Ecology and the Evolution of Sex Chromosomes

Richard P. Meisel

Department of Biology and Biochemistry
University of Houston
Houston, TX USA 77204-5001
rpmeisel@uh.edu
https://orcid.org/0000-0002-7362-9307

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Abstract

This article reviews and discusses ecological factors that affect sex chromosome evolution. Sex chromosomes are common features of animal genomes, and are often the location where master sex determination genes are found. Many important aspects of sex chromosome evolution are thought to be driven by sex-specific selection pressures, such as sexual antagonism and sexual selection. Sex-specific selection affects both the formation of sex chromosomes from autosomes and differences in the evolutionary trajectories between sex chromosomes and autosomes. Most population genetic models are agnostic as to whether the sex-specific selection pressures arise from intrinsic features of organismal biology or extrinsic factors that depend on environment. Here, I review the evidence that extrinsic, or ecological, factors are important determinants of sex-specific selection pressures that shape sex chromosome evolution.

Introduction

Sex chromosomes are a common feature of eukaryotic genomes, especially in animal species where sex is determined by genetics (Bachtrog *et al.*, 2014). When sex is determined by heritable genetic variation, a master sex determining gene that initiates either male or female development can be found on a sex chromosome (Beukeboom & Perrin, 2014). Most research on the evolution of sex chromosomes is focused on two key areas (Abbott *et al.*, 2017). First, there is a large body of work on how sex chromosomes arise from autosomes (e.g., van Doorn, 2014; Pennell *et al.*, 2015; Vicoso & Bachtrog, 2015). Second, there is a comparable amount of research on the unique evolutionary trajectories of sex chromosomes, which frequently differ from the autosomes (e.g., Bachtrog, 2013; Meisel & Connallon, 2013).

Many of the unique evolutionary dynamics of sex chromosomes have been hypothesized to result from their sex-limited or sex-biased mode of inheritance (Charlesworth & Charlesworth, 1980; Rice, 1987; Bachtrog, 2006; van Doorn & Kirkpatrick, 2007). Biased transmission via males or females can allow for selection pressures in one sex to be the predominant selective force shaping sex chromosome evolution (Rice, 1984; Charlesworth *et al.*, 1987). These sex-specific effects can be especially important if they are sexually antagonistic, i.e., in opposite directions in males and females (van Doorn & Kirkpatrick, 2007, 2010; Blackmon & Brandvain, 2017; Rowe *et al.*, 2018).

Here, I describe how the sex-specific selection pressures that drive sex chromosome evolution can arise from ecological factors that males and females encounter in their natural environments. Most population genetic models of sex chromosome formation and subsequent evolution are agnostic as to whether selection pressures are intrinsic to the organisms or come from extrinsic (i.e., ecological) factors. Intrinsic factors include fixed aspects of cellular or physiological features that differ between the sexes. Extrinsic or ecological factors, in comparison, include differences between the sexes in how they use their natural environment (Shine, 1989), as well as variation in the environment across the species range (Delcourt *et al.*, 2009; Delph *et al.*, 2011). There are important aspects of ecological selection pressures that should be considered when studying sex chromosome evolution, which I highlight and explain below.

Sex-Specific Selection and the Evolution of Sex Chromosomes

Sex-specific selection pressures are thought to be important for the formation of new sex chromosomes and the subsequent evolution of sex chromosomes. Sex-specific selection can involve selection operating in only one sex or in different directions in males and females. The same general concepts apply to the two major types of sex chromosome systems found animals. In XY systems, such as in mammals and *Drosophila* (Graves, 1995; Salz & Erickson, 2010), males are heterogametic (XY) and females are homogametic (XX). In ZW systems, such as in Lepidoptera and birds (Sahara *et al.*, 2012; Zhou *et al.*, 2014), females are heterogametic (ZW) and males are homogametic (ZZ). The relevant sex-specific selection pressures are often reversed depending on whether a species has an XY or ZW system, and there are some important differences between XY and ZW systems that are beyond the scope of this review (Mank *et al.*, 2014). Nonetheless, many of the same principles apply to both XY and ZW systems.

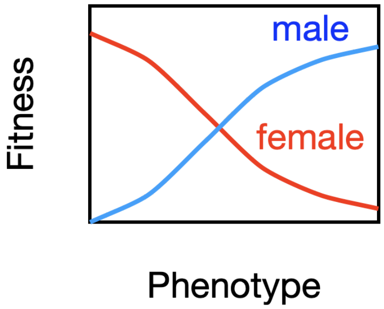

Figure 1. Example of sexually antagonistic phenotypic variation. The fitness of males (blue) and females (red) are shown for a continuum of phenotypic values. Phenotypes that maximize female fitness are deleterious to males, and phenotypes that maximize male fitness are costly to females.

Sexual antagonism is a specific type of sex-specific selection that is important for sex chromosome evolution. Sexually antagonistic selection, or inter-sexual conflict, refers to the phenomenon whereby males and females have different fitness optima for alleles or traits (Figure 1), and it is conventionally divided into two categories (Arnqvist & Rowe, 2013; Schenkel *et al.*, 2018). First, intralocus sexual antagonism arises when males and females differ in which allele (at a single locus) maximizes fitness (Lande, 1980; Bonduriansky & Chenoweth, 2009). Intralocus conflicts can be especially pronounced in adults (Chippindale *et al.*, 2001), where males and females are likely to have different phenotypic optima (Figure 1). Second, intergenic sexual conflicts occur when an allele of one gene expressed in one sex has antagonistic effects on at least one allele in at least one another gene that is expressed in the other sex (Rice & Holland, 1997). Intergenic conflicts may be an important aspect of sexual selection, where alleles could increase mating success in one sex at a cost to the other (Arnqvist & Rowe, 1995). Both intralocus and intergenic sexual antagonism can be important for the evolution of sex chromosomes.

Sex-specific selection pressures are thought to contribute to the formation of new sex chromosomes (van Doorn, 2014). These large-scale chromosomal changes generally occur via two different mechanisms (Figure 2). First, a fusion between an autosome and one of the sex chromosomes will create a neo-sex chromosome (Steinemann, 1982; Castillo *et al.*, 2010; Pennell *et al.*, 2015). Y-autosome fusions, in particular, are expected to be favored to invade a population if the autosome carries a male-beneficial allele (Charlesworth & Charlesworth, 1980), or female-beneficial allele for a W-autosome fusion. This is because sex-limited inheritance of a sex-beneficial allele can resolve a sexual conflict if the allele is deleterious when expressed in the other sex (Figure 2).

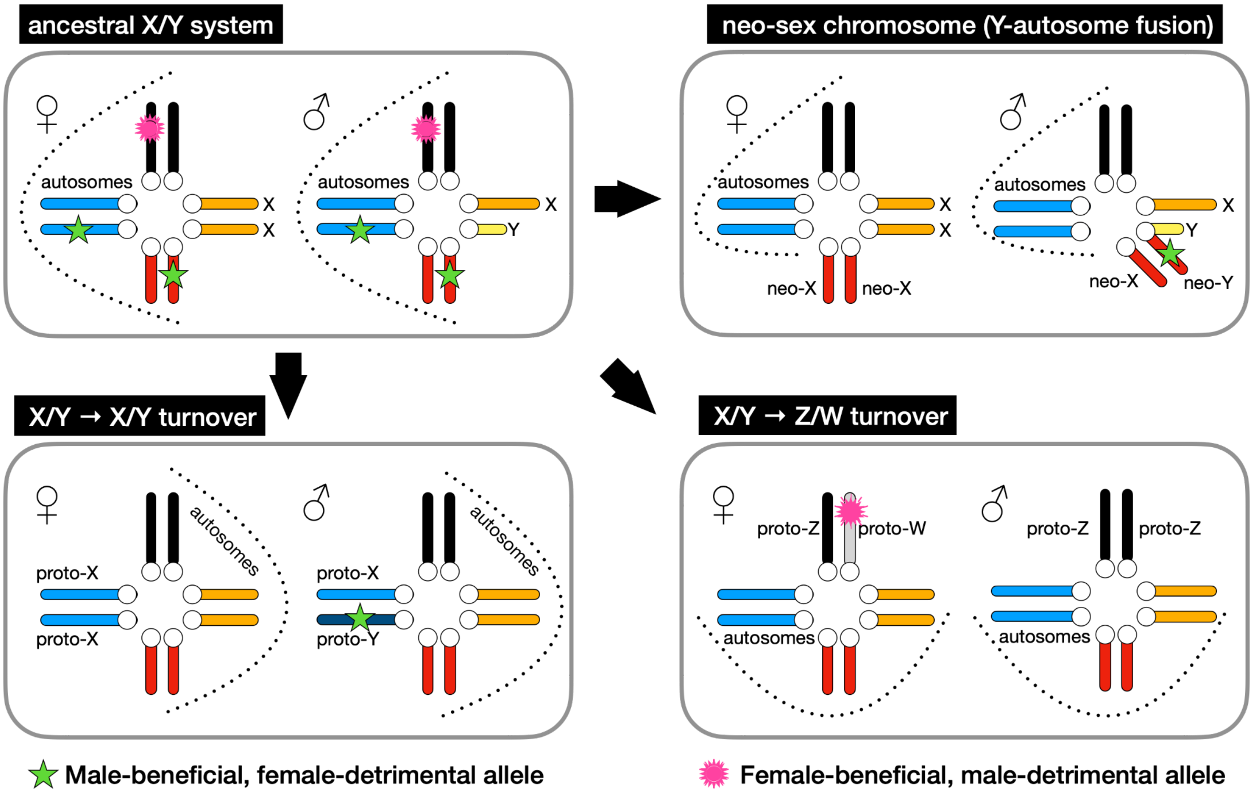

Figure 2. Sex chromosome transformations can occur via multiple evolutionary pathways. In the examples shown here, the ancestral karyotype has a sex chromosome pair along with three autosomal pairs of chromosomes (top left). In the ancestral karyotype, male-beneficial sexually antagonistic alleles (green stars) are found on some autosomes, and a female-beneficial sexually antagonistic allele is found on another autosome. Neo-sex chromosomes can be created when an autosome (red) fuses to the Y chromosome (top right). An autosome can be converted into a proto- X/Y or Z/W chromosome when it acquires a new master sex deterrmining locus (bottom), with the ancestral sex chromosome reverting to an autosome. The creation of neo- and proto-sex chromosomes can resolve a sexual conflict by allowing a sexually antagonistic allele to be inherited only by the sex in which it is beneficial.

A second type of large-scale change involves a chromosomes transitioning from sex-linked to autosomal and *vice versa*, in a process I will refer to as sex chromosome turnover (Figure 2). For example, in a species with an XY system, an autosome can become a proto-X/proto-Y chromosome pair with the acquisition of a male-determining locus; the ancestral

X and/or Y chromosome can subsequently revert to an autosome (Carvalho & Clark, 2005; Larracuente *et al.*, 2010; Vicoso & Bachtrog, 2013). Alternatively, an XY system can evolve into a ZW system if an autosome acquires a female-determining allele, and the ancestral X and/or Y chromosome can revert to an autosome. An existing ZW system can similarly transition to a different ZW system or evolve into an XY system. In all scenarios, sexually antagonistic selection is thought to increase the probability of a sex chromosome turnover because Y- or Z-linkage of a sexually antagonistic allele can resolve the inter-sexual conflict (van Doorn & Kirkpatrick, 2007, 2010). An example of this phenomenon has been documented in cichlid fish, where different pigmentations and patterns are favored in males and females, and W-linkage of the female-beneficial allele resolved the inter-sexual conflict (Roberts *et al.*, 2009). This is one of the examples of an ecological selection pressure that I describe in more detail below.

Sex-specific selection pressures are also thought to explain differences in the evolutionary dynamics of sex chromosomes relative to autosomes. For example, Y (or W) chromosomes have male- (female-) limited inheritance and little to no recombination along most or all of their length (Charlesworth, 1991; Rice, 1996a). These factors favor the fixation of male- (female-) beneficial alleles on the Y (W) chromosome, and promote the degeneration of the Y (W) chromosome via a combination of Muller's ratchet and genetic hitchhiking (Charlesworth & Charlesworth, 2000; Charlesworth *et al.*, 2005; Bachtrog, 2013). Experiments in *Drosophila* have demonstrated that male-limited inheritance allows male-beneficial, female-detrimental sexually antagonistic alleles to accumulate (Rice, 1996b, 1998; Prasad *et al.*, 2007; Zhou & Bachtrog, 2012). However, the extent to which the male-beneficial effects depend on ecological contexts is not always considered. I discuss this in further detail below.

The sexually asymmetrical inheritance of X and Z chromosomes may also favor the accumulation of alleles with sex-specific fitness effects. X chromosomes are carried by females 2/3 of the time and are haploid in males, while Z chromosomes are preferentially transmitted by males and haploid in females. These factors may favor the invasion of recessive male-beneficial or dominant female-beneficial X-linked mutations, and *vice versa* for Z chromosomes (Rice, 1984; Charlesworth *et al.*, 1987; Orr & Betancourt, 2001). Other factors may further affect the maintenance sexually antagonstic polymorphisms or fixation of sexually antagonistic alleles on X or Z chromosomes (Patten & Haig, 2009; Fry, 2010; Ruzicka & Connallon, 2020). For example, there is some evidence that the *Drosophila* X chromosome is enriched for alleles with sexually antagonistic fitness effects (Gibson *et al.*, 2002; Innocenti & Morrow, 2010). Moreover, there is evidence that X-linked (or Z-linked) genes evolve faster than autosomal genes, possibly because selection in males (females) drives the fixation of recessive beneficial alleles (Meisel &

Connallon, 2013). Below, I discuss how these evolutionary dynamics of sex chromosomes could be affected by ecological factors.

The Ecology of Sex-Specific Selection and Sexual Antagonism

Before discussing how ecological factors affect the evolution of sex chromosomes, I will review some of the evidence that sex-specific selection pressures can depend on the environment that organisms experience. This is important to consider in light of ecological factors that affect sex chromosome evolution because so many aspects of sex chromosome evolution depend on sex-specific selection pressures (see above). I will focus on both sexually antagonistic and sexually selected traits. Sexual selection involves a specific class of sex-specific or sexually dimorphic traits that are involved in the competitive access to mates (Jones, 2016).

Sex-specific selection pressures can arise from differences in how males and females use their environment (including niche partitioning or different dietary strategies), which could be a selective force in favor of sexual dimorphism (Slatkin, 1984; Shine, 1989). For example, Selander (1966) observed sexual dimorphism in size and foraging behavior in two woodpecker species, suggesting sex differences in niche utilization. Similarly, in carpet pythons (*Morelia spilota*), females have larger heads and consume larger prey than males (Pearson *et al.*, 2002). Sex differences in niche utilization could potentially arise from sex differences in parental care, which could limit the foraging or hunting capacity of one sex (Kernaléguen *et al.*, 2015).

Sex-specific selection pressures can also differ across ecological habitats within a species' range (Rhen & Crews, 2002; Connallon *et al.*, 2018a). In the dioescious plant *Silene latifolia*, for instance, intralocus sexual conflict for leaf area depends on water availability in the environment (Delph *et al.*, 2011). In *Drosophila serrata*, whether genetic variation has sexually antagonistic fitness effects, and the extent of those effects, depends on the diet on which the flies are raised (Delcourt *et al.*, 2009; Punzalan *et al.*, 2014). Theory also predicts that sexually antagonistic selection should decrease in more extreme environments, variable conditions, or near the limits of the species range (Lande, 1980; Connallon, 2015). This prediction is supported by data from some natural and experimental populations (Berger *et al.*, 2014; Holman & Jacomb, 2017; De Lisle *et al.*, 2018; Martinossi-Allibert *et al.*, 2018). However, the clinal distribution of traits in *Drosophila melanogaster* is concordant between males and females, suggesting that sex-specific selection pressures do not differ across ecological habitats (Lasne *et al.*, 2018). Therefore, while sex-specific selection pressures frequently vary across habitats and environments, the pattern is not universal.

There are myriad consequences of geographical variation in sex-specific selection pressures. For example, one meta-analysis across animals found that male body size varies more across latitudes than female body size (Blanckenhorn *et al.*, 2006). Another consequence arises under scenarios of female demographic dominance, or the situation whereby population size depends on female reproductive output. In those cases, sexually antagonistic selection pressures that differ across populations can allow alleles that increase female fitness within each population to become more common than expected without sexual asymmetries in reproductive contributions (Harts *et al.*, 2014). However, if selection pressures change over time (e.g., environmental change, seasonal cycling), this can dampen the effect of sexual antagonism by causing male and female selection pressures to be aligned (Connallon & Hall, 2016).

Pathogens are an especially intriguing ecological factor that could affect sex-specific selection pressures. Exposure to pathogens depends on the ecological environment (Ostfeld *et al.*, 2010), and there are sex differences in immune responses to infections (Klein & Flanagan, 2016; Belmonte *et al.*, 2019). These sex differences could be a cause of sexual conflict, or they could be explained by the resolution of historical conflict. One specific cause of conflict may be the effect of mating on the induction of the female immune system (Morrow & Innocenti, 2012), which provides an interface between disease ecology and sexual selection (see below).

Sexually selected traits can depend on condition—which can include diet, parasite infection, and other ecologically-dependent factors—or vary across environments (Hamilton & Zuk, 1982; Rowe & Houle, 1996; Bonduriansky, 2007; Hunt & Hosken, 2014; Miller & Svensson, 2014). For example, sexual selection on body size and color morphs vary across populations in the damselfly *Ischnura elegans* (Gosden & Svensson, 2008). In addition, larval diet affects some sexually selected traits in flies with extreme sexual dimorphisms (David *et al.*, 2000; Cotton *et al.*, 2004; Bonduriansky & Rowe, 2005). The strength of sexual selection can further depend on the environment—female diet affects copulation behavior in *Gerris buenoi* water striders, which has implications for the mating advantage experienced by large males (Ortigosa & Rowe, 2002). Genotype-by-environment (GxE) interactions could be especially important for sexual selection (Ingleby *et al.*, 2010). One such example comes from the lesser waxmoth, *Achroia grisella*, where GxE interactions affect multiple male signal characters, as well as female choice for those signals (Jia *et al.*, 2000; Rodríguez & Greenfield, 2003; Danielson-François *et al.*, 2006).

Interactions between sexually selected traits and environments can also have important consequences for the evolution of secondary sexual characteristics. Population genetics theory predicts that spatial variation in natural selection can promote runaway sexual selection on exagerated male traits in one part of the species' range (Lande, 1982). Variation in selection along a species' range can even allow for the evolution of female preference that comes at a cost, in the form of predation risk or lost time and energy (Day, 2000). Costly female choice can further evolve if phenotypes depend on GxE interactions (Kokko & Heubel, 2008).

Sexual selection can also inhibit or promote local adaptation, depending on the extent of migration across populations and strength of selection within populations (Servedio & Boughman, 2017). A study comparing *D. melanogaster* adapted to cadmium- and ethanol-containing diets found that whether sexual selection produces ecologically well-adapted progeny can depend on the alleles segregating in the population (Long *et al.*, 2012). Other work in *D. melanogaster* has shown that sexual selection impedes adaptation (Hollis & Houle, 2011; Arbuthnott & Rundle, 2012), possibly because sexual conflict interferes with natural selection purging deleterious alleles. Together, all the work presented in this section demonstrates that ecological factors affect sex-specific selection, and sex-specific selection affects adaptation to specific environments.

The Ecology of Sex Chromosome Evolution

The formation of sex chromosomes from autosomes, along with the subsequent evolutionary dynamics of sex chromosomes that differ from the autosomes, are greatly affected by sex-specific selection. As described above, sex-specific selection pressures can differ across environments, and those environmental effects can cause different responses to selection than expected under uniform selection pressures. Combining these concepts, it is likely that sex chromosome evolution is affected by sex-specific selection that depends on ecological factors. Below, I review the evidence from both population genetic theory and studies of natural genetic variation that sex chromosome evolution is affected by ecology.

Clinal sex chromosomes

Geographic clines, with a gradient in selection pressures along a species' range (Huxley, 1938; Endler, 1977), are especially informative of sex-specific selection pressures that differ across environments. As mentioned above, theory predicts that the evolution of sexually selected traits can be affected by clinal variation in natural selection (Lande, 1982; Day, 2000). Owen (1986) showed that sex-specific selection along a cline can create differences in the frequencies of X-linked alleles between males and females. Lasne *et al.* (2017) further demonstrated that X-linked genes could contribute more to local adaptation than autosomal genes if migration is male-biased. Selection within local environments is also predicted to increase the rate of fixation of chromosomal inversions on the X chromosome relative to the autosomes (Connallon *et al.*, 2018b), a phenomenon that has been observed in *Drosophila* (Bhutkar *et al.*, 2008).

Despite the theoretical predictions described above, empirical tests of “large X” effects on local adaptation have produced mixed results. Lasne *et al*. (2019) failed to find evidence that the *D. melanogaster* X chromosome contributes to meaningful to clinal variation in multiple traits, although they did not consider sex-specific effects. In contrast, wing melanization in the butterfly *Colias philodice eriphyle* increases with elevation and depends largely on W-linked genetic variation (Ellers & Boggs, 2002). Sexually dimorphic gene expression variation may be an especially promising phenotype to study between sexes and across environments (Ingleby *et al.*, 2014). There is evidence that the expression levels of X-linked genes evolve faster than autosomal genes (Brawand *et al.*, 2011; Kayserili *et al.*, 2012; Meisel *et al.*, 2012). Across populations of *D. serrata*, X-linked gene expression divergence in females is elevated, relative to the autosomes (Allen *et al.*, 2017). Further work is needed to evaluate if X or Z chromosomes disproportionately contribute to local adaptation, and if those contributions depend on whether the alleles under selection have sex-specific fitness effects.

Thermal effects on sex chromosome evolution

Temperature is an intriguing ecological factor that could vary across populations or clines and have sex-specific effects. Notably, sex is often determined by the incubation temperature of eggs in species without sex chromosomes, including many reptiles and some other vertebrates (Valenzuela & Lance, 2004). Temperature-dependent sex determination can be selectively favored under certain thermal regimes (Charnov & Bull, 1977; Janzen & Phillips, 2006), but temperature-dependent systems are also capable of evolving into systems with a heritable sex determiner on a sex chromosome (Sarre *et al.*, 2004). Evolutionary transitions from temperature-dependent to heritable (i.e., genetic or sex chromosome) sex determination can be favored if the thermal environment that determines each sex is not well-aligned with the environment that maximixes the fitness of the sexes (Bulmer & Bull, 1982). However, sexual development is maleable, and genetic sex determination systems can also be sensitive to temperature in ways that over-ride the sex chromosome genotype (Sarre *et al.*, 2004; Holleley *et al.*, 2015). This fluidity between genetic and temperature-dependent sex determination provides a direct link between thermal ecology and sex chromosome evolution (Table 1).

Other examples demonstrate additional ways in which temperature-dependent selection pressures can affect sex chromosome evolution (Table 1). For example, there is an enrichment of X-linked alleles associated with divergence in cold tolerance and climatic variables across populations of *Drosophila montana* (Wiberg *et al.*, 2021). In other *Drosophila* species, Y chromosomes can harbor alleles with large fitness effects, despite having very few genes (Chippindale & Rice, 2001; Carvalho *et al.*, 2009). It is not yet determined whether the fitness effects of these Y-linked alleles depend on ecological factors.

Table 1. Effect of temperature on sex chromosome evolution

Sex chromosome turnover
Temperature override of genetic sex determination in the Australian bearded dragon, *Pogona vitticeps* (Holleley *et al.*, 2015)
Sex chromosome evolution
Alleles associated with cold tolerance and climate are enriched on the *Drosophila montana* X chromosome (Wiberg *et al.*, 2021)
Temperature-dependent fitness effects maintain a cline of house fly proto-Y chromosome (Delclos *et al.*, 2021)

The best evidence for temperature-dependent fitness effects of Y chromosomes comes from the house fly, *Musca domestica* (Table 1). House fly has a polygenic sex determination system, and the male-determining gene is frequently found on one of two different proto-Y chromosomes (Hamm *et al.*, 2015; Sharma *et al.*, 2017). One of these male-determining proto-Y chromosomes is most common at northern latitudes, and the other is predominantly found at southern latitudes (Denholm *et al.*, 1986; Tomita & Wada, 1989; Hamm *et al.*, 2005; Kozielska *et al.*, 2008). As predicted by their clinal distributions, the frequencies of these two proto-Y chromosomes is associated with temperature variation across populations (Feldmeyer *et al.*, 2008). Moreover, the northern proto-Y chromosome confers greater cold tolerance and preference for colder temperatures, while the southern proto-Y confers heat tolerance and preference (Delclos *et al.*, 2021). Transcriptome-wide gene expression analysis has identified candidate genes whose temperature-dependent expression may be responsible for the phenotypes under selection (Adhikari *et al.*, 2021). These patterns suggest that the polymorphism is maintained by temperature-dependent fitness effects of the proto-Y chromosomes, but it is not yet resolved if these effects are sex-specific.

Pigmentation, predation, and sex chromosome evolution in fish

Pigmentation, specifically sexual dichromatism, is a phenotype with environment-dependent fitness effects that contributes to sex chromosome evolution in teleost fish. Many evolutionary transitions in sex chromosomes, as well as complex sex chromosome systems, have been documented in teleosts (Mank & Avise, 2009; Sember *et al.*, 2021).

Intriguingly, sexually dimorphic pigmentation in fish is often controlled by genes on the sex chromosomes (Kottler & Schartl, 2018). Pigmentation in fish is often used for signaling to potential mates, but those same signals can attract predators (Reznick *et al.*, 1996; Zuk & Kolluru, 1998). Moreover, pigmentation patterns that provide camouflage from predators can depend on specific aspects of the natural environment (Cott, 1940; Endler, 1978). All of this taken together raises the possibility that sex-specific and environment-dependent selection on pigmentation contributes to the evolution of sex chromosomes in teleosts. Below, I review one clear example of sex chromosome turnover driven by intersexual conflict over signaling and camouflage (Roberts *et al.*, 2009). I also describe additional fish taxa where selection on sexual dichromatism may drive sex chromosome turnover or the evolution of sex chromosomes (Table 2).

Table 2. Effect of pigmentation, sexual selection, and predator avoidance on sex chromosome evolution

Sex chromosome turnover

Lake Malawi cichlid W chromosome with a female-determining locus linked to an allele that improves female camouflage but negatively affects male courtship display (Roberts *et al.*, 2009)

Sex chromosome evolution

Guppy Y chromosome affects pigmentation phenotype under sexually selection but also associated with predation risk (Gordon *et al.*, 2012, 2017)

Swordtail fish Y-linked allele affects sexually selected pigmentation (Kingston *et al.*, 2003)

Y-linked allele in a mosquitofish with temperature-dependent effects on melanization that is involved in mate signaling and predator avoidance (Angus, 1989; Horth, 2004, 2006; Horth *et al.*, 2013)

The clearest example of intralocus sexual conflict driving a sex chromosome turnover comes from cichlid fish in Lake Malawi (Roberts *et al.*, 2009). In these fish, bright pigmentation is favored in males because it increases mate recognition (Van Oppen *et al.*, 1998), but a different coloration allows females to camouflage against the rock substrate of the lakes they inhabit. This creates a conflict between natural selection in females (for predation avoidance) and sexual selection in males. This conflict was resolved when a female-determining allele arose that is genetically linked to the allele that determines the female-preferred color pattern (Figure 2). This is a clear example of an ecological selection pressure (camouflage for predator avoidance) driving the evolutionary turnover of a sex chromosome system (Table 2).

There has been extensive sex chromosome turnover during the evolution of cichlids from Lake Malawi, Lake Tanganyika, and other East African lakes (Gammerdinger & Kocher, 2018; El

Taher *et al.*, 2021). Closely related cichlid species often differ in which chromosome is sex-linked, and some species have polygenic sex determination systems with multiple sex-linked chromosomes (Ser *et al.*, 2010; Roberts *et al.*, 2016; Böhne *et al.*, 2019). Cichlid fish are also one of the best examples of an adaptive radiation that involved a high rate of speciation giving rise to many new species in a short period of time, possibly as a result of niche specialization for a diversity of ecological habitats (Ronco *et al.*, 2021). Sex chromosomes are thought to have a large effect on speciation because they may be more likely to harbor loci for reproductive isolation (Payseur *et al.*, 2018), providing a link between sex chromosome turnover and speciation in cichlid fish (El Taher *et al.*, 2021). Moreover, alleles responsible for color variation in cichlids tend to be sex-linked (Lande *et al.*, 2001), suggesting that sexual conflicts over camouflage and mate attraction at pigmentation loci could be partially responsible for both sex chromosome turnover and speciation in cichlid fish. This is notable because it ties together ecological factors that promote speciation with ecological factors that drive sex chromosome turnover.

When sex chromosome turnovers are common, the same chromosome is likely to become sex-linked in multiple evolutionary lineages. There has indeed been repeated recruitment of the same chromosome to be an X-Y or Z-W chromosome across cichlids, with rates of sex chromosome re-use exceeding random expectations (Gammerdinger & Kocher, 2018; Böhne *et al.*, 2019; El Taher *et al.*, 2021; Feller *et al.*, 2021). There are at least two explanations for the same chromosome repeatedly being recruited to be a sex chromosome in multiple evolutionary lineages (O'Meally *et al.*, 2012; Furman & Evans, 2016). First, some chromosomes may possess genes that are able to mutate into sex determiners, such as *Sox9* in *Oryzias* rice fishes (Takehana *et al.*, 2007, 2014; Myosho *et al.*, 2015). Alternatively, some chromosomes may be more likely to harbor sexuallly antagonistic alleles whose conficts can be resolved by Y- or W-linkage, e.g., genes involved in pigmentation that have dual roles in camouflage and mate attraction (Roberts *et al.*, 2009). Additional work to distinguish between these hypotheses would be informative of the role that ecology plays in sex chromosome turnover.

Connections between sex chromosomes, pigmentation, and predation have been observed in other fish, including those in the family Poeciliidae (Table 2). The poeciliid fishes are classic models for the evolution of sex chromosomes and sex determiantion (Volff & Schartl, 2001; Schultheis *et al.*, 2009). Loci controlling color polymorphisms in *Poecilia spp.*, including the guppy, are often Y-linked (Winge, 1927; Lindholm & Breden, 2002; Lindholm *et al.*, 2004; Morris *et al.*, 2018). In the guppy, *P. reticulata*, male mate choice depends on male color patterns (Houde, 1987). In addition, male guppies from high predation environments are less colorful than those from locations with lower predation (Endler, 1980; Magurran, 2005), and the extent of Y-linkage of color traits is greater in high predation than low predation environments (Gordon *et al.*, 2012, 2017). There are also likely to be tradeoffs and complex interactions between sexually selected traits, predator avoidance, and other ecologically relevant phenotypes (Endler, 1995; Godin & McDonough, 2003), similar to the cichlid fish described above. For example, frequency-dependent survival favors rare color morphs in *P. reticulata*, possibly because predators are more likely to capture the more common morph as a result of selective search strategies (Olendorf *et al.*, 2006). *Poecilia parae* also has multiple male color morphs that are determined by Y chromosome genetic variation (Sandkam *et al.*, 2021). Rare color morphs of *P. parae* are preferred by females (Lindholm *et al.*, 2004), suggesting that the polymorphism may be maintained because of trade-offs across alternative mating strategies (Hurtado-Gonzales & Uy, 2009). These findings provide additional evidence that conflicts involving pigmentation that attracts both mates and predators are likely to be mediated by sex-linked alleles.

Xiphophorus is another genus of poeciliid fish that is a classic model for the evolution of sex chromosomes and sexual conflict. For example, *Xiphophorus maculatus* has a polygenic sex determination system that is thought to be maintained by sexually antagonstic selection (Orzack *et al.*, 1980). In addition, pigmentation patterns are frequently Y-linked in *Xiphophorus spp*. (Zimmerer & Kallman, 1988), and the pigmentation affects both sexual selection and predator avoidance (Table 2). In the pygmy swordtail, *Xiphophorus pygmaeus*, a polymorphic Y-linked locus controls body color, with both blue and gold males found in natural populations (Kallman, 1989; Baer *et al.*, 1995). Females from populations with few predators prefer blue males, but females from high predation risk populations have no color preference (Kingston *et al.*, 2003). This is consistent with sexual selection (female choice) being weaker in populations with more risk of predators because of tradeoffs between sexual and natural selection (Zuk, 1992). The examples from *Xiphophorus* provide yet more evidence for a relationship between sex chromosomes, sexual selection, and predation.

Sex-linkage of pigmentation alleles is oberved in other, non-poeciliid fish, as well. For example, penetrance of a Y-linked melanism allele in the eastern mosquitofish, *Gambusia holbrooki*, depends on temperature (Angus, 1989; Horth, 2006). Non-melanic mosquitofish males are preferred by females, possibly because the melanism resembles a parasitic infection (Horth *et al.*, 2013). However, melanic males have an advantage in the presence in predators (Horth, 2004), suggesting an environment-dependent selective advantage that could maintain genetic variation at this sexually selected Y-linked locus (Table 2). There is also a Y-linked color allele in the Japanese rice fish, *Oryzias latipes* (Aida, 1921), a member of a genus with a high rate of sex chromosome turnover (Takehana *et al.*, 2014; Myosho *et al.*, 2015). Future work could test if there is a relationship between pigmentation, ecological factors (e.g., predation), and sex chromosome turnover in rice fishes.

Body size and sex chromosome evolution

Body is size is another phenotype that can be affected by sex chromosome genotypes, but it is not clear how selection on body size affects sex chromosome evolution. Sexual size dimorphism is ubiquitous across animals, with size differences evolving under the influence of sexual selection, ecological factors, and developmental constraints (Hedrick & Temeles, 1989; Abouheif & Fairbairn, 1997; Blanckenhorn, 2005; Janicke & Fromonteil, 2021). The potential for interplay between sexual selection and ecology is of particular relevance here.

Effects of sex chromosomes on sexual size dimorphisms have been documented in multiple fish species. For example, differences in adult male size and age at sexual maturity in a population of *Xiphophorus nigrensis* are controlled by genetic variation at a Y-linked locus (Lampert *et al.*, 2010). Females prefer large males, and small males often employ a “sneaker” strategy to mate with females (Zimmerer & Kallman, 1989). While it is possible that large and small males have equal fitness (Ryan *et al.*, 1992), there may also be undescribed ecological factors that favor one morph in specific environments. In one population of *P. reticulata*, GxE interactions affect male body size (the environmental variable manipulated was food amount), with some of the alleles for body size on the Y chromosome (Hughes *et al.*, 2005). Lastly, alleles associated with phenotypic and behavioral divergence, including body size, between sympatric stickleback species in the *Gasterosteus aculeatus* complex are located on the ancestral- and neo-sex chromosomes (Kitano *et al.*, 2009; Yoshida *et al.*, 2014). It remains to be determined if these sex-linked body size alleles have context-dependent fitness effects across ecological habitats.

Future Directions

There are numerous examples of ecological factors affecting sex chromosome evolution, including temperature (Table 1) and predation (Table 2). In some cases, there are intersexual conflicts between pigmentation patterns in males that attract mates and those that provide females with camouflage. There is clear evidence that these conflicts can be resolved by a sex chromosome turnover that limits inheritance of one allele to the sex in which it is beneficial (Roberts *et al.*, 2009). In other cases, temperature affects the sex determination pathway in a way that over-rides an existing genetic or chromosomal sex determination system (Holleley *et al.*, 2015). However, temperature can affect the evolution of sex chromosomes independently of the sex determination pathway by, for example, maintaining polymorphisms in which different sex chromosomes have temperature-dependent effects on fitness (Adhikari *et al.*, 2021; Wiberg *et al.*, 2021). Each of these phenomena is illustrated by a small number of examples (Tables 1 and 2), and future work should examine the generalities of these patterns. Below, I describe some model systems for examining specific ways in which ecological factors could affect sex chromosome evolution.

Examining conflicts over pigmentation that attracts both mates and predators may be the most promising way forward to investigate how ecological factors affect sex chromosome evolution. Intersexual conflicts over pigmentation in cichlid fish is the best example of a selection pressure driving sex chromosome turnover, and the poecillid fish Y chromosome polymorphisms are a classic model for sexually selected pigmentation (Table 2). Continuing work in both of these systems is likely to reveal more examples of sex-specific and ecologically dependent selection pressures that shape sex chromosome evolution. Cichlids are an especially promising system for future work because of the high rate of both sex chromosome turnover and ecological adaptation that has happened in a very short period of time (El Taher *et al.*, 2021; Ronco *et al.*, 2021)

Sexual dichromatism is extensive across animals, raising the possibility that conflicts between sexual selection and predator avoidance may be important for sex chromosome turnover more broadly. Of note here are the sexually dichromatic in fish beyond cichlids and poeciliids (Miller *et al.*, 2021), as well as the extensive sexual dichromatism in frogs (Bell & Zamudio, 2012). Frogs, like fish, have experienced very high rates of sex chromosome turnover during their evolution (Jeffries *et al.*, 2018; Ma & Veltsos, 2021). However, unlike fish, no clear links have been drawn between pigmentation, ecology, and sex chromosome evolution in frogs. Frogs may therefore represent a promising, untapped system to investigate the ecology of sex chromsoome evolution.

An additional area of investigation that should be explored is how sex-linked genetic variation affects ecologically relevant phenotypes in an environment-dependent manner. Theory predicts that sex-specific and/or local adaptation can disproportionately affect sex chromosome evolution more than autosoms (Owen, 1986; Lasne *et al.*, 2017; Connallon *et al.*, 2018b). However, empirical studies of natural populations have revealed mixed support for this predicted result (Lasne *et al.*, 2018, 2019; Wiberg *et al.*, 2021). Of note are clines of proto-Y chromosomes in the house fly, which have significant effects on thermal phenotypes, although it remains to be determined if the effects are sex-specific (Delclos *et al.*, 2021).

One possible explanation for the mixed evidence for effects of sex chromosomes on local adaptation is that sex-specific fitness effects were not always considered in previous experiments. Specifically, GxE interactions that depend on sex (i.e., GxSxE effects) may be important for sexual selection and the evolution of sexual dimorphism (Ingleby *et al.*, 2010; Delph *et al.*, 2011). Given the importance of sex-specific selection on sex chromosome evolution, it is likely worth considering sex-specific fitness effects in any study of the relationship between sex chromosomes and local adaptation. However, it is also worth noting that not all sexually selected traits depend on the environment (e.g., Arbuthnott & Rundle, 2014), and it is not clear the extent to which sexual selection varies across environments. Future work could compare the effect of environmental conditions on sexually selected traits that map to either the sex chromosomes or autosomes to test of GxE interactions are more common for autosomal or sex-linked sexually selected traits.

Conclusions

Sex chromosome evolution is greatly affected by sex-specific selection pressures, and there is extensive evidence that sex-specific selection pressures often depend on ecological factors. It therefore should not be surprising that there are multiple examples of ecological effects on sex chromosome evolution (Tables 1 and 2). Nonetheless, these examples are limited, and multiple open questions remain about how ecology affects sex chromosome evolution. For example, do sex chromosomes play a disproportionate role in sex-specific or sexually antagonistic ecological adaptation? In addition, while sexual conflict arising from ecological factors can drive sex chromosome turnover (e.g., Roberts *et al.*, 2009), it is not clear if ecologically relevant selection pressures are a common factor in sex chromosome turnover. These should be motivating questions for researchers interested in ecology and the evolution of sex chromosomes going forward.

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