

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-determining systems where we also include 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 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 the same species, including cichlid species (Ser et al. 2010) and *Rana rugosa* (Ogata et al. 2007).

Depending on the prominence of transitions to ESD in the manuscript include something like (currently quoted):

“Transitions have repeatedly occurred between environmental sex determination and genotypic sex determination, as exemplified by the distribution of temperature sex determination among reptiles: either temperature or genes provide the initial trigger in closely related species (Ewert and Nelson 1991; Pokorna and Kratochvil 2009; Ezaz et al. 2009) or even conspecific populations (Pen et al. 2010). Similar situations are found in fishes (e.g.,

Conover and Heins 1978a).”

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 oramong populations has been reported in many speciesincluding houseflies, midges, woodlice, platyfish, cichlidfish, and frogs (Gordon, 1944; Kallman, 1970; Thomp-son, 1971; Macdonald, 1978; Bull, 1983; Rigaud et al., 1997; Caubet et al., 2000; Lande et al., 2001; Ogataet al., 2003; Lee et al., 2004; Mank et al., 2006).

Brief description of sex ratio adjustment and sexual antagonism theories:

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 example, 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.

Sex ratio selection might be a particularly important force driving transitions between sex-determining systems (Beukeboom and Perrin 2014, Chap-

ter 7). For example, feminizing mutations may invade when female biased sex ratios are favoured due to interdemic selection (Wilson and Colwell 1981, Vuilleumier et al. 2007). In other cases, flexible sex determination systems may be favoured in order to exploit environmental conditions that are optimal for males or females, creating locally biased sex ratios (Charnov and Bull 1977, Werren and Taylor 1984, Pen et al. 2010). 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., driving X or Y chromosomes are inherited disproportionately often), which leads to biased sex ratios. They find that new, unlinked sex-determining loci (masculinizing or feminizing mutations) can then spread, restoring an even sex ratio.

We add haploid selection:

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. **FROM PREVIOUS PAPER:** In plants, selection among haploid male gametophytes is thought to be pervasive Skogsmyr and Lankinen (2002), Moore and Pannell (2011), Marshall and Evans (2016); in *Arabidopsis*, 60-70% of all genes are expressed during the haploid phase Borg et al. (2009), and pollen expressed genes exhibit stronger signatures of purifying selection and positive selection Arunkumar et al. (2013), Gossmann et al. (2014). For agricultural breeding, pollen has been exposed to a variety of selection pressures *in vivo* and *in vitro*, including temperature Hedhly et al. (2004), Clarke et al. (2004), herbicides Frascaroli and Songstad (2001), metals Searcy and Mulcahy (1985), water stress Ravikumar et al. (2003), and pathogens Ravikumar et al. (2012), resulting in an increased frequency of resistant genotypes among the diploid sporophytic offspring. In animals, expression during the haploid sperm stage is traditionally thought to be suppressed Hecht (1998), although recent evidence suggests that the extent and selective importance of postmeiotic gene

expression may be underestimated Zheng et al. (2001), Joseph and Kirkpatrick (2004), Vibranovski et al. (2010), Immler et al. (2014).

Here, suggest that the canonical view (no haploid expression in animals, genome highly chromatinized in sperm and not expressed) might be based on model organisms, such as mice, where sperm is sufficiently short-lived that transcripts provisioned during spermatogenesis may be sufficient without further haploid transcription (although note that the Vibranovski lab results are in mice showing some transcription does occur). In broadcast spawning animal species (e.g., corals, many fish) and species where sperm typically requires greater longevity, expression of the haploid genotype may be required (Immler paper indicates this, but not that strongly - as I remember). We can use this suggestion in discussion to speculate in what species the processes we study might be looked for (i.e., animals with multiple matings, broadcast spawning and/or long-lived sperm and outcrossing/non-pollen-limited plants).

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.

We add haploid selection (and justification, see below)

Also discuss the fact that, in terms of recombination suppression, haploid selection among male gametes generates selection pressure similar to that of male specific selection.

What will be the result: where there is sex biases and sex-specific 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???

Discussion

2 DRAFT (improve): In Úbeda et al. (2015), the new sex determining locus
spreads because it arises in linkage with a locus that experiences drive. They
4 assume that drive occurs predominantly in one sex, e.g., during spermatogenesis or a 'killer' sperm. A driving allele is maintained at an intermediate
6 frequency by selection, e.g., because it causes male sterility when homozygous (because all male sperm are killed). Y chromosomes that arise in linkage
8 with the driving allele spread because they allow drive to occur more often, thus genetic sex determination with a sex ratio bias evolves. Thus Úbeda
10 et al. (2015) also find that genetic sex determiners can invade, despite causing sex ratios to become biased. Finally, they show that autosomal 'restorers'
12 that negate the effects of meiotic drive can invade and restore an equal sex ratio. When sex ratio bias occurs due to haploid selection, a natural class
14 of sex ratio 'restorers' exist because haploid selection often occurs in a context that is determined by the diploid parents. For example, the intensity of
16 pollen competition can be manipulated by altering style length (Travers and Shea 2001, Lankinen and Skogsmyr 2001, Ruane 2009), delaying stigma receptivity
18 (Galen et al. 1986, Lankinen and Madjidian 2011) and/or delaying pollen tube growth in the pistil (Herrero 2003). Where the X and Y have
20 fitness differences, Hough et al. (2013) and Otto et al. (2015) demonstrated that mothers should generally evolve to balance sex ratios by reducing the
22 intensity of haploid competition.

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

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

FROM THESIS: Generally, any sex-linked gene that harbours genetic
44 variation in haploid fitness should cause sex ratios to become biased. Sex
ratio bias caused by pollen competition has previously been discussed in
46 the context of Y-linked deleterious mutations, which are thought to build
up after recombination suppression evolves (Lloyd 1974, Stehlik and Barrett
48 2005). Sex ratios can also become biased due to meiotic drive; in a classic
paper, Hamilton (1967) showed that X- or Y-linked alleles that experience
50 meiotic drive will bias sex ratios. He assumed that driving alleles are un-
der directional selection and spread to fixation but such alleles can also be
52 maintained at intermediate frequencies by selection (Feldman and Otto 1989,

Holman et al. 2015). When sex ratios are biased, other loci are expected to
54 evolve to restore equal sex ratios. Indeed, alleles that negate the effect of
sex-linked meiotic drivers and restore equal sex ratios have been identified
56 (Stalker 1961, Smith 1975). A similar process occurs with cytoplasmic male
sterility alleles (that cause biased sex ratios) and nuclear ‘restorer’ genotypes
58 (Frank 1989).

Several aspects of the relationship between haploid selection (e.g., pollen
60 or sperm competition) and sex ratios remain to be explored. For example,
new sex-determining systems (particularly transitions between male and fe-
62 male heterogamety) can be favoured in order to restore equal sex ratios in
populations that have a sex ratio bias (Bull 1983, Kozielska et al. 2010, Úbeda
64 et al. 2015). Based on the results of Chapter ??, we would expect that sex
ratio biases would occur via associations between sex-determining loci and
66 loci that experience haploid selection. However, these associations should
also select against transitions between sex-determining systems, as has been
68 found with sexually antagonistic selection (van Doorn and Kirkpatrick 2007;
2010). It is not clear how the spread of new sex determination systems would
70 be influenced by the combination of sex ratio biases and favourable associ-
ations between haploid selected loci and sex-determining regions. Finally,
72 Hamilton (1967) pointed out that biased sex ratios can affect population size
because the number of offspring in each generation is typically determined by
74 the number of females. Population density can, in turn, affect the intensity
of pollen/sperm competition in future generations because fewer males are
76 available to donate pollen/sperm in a particular area. Thus, a feedback could
occur between population densities and haploid selection, which has not yet
78 been investigated.

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