

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

Michael F Scott*¹ and Matthew M Osmond*², and Sarah P Otto²

* These authors contributed equally to this work

¹ Department of Botany, University of British Columbia, #3529 - 6270 University
Boulevard, Vancouver, BC, Canada V6T 1Z4

² Department of Zoology, University of British Columbia, #4200 - 6270 University
Boulevard, Vancouver, BC, Canada V6T 1Z4

email: mfscott@biodiversity.ubc.ca, mmosmond@zoology.ubc.ca

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 sex-specific selection on their haploid genotypes during ga-
10 metic competition (e.g., pollen/sperm competition) or meiosis (i.e., meiotic
drive); selective processes that typically occur in one sex or the other. In
12 addition, haploid selection can cause the zygotic sex ratio to become biased
because sex ratios are determined by the production and fertilization success
14 of X- versus Y-bearing pollen/sperm. Notably, we find that the spread of new
genetic sex determination systems is not affected by sex ratio biases that are
16 caused by haploid selection. In addition, we find that, with haploid selection,
transitions between male and female heterogamety (XY to ZW or ZW to XY)
18 can occur despite breaking up favourable associations the between ancestral
sex-determining locus and selected loci. These transitions occur because an
20 unlinked neo-Y (neo-W) can have higher fitness in males (females), even if
the population mean fitness is reduced. Such transitions are not possible
22 with diploid selection alone, in which case tighter linkage increases the fit-
ness of both males and females. Furthermore, a period of selection among
24 haploids can favour the stable maintenance of polymorphic sex determina-
tion systems. Thus, our models offer several new insights to be explored as
26 information about sex determination in non-model taxa accumulates.

Introduction

28 Animals and angiosperms exhibit extremely diverse sex determination systems (re-
viewed in Bull 1983, Charlesworth and Mank 2010, Beukeboom and Perrin 2014,
30 Bachtrog et al. 2014). Among species with genetic sex determination of diploid
sexes, some taxa have heterogametic males (XY) and homogametic females (XX),
32 including mammals and most dioecious plants (Ming et al. 2011); whereas other
taxa have homogametic males (ZZ) and heterogametic females (ZW), including
34 Lepidoptera and birds. Within several taxa, the chromosome that harbours the
master sex-determining region changes. For example, transitions of the master
36 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),
38 Diptera (Vicoso and Bachtrog 2015), and *Oryzias* (Myosho et al. 2012). In ad-
dition, many gonochoric/dioecious clades with genetic sex determination exhibit
40 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
42 flies (Tephritids, Vicoso and Bachtrog 2015), amphibians (Hillis and Green 1990),
the angiosperm genus *Silene* (Slancarova et al. 2013), Coleoptera and Hemiptera
44 (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,
46 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
48 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
50 et al. 2010, Holleley et al. 2015).

Predominant theories in which new sex determination systems are favoured by
52 selection involve fitness differences between sexes (e.g., sexually antagonistic se-
lection) or sex ratio selection. van Doorn and Kirkpatrick (2007; 2010) show that
54 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
56 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
58 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
60 and Kirkpatrick 2010). However, any sexually-antagonistic loci that are linked to
the ancestral sex-determination locus will develop similar, favourable associations
62 and select against the spread of a new sex-determination system.

It has been suggested that sex ratio selection could be a particularly impor-
64 tant force driving transitions between sex-determining systems (Beukeboom and
Perrin 2014, Chapter 7). For example, flexible sex determination systems may be
66 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,
68 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
70 (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,
72 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
74 disproportionately often), which causes sex ratios to become biased (Hamilton
1967). They find that new, unlinked sex-determining loci (masculinizing or femi-
76 nizing mutations, i.e., neo-Y or neo-W loci) can then spread, restoring an even sex
ratio.

78 Here, we use mathematical models to find the conditions under which new
sex determination systems are favoured when loci experience haploid selection.
80 Haploid genotypes at many loci experience selection during gamete competition
and/or meiotic drive (Mulcahy et al. 1996, Joseph and Kirkpatrick 2004). We
82 use the term ‘meiotic drive’ to refer to the biased (non-Mendelian) segregation of
genotypes during gamete production and the term ‘gametic competition’ to refer
84 to selection upon haploid genotypes within a gamete/gametophyte pool; the term
‘haploid selection’ encompasses both processes. Meiotic drive generally occurs
86 either during the production of male or female gametes only (Ubeda and Haig,

2005; Lindholm et al. 2016). Because there are typically more pollen/sperm than
88 required for fertilization, gametic competition is also typically sex specific, oc-
curring primarily among male gametes. Gametic competition may be particularly
90 common in plants, in which 60-70% of all genes are expressed in the male game-
tophyte and these genes exhibit stronger signatures of selection than random genes
92 (Borg et al. 2009, Arunkumar et al. 2013, Gossmann et al. 2014). In addition, ar-
tificial selection pressures applied to male gametophytes cause the frequency of
94 resistant alleles to increase (e.g., Hormaza and Herrero 1996, Ravikumar et al.
2003, Hedhly et al. 2004, Clarke et al. 2004). A smaller (but non-negligible) pro-
96 portion of genes are thought to be expressed and selected during competition in
animal sperm, although precise estimates are uncertain (Zheng et al. 2001, Joseph
98 and Kirkpatrick 2004, Vibranovski et al. 2010).

There are various ways in which a period of haploid selection could influence
100 transitions between sex determination systems. Firstly, if we assume that haploid
selection at any particular locus predominantly occurs in one sex (e.g., meiotic
102 drive during spermatogenesis), then such loci experience a form of sex-specific
selection. In this respect, we might expect that haploid selection might affect
104 transitions between sex determination systems in a similar manner to sex-specific
diploid selection (as explored by van Doorn and Kirkpatrick 2007; 2010). That
106 is, new masculinizing mutations (neo-Y chromosomes) could be favoured via asso-
ciations with alleles that are beneficial in the male haploid stage. However, sex
108 ratios can also become biased by linkage between the sex-determining region and
a locus that harbours genetic variation in haploid fitness. For example, there are
110 several known cases of sex ratio bias caused by sex-linked meiotic drive alleles
(?, , Chapter 3) or selection among X- and Y-bearing pollen (Lloyd 1974, Conn
112 and Blum 1981, Stehlik and Barrett 2005; 2006, Field et al. 2012; 2013). It is not
immediately clear how the spread of new sex determination systems would be in-
114 fluenced by the combination of sex ratio biases and associations between haploid
selected loci and sex-determining regions.

116 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 determination 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 associations 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 selection. This does not occur in models that do not include haploid selection.

Model

We consider the transition between an ancestral and novel sex determination systems 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 alleles 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 evaluate 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 epistatically 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 determination such that zygotes develop as females in a proportion (k) of the environments they experience. Finally, we also analyze a model of maternally-controlled environmental sex-determination (ESD), where mothers with at least one m allele produce daughters with probability k .

In each generation, we census the genotype frequencies in male and female
 gametes/gametophytes (hereafter gametes) before gametic competition (see Sup.
 Mat. for recursion equations). First, competition occurs among male gametes
 (sperm/pollen competition) and among female gametes (egg/ovule competition)
 separately. Selection during gametic competition depends on the **A** locus geno-
 type, relative fitnesses are given by w_A^{ϕ} and w_a^{ϕ} ($\phi \in \{\text{♀}, \text{♂}\}$; see table 1). We as-
 sume that all gametes compete for fertilization during gametic competition, which
 is not the case for monogamous mating systems where gametes from only one mat-
 ing partner are present. Gametic competition in monogamous mating systems is
 equivalent to meiotic drive in our model, which only alters the frequency of ga-
 metes produced by heterozygotes. After gametic competition, random mating oc-
 curs between male and female gametes. The resulting zygotes develop as males or
 females, depending on their genotypes at the **X** and **M** loci (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 given by w_g^{δ} in males and
 $w_g^{\text{♀}}$ 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 by meiosis, during which recom-
 bination and sex-specific meiotic drive can occur. Recombination occurs between
 loci **X** and **A** with probability r , between loci **A** and **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 Table S.1). Males/females
 that are heterozygous at the **A** locus experience meiotic drive; Aa heterozygotes of
 sex ϕ produce gametes bearing allele A with probability α^{ϕ} . Thus, the **A** locus
 can experience sex-specific gametic competition, diploid selection and/or meiotic
 drive.

Results

The only asymmetry between males and females in our model is that, under the
 ancestral sex determination system, males develop with genotype XY (or ZZ) and

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

Genotype	Relative fitness during gametic 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	$(1 - \alpha^\phi) = 1/2 - \alpha_\Delta^\phi/2$

females with genotype XX (or ZW). Therefore, without loss of generality, we
174 primarily present results for ancestral XY sex determination. Ancestral ZW sex
determination can be considered by changing the notation such that X becomes Z ,
176 Y becomes W and the labelling of male and female selection terms are reversed.

Resident equilibrium and stability

178 In the resident population (allele M fixed), we follow the frequency of A in female
gametes (eggs) from an XX female, p_X^ϕ , and in X -bearing, p_X^ϕ , and Y -bearing,
180 p_Y^ϕ , 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.

182 Various forms of selection can maintain a polymorphism at the **A** locus, includ-
ing sexually antagonistic selection, overdominance and conflicts between diploid
184 selection and selection upon haploid genotypes (ploiddally antagonistic selection,
Immler et al. 2012) or a combination of these selective regimes. Here, we assume
186 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

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

188 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
 190 ($s^\delta = s^\varphi$, $h^\delta = h^\varphi$, and $\alpha^\delta = \alpha^\varphi = 1/2$), the equilibrium allele frequency and
 stability can be calculated analytically without assuming weak selection. How-
 192 ever, here, we focus on weak selection in order to make fewer assumptions about
 fitnesses.

194 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
 196 gamete are the same ($\hat{p}_X^\varphi = \hat{p}_X^\delta = \hat{p}_Y^\delta = \bar{p}$) and given by

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

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

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

where $V_A = \bar{p}(1 - \bar{p})$ is the variance in the frequency of *A* and $D^\varphi = (\bar{p}s^\varphi +$
 200 $(1 - \bar{p})h^\varphi s^\varphi) - (\bar{p}h^\varphi s^\varphi + (1 - \bar{p}))$ 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
 202 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
 204 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 gametic competition or drive

206 $(\alpha_{\Delta}^{\phi} = t^{\phi} = 0)$, these results reduce to those of van Doorn and Kirkpatrick (2007).

Turnover between sex-determination systems

208 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
 210 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
 212 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
 214 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
 216 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
 218 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
 220 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
 222 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, $c =$
 224 $\lambda_{mA}\lambda_{ma} + \rho_{mA}\rho_{ma}$ (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
see Table S.2 for mean fitnesses.

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 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 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).

240 Thus, eggs with and without a neo-W differ in the frequency of A alleles they obtain from mating with male gametes.

242 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
244 solves (4) is greater than one. If the average change in frequency of the two haplotypes that carry the m allele (Am and am) is positive, invasion will always occur
246 (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-determining allele increases in frequency on one \mathbf{A} background and declines on
248 the other, and invasion requires

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

250 for the neo-Y, and

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

252 **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
254 expected to invade for any recombination rate, R , when the net flow of recombinants is from the less fit (smaller λ_{mi}) to the more fit \mathbf{A} background (making the
256 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?**

258 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 between 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 it might be better to have slightly different phrasing here.**
262

264 We can explicitly determine the conditions under which invasion occurs if we assume that the A allele reaches an equilibrium frequency under the ancestral sex-

determination system before the neo-sex-determination system (m) arises. The
 266 equilibrium frequency of A on different ancestral backgrounds (\hat{p}_Y^δ , \hat{p}_X^δ , and \hat{p}_X^\varnothing) is
 given by equations (2) and (3) where we assume selection and meiotic drive are
 268 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
 270 neo-W ($k = 0$) into an ancestrally XY system by $\lambda_{Y',XY}$ and $\lambda_{W',XY}$, respectively,
 which are given by

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

272 and

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

where $V_A = \bar{p}(1 - \bar{p})$ is the variance in the frequency of A and $S_A = (D^\delta + \alpha_\Delta^\delta + t^\delta) -$
 274 $(D^\varnothing + \alpha_\Delta^\varnothing + t^\varnothing)$ is the difference in fitness in males versus females for the A allele
 against the a allele across diploid selection, gametic competition, and meiosis.

276 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
 278 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
 280 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-
 282 determining locus is more closely linked to a locus under sexually-antagonistic
 selection.

284 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
 286 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
 288 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

290 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
 292 $R > r$, associations that build up by selection between sex and alleles will be
 weakened. Therefore, mean fitness can decrease, see Figure S.1.

294 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-
 296 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
 298 $(\hat{p}_Y^\delta - \hat{p}_X^\delta) = 0$ 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
 300 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
 302 $R = 1/2$ 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
 304 sex (e.g., during male meiosis only) and equal dominance, $h^\varrho = h^\delta$. Where there
 is no gametic competition and meiotic drive in one sex only, an unlinked neo-W
 306 can invade as long as the same allele is favoured in male and female diploid selec-
 tion ($s^\varrho s^\delta > 0$, see Figure 2B), which is 50% of the parameter space. Where there
 308 is no meiotic drive and gametic 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
 310 selection and there are sex differences in selection of one type ($-s^\varrho(s^\varrho - s^\delta) > 0$,
 see Figure 2C,D), which is 25% of the parameter space. These special cases in-
 312 dicate that neo-W invasion can occur for a relatively large fraction of parameter
 space, even if $R > r$.

314 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
 316 sex-determining locus invades in order to restore equal sex ratios (Kozielska et al.
 2010). Our model provides a good opportunity to determine whether Fisherian
 318 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**

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
$h^\delta = h^\varphi, t^\varphi = t^\delta = \alpha_{\Delta}^\varphi = 0$	$s^\varphi s^\delta > 0$
$h^\delta = h^\varphi, t^\varphi = t^\delta = \alpha_{\Delta}^\delta = 0$	$s^\varphi s^\delta > 0$
$h^\delta = h^\varphi, t^\varphi = \alpha_{\Delta}^\varphi = \alpha_{\Delta}^\delta = 0$	$-s^\varphi(s^\varphi - s^\delta) > 0$
$h^\delta = h^\varphi, t^\delta = \alpha_{\Delta}^\varphi = \alpha_{\Delta}^\delta = 0$	$-s^\varphi(s^\varphi - s^\delta) > 0$

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, $\alpha^\delta \neq 1/2$, $\alpha^\varphi = 1/2$). We will also disregard gametic competition ($t^\varphi = t^\delta = 0$) such that zygotic sex ratios can only be biased by meiotic drive in males. In this case, the zygotic sex ratio can be initially biased only if the ancestral sex-determining system is XY (Figure 1B). If the ancestral sex-determining system is ZW, the zygotic 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, 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 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) 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.

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 (since $\lambda_{Y,XY} =$
 338 $\lambda_{W,ZW}$, $\lambda_{W,XY} = \lambda_{Y,ZW}$). Thus with $k = 1/2$ the neo-ESD gets half of the advan-
 340 tages 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
 342 locus, R , doesn't enter into the $k = 1/2$ results because sex is essentially random-
 ized each generation, preventing associations from building up between allele A
 344 and sex.

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

Maternally-controlled neo-ESD

348 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
 350 find that, as with offspring control, under weak selection the invasion fitness of a
 sex-determiner that is maternally controlled can be written

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

352 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
 354 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
 356 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 ?? – ??).

358 Discussion

One might expect Fisherian sex ratio selection to influence the spread of new
 360 sex-determining systems because linkage between haploid selected loci and sex-

determining regions cause biased zygotic sex ratios (Hamilton 1967, ?, Field et al. 2012; 2013). Fisherian sex ratio selection follows from the fact that, for an autosomal locus, half of the genetic 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 genetic 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 increases investment in males will spread via the higher per-individual contributions made by males. That is, under Fisherian sex ratio selection, the success of 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 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-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 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 autosomal if they determine sex. Thus, despite the fact that sex ratio biases caused by gametic competition or meiotic drive have been shown to exert selection on 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 sex ratio selection acting upon neo-sex-determination systems (e.g., see Figure 1 and Úbeda et al. 2015, in which a neo-Y invades despite biasing sex ratios).

It has previously been demonstrated that new sex-determining systems can evolve if there is genetic variation maintained by sexually-antagonistic selection (van Doorn and Kirkpatrick 2007; 2010). In particular, transitions to new sex-determining systems can occur when new sex-determining regions are more closely linked to a sexually-antagonistic locus. Our results show that genetic variation at loci that experience haploid selection can also generate selection in favour of new sex-determining systems. New sex-determining alleles are again favoured if they

are more closely linked with a locus under haploid selection. However, with hap-
392 loid selection, heterogametic transitions (XY to ZW or ZW to XY) can also occur
when the new sex-determining region is less closely linked to the locus under se-
394 lection.

Neo-W (neo-Y) alleles invade when their fitness in females (males) is greater
396 than the mean fitness of females (males) under the ancestral sex determination
system. With sexually antagonistic selection (between diploid sexes) only, linkage
398 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-
400 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-
402 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
404 haploid selection on loci linked to an XY (ZW) sex-determining region, polymor-
phisms can be maintained at which the mean fitness of females (males) or males
406 is lower than it would be without sex-linkage, allowing unlinked neo-W (neo-Y)
alleles to invade, see figure S.1.

408 We assume that sex-determining alleles do not experience direct selection ex-
cept via their associations with sex and alleles at a selected locus. However, in
410 some cases, there may be significant degeneration around the sex-limited allele (Y
or W) in the ancestral sex determining region because recessive deleterious muta-
412 tions and/or deletions may fix around the Y or W allele (Rice 1996, Charlesworth
and Charlesworth 2000, Bachtrog 2006, Marais et al. 2008). During heterogametic
414 transitions (XY to ZW or ZW to XY), the formally sex-limited allele fixes such
that all individuals have YY or WW genotypes (Figure 1). Any recessive deleter-
416 ious alleles linked to the Y or W will therefore be revealed to selection during a
heterogametic transition. This phenomenon was studied by van Doorn and Kirk-
418 patrick (2010), who found that degeneration can prevent fixation of a neo-W or
a neo-Y allele, leading to a mixed sex determination system where the ancestral-
420 and neo- sex-determining loci are both polymorphic. However, they noted that

very rare recombination events around the ancestral sex-determining region can
422 allow these heterogametic transitions to complete.

Our model of meiotic drive is very simple, involving a single locus with two
424 alleles. However, many meiotic drive systems involve an interaction with another
locus at which alleles may ‘suppress’ the action of meiotic drive (?) (Lindholm et
426 al. 2016). Thus, the dynamics of meiotic drive alleles can be heavily dependent on
the interaction between two loci and the recombination rate between them, which
428 in turn can be affected by sex-linkage if there is reduced recombination between
sex chromosomes (Hurst and Pomiankowski, 1991). Furthermore, in some cases, a
430 driving allele may act by killing any gametes that carry a ‘target’ allele at another
locus, in which case there is a two-locus drive system and the total number of
432 gametes produced can be reduced by meiotic drive (here, we assume that the total
gamete number is not affected by drive). Thus, the number of mates competing
434 for fertilization (mating system) can further affect the frequency of a meiotic drive
allele (Holman et al., 2015). Finally, the intensity of pollen/sperm competition
436 under a particular mating system can depend on the density of males available to
donate pollen/sperm, which can depend on the sex ratio and population size (Taylor
438 and Jaenike, 2002). Here, we do not consider feedbacks between sex ratios and
the intensity of haploid selection. It remains to be investigated how the evolution
440 of new sex-determining mechanisms could be influenced by ecological feedbacks
under different mating systems and by two-locus meiotic drive.

442 The hypotheses presented here can be investigated in a similar manner to the
idea that transitions between sex-determining systems are favoured by linkage to
444 sexually antagonistic variation. In the case of sexually antagonistic variation, one
supporting observation is that genes that appear to experience sexually-antagonistic
446 selection have been found on recently derived sex chromosomes CHECK (Kallman
1973; Wada et al. 1998; Lande et al. 2001; Lindholm and Breden 2002; Streelman
448 et al. 2003; Fernandez and Morris 2008; Kitano et al. 2009; Roberts et al. 2009).
However, it is possible that sexually antagonistic variation accumulated after sex
450 chromosome transitions because linkage with the sex-determining regions allows

sexually antagonistic selection to maintain polymorphisms under a larger parameter space (Rice, 1987, Jordan and Charlesworth, 2010-ish). We note that linkage with sex chromosomes is not, a priori, more permissive to the maintenance of ploidally antagonistic variation (Immler et al. 2012). Secondly, we note that new sex-determination systems can be favoured if either the ancestral sex-determining region or the new sex-determining region are linked to loci under haploid selection. Therefore, the presence of haploid selected loci around ancestral- or new-sex-determining regions could support their role in sex chromosome turnover.

Do we have any cool examples? Meiotic drive alleles certainly more common on the sex chromosomes - although there are other explanations: (1) Divergence between X and Y provides a ready supply of target alleles for meiotic drive. (2) sex-linked meiotic drive has a more obvious phenotype to detect, sex ratio bias.

Taken at face value, our results indicate that transitions in heterogamety (XY to ZW or vice versa) are more likely to be favoured by selection if there is selection upon both haploid and diploid genotypes rather than diploid selection alone. Thus, In broadcast spawning animal species (e.g., corals, many fish) and species where sperm typically requires greater longevity, haploid selection may be stronger because transcripts shared during spermatogenesis may become depleted (Immler et al. 2014). also, mating systems (e.g., fewer alleles are available during gametic competition in monogamous species), selfing rates, and estimates of pollen limitation could be used as indicators of the intensity of haploid selection We have results where polygenic sex determination is sometimes stable, may be worth mentioning:

“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. 2012), crustaceans (e.g. Battaglia 1958; Battaglia & Malesani 1959; Voordouw & Anholt 2002), bivalves (Haley 1977; Saavedra et al. 1997), gastropods (Yusa 2007a,b), and polychaetes (Bacci 1965, 1978; Premoli et al. 1996).” From Vuilleumier et al. 2007: “Polymorphism for sex-determining genes within or among populations has been reported in many species including houseflies, midges, woodlice,

platyfish, cichlid fish, and frogs (Gordon, 1944; Kallman, 1970; Thompson, 1971;
482 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).” Also check
484 Kallman (1984) -from vD&K, 2010.

vD&K also suggest that this build up of sex-antagonistic polymorphisms may
486 help to stabilize the ancestral sex-determining system, which would not be the case
with haploid selection.

488 **References**

Arun Kumar, R., E. B. Josephs, R. J. Williamson, and S. I. Wright. 2013. Pollen-
490 specific, but not sperm-specific, genes show stronger purifying selection and
higher rates of positive selection than sporophytic genes in *Capsella grandiflora*.
492 Molecular biology and evolution 30:2475–2486.

Bachtrog, D. 2006. A dynamic view of sex chromosome evolution. Current opin-
494 ion in genetics & development 16:578–585.

Bachtrog, D., J. E. Mank, C. L. Peichel, M. Kirkpatrick, S. P. Otto, T.-L. Ashman,
496 M. W. Hahn, J. Kitano, I. Mayrose, R. Ming, N. Perrin, L. Ross, N. Valenzuela,
J. C. Vamosi, and Tree of Sex Consortium. 2014. Sex determination: why so
498 many ways of doing it? PLoS Biol 12:e1001899.

Beukeboom, L. W., and N. Perrin. 2014. The evolution of sex determination.
500 Oxford University Press, Oxford, UK.

Borg, M., L. Brownfield, and D. Twell. 2009. Male gametophyte development: a
502 molecular perspective. Journal of Experimental Botany 60:1465–1478.

Bull, J. J. 1983. Evolution of sex determining mechanisms. The Benjamin Cum-
504 mings Publishing Company.

- Charlesworth, B., and D. Charlesworth. 2000. The degeneration of Y chromosomes. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 355:1563–1572.
- Charlesworth, D., and J. E. Mank. 2010. The birds and the bees and the flowers and the trees: lessons from genetic mapping of sex determination in plants and animals. Genetics 186:9–31.
- Charnov, E. L., and J. Bull. 1977. When is sex environmentally determined? Nature 266:828–830.
- Clarke, H. J., T. N. Khan, and K. H. M. Siddique. 2004. Pollen selection for chilling tolerance at hybridisation leads to improved chickpea cultivars. Euphytica 139:65–74.
- Conn, J. S., and U. Blum. 1981. Sex ratio of *Rumex hastatulus*: the effect of environmental factors and certation. Evolution 35:1108–1116.
- Conover, D. O., and S. W. Heins. 1987. Adaptive variation in environmental and genetic sex determination in a fish. Nature 326:496–498.
- Ezaz, T., S. D. Sarre, and D. O’Meally. 2009. Sex chromosome evolution in lizards: independent origins and rapid transitions. Cytogenetic and Genome Research 127:249–260.
- Field, D. L., M. Pickup, and S. C. H. Barrett. 2012. The influence of pollination intensity on fertilization success, progeny sex ratio, and fitness in a wind-pollinated, dioecious plant. International Journal of Plant Sciences 173:184–191.
- . 2013. Comparative analyses of sex-ratio variation in dioecious flowering plants. Evolution 67:661–672.
- Frank, S. A. 1989. The Evolutionary Dynamics of Cytoplasmic Male Sterility. American Naturalist 133:345–376.

- Gossmann, T. I., M. W. Schmid, U. Grossniklaus, and K. J. Schmid. 2014.
 532 Selection-driven evolution of sex-biased genes Is consistent with sexual selec-
 tion in *Arabidopsis thaliana*. *Molecular biology and evolution* 31:574–583.
- 534 Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Hedhly, A., J. I. Hormaza, and M. Herrero. 2004. Effect of temperature on pollen
 536 tube kinetics and dynamics in sweet cherry, *Prunus avium* (Rosaceae). *Ameri-
 can journal of botany* 91:558–564.
- 538 Hillis, D. M., and D. M. Green. 1990. Evolutionary changes of heterogametic
 sex in the phylogenetic history of amphibians. *Journal of Evolutionary Biology*
 540 3:49–64.
- Holleley, C. E., D. O’Meally, S. D. Sarre, J. A. Marshall Graves, T. Ezaz, K. Mat-
 542 subara, B. Azad, X. Zhang, and A. Georges. 2015. Sex reversal triggers the
 rapid transition from genetic to temperature-dependent sex. *Nature* 523:79–82.
- 544 Hormaza, J. I., and M. Herrero. 1996. Male gametophytic selection as a plant
 breeding tool. *Scientia horticultrae* 65:321–333.
- 546 Hough, J., S. Immler, S. Barrett, and S. P. Otto. 2013. Evolutionarily stable sex
 ratios and mutation load. *Evolution* 7:1915–1925.
- 548 Immler, S., G. Arnqvist, and S. P. Otto. 2012. Ploidally antagonistic selection
 maintains stable genetic polymorphism. *Evolution* 66:55–65.
- 550 Immler, S., C. Hotzy, G. Alavioon, E. Petersson, and G. Arnqvist. 2014. Sperm
 variation within a single ejaculate affects offspring development in Atlantic
 552 salmon. *Biology letters* 10:20131040.
- Joseph, S., and M. Kirkpatrick. 2004. Haploid selection in animals. *Trends in*
 554 *Ecology & Evolution* 19:592–597.

- Kozielska, M., F. J. Weissing, L. W. Beukeboom, and I. Pen. 2010. Segregation
556 distortion and the evolution of sex-determining mechanisms. *Heredity* 104:100–
112.
- 558 Li, J., R. B. Phillips, A. S. Harwood, B. F. Koop, and W. S. Davidson. 2011. Ident-
tification of the Sex Chromosomes of Brown Trout (*Salmo trutta*) and Their
560 Comparison with the Corresponding Chromosomes in Atlantic Salmon (*Salmo*
salar) and Rainbow Trout (*Oncorhynchus mykiss*). *Cytogenetic and Genome*
562 *Research* 133:25–33.
- Lloyd, D. G. 1974. Female-predominant sex ratios in angiosperms, vol. 32. *Hered-*
564 *ity*.
- Mank, J. E., D. E. L. Promislow, and J. C. Avise. 2006. Evolution of alterna-
566 tive sex-determining mechanisms in teleost fishes. *Biological Journal of the*
Linnean Society 87:83–93.
- 568 Marais, G. A. B., M. Nicolas, R. Bergero, P. Chambrier, E. Kejnovsky, F. Monéger,
R. Hobza, A. Widmer, and D. Charlesworth. 2008. Evidence for degeneration
570 of the Y chromosome in the dioecious plant *Silene latifolia*. *Current Biology*
18:545–549.
- 572 Ming, R., A. Bendahmane, and S. S. Renner. 2011. Sex chromosomes in land
plants. [dx.doi.org 62:485–514](https://doi.org/10.1093/aob/mbr244).
- 574 Mulcahy, D. L., M. Sari-Gorla, and G. B. Mulcahy. 1996. Pollen selection - past,
present and future. *Sexual Plant Reproduction* 9:353–356.
- 576 Myosho, T., H. Otake, H. Masuyama, M. Matsuda, Y. Kuroki, A. Fujiyama,
K. Naruse, S. Hamaguchi, and M. Sakaizumi. 2012. Tracing the Emergence
578 of a Novel Sex-Determining Gene in Medaka, *Oryzias luzonensis*. *Genetics*
191:163–170.

- 580 Ogata, M., Y. Hasegawa, H. Ohtani, M. Mineyama, and I. Miura. 2007. The
ZZ/ZW sex-determining mechanism originated twice and independently during
582 evolution of the frog, *Rana rugosa*. *Heredity* 100:92–99.
- Otto, S. P., M. F. Scott, and S. Immler. 2015. Evolution of haploid selection in
584 predominantly diploid organisms. *Proceedings of the National ...*
- Pen, I., T. Uller, B. Feldmeyer, A. Harts, G. M. While, and E. Wapstra. 2010.
586 Climate-driven population divergence in sex-determining systems. *Nature*
468:436–438.
- 588 Pokorná, M., and L. Kratochvíl. 2009. Phylogeny of sex-determining mecha-
nisms in squamate reptiles: are sex chromosomes an evolutionary trap? *Zoo-
590 logical Journal of the ...* 156:168–183.
- Ravikumar, R. L., B. S. Patil, and P. M. Salimath. 2003. Drought tolerance in
592 sorghum by pollen selection using osmotic stress. *Euphytica* 133:371–376.
- Rice, W. R. 1996. Evolution of the Y Sex Chromosome in Animals. *BioScience*
594 46:331–343.
- Ser, J. R., R. B. Roberts, and T. D. Kocher. 2010. Multiple interacting loci control
596 sex determination in lake Malawi cichlid fish. *Evolution* 64:486–501.
- Slancarova, V., J. Zdanska, B. Janousek, M. Talianova, C. Zschach, J. Zluvova,
598 J. Siroky, V. Kovacova, H. Blavet, J. Danihelka, B. Oxelman, A. Widmer, and
B. Vyskot. 2013. Evolution of sex determination systems with heterogametic
600 males and females in *Silene*. *Evolution* 67:3669–3677.
- Smith, D. A. S. 1975. All-female broods in the polymorphic butterfly *Danaus*
602 *chrysippus* L. and their ecological significance. *Heredity* 34:363–371.
- Stalker, H. D. 1961. The Genetic Systems Modifying Meiotic Drive in *Drosophila*
604 *Paramelanica*. *Genetics* .

- 606 Stehlik, I., and S. Barrett. 2005. Mechanisms governing sex-ratio variation in
dioecious *Rumex nivalis*. *Evolution* 59:814–825.
- 608 Stehlik, I., and S. C. H. Barrett. 2006. Pollination intensity influences sex ratios in
dioecious *Rumex nivalis*, a wind-pollinated plant. *Evolution* 60:1207–1214.
- 610 Úbeda, F., M. M. Patten, and G. Wild. 2015. On the origin of sex chromosomes
from meiotic drive. *Proceedings of the Royal Society B: Biological Sciences*
282:20141932.
- 612 van Doorn, G. S., and M. Kirkpatrick. 2007. Turnover of sex chromosomes in-
duced by sexual conflict. *Nature* 449:909–912.
- 614 ———. 2010. Transitions Between Male and Female Heterogamety Caused by
Sex-Antagonistic Selection. *Genetics* 186:629–645.
- 616 Vibrationovski, M. D., D. S. Chalopin, H. F. Lopes, M. Long, and T. L. Karr. 2010.
Direct evidence for postmeiotic transcription during *Drosophila melanogaster*
618 spermatogenesis. *Genetics* 186:431–433.
- Vicoso, B., and D. Bachtrog. 2015. Numerous transitions of sex chromosomes in
620 Diptera. *PLoS Biol* 13:e1002078.
- Vuillleumier, S., R. Lande, J. J. M. van Alphen, and O. Seehausen. 2007. Invasion
622 and fixation of sex-reversal genes. *Journal of Evolutionary Biology* 20:913–920.
- Werren, J. H., and P. D. Taylor. 1984. The effects of population recruitment on sex
624 ratio selection. *The American Naturalist* 124:143–148.
- Wilson, D. S., and R. K. Colwell. 1981. Evolution of sex ratio in structured demes.
626 *Evolution* 35:882–897.
- Yano, A., B. Nicol, E. Jouanno, E. Quillet, A. Fostier, R. Guyomard, and
628 Y. Guiguen. 2012. The sexually dimorphic on the Y-chromosome gene (sdY)
is a conserved male-specific Y-chromosome sequence in many salmonids. *Evo-
630 lutionary Applications* 6:486–496.

632 Zheng, Y., X. Deng, and P. A. Martin-DeLeon. 2001. Lack of sharing of Spam1
(Ph-20) among mouse spermatids and transmission ratio distortion. *Biology of
Reproduction* 64:1730–1738.

634 **Figures**

Appendix

Recursion Equations

In each generation we census the genotype frequencies in male and female gametes/gametophytes (hereafter, gametes) before gametic competition. Before gametic 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 gametic competition are $X_i^{\varphi,s} = w_g X_i^\varphi / \bar{w}_H^\varphi$ and $Y_i^{\varphi,s} = w_g Y_i^\varphi / \bar{w}_H^\varphi$, where $\bar{w}_H^\varphi = \sum_{i=1}^4 w_g X_i^\varphi + w_g Y_i^\varphi$ is the mean fitness of male ($\varphi = \delta$) or female ($\varphi = \varphi$) 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 epistatic 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

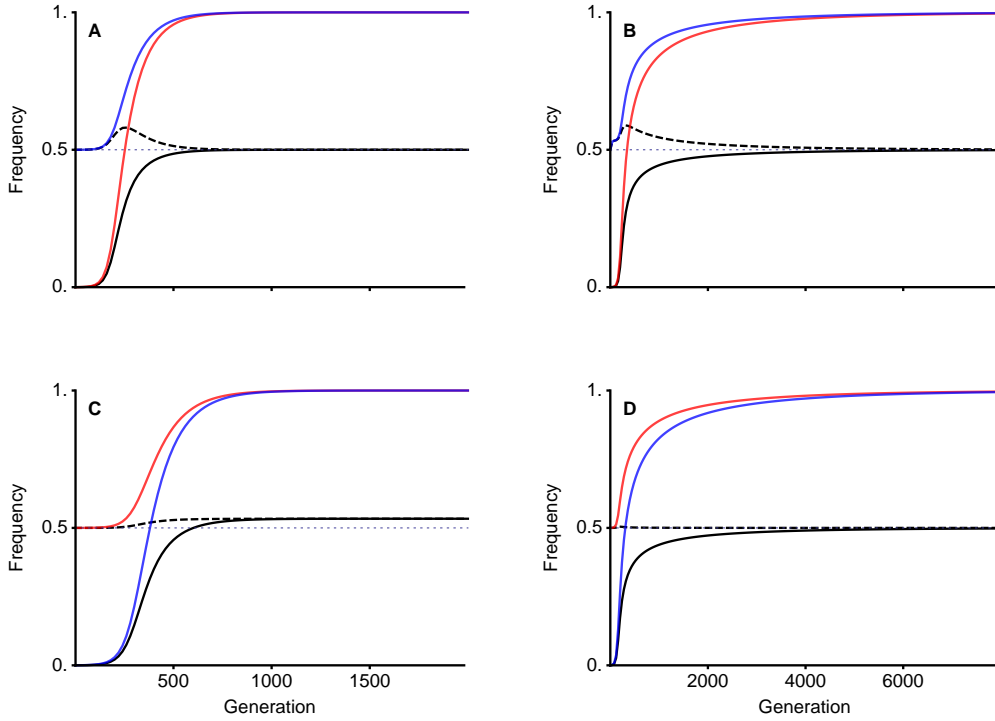


Figure 1: Heterogametic transitions from XY to ZW sex determination (neo-W frequency shown by black lines, panels A and B) or from ZW to XY (neo-Y frequency shown by black lines, panels C and D) occurs similarly regardless of sex ratio biases present before (B versus D) or after (C versus A, dashed lines 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 gametic competition ($r^{\varnothing} = r^{\sigma} = 0$) and meiotic drive occurs during male meiosis only ($\alpha_{\Delta}^{\varnothing} = 0$, $\alpha_{\Delta}^{\sigma} = -1/5$). 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, $s^{\varnothing} = s^{\sigma} = 1/5$, $h^{\varnothing} = h^{\sigma} = 7/10$. **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).

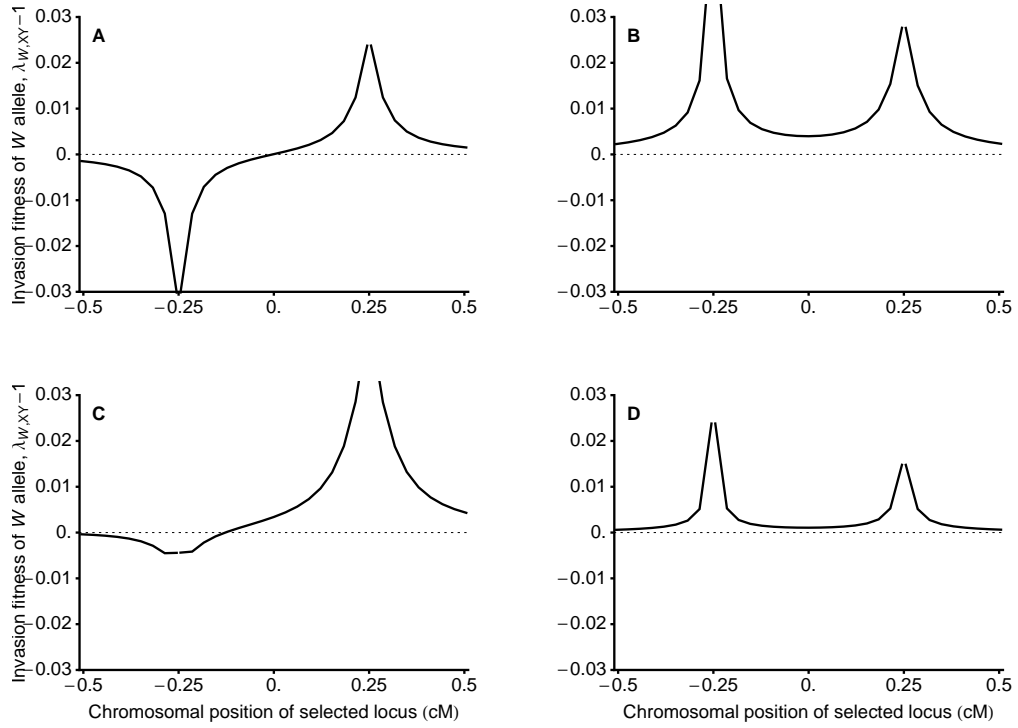


Figure 2: A sexual antagonism (no haploid selection), B drive (no gametic competition), equal selection in sexes ($s^{\varnothing} = s^{\sigma}$), C & D Pollen/Sperm competition only (no drive). C allele favoured in pollen/sperm competition selected against less in males ($t < 0$, $s^{\varnothing}, s^{\sigma} > 0$, $s^{\varnothing} < s^{\sigma}$). 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)

664 $k_{MMXY} = k_{MYY} = 0$) and epistatically recessive to a dominant novel sex-determining locus, \mathbf{M} ($k_{Mmc} = k_{mmc} = k$).

666 Selection among diploids then occurs according to the diploid genotype at the \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 $xx_{ij}^{\phi,s} = w_h^{\phi}xx_{ij}/\bar{w}^{\phi}$, $xy_{ij}^{\phi,s} = w_h^{\phi}xy_{ij}/\bar{w}^{\phi}$, 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 .

672 Finally, these diploids undergo meiosis to produce the next generation of gametes. Recombination and sex-specific meiotic drive occur during meiosis. Here, we allow the relative locations of the SDR, \mathbf{A} , and \mathbf{M} loci to be generic by using 674 three parameters to describe the recombination rates between them. R is the recombination rate between the \mathbf{A} locus and the \mathbf{M} locus, χ is the recombination rate 676 between the \mathbf{M} locus and the \mathbf{X} locus, and r is the recombination rate between the \mathbf{A} locus and the \mathbf{X} locus. Table S.1 gives substitutions for χ for defined relative 678 locations of these loci. During meiosis in sex d , meiotic drive occurs such that, in Aa heterozygotes, a fraction α_d of gametes produced carry the A allele and $(1 - \alpha_d)$ 680 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	$\chi = (R - r)/(1 - 2r)$

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

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

684

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

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

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

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

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

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

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

The full system is therefore described by 16 recurrence equations (three loci, each with two alleles, and two gamete sexes yields 16 combinations). However, some diploid types are not produced under a given sex determination system. For example, with the M allele fixed and ancestral XY sex determination, there are no XX males, XY females, or YY females ($xx_{11}^{\phi}, xx_{12}^{\phi}, xx_{22}^{\phi}, xy_{11}^{\phi}, xy_{12}^{\phi}, xy_{22}^{\phi}, yy_{11}^{\phi}, yy_{12}^{\phi}$, and yy_{22}^{ϕ} are all 0). In this case, the system only involves six recursion equations because there is only one M locus allele and no Y -bearing female gametes. This six-equation system yields equilibrium (2). Within this resident population (when m is absent) we describe frequencies among different gamete types, which are given by $X_{MA}^{\phi} = p_{Xf}$, $X_{Ma}^{\phi} = (1 - p_{Xf})$, $X_{MA}^{\delta} = (1 - q)p_{Xm}$, $X_{Ma}^{\delta} = (1 - q)(1 - p_{Xm})$, $Y_{MA}^{\delta} = qp_{Ym}$, and $Y_{Ma}^{\delta} = q(1 - p_{Ym})$. In this resident population, the mean fitnesses 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)	$\frac{\{p_X^\varnothing w_A^\varnothing q p_Y^\delta w_A^\delta w_{AA}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q p_Y^\delta w_A^\delta w_{Aa}^\delta + p_X^\varnothing w_A^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{Aa}^\delta + (1 - p_X^\varnothing) w_a^\varnothing q (1 - p_Y^\delta) w_a^\delta w_{aa}^\delta\}}{\{\bar{w}_H^\delta \bar{w}_H^\delta\}}$

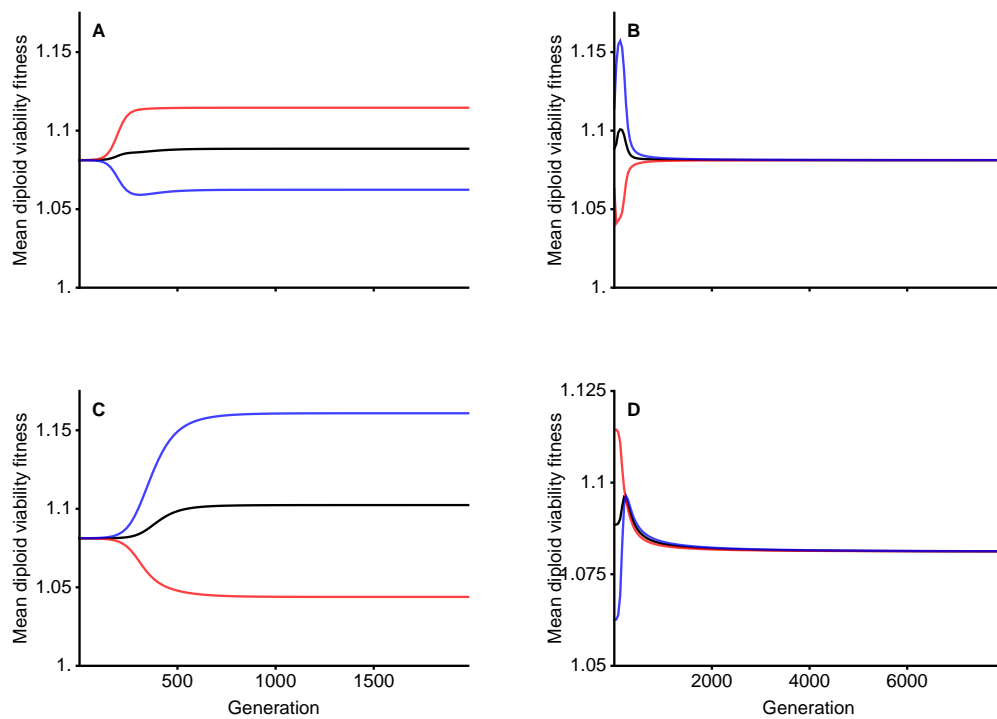


Figure S.1: Could add titles to the columns/rows: neo-W for row 1, neo-Y for row 3, $r = 0.5$, $R = 0.05$ for column 1 and $r = 0.05$, $R = 0.5$ for column 2. & possibly adjust padding (too much whitespace?). Matt - could you uncomment the line legends in the Mathematica file (function not included in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