2 illustrate a number of key points about the invasion of neo-Y and neo-W mutations. For a neo-Y, invasion depends on the relative lifetime fitness of A -bearing and a -bearing male gametes (i.e., in sperm only). The lifetime fitness of male gametes partly depends on the allele carried by the female gamete that they mate with (e.g., A with probability $p_X^\varnothing w_A^\varnothing / \bar{w}_H^\varnothing$). Similarly, invasion of a neo-W depends on the relative lifetime fitness of A -bearing and a -bearing female gametes (i.e., in eggs only). However, in the case of a neo-W, the allele carried by the male gamete that they mate with can come from either an X-bearing or a Y-bearing sperm (e.g., A with probability $\bar{p}^\delta w_A^\delta / \bar{w}_H^\delta$). In either case, the zygote will then develop as a female due to the presence of a neo-W. By contrast, females

234 that do not carry the neo-W only result from matings with X-bearing sperm (e.g.,
 matings with A-bearing sperm occur with probability $\bar{p}_X^\delta w_A^\delta / \bar{w}_H^\delta$). If the **A** locus
 236 is initially linked to the ancestral sex-determining locus, **X**, (i.e., $r < 1/2$) the
 frequency of the A allele among X- and Y-bearing sperm can differ (equation 3).
 238 Thus, eggs with and without a neo-W differ in the frequency of A alleles they
 obtain from mating with male gametes.

240 We are particularly concerned with whether or not a rare neo-sex-determining
 allele increases in frequency, which occurs when the largest eigenvalue, λ , that
 242 solves (4) is greater than one. If the average change in frequency of the two hap-
 lotypes that carry the m allele (Am and am) is positive, invasion will always occur
 244 (if $\{(\lambda_{mA} - 1) + (\lambda_{ma} - 1)\} / 2 > 0$, $\lambda > 1$). If neither haplotype increases in
 frequency ($\lambda_{mA}, \lambda_{ma} < 1$), the m allele will not invade. Otherwise, the new sex-
 246 determining allele increases in frequency on one **A** background and declines on
 the other, and invasion requires

$$R \left[\frac{p_X^\delta w_A^\delta w_a^\delta (1 - \alpha^\delta)}{\bar{w}_H^\delta \bar{w}_H^\delta (\lambda_{mA} - 1)} + \frac{(1 - p_X^\delta) w_a^\delta w_A^\delta \alpha^\delta}{\bar{w}_H^\delta \bar{w}_H^\delta (\lambda_{ma} - 1)} \right] \frac{w_{Aa}^\delta}{\bar{w}^\delta} < 1, \quad (5)$$

248 for the neo-Y, and

$$R \left[\frac{\bar{p}^\delta w_A^\delta w_a^\delta (1 - \alpha^\delta)}{\bar{w}_H^\delta \bar{w}_H^\delta (\lambda_{mA} - 1)} + \frac{(1 - \bar{p}^\delta) w_a^\delta w_A^\delta \alpha^\delta}{\bar{w}_H^\delta \bar{w}_H^\delta (\lambda_{ma} - 1)} \right] \frac{w_{Aa}^\delta}{\bar{w}^\delta} < 1, \quad (6)$$

250 **FIX THESE EQUATIONS... i changed them a little, is this okay now? (mmo)** for
 the neo-W. Equations (5) and (6) show that the new sex-determining allele, m , is
 252 expected to invade for any recombination rate, R , when the net flow of recombi-
 nants is from the less fit (smaller λ_{mi}) to the more fit **A** background (making the
 254 terms inside the square brackets in Equations 5 and 6 negative). **Q: is it definitely**
possible to have negative square brackets for a equilibria maintained by selection?
 256 When the net flow of recombinants is from the more fit to the less fit haplotype,
 the new sex-determining allele can still invade when the rate of recombination be-
 258 tween it and the selected locus, R , is small enough. **Q:Is it the case that sometimes**
the square brackets are positive and invasion occurs for $R = 1/2$? In which case

260 it might be better to have slightly different phrasing here.

We can explicitly determine the conditions under which invasion occurs if we
 262 assume that the A allele reaches an equilibrium frequency under the ancestral sex-
 determination system before the neo-sex-determination system (m) arises. The
 264 equilibrium frequency of A on different ancestral backgrounds (\hat{p}_Y^δ , \hat{p}_X^δ , and \hat{p}_X^σ) is
 given by equations (2) and (3) where we assume selection and meiotic drive are
 266 weak relative to recombination (s^δ , t^δ , α_Δ^δ of order ϵ). Under weak selection, we
 denote the leading eigenvalue describing the invasion of a neo-Y ($k = 0$) and a
 268 neo-W ($k = 0$) into an ancestrally XY system by $\lambda_{Y',XY}$ and $\lambda_{W',XY}$, respectively,
 which are given by

$$\lambda_{Y',XY} = 1 + \frac{V_A(r-R)(S_A)^2}{rR} + O(\epsilon^3) \quad (7)$$

270 and

$$\lambda_{W',XY} = \lambda_{Y',XY} + (2\alpha_\Delta^\delta - 2\alpha_\Delta^\sigma + t^\delta - t^\sigma)(\hat{p}_Y^\delta - \hat{p}_X^\delta) + O(\epsilon^3) \quad (8)$$

where $V_A = \bar{p}(1-\bar{p})$ is the variance in the frequency of A and $S_A = (D^\delta + \alpha_\Delta^\delta + t^\delta) -$
 272 $(D^\sigma + \alpha_\Delta^\sigma + t^\sigma)$ is the difference in fitness in males versus females for the A allele
 against the a allele across diploid selection, haploid competition, and meiosis.

274 The neo-sex-determining allele m will spread if $\lambda_{m,XY} > 1$. Equation (7)
 demonstrates that a neo-Y will invade if and only if it is more closely linked to
 276 the selected locus than the ancestral sex-determining region (i.e., if $R < r$, note
 that V_A and $(S_A)^2$ are strictly positive). This result echoes that of van Doorn and
 278 Kirkpatrick (2007), who considered diploid selection only and also found that ho-
 mogametic transitions (XY to XY or ZW to ZW) can occur when the neo-sex-
 280 determining locus is more closely linked to a locus under sexually-antagonistic
 selection.

282 If there is no selection upon haploid genotypes ($t^\delta = \alpha_\Delta^\delta = 0$), as considered
 by van Doorn and Kirkpatrick (2010), the spread of a neo-W is equivalent to the
 284 spread of a neo-Y ($\lambda_{W',XY} = \lambda_{Y',XY}$) such that heterogametic transitions (XY to

ZW or ZW to XY) can also occur only if the neo-sex-determining region is more
 286 closely linked to a locus under selection ($R < r$). However, if there is any haploid
 selection, the additional term in equation (8) can be positive, which can allow
 288 invasion ($\lambda_{W',XY} > 1$) even when the neo-sex-determining region is less closely
 linked to the selected locus ($R > r$). These transitions are unusual because, when
 290 $R > r$, associations that build up by selection between sex and alleles will be
 weakened. Therefore, mean fitness can decrease, see Figure S.1.

292 We find that neo-W alleles can invade for a large number of selective regimes.
 To clarify the parameter space under which $\lambda_{W',XY} > 1$, we consider several spe-
 294 cial cases. Firstly, if the **A** locus is unlinked to the ancestral sex-determining re-
 gion ($r = 1/2$), a more closely linked neo-W ($R < 1/2$) can always invade because
 296 $(\hat{p}_Y^\delta - \hat{p}_X^\delta) = 0$ such that the second term in (8) disappears and invasion depends
 on the sign of $(r - R)$. Indeed, invasion typically occurs when the neo-W is more
 298 closely linked to the selected locus than the ancestral sex-determining region, Fig-
 ure 2. Secondly, we can simplify cases where $R > r$ using the special case where
 300 $R = 1/2$ and $r < 1/2$. In table 3 we give the conditions where invasion occurs
 where we further assume that haploid selection only occurs during one phase in one
 302 sex (e.g., during male meiosis only) and equal dominance, $h^\varnothing = h^\delta$. Where there
 is no haploid competition and meiotic drive in one sex only, an unlinked neo-W can
 304 invade as long as the same allele is favoured in male and female diploid selec-
 tion ($s^\varnothing s^\delta > 0$, see Figure 2B), which is 50% of the parameter space. Where there is no
 306 meiotic drive and haploid competition occurs in one sex only, an unlinked neo-W
 can invade as long as the same allele is favoured in male and female diploid selec-
 308 tion and there are sex differences in selection of one type ($-s^\varnothing(s^\varnothing - s^\delta) > 0$, see
 Figure 2C,D), which is 25% of the parameter space. These special cases indicate
 310 that neo-W invasion can occur for a relatively large fraction of parameter space,
 even if $R > r$.

312 Previous research suggests, when the ancestral sex-determining locus is linked
 to a locus that experiences haploid selection (e.g., meiotic drive), a new, unlinked
 314 sex-determining locus invades in order to restore equal sex ratios (Kozielska et al.

Table 3: Invasion conditions for unlinked neo-W ($R = 1/2$, $r < 1/2$) with one form of haploid selection only

Assumptions	neo-W spreads ($\lambda_{W',XY} > 1$) if
$h^\delta = h^\varnothing, t^\varnothing = t^\delta = \alpha_{\Delta}^\varnothing = 0$	$s^\varnothing s^\delta > 0$
$h^\delta = h^\varnothing, t^\varnothing = t^\delta = \alpha_{\Delta}^\delta = 0$	$s^\varnothing s^\delta > 0$
$h^\delta = h^\varnothing, t^\varnothing = \alpha_{\Delta}^\varnothing = \alpha_{\Delta}^\delta = 0$	$-s^\varnothing(s^\varnothing - s^\delta) > 0$
$h^\delta = h^\varnothing, t^\delta = \alpha_{\Delta}^\varnothing = \alpha_{\Delta}^\delta = 0$	$-s^\varnothing(s^\varnothing - s^\delta) > 0$

2010). Our model provides a good opportunity to determine whether Fisherian
316 sex ratio selection provides a useful explanation for the evolution of new sex-
determining loci in other contexts. Consider, for example, the case where the **A**
318 locus is linked to the ancestral-SDR ($r < 1/2$) and experiences meiotic drive in
males only (e.g., during spermatogenesis but not during oogenesis, $\alpha^\delta \neq 1/2$,
320 $\alpha^\varnothing = 1/2$). We will also disregard haploid competition ($t^\varnothing = t^\delta = 0$) such that
zygotic sex ratios can only be biased by meiotic drive in males. In this case, the
322 zygotic sex ratio can be initially biased only if the ancestral sex-determining sys-
tem is XY (Figure 1B). If the ancestral sex-determining system is ZW, the zygotic
324 sex ratio will be 1:1 because diploid sex is determined by the proportion of Z-
bearing versus W-bearing eggs (and meiosis in females is fair, Figure 1D). Thus,
326 if the zygotic sex ratio is crucial to the evolution of new genetic sex-determining
systems, invasion into ZW and XY systems will be distinct. However, we find
328 that invasion by a homogametic neo-sex-determining allele (XY to XY, or ZW to
ZW) or by a heterogametic neo-sex-determining allele (XY to ZW or ZY to XY)
330 occur under the same conditions. That is, we can show that $\lambda_{Y',XY} = \lambda_{W',ZW}$ and
 $\lambda_{Y',ZW} = \lambda_{W',XY}$, for a numerical example, compare Figure 1A,B to Figure 1C,D.

332 Offspring-controlled neo-ESD

The growth rate of a rare, dominant offspring-controlled neo-ESD region that produces males or females with equal probability ($k = 1/2$) is

$$\lambda_{ESD} \approx 1 + \frac{1}{2} \frac{(\lambda_{Y,XY} - 1) + (\lambda_{W,XY} - 1)}{2} \Big|_{R=1/2}, \quad (9)$$

which is the same for invasion into an ancestrally XY or ZW system. Thus with $k = 1/2$ the neo-ESD gets half of the advantages of a neo- W and half that of a neo- Y , but only has an effect one half of the time (the other half of the time it produces the same sex as the ancestral system would have). Recombination between the selected locus and the novel sex-determining locus, R , doesn't enter into the $k = 1/2$ results because sex is essentially randomized each generation, preventing associations from building up between allele A and sex.

Depends 50% on its fitness relative to non-mutant males and 50% on its fitness relative to non-mutant females.

344 Maternally-controlled neo-ESD

One might think that when the sex of zygotes is under the control of mothers, there would be strong selection to balance the sex ratio among zygotes. However, we find that, as with offspring control, under weak selection the invasion fitness of a sex-determiner that is maternally controlled can be written

$$\lambda_{k,XY} \approx 1 + V_A S_A C_k, \quad (10)$$

where C_k is a term that depends on k . Of particular interest is $k = 1/2$ (i.e., when the mother perfectly balances the sex ratio of her offspring). When both recombination rates are small we have $C_{1/2} \approx R(s^\delta - s^\varnothing)/8 = \lim_{r \rightarrow 0} C_1/4$. This implies that, at least under tight linkage, the invasion of maternally-controlled ESD is independent of R (because $S_A \propto R^{-1}$) and can invade whenever a neo- W can (which can invade even when it biases the sex ratio further; Figures ?? – ??).

Discussion

356 If there is genetic variation maintained by sexually-antagonistic selection, new sex-
determining systems can evolve. In particular, transitions to new sex-determining
358 systems can occur when new sex-determining regions are more closely linked to
a sexually-antagonistic locus. Here, we show that genetic variation at loci that
360 experience haploid selection can also generate selection in favour of new sex-
determining systems. Closer linkage can again favour new sex-determining alleles.
362 However, with haploid selection, heterogametic transitions (XY to ZW or ZW to
XY) can also occur when the new sex-determining region is less closely linked to
364 the locus under selection.

Neo-W (neo-Y) alleles invade when their fitness in females (males) is greater
366 than the mean fitness of females (males) under the ancestral sex determination
system. With sexually antagonistic selection (between diploid sexes) only, linkage
368 between a selected locus and the sex-determining region strengthens associations
between male beneficial alleles and the male-determining allele (Y or Z) and be-
370 tween female beneficial alleles and the female-determining allele (X or W). Thus,
the mean fitness of both males and females increases with closer linkage to the sex-
372 determining region. Therefore, new sex-determining alleles only invade if they are
more closely linked than the ancestral sex-determining region. However, if there is
374 haploid selection on loci linked to an XY (ZW) sex-determining region, there are
equilibria for which the mean fitness of females (males) or males is lower than it
376 would be without sex-linkage, allowing unlinked neo-W (neo-Y) alleles to invade,
see figure S.1.

378 Linkage between a locus that experiences haploid selection and a sex-determining
region causes zygotic sex ratios to become biased (REFERENCES), which we
380 might then expect to exert sex ratio selection upon new modifiers. Fisherian sex
ratio selection follows from the fact that, for an autosomal locus, half of the genetic
382 material is inherited from a male, and half from a female. Thus, if the population
sex ratio is biased towards females, the average per-individual contribution of ge-
384 netic material to the next generation from males is greater than the contribution

from females (and vice versa for male-biased sex ratios). Therefore, a mutant that
386 increases investment in males will spread via the higher per-individual contribu-
tions made by males. That is, under Fisherian sex ratio selection, the success of
388 a mutant relative to the non-mutant depends, in equal parts, on the contributions
made by males and females to the next generation. An implicit assumption of
390 Fisherian sex ratio selection is that the mutant allele is autosomal and has the same
inheritance pattern as the non-mutant allele. The mutations we consider here, neo-
392 sex-determining alleles, break this assumption. For example, the success of neo-Y
mutations depends only on the number of alleles contributed by males (equation 4
394 and Table 2). Even mutants that are equally likely to be found in males or females,
such as an environmental sex determination mutation (equation 9), are not strictly
396 autosomal if they determine sex. Thus, despite the fact that sex ratio biases caused
by haploid competition or meiotic drive have been shown to exert selection on
398 various autosomal modifiers (Stalker 1961, Smith 1975, Frank 1989, Hough et al.
2013, Úbeda et al. 2015, Otto et al. 2015), we do not find evidence of Fisherian
400 sex ratio selection acting upon neo-sex-determination systems (e.g., see Figure 1).

We only consider selection at the **A** locus, the sex-determining regions do not
402 experience direct selection except via their associations with sex and **A** locus al-
leles. However, in some cases, there may be significant degeneration around the
404 sex-limited allele (Y or W) in the ancestral sex determining region. That is, reces-
sive deleterious mutations and/or deletions may fix around the Y or W allele Rice
406 1996, Charlesworth and Charlesworth 2000, Bachtrog 2006, Marais et al. 2008).
Degenerated Y could prevent fixation, this was studied by vD&K 2010, which is
408 why we didn't do it. They note that YY lethality can prevent neo-W (and Y) fixing
but that even very small amounts of recombination between X and Y can complete
410 the process.

Discuss patterns that might be looked for:

412 Evolutionary events, such as the transition between one sex-determination sys-
tem and another, are generally difficult to observe directly. One observation would
414 be the presence of sexually antagonistic variation linked to neo-sex chromosomes

- example from cichlids (debated, i believe). Our model could be examined in
416 a similar manner, although we find that genes that experience haploid selection
that are near either the neo- or ancestral-sex-determining locus could have been
418 involved in favouring a transition between sex-determining systems.

A complementary method of investigating evolutionary transitions is via com-
420 parative methods. Taken at face value, our results indicate that transitions in het-
erogamety (XY to ZW or vice versa) are more likely to be favoured by selection
422 if there is selection upon both haploid and diploid genotypes rather than diploid
selection alone.

424 In broadcast spawning animal species (e.g., corals, many fish) and species
where sperm typically requires greater longevity, haploid selection may be stronger
426 because transcripts shared during spermatogenesis may become depleted (Immler
et al. 2014). also, mating systems (e.g., fewer alleles are available during hap-
428 loid competition in monogamous species), selfing rates, and estimates of pollen
limitation could be used as indicators of the intensity of haploid selection

430 We have results where polygenic sex determination is sometimes stable, may be
worth mentioning:

432 “Polygenic sex determination has been reported in many plants (e.g. Shannon
& Holsinger 2007), fishes (Vandeputte et al. 2007; Ser et al. 2010; Liew et al.
434 2012), crustaceans (e.g. Battaglia 1958; Battaglia & Malesani 1959; Voordouw
& Anholt 2002), bivalves (Haley 1977; Saavedra et al. 1997), gastropods (Yusa
436 2007a,b), and polychaetes (Bacci 1965, 1978; Premoli et al. 1996).” From Vuilleu-
mier et al. 2007: “Polymorphism for sex-determining genes within or among pop-
438 ulations has been reported in many species including houseflies, midges, woodlice,
platyfish, cichlid fish, and frogs (Gordon, 1944; Kallman, 1970; Thomp-son, 1971;
440 Macdonald, 1978; Bull, 1983; Rigaud et al., 1997; Caubet et al., 2000; Lande et
al., 2001; Ogata et al., 2003; Lee et al., 2004; Mank et al., 2006).”

442 We caution that our model of meiotic drive is very simple, involving a single
locus with two alleles. Many meiotic drive systems involve an interaction with
444 another locus at which alleles may ‘suppress’ the action of meiotic drive. Further-

more, in some cases, a driving allele may act by killing any gametes that carry a
446 ‘target’ allele at another locus, in which case the total number of gametes produced
will be reduced (here, we assume total gamete number is not affected by drive).

448 Mix pollen competition and sex-ratio affects in here? Kokko paper addresses
some of these issues, but not related to sex-determination. These feedbacks be-
450 tween population densities and meiotic drive or haploid competition for different
sexual/mating systems deserve further attention.

452 Here, we have not considered any population size dynamics

(Check with Jim Bull that it’s ok before including this speculation:) Finally,
454 Hamilton (1967) pointed out that biased sex ratios can affect population size be-
cause the number of offspring in each generation is typically determined by the
456 number of females. Population density can, in turn, affect the intensity of pollen/sperm
competition in future generations because fewer males are available to donate
458 pollen/sperm in a particular area. Thus, a feedback could occur between popu-
lation densities and haploid selection, which has not yet been investigated.

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606 **Figures**

Appendix

608 Recursion Equations

In each generation we census the genotype frequencies in male and female gametes/gametophytes (hereafter, gametes) before haploid competition. Before haploid competition, the frequencies of X-bearing male and female gametes are given by X_i^δ and X_i^φ and the frequencies of Y-bearing gametes are given by Y_i^δ and Y_i^φ where the index i specifies genotypes $MA = 1$, $Ma = 2$, $mA = 3$, and $ma = 4$. Competition then occurs among gametes of the same sex (e.g., among eggs and among sperm separately) according to the **A** locus allele, g ($g \in A, a$, see Table 1), carried by individuals with genotype i . The genotype frequencies after haploid competition are $X_i^{\delta,s} = w_g X_i^\delta / \bar{w}_H^\delta$ and $Y_i^{\delta,s} = w_g Y_i^\delta / \bar{w}_H^\delta$, where $\bar{w}_H^\delta = \sum_{i=1}^4 w_g X_i^\delta + w_g Y_i^\delta$ is the mean fitness of male ($\delta = \delta$) or female ($\delta = \varphi$) gametes. Random mating then occurs between gametes to produce diploid zygotes with genotype ij at the **A** and **M** loci, such that XX zygotes are denoted xx_{ij} , XY zygotes are xy_{ij} , and YY zygotes are yy_{ij} . In XX and YY zygotes, individuals with genotype ij are equivalent to those with genotype ji . For simplicity, we denote the frequency of genotype ij in XX and YY zygotes to the average of these frequencies, $xx_{ij} = (X_i^{\varphi,s} X_j^{\delta,s} + X_j^{\varphi,s} X_i^{\delta,s})/2$ and $yy_{ij} = (Y_i^{\varphi,s} Y_j^{\delta,s} + Y_j^{\varphi,s} Y_i^{\delta,s})/2$.

Denoting the **M** locus genotype by b ($b \in MM, Mm, mm$) and the **X** locus genotype by c ($c \in XX, XY, YY$), zygotes develop as females with probability k_{bc} . Therefore, the frequencies of XX females are given by $xx_{ij}^\varphi = k_{bc} xx_{ij}$, XY females are given by $xy_{ij}^\varphi = k_{bc} xy_{ij}$, and YY females are given by $yy_{ij}^\varphi = k_{bc} yy_{ij}$. Similarly, XX male frequencies are $xx_{ij}^\delta = (1 - k_{bc}) xx_{ij}$, XY male frequencies are $xy_{ij}^\delta = (1 - k_{bc}) xy_{ij}$, and YY males frequencies are $yy_{ij}^\delta = (1 - k_{bc}) yy_{ij}$. This notation allows both the ancestral and novel sex-determining regions to determine zygotic sex according to an XY system, a ZW system, or an environmental sex-determining system. In addition, we can consider any dominance relationship between the two sex-determining loci. Typically, we assume that the ancestral sex-determining system (**X** locus) is XY ($k_{MMXX} = 1$ and $k_{MMXY} = k_{MYY} = 0$)

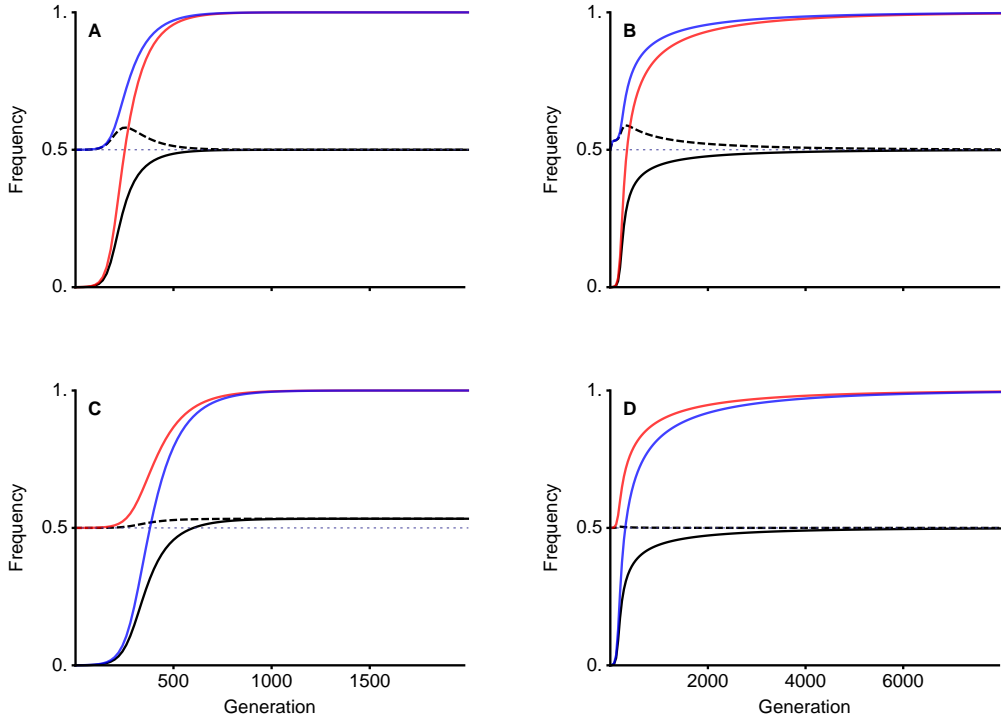


Figure 1: Heterogametic transitions from XY to ZW sex determination (neo-W frequency shown by black lines, panels A and B) or from ZW to XY (neo-Y frequency shown by black lines, panels C and D) occurs similarly regardless of sex ratio biases present before (B versus D) or after (C versus A, dashed lines show male frequency). During the invasion of a neo-ZW sex determination system (A and B), the ancestral Y fixes in both males and females (blue and red lines). Similarly, the ancestral W allele fixes in males and females (blue and red lines) during a ZW to XY transition. In this plot, there is no haploid competition ($t^{\varnothing} = t^{\delta} = 0$) and meiotic drive occurs during male meiosis only ($\alpha_{\Delta}^{\varnothing} = 0$, $\alpha_{\Delta}^{\delta} = -1/5$). Therefore, sex ratio biases can only arise when the A locus is linked to an XY sex-determining locus. In panels A and C, the neo-sex-determining locus is more closely linked to the A locus than the ancestral sex-determining region ($r = 1/2$, $R = 1/20$) such that a neo-Y can cause biased sex ratios (panel C). Unlike with diploid selection alone, when there is haploid selection (in this case meiotic drive), neo-sex-determining loci that are less closely linked to the A locus can also spread (panels B and D, $r = 1/20$, $R = 1/2$), see equation (8) and Figure 2B. These transitions are unusual because linkage generally allows favourable associations to arise via selection and the new sex determination systems in B and D have looser linkage. Thus, diploid mean fitness decreases over the course of the transitions in B and D, see Figure S.1. However, the mean fitness of females increases during the spread of dominant neo-W alleles and the mean fitness of males increases during the spread of dominant neo-Y alleles, Figure S.1. In this plot there are no sex differences in selection and an equilibrium is maintained because selection in diploids opposes meiotic drive, $s^{\varnothing} = s^{\delta} = 1/5$, $h^{\varnothing} = h^{\delta} = 7/10$. **Aesthetic adjustments:** Could add titles to the columns/rows: neo-W for row 1, neo-Y for row 3, $r = 0.5$, $R = 0.05$ for column 1 and $r = 0.05$, $R = 0.5$ for column 2. Could adjust padding (too much whitespace where there is no axis label). It also seems could increase ratio of font size relative to plot size to make figure more compact. Could make sex ratio biases more extreme by reducing the r in A and C and reducing R in B and D. Matt - could you uncomment the line legends in the Mathematica file (function not included in my Mathematica version).

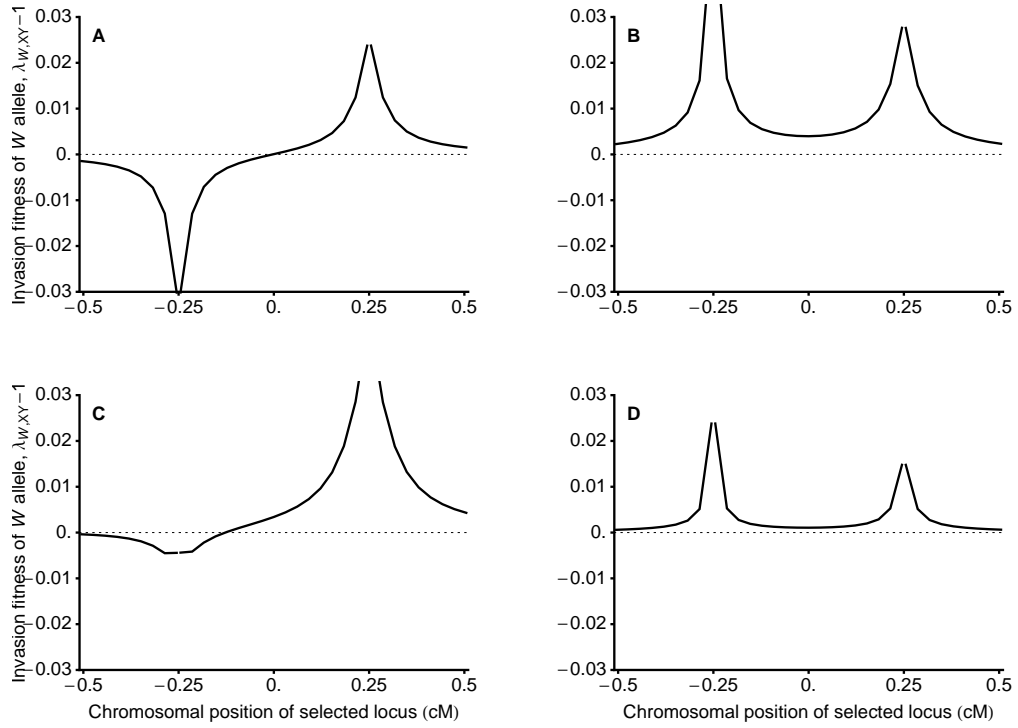


Figure 2: A sexual antagonism (no haploid selection), B drive (no haploid competition), equal selection in sexes ($s^{\varnothing} = s^{\sigma}$), C & D Pollen/Sperm competition only (no drive). C allele favoured in pollen/sperm competition selected against less in males ($t < 0$, $s^{\varnothing}, s^{\sigma} > 0$, $s^{\varnothing} < s^{\sigma}$). D allele favoured in pollen/sperm competition selected against more in males than females ($t < 0$, $s^{\varnothing}, s^{\sigma} > 0$, $s^{\varnothing} > s^{\sigma}$). I suspect that panel C has a region where no equilibrium is maintained (CHECK! Maybe include different parameters here). Currently use different parameters for B than using in figure 1 (selection/drive twice as strong in turnover figure)

636 and recessive to a dominant novel sex-determining locus, \mathbf{M} ($k_{Mmc} = k_{mmc} = k$).

Selection among diploids then occurs according to the diploid genotype at the
 638 \mathbf{A} locus, h , for an individual of type ij ($h \in AA, Aa, aa$, see Table 1). The diploid
 frequencies after selection in sex d are given by $xx_{ij}^{\phi,s} = w_h^{\phi} xx_{ij} / \bar{w}^{\phi}$, $xy_{ij}^{\phi,s} =$
 640 $w_h^{\phi} xy_{ij} / \bar{w}^{\phi}$, and $yy_{ij}^{\phi,s} = w_h^{\phi} yy_{ij} / \bar{w}^{\phi}$, where $\bar{w}^{\phi} = \sum_{i=1}^4 \sum_{j=1}^4 w_h^{\phi} xx_{ij} + w_h^{\phi} xy_{ij} +$
 $w_h^{\phi} yy_{ij}$ is the mean fitness of individuals of sex d .

642 Finally, these diploids undergo meiosis to produce the next generation of gametes. Recombination and sex-specific meiotic drive occur during meiosis. Here,
 644 we allow the relative locations of the SDR, \mathbf{A} , and \mathbf{M} loci to be generic by using
 three parameters to describe the recombination rates between them. R is the re-
 646 combination rate between the \mathbf{A} locus and the \mathbf{M} locus, χ is the recombination rate
 between the \mathbf{M} locus and the \mathbf{X} locus, and r is the recombination rate between the
 648 \mathbf{A} locus and the \mathbf{X} locus. Table S.1 gives substitutions for χ for defined relative
 locations of these loci. During meiosis in sex d , meiotic drive occurs such that, in
 650 Aa heterozygotes, a fraction α_d of gametes produced carry the A allele and $(1 - \alpha_d)$
 carry the a allele.

Table S.1: χ substitutions for different loci orders (assuming no interference)

Order of loci	
SDR-A-M	$\chi = R(1 - r) + r(1 - R)$
SDR-M-A	$\chi = (r - R)/(1 - 2R)$
A-SDR-M	$\chi = (R - r)/(1 - 2r)$

652 Among gametes from sex ϕ (sperm/pollen when $\phi = \sigma$, eggs/ovules when $\phi =$
 φ), the frequency of haplotypes (before haploid competition) in the next generation
 654 are given by

$$\begin{aligned}
X_{MA}^{\tilde{\varphi}'} = & xx_{11}^{\tilde{\varphi},s} + xx_{13}^{\tilde{\varphi},s}/2 + (xx_{12}^{\tilde{\varphi},s} + xx_{14}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& - R(xx_{14}^{\tilde{\varphi},s} - xx_{23}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& + (xy_{11}^{\tilde{\varphi},s} + xy_{13}^{\tilde{\varphi},s})/2 + (xy_{12}^{\tilde{\varphi},s} + xy_{14}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& - r(xy_{12}^{\tilde{\varphi},s} - xy_{21}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} - \chi(xy_{13}^{\tilde{\varphi},s} - xy_{31}^{\tilde{\varphi},s})/2 \\
& + \{ -(R+r+\chi)xy_{14}^{\tilde{\varphi},s} + (r+\chi-R)xy_{41}^{\tilde{\varphi},s} \\
& + (R+r-\chi)xy_{23}^{\tilde{\varphi},s} + (R+\chi-r)xy_{32}^{\tilde{\varphi},s} \}\alpha^{\tilde{\varphi}}/2
\end{aligned} \tag{S.1a}$$

$$\begin{aligned}
X_{Ma}^{\tilde{\varphi}'} = & xx_{22}^{\tilde{\varphi},s} + xx_{24}^{\tilde{\varphi},s}/2 + (xx_{12}^{\tilde{\varphi},s} + xx_{23}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& - R(xx_{23}^{\tilde{\varphi},s} - xx_{14}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& (xy_{22}^{\tilde{\varphi},s} + xy_{24}^{\tilde{\varphi},s})/2 + (xy_{21}^{\tilde{\varphi},s} + xy_{23}^{\tilde{\varphi},s})(1-\alpha^{\tilde{\varphi}}) \\
& - r(xy_{21}^{\tilde{\varphi},s} - xy_{12}^{\tilde{\varphi},s})(1-\alpha^{\tilde{\varphi}}) - \chi(xy_{24}^{\tilde{\varphi},s} - xy_{42}^{\tilde{\varphi},s})/2 \\
& + \{ -(R+r+\chi)xy_{23}^{\tilde{\varphi},s} + (r+\chi-R)xy_{32}^{\tilde{\varphi},s} \\
& + (R+r-\chi)xy_{14}^{\tilde{\varphi},s} + (R+\chi-r)xy_{41}^{\tilde{\varphi},s} \}(1-\alpha^{\tilde{\varphi}})/2
\end{aligned} \tag{S.1b}$$

$$\begin{aligned}
X_{mA}^{\tilde{\varphi}'} = & xx_{33}^{\tilde{\varphi},s} + xx_{13}^{\tilde{\varphi},s}/2 + (xx_{23}^{\tilde{\varphi},s} + xx_{34}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& - R(xx_{23}^{\tilde{\varphi},s} - xx_{14}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& (xy_{33}^{\tilde{\varphi},s} + xy_{31}^{\tilde{\varphi},s})/2 + (xy_{32}^{\tilde{\varphi},s} + xy_{34}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} \\
& - r(xy_{34}^{\tilde{\varphi},s} - xy_{43}^{\tilde{\varphi},s})\alpha^{\tilde{\varphi}} - \chi(xy_{31}^{\tilde{\varphi},s} - xy_{13}^{\tilde{\varphi},s})/2 \\
& + \{ -(R+r+\chi)xy_{32}^{\tilde{\varphi},s} + (r+\chi-R)xy_{23}^{\tilde{\varphi},s} \\
& + (R+r-\chi)xy_{41}^{\tilde{\varphi},s} + (R+\chi-r)xy_{14}^{\tilde{\varphi},s} \}\alpha^{\tilde{\varphi}}/2
\end{aligned} \tag{S.1c}$$

$$\begin{aligned}
X_{ma}^{\tilde{\phi}'} = & xx_{44}^{\tilde{\phi},s} + xx_{34}^{\tilde{\phi},s}/2 + (xx_{14}^{\tilde{\phi},s} + xx_{24}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& - R(xx_{14}^{\tilde{\phi},s} - xx_{23}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& (xy_{44}^{\tilde{\phi},s} + xy_{42}^{\tilde{\phi},s})/2 + (xy_{41}^{\tilde{\phi},s} + xy_{43}^{\tilde{\phi},s})(1 - \alpha^{\tilde{\phi}}) \\
& - r(xy_{43}^{\tilde{\phi},s} - xy_{34}^{\tilde{\phi},s})(1 - \alpha^{\tilde{\phi}}) - \chi(xy_{42}^{\tilde{\phi},s} - xy_{24}^{\tilde{\phi},s})/2 \\
& + \{ -(R + r + \chi)xy_{41}^{\tilde{\phi},s} + (r + \chi - R)xy_{14}^{\tilde{\phi},s} \\
& + (R + r - \chi)xy_{32}^{\tilde{\phi},s} + (R + \chi - r)xy_{23}^{\tilde{\phi},s} \}(1 - \alpha^{\tilde{\phi}})/2
\end{aligned} \tag{S.1d}$$

$$\begin{aligned}
Y_{MA}^{\tilde{\phi}'} = & yy_{11}^{\tilde{\phi},s} + yy_{13}^{\tilde{\phi},s}/2 + (yy_{12}^{\tilde{\phi},s} + yy_{14}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& - R(yy_{14}^{\tilde{\phi},s} - yy_{23}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& (xy_{11}^{\tilde{\phi},s} + xy_{31}^{\tilde{\phi},s})/2 + (xy_{21}^{\tilde{\phi},s} + xy_{41}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& - r(xy_{21}^{\tilde{\phi},s} - xy_{12}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} - \chi(xy_{31}^{\tilde{\phi},s} - xy_{13}^{\tilde{\phi},s})/2 \\
& + \{ -(R + r + \chi)xy_{41}^{\tilde{\phi},s} + (r + \chi - R)xy_{14}^{\tilde{\phi},s} \\
& + (R + r - \chi)xy_{32}^{\tilde{\phi},s} + (R + \chi - r)xy_{23}^{\tilde{\phi},s} \}\alpha^{\tilde{\phi}}/2
\end{aligned} \tag{S.1e}$$

$$\begin{aligned}
Y_{Ma}^{\tilde{\phi}'} = & yy_{22}^{\tilde{\phi},s} + yy_{24}^{\tilde{\phi},s}/2 + (yy_{12}^{\tilde{\phi},s} + yy_{23}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& - R(yy_{23}^{\tilde{\phi},s} - yy_{14}^{\tilde{\phi},s})\alpha^{\tilde{\phi}} \\
& (xy_{22}^{\tilde{\phi},s} + xy_{42}^{\tilde{\phi},s})/2 + (xy_{12}^{\tilde{\phi},s} + xy_{32}^{\tilde{\phi},s})(1 - \alpha^{\tilde{\phi}}) \\
& - r(xy_{12}^{\tilde{\phi},s} - xy_{21}^{\tilde{\phi},s})(1 - \alpha^{\tilde{\phi}}) - \chi(xy_{42}^{\tilde{\phi},s} - xy_{24}^{\tilde{\phi},s})/2 \\
& + \{ -(R + r + \chi)xy_{32}^{\tilde{\phi},s} + (r + \chi - R)xy_{23}^{\tilde{\phi},s} \\
& + (R + r - \chi)xy_{41}^{\tilde{\phi},s} + (R + \chi - r)xy_{14}^{\tilde{\phi},s} \}(1 - \alpha^{\tilde{\phi}})/2
\end{aligned} \tag{S.1f}$$

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$$\begin{aligned}
Y_{mA}^{\phi'} = & yy_{33}^{\phi,s} + yy_{13}^{\phi,s}/2 + (yy_{23}^{\phi,s} + yy_{34}^{\phi,s})\alpha^{\phi} \\
& - R(yy_{23}^{\phi,s} - yy_{14}^{\phi,s})\alpha^{\phi} \\
& (xy_{33}^{\phi,s} + xy_{13}^{\phi,s})/2 + (xy_{23}^{\phi,s} + xy_{43}^{\phi,s})\alpha^{\phi} \\
& - r(xy_{43}^{\phi,s} - xy_{34}^{\phi,s})\alpha^{\phi} - \chi(xy_{13}^{\phi,s} - xy_{31}^{\phi,s})/2 \\
& + \{ -(R+r+\chi)xy_{23}^{\phi,s} + (r+\chi-R)xy_{32}^{\phi,s} \\
& + (R+r-\chi)xy_{14}^{\phi,s} + (R+\chi-r)xy_{41}^{\phi,s} \}\alpha^{\phi}/2
\end{aligned} \tag{S.1g}$$

$$\begin{aligned}
Y_{ma}^{\phi'} = & yy_{44}^{\phi,s} + yy_{34}^{\phi,s}/2 + (yy_{14}^{\phi,s} + yy_{24}^{\phi,s})\alpha^{\phi} \\
& - R(yy_{14}^{\phi,s} - yy_{23}^{\phi,s})\alpha^{\phi} \\
& (xy_{44}^{\phi,s} + xy_{24}^{\phi,s})/2 + (xy_{14}^{\phi,s} + xy_{34}^{\phi,s})(1-\alpha^{\phi}) \\
& - r(xy_{34}^{\phi,s} - xy_{43}^{\phi,s})(1-\alpha^{\phi}) - \chi(xy_{24}^{\phi,s} - xy_{42}^{\phi,s})/2 \\
& + \{ -(R+r+\chi)xy_{14}^{\phi,s} + (r+\chi-R)xy_{41}^{\phi,s} \\
& + (R+r-\chi)xy_{23}^{\phi,s} + (R+\chi-r)xy_{32}^{\phi,s} \}(1-\alpha^{\phi})/2
\end{aligned} \tag{S.1h}$$

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The full system is therefore described by 16 recurrence equations (three loci, each
 664 with two alleles, and two gamete sexes yields 16 combinations). However, some
 diploid types are not produced under a given sex determination system. For exam-
 666 ple, with the M allele fixed and ancestral XY sex determination, there are no XX
 males, XY females, or YY females ($xx_{11}^{\phi}, xx_{12}^{\phi}, xx_{22}^{\phi}, xy_{11}^{\phi}, xy_{12}^{\phi}, xy_{22}^{\phi}, yy_{11}^{\phi}, yy_{12}^{\phi}$,
 668 and yy_{22}^{ϕ} are all 0). In this case, the system only involves six recursion equations be-
 cause there is only one M locus allele and no Y-bearing female gametes. This six-
 670 equation system yields equilibrium (2). Within this resident population (when m
 is absent) we describe frequencies among different gamete types, which are given
 672 by $X_{MA}^{\phi} = p_{Xf}$, $X_{Ma}^{\phi} = (1 - p_{Xf})$, $X_{MA}^{\delta} = (1 - q)p_{Xm}$, $X_{Ma}^{\delta} = (1 - q)(1 - p_{Xm})$,
 $Y_{MA}^{\phi} = qp_{Ym}$, and $Y_{Ma}^{\phi} = q(1 - p_{Ym})$. In this resident population, the mean fitnesses
 674 are given in table S.2.

Table S.2: mean fitnesses in resident (M fixed, XY sex determination)

Sex & Life Cycle Stage	Mean Fitness
female gametes (\bar{w}_H^\varnothing)	$p_X^\varnothing w_A^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing$
male gametes (\bar{w}_H^δ)	$\bar{p}^\delta w_A^\delta + (1 - \bar{p}^\delta) w_a^\delta$
females (\bar{w}^\varnothing)	$\frac{\{p_X^\varnothing w_A^\varnothing (1 - q) p_X^\delta w_A^\delta w_{AA}^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing (1 - q) p_X^\delta w_A^\delta w_{Aa}^\varnothing + p_X^\varnothing w_A^\varnothing (1 - q) (1 - p_X^\delta) w_a^\delta w_{Aa}^\varnothing + (1 - p_X^\varnothing) w_a^\varnothing (1 - q) (1 - p_X^\delta) w_a^\delta w_{aa}^\varnothing\}}{\{\bar{w}_H^\varnothing \bar{w}_H^\delta\}}$
males (\bar{w}^δ)	$\frac{\{p_X^\varnothing w_A^\varnothing q p_Y^\delta w_A^\delta w_{AA}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q p_Y^\delta w_A^\delta w_{Aa}^\delta + p_X^\varnothing w_A^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{Aa}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{aa}^\delta\}}{\{\bar{w}_H^\delta \bar{w}_H^\varnothing\}}$

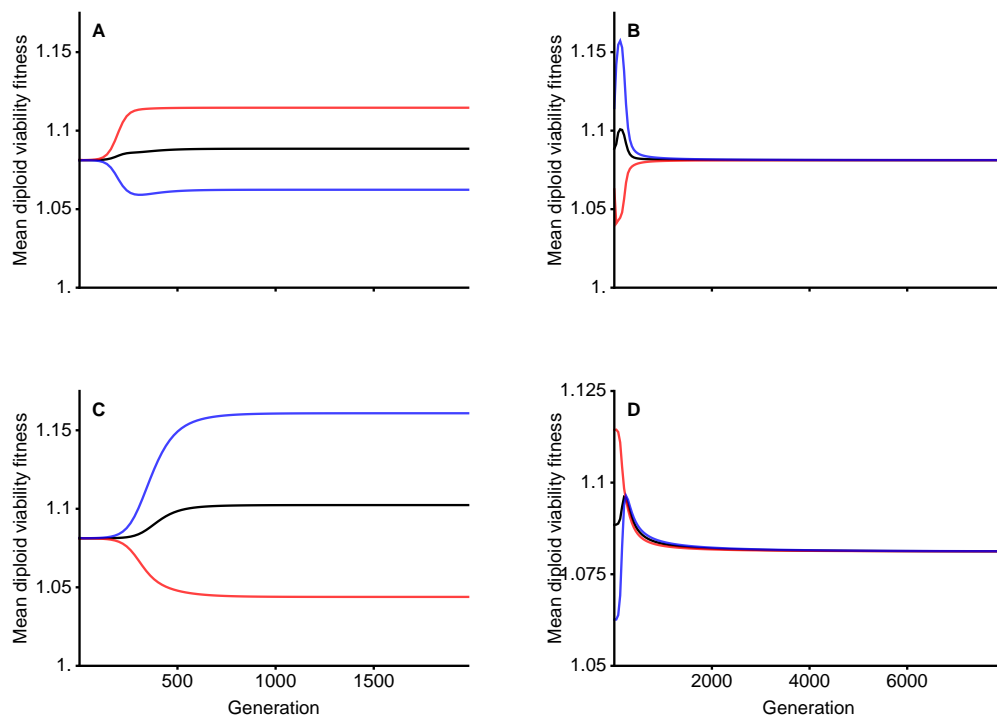


Figure S.1: Could add titles to the columns/rows: neo-W for row 1, neo-Y for row 3, $r = 0.5$, $R = 0.05$ for column 1 and $r = 0.05$, $R = 0.5$ for column 2. & possibly adjust padding (too much whitespace?). Matt - could you uncomment the line legends in the Mathematica file (function not included in my Mathematica version).