

Sexual Behavior, Genes, and Evolution in *Xiphophorus*

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ABSTRACT

A century of research into both behavior and genetics in *Xiphophorus* has yielded important insights into the genetic architecture underlying sexual behavior, particularly as concerns male courtship and mating strategies. Two Y-linked loci underlie much of the variation in male mating strategies, possibly reflecting selection for modularization. Courtship behavior elements, in contrast, are under polygenic control. Little is known about the genetics of female mating preferences, yet behavioral evidence suggests that female preference complexes typically do not map on to suites of male traits. Natural hybrid zones in *Xiphophorus* present an ideal system for studying the evolutionary genetics of male traits and female preferences using contemporary molecular techniques.

INTRODUCTION

SEXUAL BEHAVIOR is central to the evolutionary processes of speciation, hybridization, sexual conflict, and sexual selection, making it essential to understand the genetics underlying courtship and mate choice. Few model systems can claim the deep roots of *Xiphophorus* in both genetics and behavior. Already popular aquarium fishes in the early twentieth century, swordtails and platyfishes proved amenable to interspecific crosses,^{1,2} and they exhibited several independently segregating Mendelian pigment-pattern variants which made them useful for early genetic mapping studies. Myron Gordon¹ saw a parallel between his work and that of his predecessor T.H. Morgan, predicting that *Xiphophorus* would become the "*Drosophila* of fish genetics." *Xiphophorus* continued to be an important model in classical genetics. With the advent of molecular techniques, the classical pigment-pattern work shifted to explicitly address genes involved in melanoma formation.³⁻⁵

Xiphophorus also proved highly tractable for

early studies of behavior.^{6,7} From the beginning, behavioral research has focused on courtship and mating behavior, which vary widely among species. Into the 1980s, much of the behavioral work explicitly addressed genetic influences, such as the inheritance of behavioral characteristics in artificial hybrid crosses⁸ and the effects of the Y-linked P gene on male mating behavior.⁹

By and large, however, contemporary work on *Xiphophorus* behavior has remained separate from work using state-of-the-art genetic techniques. This article reviews what is known about the evolutionary genetics of behavior in swordtails and platyfishes and suggests approaches for future research on this topic.

EVOLUTIONARY GENETICS OF MALE COURTSHIP BEHAVIOR

The most instructive insights into behavior genetics in *Xiphophorus* have come from polymorphisms in male sexual behavior. Two loci, both linked to the Y chromosome, have large,

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pleiotropic effects on male body patterns, life history, and behavior.

The *P* locus, on the Y chromosome of male swordtails, is reviewed in this issue by Ryan.¹⁰ The *P* gene appears to regulate the timing of maturity via the hypothalamic—pituitary—gonadal axis,¹¹ and allelic variation at *P* is associated with a suite of correlated effects. Wild populations and species can be fixed or polymorphic at the *P* locus, with up to four alleles in some populations of *X. multilineatus*.⁹ Males with the “large” allele of *P*, *P-L*, are larger, more robust, and more ornamented than small (*P-s*) males⁹ and also exhibit greater swimming endurance.¹² Further, *P-L* males perform elaborate multicomponent courtship displays to females. *P-s* males, in contrast, lack courtship behavior and “sneak” copulations. Males with intermediate alleles exhibit a mix of courting and noncourting strategies. Females prefer to mate with ornamented, courting males.¹³

Whereas *P-L* males are favored by sexual selection, they are at a distinct disadvantage with respect to natural selection, which likely explains how *P*-gene polymorphisms are maintained in natural populations. The delayed maturity of large males is a disadvantage because of the reduced probability of surviving to maturity, but is an advantage because males that do survive to maturity are preferred by females. Ryan et al.¹⁴ showed that *P-s* and *P-L* males could have equal fitness simply based on the difference in the timing of maturity, even assuming the same per capita mortality in small and large males. *P-L* males in *X. multilineatus* are more attractive to predators, suggesting that per capita mortality may in fact be higher in these males.¹⁵

Countervailing selection also explains the maintenance of another Y-linked polymorphism, in this case associated with color variation. Males carrying the + and *cp* alleles express blue body color, with *cp* males expressing a gold caudal fin. *Con* males have both a gold body and caudal fin.^{11,16} The *con* allele occurs only in *P-s* males, while the + and *cp* alleles occur in males of all size classes.¹¹ In *X. pygmaeus*, males are fixed for the small, noncourting allele at the *P* locus, but males are polymorphic for body color; 13–25% of small males are gold.¹⁶

Kingston et al.¹⁷ showed that while female *X. pygmaeus* in one population preferred to mate with blue (+) males, gold (*con*) males dominated blue males in aggressive interactions and forced copulations on females. While the blue allele thus appears to be favored by intersexual selection, the gold allele is favored by intrasexual competition. In addition to balancing selection on phenotypes, what mechanisms might be maintaining polymorphisms in these single genes of large effect? It is likely that frequency-dependent selection would favor rare alleles at both loci: rare attractive males would enjoy an advantage with respect to mate choice, while rare sneaker males would presumably benefit from decreased female vigilance. In guppies, another poeciliid fish, females show a preference for rare male phenotypes,⁵³ suggesting that rare males could in fact have a mating advantage.

For both the *P* and body-color loci, then, single, Y-linked genes of large effect appear to regulate the expression of distinct and contrasting behavioral strategies. Male display traits are sexually antagonistic traits¹⁸ that are beneficial when expressed in males (since they increase attractiveness to females) but deleterious when expressed in females (since they do not enhance attractiveness and only incur predation and production costs). Since males are the heterogametic sex in swordtails, these genes should accumulate on the Y chromosome,^{18–20} which in turn favors a reduction in recombination between the sex chromosomes. A recent review²¹ suggests that this is the case particularly in taxa like *Xiphophorus*, where males have a nondegenerate heterogametic sex chromosome.

Selection might also favor the coordinated expression of behavioral and morphological traits corresponding to a distinct mating strategy. Such “selection for modularization,”^{22–24} favoring alleles with appropriate pleiotropic or epistatic effects on functionally associated traits, may be acting on the suite of traits associated with these Y-linked polymorphisms. Selection would thus favor a genetic architecture yielding coordinated expression or suppression of courtship and ornamentation. Since *P* genotype is tightly correlated with age and size at maturity, selection on life-history traits can

have strong effects on sexual traits and vice-versa.²⁵

Whereas the presence or absence of courtship is determined by single loci, the specific form of courtship behavior appears to be under polygenic control. In those *Xiphophorus* that court, males exhibit a complex array of motor patterns which vary among species. In *X. nigrensis* and *X. multilineatus*, for example, males perform a lateral display involving rapid 180° turns in front of and perpendicular to the female.^{13,26} Male *X. helleri*, in contrast, position themselves in front of the female and perform a backward swim. The specific form of courtship is meaningful to females: males performing a backward swim and other courtship-specific motor patterns are more attractive than the same males exhibiting the same degree of motion in noncourtship swimming.²⁷

Franck⁸ performed a series of reciprocal crosses between species differing in the expression of courtship behavior. Analysis of the courtship patterns of male F₁, F₂, and backcross progeny revealed that the backward swim ("backing from behind", Franck⁸) in *X. helleri* and lateral display components ("sword-bending" and "frontal position") in *X. montezumae* were each polygenic and inherited independently from one another. This genetic architecture may help to maintain heritable variation in courtship behavior. While there may be strong selection for modularization with respect to the presence or absence of courtship, this may not be the case for the expression of individual components; in fact, female preferences for novel traits (e.g., Burley and Syman-ski²⁸) may exert diversifying selection on quantitative differences in courtship displays.

Mating behavior, of course, involves the presentation of a suite of morphological traits, many of which have been the focus of genetic studies. The sword, a conspicuous extension of the caudal fin, is a target of female mating preferences²⁹ and, in the secondarily swordless *X. birchmanni*, of female disdain.³⁰ Hybridization experiments between *X. helleri* and *X. montezumae* revealed that the sword is under the control of multiple genes of small effect.³¹ Swords of some F₁ hybrids were longer than those observed in parental species, indicating epistatic interactions among sword-determining loci.

Allometric growth of the sexually-dimorphic dorsal fin in *X. nigrensis* is also a polygenic trait.¹¹

Franck et al.³² examined female preference for macromelanophore patterns determined by the *Mdl* locus. *Mdl* is closely linked to *ONC-Xmrk*, a dominant oncogene associated with melanoma. *Mdl* males (as well as female shoal mates) were preferred by females in turbid water but not in clear water. Franck et al.³² argued that the potentially harmful oncogene could persist in *X. helleri* populations by hitchhiking along with *Mdl*.

It has been difficult to detect female mating preferences for other Mendelian pigment-pattern traits. The caudal blotch (*Cb*) and spotted caudal (*Sc*) polymorphisms in *X. malinche* and *X. birchmanni*, respectively,³³ do not elicit repeatable female preferences (BBM Wong and GG Rosenthal, unpublished data), and *X. variatus* mate randomly with respect to tailspot polymorphism.³⁴ *X. maculatus*, however, mate disassortively with respect to tailspots,³⁵ which Borowsky³⁶ suggested might reflect inbreeding avoidance.

GENETIC ARCHITECTURE OF FEMALE MATING PREFERENCES AND THE EVOLUTION OF SEXUAL COMMUNICATION

Female *Xiphophorus* exhibit mating preferences with respect to numerous, distinct male traits: swords,^{29,30,37} color,^{17,38,39} pheromone cues,³⁹ courtship,²⁷ body size,^{29,40} and vertical barring patterns.⁴¹ Within species, females express a patchwork of ancestral and derived preferences. For example, females of several species whose males have never evolved, or have secondarily lost, swords or large body size nevertheless prefer males expressing those traits;^{37,40,42} the same females exhibit preferences for the olfactory signals of conspecific males.⁴³ Female preferences vary greatly among populations and species: females in several species show strong preferences for conspecific olfactory signals;³⁹ populations of *X. pygmaeus* vary in their preference for male body size,⁴⁰ body color,¹⁷ courtship, swords, and body shape;²⁵ and *X. nigrensis*²⁶ and *X. birch-*

*manni*³⁰ have secondarily lost the preference for swords.

While there has been little work explicitly addressing the genetic basis of female mating preferences in *Xiphophorus*, there is ample evidence to suggest that preference variation has a strong genetic component. Preference differences among populations and species persist in laboratory-reared females and those reared in the absence of males.²⁶ The only study to explicitly address female mate choice and genotype was Borowsky and Kallman's³⁵ finding that female *X. maculatus* mated disassortatively with respect to tailspot genotype; this could reflect physical linkage or linkage disequilibrium of tailspot genes with preference genes, or the result of experience with one's own phenotype or that of similar individuals.⁴⁴

The genetic architecture of female preference has tremendous implications for the evolution of male traits and female preferences. First, there may be pleiotropic effects of the same gene regions on both traits and preferences,⁴⁵ although this may be challenging to achieve by a single genetic mechanism in fish communication. For example, the same locus might influence the temporal frequency of a courtship motor pattern, and the temporal-frequency response of the optic tectum.

Second, genetic architecture constrains how multiple preferences and multiple traits might interact. The existing evidence strongly suggests that there is not a one-to-one mapping between genetically correlated male trait complexes and suites of female preferences. For example, courtship expression and body size are strongly correlated in species with *P* gene polymorphisms,¹¹ yet these signals address different sensory mechanisms and the resulting preferences may be under distinct genetic control. Conversely, while the sword is a polygenic trait and body size is linked to *P*,¹¹ the female preference for swords reflects a broader bias for large apparent size.²⁹ *X. birchmanni* females prefer males of larger size, yet avoid males with allometrically larger dorsal fins (HS Fisher and GG Rosenthal, unpublished data). Suites of traits and preferences can thus interact through complementary, opposing, or orthogonal processes.

Selection might favor the coordinated expression of preferences for correlated male

phenotypes. If females express preferences congruent with the correlation between male traits, the traits would essentially represent redundant aspects of the same signal, thereby reducing the cost of information and possibly reducing the time females require to sample each male. Thus, "selection for modularization",²²⁻²⁴ favoring alleles with appropriate pleiotropic or epistatic effects on functionally associated traits, may be acting on both traits and preferences.

The heritability of male traits, female preferences, and their association is poorly understood. Both male traits and female preferences can show flexible responses to their environment. In *X. helleri*, females allocate differential amounts of tissue to the sword versus body size depending on feeding regime,³⁷ and in guppies *Poecilia reticulata*, female preference for carotenoid-based color patches on males depends on carotenoid availability in the environment.⁵⁴ Environmental influences can thus affect suites of traits, suites of preferences, and their interactions.

HYBRIDIZATION AND SEXUAL BEHAVIOR

Artificial crosses between species have always been instrumental in studying *Xiphophorus* genetics.¹⁻³ More recently, we have found several natural hybrid zones between *X. malinche* and *X. birchmanni*,⁴⁶ and we and other workers have observed morphological and molecular evidence of hybridization between several other species pairs. These hybrid zones offer an opportunity to study how species-specific trait and preference complexes are disrupted in nature. In the *X. malinche*—*birchmanni* hybrid zone, males exhibit transgressive combinations of sexual traits—phenotypes not observed in either parental species. These include melanotic caudal patterns.⁴⁶ Female hybrids exhibit a mixture of preferences found in the two species (GGR, unpublished data). *X. birchmanni* females avoid males with swords, preferring the swordless, conspecific phenotype.³⁰ *X. malinche* show no preference for swords, and the sword is lost in hybrid populations with a largely *X. malinche* genetic background (GGR, FJGL, unpublished data). Naturally-hybridiz-

ing species offer an opportunity for the genetic dissection of traits and preferences and for the study of how selection acts on trait and preference genes in the wild.

MOLECULAR APPROACHES TO THE EVOLUTIONARY GENETICS OF SEXUAL BEHAVIOR

As Gordon¹ was perhaps the first to recognize, *Xiphophorus* occupy a unique position when it comes to the study of animal genetics. This is particularly true when it comes to the genetic architecture of sexual communication. *Xiphophorus* has been intensively studied with respect to male traits and female preferences, and techniques like playback of computer animations⁴⁷ permit high-throughput behavioral phenotyping. The *Xiphophorus* genome has been extensively mapped,^{48–50} which should make it straightforward to identify quantitative trait loci (QTL) associated with male traits and preferences. There is extensive conservation of very large linkage groups among teleosts.^{49,51,52} Comparative data from other fish genome projects should, in the near future, allow identification of candidate genes responsible for interspecific divergence in sexual communication systems.

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