

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

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Contributions:

Abstract

Sex determination systems are remarkably dynamic; many studied taxa display transitions of sex-determining genes between chromosomes or the evolution of new sex-determining systems. Here, we utilize population genetic models to study the spread of novel sex-determiners in systems with haploid gametic selection, e.g., pollen or sperm competition. Haploid selected loci experience a form of sex-specific selection (because gametic competition occurs predominantly among haploids produced by males) and can also cause sex ratios at birth to become biased (because sex ratios are determined by the fertilization success of X- versus Y-bearing pollen/sperm). We find that the evolution of sex determination systems where mothers determine sex at birth (e.g., environmental sex determination where sex is determined at birth) is influenced by classic Fisherian sex ratio selection. (Maybe not true???) However, notably, we find that the spread of new genetic sex determination systems is not affected by sex ratio biases that are caused by gametic selection because sex ratios become biased after parental provisioning has occurred (even if pollen/sperm competition occurs within the mother). In addition, we find that linkage of an ancestral sex chromosome to a locus under haploid selection can favour transitions between male and female heterogamety (e.g., XY to ZW), which is not the case for any forms of diploid sex specific selection (e.g., sexually antagonistic selection). During these transitions, new sex-determining alleles spread despite breaking up favourable associations that build up between ancestral sex-determining loci and selected loci, reducing population mean fitness. Furthermore, a period of selection among haploids can favour the stable maintenance of polymorphic sex determination systems. Thus, our models offer several new insights to be explored as information about sex determination in non-model taxa accumulates.

Introduction

Animals and angiosperms exhibit extremely diverse sex determination systems, as reviewed by Bull (1983), Charlesworth and Mank (2010), Beukeboom and Perrin (2014), Bachtrog et al. (2014). Among species with genetic sex determination of diploid sexes, some taxa have heterogametic males (XY) and homogametic females (XX), including mammals and most dioecious plants (Ming et al. 2011); whereas other taxa have homogametic males (ZZ) and heterogametic females (ZW), including Lepidoptera and birds. Within several taxa, the chromosome that harbours the master sex-determining region changes. For example, transitions of the master 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), Diptera (Vicoso and Bachtrog 2015), and *Oryzias* (Myosho et al. 2012). In addition, many gonochoric/dioecious clades with genetic sex determination exhibit 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 flies (Tephritids, Vicoso and Bachtrog 2015), amphibians (Hillis and Green 1990), the angiosperm genus *Silene* (Slancarova et al. 2013), Coleoptera and Hemiptera (Beukeboom and Perrin 2014, plate 2). Indeed, in some cases, both male and female heterogametic sex determination systems can be found in the same species, 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 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 et al. 2010, Holleley et al. 2015).

Predominant theories in which new sex determination systems are favoured by selection involve fitness differences between sexes (e.g., sexually antagonistic selection) or sex ratio selection. van Doorn and Kirkpatrick (2007; 2010) show that new sex determination loci can be favoured if they arise in close linkage with a locus that experiences sexual antagonism. For ex-

ample, linkage allows favourable associations to build up between a male-beneficial allele and a neo-Y chromosome. Such associations can favour a new master sex-determining gene on a new 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 and Kirkpatrick 2010). However, any sexually-antagonistic loci that are linked to the ancestral sex-determination locus will develop similar, favourable associations and select against the spread of a new sex-determination system.

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

Here, we use mathematical models to find the conditions under which new sex determination systems are favoured by selection where we include a period of selection among haploid gametes/gametophytes. Selection among haploid genotypes is thought to occur primarily among pollen/sperm, which can compete whenever there are more pollen/sperm than required for fertilization (Mulcahy et al. 1996, Joseph and Kirkpatrick 2004). Haploid selection

may be particularly common in plants, in which 60-70% of 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, Gossmann et al. 2014). In addition, artificial selection pressures applied to male gametophytes cause the frequency of 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) proportion of genes are thought to be expressed and selected in animal sperm, although precise estimates are uncertain (Zheng et al. 2001, Joseph and Kirkpatrick 2004, Vibranovski et al. 2010). **add something about drive**

There are various ways in which a period of haploid selection could influence transitions between sex determination systems. Firstly, if we assume that haploid selection at any particular locus predominantly occurs in one sex (e.g., pollen/sperm competition), then such loci experience 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 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 favoured via linkage associations with alleles that are beneficial in pollen/sperm. However, sex ratios can also become biased if there is linkage between the sex-determining region and a locus that harbours genetic variation in haploid fitness. For example, differences in fitness between X- and Y-bearing pollen tubes can cause the sex ratio among seeds to become biased when there is pollen competition (Lloyd 1974, Conn 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 influenced by the combination of sex ratio biases and favourable 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 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-Z/neo-W 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.

NOTE RE: DRIVE. I expect drive (that occurs specifically in one sex, e.g., during spermatogenesis) to behave almost exactly like haploid selection. That is, I think that a XY-linked driver that is maintained by selection (e.g., because it causes sterility when homozygous, which is common in known drive systems) will only favour invasion of a more tightly linked neo-Y (worsening sex ratio biases) and could favour invasion of a neo-W. This may run counter to generic expectations from new sex chromosome systems evolving to balance the sex ratio. So, do you think it would significantly enhance the paper to model drive explicitly or just discuss it as being similar???

FOR RESULTS?

FROM PREVIOUS PAPER: The maintenance of polymorphism at loci that experience sex specific selection in both haploid and diploid phases was considered by Immler et al. Immler et al. (2012), demonstrating that polymorphisms can be maintained by sexually antagonistic selection or overdominance as well as by conflicting selection pressures in haploids and diploids (haploid-diploid conflict or ploidy antagonistic selection) or a combination of these selective regimes.

Model

We will consider a three locus model. Locus **X** is the ancestral sex-determining region (SDR), with alleles X and Y (or Z and W). Locus **A** is a region under selection, with alleles A and a . And locus **M** is a novel sex-determining region, with alleles M and m . With genotype MM at locus **M**, the sex of a zygote is determined by the genotype at locus **X** (XX become females and XY males, or ZW become females and ZZ males). With at least one m allele at locus **M**, a zygote develops as a female with probability k and as a male with probability $1 - k$. With $k = 0$, the novel sex determiner is a masculinizer (e.g., a neo-Y chromosome) and with $k = 1$ the novel sex determiner is a feminizer (e.g., a neo-W chromosome). With intermediate k , locus **M** is interpreted as an environmental sex-determining region.

The life-cycle begins with competition between haploid gametes/gametophytes within each sex, where selection depends on the sex of the diploid they came from and their allele at the **A** locus. Gametes/gametophytes from males then mate randomly with gametes/gametophytes from females. The resulting zygotes develop as males or females, depending on their genotypes at the **X** and **M** loci. Diploids then compete with others of the same sex, where selection depends on the sex of the individual and its genotype at the **A** locus. This is followed by meiosis with recombination. 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 . Any order of the loci can be modelled with appropriate choices of r , R , and χ . We track the frequency of haploid genotypes produced by each sex from one generation to the next (recursion equations in Sup. Mat.).

With allele M fixed at the **M** locus, sex is determined by locus **X** and an equilibrium is reached at locus **A**. We then examine the ability of a rare, novel sex-determiner m to increase in frequency at this equilibrium. Numerical simulations are used to examine when an invading mutation goes to fixation.

Results

Resident equilibrium and stability

With allele M fixed, we follow the dynamics of the frequency of A in gametes/gametophytes from the homogametic sex (e.g., in eggs from an XX female, p_{Xf}) and the frequencies of A in the two types of gametes/gametophytes from the heterogametic sex (e.g., in sperm from an XY male that are X-bearing, p_{Xm} , and Y-bearing, p_{Ym}). Assuming selection is weak relative to recombination, the differences in the frequencies of A in each type of gamete/gametophyte are small, and we can solve for the mean frequency of A across all types (p_A) as well as the difference in the frequencies of A between two of the three types, to first order in selection. Linear stability analysis can then be used to determine the stability of this equilibrium. With no haploid selection and $k = 0$ (neo- Y invading a ZW system) or $k = 1$ (neo- W invading an XY system), our results reduce to those of van Doorn and Kirkpatrick (2010).

Sex chromosome turnover

The spread of a rare mutant m at the \mathbf{M} locus in such a population is determined by the leading eigenvalue, λ , of the system described by the equations for the next generation frequency of haploid genotypes with the mutation. Below we present the results for invasion into an XY system assuming equal dominance coefficients in the two sexes, no competition among gametes/gametophytes from females, and linear arrangement **XAM**. Equivalent results for invasions into a ZW system are given in the Sup. Mat.

Neo-Y

The growth rate of a rare, dominant neo-Y region ($k = 0$) is

$$\lambda_{Y,XY} = 1 + V_A \frac{(r - R)}{rR} \frac{s_f^2}{(s_f + s_m)^2} t_m^2, \quad (1)$$

where $V_A = p_A(1 - p_A)$ is the variance at the **A** locus, s_f and s_m are the respective selection coefficients for A in diploid females and males, and t_m is the selection coefficient for A in gametes/gametophytes from males. The neo-Y can therefore invade whenever it is in tighter linkage with the selected locus than is the ancestral sex-determining locus, $r > R$, provided locus **A** is polymorphic ($V_A > 0$) and there is selection among both females ($s_f \neq 0$) and gametes/gametophytes from males ($t_m \neq 0$).

Neo-W

The growth rate of a rare, dominant neo-W region ($k = 1$) is

$$\lambda_{W,XY} = 1 + V_A \frac{s_f ((2r(1 - R) + R)s_f + (1 - 2r)Rs_m)}{2rR(s_f + s_m)^2} t_m^2. \quad (2)$$

In this case, even when the novel sex-determining locus is in looser linkage with the selected locus than is the ancestral sex-determining locus, $r < R$, a novel sex-determiner can invade. For example, with $R = 1/2$ the neo-W invades if there is some linkage between the ancestral sex-determining and selected loci ($r < 1/2$), there is selection among gametes/gametophytes in males ($t_m \neq 0$), and there is selection for or against A in both males and females ($s_m s_f > 0$) that is stronger in females than in males ($|s_f| > |s_m|$).

Neo-ESD

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

$$\lambda_{ESD,XY} = 1 + \frac{(\lambda_{Y,XY} - 1) + (\lambda_{W,XY} - 1)}{4} \Big|_{R=1/2} \quad (3)$$

Thus the $k = 1/2$ case gets half of the advantages of a neo- W and half that of a neo- Y . 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.

Discussion

2 Brief results summary.

DRAFT (improve): In Úbeda et al. (2015), the new sex determining locus
4 spreads because it arises in linkage with a locus that experiences drive. They
assume that drive occurs predominantly in one sex, e.g., during spermatogenesis
6 or a 'killer' sperm. A driving allele is maintained at an intermediate
frequency by selection, e.g., because it causes male sterility when homozygous
8 (because all male sperm are killed). Y chromosomes that arise in linkage with
the driving allele spread because they allow drive to occur more often, thus
10 genetic sex determination with a sex ratio bias evolves. Thus Úbeda et al.
(2015) also find that genetic sex determiners can invade, despite causing sex
12 ratios to become biased. Finally, they show that autosomal 'restorers' that
negate the effects of meiotic drive can invade and restore an equal sex ratio.
14 OTHER RESTORERS. Indeed, alleles that negate the effect of sex-linked
meiotic drivers and restore equal sex ratios have been identified (Stalker
16 1961, Smith 1975). A similar process occurs with cytoplasmic male sterility
alleles (that cause biased sex ratios) and nuclear 'restorer' genotypes (Frank

18 1989). When sex ratio bias occurs due to haploid selection, a natural class
of sex ratio ‘restorers’ exist because haploid selection often occurs in a con-
20 text that is determined by the diploid parents. For example, the intensity of
pollen competition can be manipulated by altering style length (Travers and
22 Shea 2001, Lankinen and Skogsmyr 2001, Ruane 2009), delaying stigma re-
ceptivity (Galen et al. 1986, Lankinen and Madjidian 2011) and/or delaying
24 pollen tube growth in the pistil (Herrero 2003). Where the X and Y have
fitness differences, Hough et al. (2013) and Otto et al. (2015) demonstrated
26 that mothers should generally evolve to balance sex ratios by reducing the
intensity of haploid competition.

28 FROM THESIS: However, reducing competition among haploids also re-
duces the potential for harmful deleterious mutations to be purged. When
30 deleterious mutations are included, the optimal intensity of haploid selection
can reflect a balance between maximizing offspring fitness and equalizing sex
32 ratios.

As part of a collaborative project (Otto et al. 2015), I considered the
34 evolution of the haploid ‘selective arena’ in cases where the X chromosome
harbours a polymorphism that affects haploid fitness. Mothers again primar-
36 ily evolve to restore equal sex ratios. However, modifying haploid selection
also affects the X-linked genotypes that are inherited by offspring. Specif-
38 ically, increasing the intensity of haploid selection increases the proportion
of daughters (all progeny of X-bearing sperm/pollen are female) that inherit
40 the allele with high haploid fitness. If this allele has high fitness in daugh-
ters, mothers can be selected to increase the intensity of haploid selection;
42 otherwise, decreased selection among haploids is favoured. Thus, because
altering haploid selection intensity affects the alleles that are inherited by
44 daughters, mothers can favour slightly biased sex ratios. In addition, I found
that stronger sex ratio biases can be favoured by paternal manipulations of
46 the haploid ‘selective arena’ because fathers are strongly selected to maximize
their own siring success (above selection to equalize the sex ratio).

48 Discuss patterns that might be looked for:

50 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 de-
pleted (Immler et al. 2014). also, mating systems (e.g., fewer alleles are
available during haploid competition in monogamous species), selfing rates,
54 and estimates of pollen limitation could be used as indicators of the intensity
of haploid selection

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

58 “Polygenic sex determination has been reported in many plants (e.g.
Shannon & Holsinger 2007), fishes (Vandeputte et al. 2007; Ser et al. 2010;
60 Liew et al. 2012), crustaceans (e.g. Battaglia 1958; Battaglia & Malesani
1959; Voordouw & Anholt 2002), bivalves (Haley 1977; Saavedra et al. 1997),
62 gastropods (Yusa 2007a,b), and polychaetes (Bacci 1965, 1978; Premoli et al.
1996).” From Vuilleumier et al. 2007: “Polymorphism for sex-determining
64 genes within or among populations has been reported in many species in-
cluding houseflies, midges, woodlice, platyfish, cichlid fish, and frogs (Gor-
don, 1944; Kallman, 1970; Thompson, 1971; Macdonald, 1978; Bull, 1983;
66 Rigaud et al., 1997; Caubet et al., 2000; Lande et al., 2001; Ogata et al.,
2003; Lee et al., 2004; Mank et al., 2006).”

(Check with Jim Bull that it’s ok before including this speculation:) Fi-
nally, Hamilton (1967) pointed out that biased sex ratios can affect popu-
70 lation size because the number of offspring in each generation is typically
determined by the number of females. Population density can, in turn, af-
fect the intensity of pollen/sperm competition in future generations because
72 fewer males are available to donate pollen/sperm in a particular area. Thus,
a feedback could occur between population densities and haploid selection,
74 which has not yet been investigated.
76

References

- 78 Arunkumar, R., E. B. Josephs, R. J. Williamson, and S. I. Wright. 2013.
Pollen-specific, but not sperm-specific, genes show stronger purifying se-
80 lection and higher rates of positive selection than sporophytic genes in
Capsella grandiflora. *Molecular biology and evolution* 30:2475–2486.
- 82 Bachtrog, D., J. E. Mank, C. L. Peichel, M. Kirkpatrick, S. P. Otto, T.-L.
Ashman, M. W. Hahn, J. Kitano, I. Mayrose, R. Ming, N. Perrin, L. Ross,
84 N. Valenzuela, J. C. Vamosi, and Tree of Sex Consortium. 2014. Sex
determination: why so many ways of doing it? *PLoS Biol* 12:e1001899.
- 86 Beukeboom, L. W., and N. Perrin. 2014. The evolution of sex determination.
Oxford University Press, Oxford, UK.
- 88 Borg, M., L. Brownfield, and D. Twell. 2009. Male gametophyte development:
a molecular perspective. *Journal of Experimental Botany* 60:1465–1478.
- 90 Bull, J. J. 1983. Evolution of sex determining mechanisms. The Benjamin
Cummings Publishing Company.
- 92 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
94 in plants and animals. *Genetics* 186:9–31.
- Charnov, E. L., and J. Bull. 1977. When is sex environmentally determined?
96 *Nature* 266:828–830.
- Clarke, H. J., T. N. Khan, and K. H. M. Siddique. 2004. Pollen selection
98 for chilling tolerance at hybridisation leads to improved chickpea cultivars.
Euphytica 139:65–74.
- 100 Conn, J. S., and U. Blum. 1981. Sex ratio of *Rumex hastatulus*: the effect of
environmental factors and certation. *Evolution* 35:1108–1116.

- 102 Conover, D. O., and S. W. Heins. 1987. Adaptive variation in environmental
and genetic sex determination in a fish. *Nature* 326:496–498.
- 104 Ezaz, T., S. D. Sarre, and D. O’Meally. 2009. Sex chromosome evolution
in lizards: independent origins and rapid transitions. *Cytogenetic and*
106 *Genome Research* 127:249–260.
- Field, D. L., M. Pickup, and S. C. H. Barrett. 2012. The influence of polli-
108 nation intensity on fertilization success, progeny sex ratio, and fitness in a
wind-pollinated, dioecious plant. *International Journal of Plant Sciences*
110 173:184–191.
- . 2013. Comparative analyses of sex-ratio variation in dioecious flow-
112 ering plants. *Evolution* 67:661–672.
- Frank, S. A. 1989. The Evolutionary Dynamics of Cytoplasmic Male Sterility.
114 *American Naturalist* 133:345–376.
- Galen, C., J. A. Shykoff, and R. C. Plowright. 1986. Consequences of stigma
116 receptivity schedules for sexual selection in flowering plants. *American*
Naturalist pages 462–476.
- 118 Gossmann, T. I., M. W. Schmid, U. Grossniklaus, and K. J. Schmid. 2014.
Selection-driven evolution of sex-biased genes Is consistent with sexual
120 selection in *Arabidopsis thaliana*. *Molecular biology and evolution* 31:574–
583.
- 122 Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Hedhly, A., J. I. Hormaza, and M. Herrero. 2004. Effect of temperature
124 on pollen tube kinetics and dynamics in sweet cherry, *Prunus avium*
(Rosaceae). *American journal of botany* 91:558–564.

- 126 Herrero, M. 2003. Male and female synchrony and the regulation of mating
in flowering plants. *Philosophical Transactions of the Royal Society B:*
128 *Biological Sciences* 358:1019–1024.
- Hillis, D. M., and D. M. Green. 1990. Evolutionary changes of heterogametic
130 sex in the phylogenetic history of amphibians. *Journal of Evolutionary*
Biology 3:49–64.
- 132 Holleley, C. E., D. O’Meally, S. D. Sarre, J. A. Marshall Graves, T. Ezaz,
K. Matsubara, B. Azad, X. Zhang, and A. Georges. 2015. Sex reversal
134 triggers the rapid transition from genetic to temperature-dependent sex.
Nature 523:79–82.
- 136 Hormaza, J. I., and M. Herrero. 1996. Male gametophytic selection as a plant
breeding tool. *Scientia horticultrae* 65:321–333.
- 138 Hough, J., S. Immler, S. Barrett, and S. P. Otto. 2013. Evolutionarily stable
sex ratios and mutation load. *Evolution* 7:1915–1925.
- 140 Immler, S., G. Arnqvist, and S. P. Otto. 2012. Ploidally antagonistic selection
maintains stable genetic polymorphism. *Evolution* 66:55–65.
- 142 Immler, S., C. Hotzy, G. Alavioon, E. Petersson, and G. Arnqvist. 2014.
Sperm variation within a single ejaculate affects offspring development in
144 Atlantic salmon. *Biology letters* 10:20131040.
- Joseph, S., and M. Kirkpatrick. 2004. Haploid selection in animals. *Trends*
146 *in Ecology & Evolution* 19:592–597.
- Kozielska, M., F. J. Weissing, L. W. Beukeboom, and I. Pen. 2010. Segrega-
148 tion distortion and the evolution of sex-determining mechanisms. *Heredity*
104:100–112.
- 150 Lankinen, A., and J. A. Madjidian. 2011. Enhancing pollen competition
by delaying stigma receptivity: Pollen deposition schedules affect siring

- 152 ability, paternal diversity, and seed production in *Collinsia heterophylla*
(Plantaginaceae). American journal of botany 98:1191–1200.
- 154 Lankinen, A., and I. Skogsmyr. 2001. Evolution of pistil length as a choice
mechanism for pollen quality. Oikos 92:81–90.
- 156 Li, J., R. B. Phillips, A. S. Harwood, B. F. Koop, and W. S. Davidson. 2011.
Identification of the Sex Chromosomes of Brown Trout (*Salmo trutta*)
158 and Their Comparison with the Corresponding Chromosomes in Atlantic
Salmon (*Salmo salar*) and Rainbow Trout (*Oncorhynchus mykiss*). Cyto-
160 genetic and Genome Research 133:25–33.
- Lloyd, D. G. 1974. Female-predominant sex ratios in angiosperms, vol. 32.
162 Heredity.
- Mank, J. E., D. E. L. Promislow, and J. C. Avise. 2006. Evolution of alter-
164 native sexdetermining mechanisms in teleost fishes. Biological Journal of
the Linnean Society 87:83–93.
- 166 Ming, R., A. Bendahmane, and S. S. Renner. 2011. Sex chromosomes in land
plants. dx.doi.org 62:485–514.
- 168 Mulcahy, D. L., M. Sari-Gorla, and G. B. Mulcahy. 1996. Pollen selection -
past, present and future. Sexual Plant Reproduction 9:353–356.
- 170 Myosho, T., H. Otake, H. Masuyama, M. Matsuda, Y. Kuroki, A. Fujiyama,
K. Naruse, S. Hamaguchi, and M. Sakaizumi. 2012. Tracing the Emergence
172 of a Novel Sex-Determining Gene in Medaka, *Oryzias luzonensis*. Genetics
191:163–170.
- 174 Ogata, M., Y. Hasegawa, H. Ohtani, M. Mineyama, and I. Miura. 2007. The
ZZ/ZW sex-determining mechanism originated twice and independently
176 during evolution of the frog, *Rana rugosa*. Heredity 100:92–99.

- 178 Otto, S. P., M. F. Scott, and S. Immler. 2015. Evolution of haploid selection
in predominantly diploid organisms. *Proceedings of the National ...*
- 180 Pen, I., T. Uller, B. Feldmeyer, A. Harts, G. M. While, and E. Wapstra.
2010. Climate-driven population divergence in sex-determining systems.
Nature 468:436–438.
- 182 Pokorná, M., and L. Kratochvíl. 2009. Phylogeny of sexdetermining mech-
anisms in squamate reptiles: are sex chromosomes an evolutionary trap?
184 *Zoological Journal of the ...* 156:168–183.
- Ravikumar, R. L., B. S. Patil, and P. M. Salimath. 2003. Drought tolerance in
186 sorghum by pollen selection using osmotic stress. *Euphytica* 133:371–376.
- Ruane, L. G. 2009. Post-pollination processes and non-random mating among
188 compatible mates. *Evolutionary Ecology Research* 11:1031–1051.
- Ser, J. R., R. B. Roberts, and T. D. Kocher. 2010. Multiple interacting loci
190 control sex determination in lake Malawi cichlid fish. *Evolution* 64:486–
501.
- 192 Slancarova, V., J. Zdanska, B. Janousek, M. Talianova, C. Zschach, J. Zlu-
vova, J. Siroky, V. Kovacova, H. Blavet, J. Danihelka, B. Oxelman, A. Wid-
194 mer, and B. Vyskot. 2013. Evolution of sex determination systems with
heterogametic males and females in *Silene*. *Evolution* 67:3669–3677.
- 196 Smith, D. A. S. 1975. All-female broods in the polymorphic butterfly *Danaus*
chrysippus L. and their ecological significance. *Heredity* 34:363–371.
- 198 Stalker, H. D. 1961. The Genetic Systems Modifying Meiotic Drive in
Drosophila Paramelanica. *Genetics* .
- 200 Stehlik, I., and S. Barrett. 2005. Mechanisms governing sex-ratio variation
in dioecious *Rumex nivalis*. *Evolution* 59:814–825.

- 202 Stehlik, I., and S. C. H. Barrett. 2006. Pollination intensity influences sex
ratios in dioecious *Rumex nivalis*, a wind-pollinated plant. *Evolution*
204 60:1207–1214.
- Travers, S. E., and K. Shea. 2001. Selection on pollen competitive ability in
206 relation to stochastic factors influencing pollen deposition. *Evolutionary*
Ecology Research 3:729–745.
- 208 Úbeda, F., M. M. Patten, and G. Wild. 2015. On the origin of sex chromo-
somes from meiotic drive. *Proceedings of the Royal Society B: Biological*
210 *Sciences* 282:20141932.
- van Doorn, G. S., and M. Kirkpatrick. 2007. Turnover of sex chromosomes
212 induced by sexual conflict. *Nature* 449:909–912.
- . 2010. Transitions Between Male and Female Heterogamety Caused
214 by Sex-Antagonistic Selection. *Genetics* 186:629–645.
- Vibranovski, M. D., D. S. Chalopin, H. F. Lopes, M. Long, and T. L. Karr.
216 2010. Direct evidence for postmeiotic transcription during *Drosophila*
melanogaster spermatogenesis. *Genetics* 186:431–433.
- 218 Vicoso, B., and D. Bachtrog. 2015. Numerous transitions of sex chromosomes
in Diptera. *PLoS Biol* 13:e1002078.
- 220 Vuilleumier, S., R. Lande, J. J. M. van Alphen, and O. Seehausen. 2007.
Invasion and fixation of sex-reversal genes. *Journal of Evolutionary Biology*
222 20:913–920.
- Werren, J. H., and P. D. Taylor. 1984. The effects of population recruitment
224 on sex ratio selection. *The American Naturalist* 124:143–148.
- Wilson, D. S., and R. K. Colwell. 1981. Evolution of sex ratio in structured
226 demes. *Evolution* 35:882–897.

- Yano, A., B. Nicol, E. Jouanno, E. Quillet, A. Fostier, R. Guyomard,
228 and Y. Guiguen. 2012. The sexually dimorphic on the Y-chromosome
gene (sdY) is a conserved male-specific Y-chromosome sequence in many
230 salmonids. *Evolutionary Applications* 6:486–496.
- Zheng, Y., X. Deng, and P. A. Martin-DeLeon. 2001. Lack of sharing of
232 Spam1 (Ph-20) among mouse spermatids and transmission ratio distortion.
Biology of Reproduction 64:1730–1738.