Patterns of inheritance of mating signals in interspecific hybrids between sailfin and shortfin mollies (Poeciliidae: *Poecilia: Mollienesia*)

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Abstract
Differences in male morphology and mating behaviors are thought to confer species sexual isolation between sailfin and shortfin species of mollies. This study used interspecific crosses between the sailfin molly, *P. latipinna*, and the shortfin molly, *P. mexicana*, to investigate patterns of inheritance of morphological traits and behavioral rates of three mating behaviors in F1 hybrid males. The two parental species showed clear species differences with respect to the length of the dorsal fin and dorsal fin ray number. First generation hybrid males were intermediate between the two parental species for dorsal fin length and fin ray number, suggesting autosomal control of this trait with little effect of dominance by genes from either parental species. Parental species showed clear species differences in their rates of courtship displays. Unlike the pattern for dorsal fin morphology, F1 hybrid males showed a clear distinction in display rates with respect to the direction of the interspecific cross. Male hybrids whose sires were *P. latipinna* had courtship display rates that were up to three times higher than the rates of displays performed by hybrid males whose fathers were *P. mexicana*. The distribution of phenotypes between the parental species and that of hybrid males sired by that parental species was nearly identical. Such a pattern suggests the influence of Y-linked genes on the inheritance of courtship display rates in mollies.

Introduction
One of the greatest challenges in evolutionary biology is to identify the forces that promote divergence in reproductive systems and ultimately speciation. Recent studies have provided much insight into how natural selection, genetic drift and sexual selection can result in population divergence and speciation (see recent reviews by Panhuis et al., 2001; Schluter, 2001; Via, 2001). Less attention however, has been given to the kinds of changes that are favored by each of these forces and our knowledge of the genetic changes that occur during speciation is very limited, especially with respect to the types of species studied (Otte & Endler, 1989; Coyne, 1992; Coyne & Orr, 1998; Macdonald & Goldstein, 1999; Orr, 2001). Much of our knowledge of the genetic basis of species differences comes from a few well-studied groups, that is, *Drosophila*, a few additional insect genera and certain plant taxa, namely *Mimulus* spp. (see Table 1, Orr, 2001).

While both prezygotic and postzygotic isolating barriers may be involved in speciation, recent models suggest that premating isolation, particularly behavioral isolation, may be more important in rapid speciation, especially rapid divergence resulting from sexual selection (Turner & Burrows, 1995; Gavrilets & Boake, 1998; Turelli, Barton & Coyne, 2001). Behavioral divergence of closely related species is a common phenomenon and sexual selection has been implicated in speciation of a variety of taxa (reviewed by Ptacek, 2000; Panhuis et al., 2001). Such studies have concentrated on the contribution of sexual selection to speciation through divergence in mating signals and preferences, yet only a few of these studies have investigated the underlying genetics of mating signal divergence (Tomaru & Oguma, 1994; Shaw, 1996;
The study of the genetics of interspecific hybrids between closely related taxa is particularly relevant for understanding the process of species isolation (Beukeboom & Assem, 2001). If sexual traits play a major role in the early stages of speciation, then these traits should show a large degree of divergence between closely related species (Civetta & Singh, 1998). To the extent that high levels of genetic divergence caused this morphological and behavioral divergence, such higher genetic divergence is also expected to translate into a stronger disruption of the phenotypes of these sexual traits in interspecific hybrids due to incompatible gene interactions (Civetta & Singh, 1998; Beukeboom & Assem, 2001). Thus comparisons of the distribution of phenotypic components of a mating signal between parental species and their hybrids provide insights into the constancy of these traits from parental to hybrid generations and provide the first step towards uncovering the underlying genetic control of species differences in the parental taxa.

Mollies (genus *Poecilia*, subgenus *Mollienesia*) are particularly amenable to the study of interspecific divergence in mating signals and its role in speciation for several reasons. First, differences in the two major species complexes of mollies, sailfins and shortfins, are found primarily in males and are strongly associated with divergence in their mating systems. Sailfin species are characterized by a sexual dimorphism in which males possess a greatly enlarged dorsal fin (Regan, 1913; Hubbs, 1933; Parzefall, 1969) that is erected and presented to the female in a courtship display (Parzefall, 1969, 1979; Farr, Travis & Trexler, 1986). Receptive females respond to this display by remaining stationary, folding the median fins, and sometimes twisting the abdomen to accept a copulation (Parzefall, 1969; personal observation). Males of the sailfin species *P. latipinna* show low levels of intramale aggression (Travis, 1994) and are not known to form permanent dominance hierarchies (Farr, 1989). Thus, reproductive success in sailfin species appears to be more a function of female choice than strong male–male competition.

In marked contrast, shortfin species do not show sexual dimorphism in fin morphology and most species rely primarily on gonopodial thrusting during mating attempts (Parzefall, 1969, 1979, 1989; Brett & Grosse, 1982; Balsano et al., 1985; Woodhead & Armstrong, 1985; Ptacek, 1998). Gonopodial thrusting is an attempt at insemination without female cooperation, whereby a male orients himself behind a female, brings his gonopodium (modified anal fin that serves as an intromittent organ during internal fertilization) to a forward position and attempts to insert it forcefully into the female’s gonopore. Males of shortfin species do not rely on female cooperation for mating and have adopted a completely different mating system than males of sailfin species. Reproductive success is determined primarily by a social structure based on male–male aggression, where dominant males aggressively keep other males from gaining access to females and females are forcibly inseminated by these males through gonopodial thrusting (Miller, 1975; Parzefall, 1969; personal observation). Thus, male–male competition appears to play a much larger role in determining male reproductive success than does female choice in shortfin molly species.

Second, in addition to the strong level of interspecific divergence in mating behaviors and associated dorsal fin morphology, most of the reproductive isolation that exists between sailfin and shortfin species of mollies appears to be primarily due to premating reproductive isolation. Despite few reported instances of interspecific hybrids occurring in natural populations (with the exception of the gynogenetic species *P. formosa*; Turner, 1982), many species of mollies are completely interfertile in laboratory crosses (Hubbs, 1933, 1936; Meyer, Wischnath & Foerster, 1985; Parzefall, 1989). This implies an important role of sexual selection through female mating preferences in promoting and maintaining the interspecific divergence in mating signals between sailfin and shortfin species of mollies (Ptacek, 1998). Thus, speciation between sailfin and shortfin mollies may have occurred through rapid divergence of male mating behavior and/or dorsal fin shape (Ptacek & Breden, 1998). While a large degree of phenotypic divergence is known to exist between males of shortfin and sailfin species (Ptacek, 1998), the underlying genetic control of these phenotypic traits is not known.

Interspecific hybrids can be generated in the laboratory and measured for their degree of trait expression of morphological and behavioral traits associated with mating signals. The phenotypic trait distributions in the F1 hybrid males can be compared to these values for males of the parental species. Such a comparison provides an initial step in understanding the genetic control of species differences between sailfin species complexes of mollies, sailfins and shortfins, particularly amenable to the study of interspecific divergence and specific divergence in mating behaviors and associated traits. Such interspecific hybrids can be generated in the laboratory and measured for their degree of trait expression of morphological and behavioral traits associated with mating signals. The phenotypic trait distributions in the F1 hybrid males can be compared to these values for males of the parental species. Such a comparison provides an initial step in understanding the genetic control of species differences between sailfin species complexes of mollies, sailfins and shortfins, particularly amenable to the study of interspecific divergence and specific divergence in mating behaviors and associated traits. Such interspecific hybrids can be generated in the laboratory and measured for their degree of trait expression of morphological and behavioral traits associated with mating signals. The phenotypic trait distributions in the F1 hybrid males can be compared to these values for males of the parental species. Such a comparison provides an initial step in understanding the genetic control of species differences between sailfin species complexes of mollies, sailfins and shortfins, particularly amenable to the study of interspecific divergence and specific divergence in mating behaviors and associated traits. Such