

Chapter 17 Precopulatory sexual selection

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17.1 Introduction

DARWIN (1871) DESCRIBED sexual selection as a struggle of two kinds: between individuals of the same sex to drive away or kill their rivals (intrasexual selection) and between individuals of the same sex to charm the opposite sex (intersexual selection). These two mechanisms of sexual selection can operate both before mating (precopulatory sexual selection) and after mating (postcopulatory sexual selection; Evans & Pilastro, **chapter 18**). Here we highlight the continuing role that poeciliid fishes play in expanding our understanding of precopulatory sexual selection (for reviews see Farr 1989; Bisazza 1993b; Houde 1997).

Two previous reviews of sexual selection within the Poeciliidae focused mainly on color dimorphisms and male aggression as possible indicators of mate choice and mating competition, respectively (Farr 1989; Bisazza 1993b). Based on these criteria and an apparent lack of courtship in most members of the family, these reviews suggested that mate choice may not be an important factor in over half of poeciliid species (Farr 1989; Bisazza 1993b). Although this is unlikely to be true (see Bisazza et al. 2001b), we still know little about the mating behaviors in most of these species, as detailed studies have focused on fewer than a dozen species. In this chapter, we do not attempt to extensively review studies of precopulatory sexual selection in the family but instead examine recent advances in which studies of poeciliid fishes have played an important role in furthering our understanding of the topic. In addition, we attempt to identify areas of research where poeciliid fishes are likely

to provide us with new insights into precopulatory sexual selection.

17.2 Mate preference

Two complementary questions can be asked about female mate choice: What role has it played in the evolution of male traits? And what drives the evolution of female mating preferences? In this section we review studies that address both of these questions and offer new insights into the evolutionary implications of female mate choice.

17.2.1 Variation in female mating preferences

The idea that variation in male mating behaviors, both among and within individuals of a species, can be adaptive is well accepted and has generated extensive research on alternative male mating strategies/tactics and the mechanisms that produce and maintain them (see below). Studies of variation in female mating behaviors, however, have lagged far behind (Jennions & Petrie 1997; Alonzo & Warner 2000; Hunt et al. 2005). Not all females prefer the same male or have the same strength of preference, nor do their preferences remain inflexible to environmental influences. Variation in female mate preferences has been detected at both population and individual levels in several species (Godin & Dugatkin 1995; Brooks & Endler 2001a; Morris et al. 2003; Rios-Cardenas et al. 2007). Wagner and Basolo (2008) argue that selection will often favor female reproductive tactics that are conditionally based on the past

costs and benefits involved in mate preference, which has particularly interesting implications for models of sexual conflict (see Magurran, **chapter 19**). Studying variation in female preferences is important to better understand the evolution of female preference, as well as the role of female preference in selecting for male traits.

Some of the first studies to report variation in female preferences in poeciliid fishes focused on *Poecilia reticulata* and revealed that these preferences covary with male color patterns among populations (Houde & Endler 1990), while both female preference for the male trait and the trait itself seem to depend on levels of predation (Endler & Houde 1995). Furthermore, in the presence of predators, female guppies from natural populations that experience high predation reduce their preferences for male coloration (Godin & Briggs 1996) and were less likely to choose males exhibiting the most conspicuous displays (Stoner & Breden 1988). These results suggest not only that there are costs associated with female mating preferences, but also that it can be adaptive for a female to be flexible about the circumstances in which some preferences are expressed. In guppies, female mating preferences can be modified based on prior experience with males (e.g., Breden et al. 1995; Dugatkin 1996) and can shift from ornamental traits to behavioral traits that indicate dominance when fighting among males is frequent (Kodric-Brown 1993). Furthermore, mate-choice copying has been shown to occur in guppies (Dugatkin 1992a; Dugatkin & Godin 1993; see Druen & Dugatkin, **chapter 20**, for more on mate-choice copying). There is some evidence to suggest that the willingness of a female to invest in mate choice, as well as the shape of her preference function, may be condition dependent (Brooks & Endler 2001a) or be influenced by the resources she has available to allocate to particular life-history functions (Hunt et al. 2005). And yet, what we have learned about variation in female preference has yet to be incorporated into models for the evolution of female preferences. One way to incorporate both environmental and genetic influences on preferences into an evolutionary model is to consider preferences as context-dependent traits (West-Eberhard 2003; Robinson & Morris, forthcoming).

Identifying the factors that influence variation in female mate preference will provide valuable insights into why females assess particular male traits. In addition, the implications of variation in female mating preference for the evolution of male traits are likely to be important. Here we highlight two evolutionary consequences of variation in female mating preferences: the maintenance of male alternative mating strategies and speciation.

Female *Xiphophorus multilineatus* have an overall significant preference for large courting males (courtiers) over small males that use sneaky matings (sneakers), and

this preference results in courting males having a higher fertilization success than sneakers (Zimmerer & Kallman 1989). However, the strength of this preference was positively related to female size, with smaller females having a weaker preference for courtiers (Rios-Cardenas et al. 2007). Since there were significant differences in mean female size among subpopulations and across time, as well as a relationship between mean female size and the relative frequencies of these two genetically distinct male strategies (courtiers were significantly more common in those samples with the largest females), Rios-Cardenas et al. (2007) suggest that variation in female preferences over space and/or time among subpopulations of *X. multilineatus* could maintain the alternative strategies in the species as a whole (without negative frequency dependence). A more recent study demonstrated that the relationship between female size and strength of preference results in smaller females being more likely to have mated with sneakers in the field, and larger females with courtiers (Morris et al. 2010). Therefore, the mating success of sneakers will be greater in populations with smaller females.

For variation in female preferences to maintain the different strategies of *X. multilineatus*, either the average size of females must vary across time, or there must be gene flow between these subpopulations. In contrast, genetic isolation between populations that vary in female preferences could lead to speciation. As described above, in guppies both female choice and selection due to predation shape male reproductive strategies, resulting in variation in male mating behavior among populations. Because different populations have consequently diverged genetically (Endler 1995), this variation in preference could provide a mechanism for the divergence in mate recognition leading to speciation (Lande 1981). Brooks (2002) argues that variation in mate choice within guppy populations, as well as enhanced mating success for new immigrants to a pool, could explain why guppy populations with divergent mate recognition have not speciated (see also Magurran 2005; Rosenthal & García de León, **chapter 10**).

17.2.2 Female preference for multiple male traits

Early models of sexual selection considered only one female mating preference for one male trait. We now know that females often prefer several different traits and that many elaborate male traits are actually complex sets of traits, with females having preferences for one or more of these components (Candolin 2003). For example, studies of female preference in guppies have found that males with a higher display rate have higher mating success (Farr 1980b). However, when a male displays, his dorsal fin is erected, allowing females to assess attributes of the dorsal

fin. Indeed, females have preferences for the size, shape, and color of the dorsal fin (Bischoff et al. 1985; Houde 1987), suggesting that the increased mating success of males that display more could be due to multiple female mating preferences. Ultimately, the presence of multiple male ornaments may be due to multiple female mating preferences (Brooks 2002). Even though several studies have demonstrated that female guppies exhibit multiple preferences (Kodric-Brown 1993; Endler & Houde 1995; Brooks 1996; Brooks & Couldridge 1999) and that females prefer different traits in different contexts (Kodric-Brown & Nicoletto 2001), how such multiple mating preferences interact to influence male sexual attractiveness is still poorly understood.

Theoretical (Iwasa & Pomiankowski 1994; Johnstone 1995, 1996) and empirical studies (Dale & Slagsvold 1996; Brooks & Couldridge 1999; Künzler & Bakker 2001) suggest that multiple mating preferences can select for multiple male traits. The question of how these preferences interact to select for male traits will require more complex analyses that examine correlations between single variables and sexual selection. Using quadratic regression analyses, along with knowledge about genetic variation and covariation in male traits, Blows et al. (2003) have highlighted the complexities of the selection on male traits. Previous work with guppies (Brooks & Endler 2001a) had identified three linear selection gradients on male sexual ornaments. Further analyses by Blows et al. (2003) suggested that there were complex interactions among traits in determining male attractiveness, including both disruptive and stabilizing selection.

Several hypotheses have emerged to explain why females assess multiple cues in mate choice; some suggest that multiple preferences are adaptive, and others suggest that they are not (see table 17.1). The multiple-message hypothesis (Møller & Pomiankowski 1993; Johnstone 1996) suggests that multiple male cues provide females with information about different male conditions. An implicit but underappreciated outcome of this hypothesis is that preferences may conflict, selecting for different males. The backup-signal

hypothesis (Johnstone 1996; similar to the redundant-signal hypothesis; see Møller & Pomiankowski 1993) is also based on benefits females gain from assessing multiple cues. Here the theory suggests that each signal gives a partial indication of a male's condition, and together the signals function to increase the accuracy of assessment. A third hypothesis, the unreliable-signal hypothesis, suggests that female preference is weak for most ornaments of multiple-signal systems because they provide unreliable information (Møller & Pomiankowski 1993).

Evidence to support both the backup- and multiple-message hypotheses comes from studies of mate preferences for conspecific versus heterospecific males in the northern swordtail fishes (*Xiphophorus* spp.). Generally, sexual selection and species recognition reinforce one another; the mechanisms of species recognition are often based on sexually selected traits (for review, see Ryan & Rand 1993; Anderson et al. 2005). However, these two components of mate choice can conflict when females have preferences for traits of conspecifics that overlap with traits of heterospecifics (Pfennig 1998). *Xiphophorus pygmaeus* females have a preference for large male size (Ryan & Wagner 1987; Morris et al. 1996), which, as the only criterion for mate choice, would drive them to mate with larger sympatric heterospecifics (*Xiphophorus cortezi*) (Hankison & Morris 2002).

In addition to body size, *X. pygmaeus* and *X. cortezi* males differ in that the latter, but not the former, have a vertical-bar pigment pattern. This pigment pattern would appear to aid *X. pygmaeus* females in species recognition, as *X. pygmaeus* females preferred barless males to naturally barred males when size was held constant (Morris 1998; Hankison & Morris 2002). And yet the presence of vertical bars did not result in a significant preference for smaller conspecifics when females were presented with a choice between smaller, barless conspecifics and larger, barred *X. cortezi* males (Hankison & Morris 2002). *Xiphophorus pygmaeus* females also prefer chemical cues from conspecific males to those from allopatric *Xiphophorus nigrensis*

Table 17.1 Hypotheses concerning the function and evolution of mate preference for multiple male traits

Proposed hypothesis	Adaptiveness of preferences	Information content of trait	Predicted change in preference strength when females are allowed to assess more cues
Multiple message	Adaptive	Informative	Increases or stays the same (depending on whether or not preferences conflict)
Redundant signal	Adaptive	Informative	Increases
Unreliable signal	Nonadaptive	Uninformative	No change

Source: Modified from Candolin 2003.

males (Crapon de Caprona & Ryan 1990) and sympatric *X. cortezi* males (Hankison & Morris 2003). However, similar to the results found with respect to vertical body bars in the previous study, preference for the chemical cues was not strong enough to reverse the preference for larger hetero-specific males (Hankison & Morris 2003). It was only when females were allowed to assess both odor and the visual vertical body bars cue (more than one species-specific cue) that they spent more time with conspecifics. These results provide support for the backup-signal hypothesis because together these two cues of odor and presence or absence of vertical bars provided enough species-specific information for females to associate with conspecifics (Hankison & Morris 2003). These results also provide support for the multiple-message hypothesis because they demonstrate that the preference for body size conflicted with the preferences for the species-specific cues.

Both vertical-bar pigment pattern and odor turn out to be more complex traits than initially realized and are not easily categorized as traits that function solely during sexual selection or species recognition. Recent studies suggest that odor is more than a species-specific cue in swordtails (McLennan & Ryan 2008) and guppies (Shohet & Watt 2004). McLennan and Ryan (2008) found that *Xiphophorus montezumae* females had a clear preference for the odor of conspecific males over that of sympatric *Xiphophorus continens* males, whereas *X. continens* females preferred the odor of *X. montezumae* males. One explanation for these results is that odor provides information not only about species identity but also about male mating strategy (McLennan & Ryan 2008). *Xiphophorus continens* males all use sneak-chase behavior (Morris et al. 2005), while *X. montezumae* males court females. A similar suggestion was made by Shohet and Watt (2004) to explain why female guppies associated with some males more than others based on olfactory cues alone. In this study, female guppies preferred the odor of females over the odor of males, and therefore, preferred males may have smelled less “male-like” (Shohet & Watt 2004). In addition, the preference based on odor conflicted with the preference based on visual cues (Shohet & Watt 2004), providing support for the multiple-message hypothesis.

As the studies on preference for odor cues and vertical bars demonstrate, the division between traits used for sexual selection and species recognition will continue to become blurred as we gain a better understanding of the role of sexual selection in speciation and the processes of speciation in general. Depending on the range of cues available, and the way in which preferences for those cues interact, comparative studies will be able to unravel the evolution of multiple mating preferences and their role in speciation. For further studies on the role of odor as a species-specific

cue for species of northern swordtails that hybridize, see Wong et al. 2005, Fisher et al. 2006, and Rosenthal and García de León, **chapter 10**.

Farr (1989) suggested that many poeciliid fishes inhabit variable environments where heterozygosity, or increased genetic variability, would be advantageous. Fluctuating asymmetry (FA) may be a cue that females use to assess heterozygosity in some cases (Vøllestad et al. 1999), and therefore, symmetry could be an important cue for mate choice in poeciliid fishes. This does not seem to be the case for guppies, since inbreeding depression does not increase FA in the sexual coloration of males (Sheridan & Pomiankowski 1997b), and even though females prefer symmetrical males (Sheridan & Pomiankowski 1997a), female guppies do not appear to discriminate against related males or their sperm (Evans et al. 2008; Pitcher et al. 2008). However, female preference for bar number symmetry has been clearly detected in *X. cortezi* (Morris & Casey 1998). These studies represent only the beginning of our understanding of female preference for symmetry. We suggest that as our understanding of both the interactions among multiple preferences and variation in female preferences increases, we will find that some of the conflicting evidence on the importance of FA is due to our lack of consideration of conflicting preferences, the role of sexual conflict in the evolution of honest signals between males and females, and overly simplified models of what it means to be a high-quality mate in variable environments. Taking into consideration our increased understanding of the interaction between multiple preferences, we believe that preference for symmetry in other poeciliid species warrants further investigation.

17.2.3 Evolution of mating preferences

Several different mechanisms have been proposed for the evolution of mating preferences, and distinguishing between these has proven to be much more difficult than demonstrating that female mating preferences influence the evolution of male traits. Models for the evolution of mate preference fall into two categories: those based on direct selection on the preference and those based on indirect selection of a preference through its genetic correlation with the preferred traits (Kirkpatrick & Ryan 1991). Here we examine some of the evidence in support of both direct- and indirect-selection models from studies of poeciliid fishes.

The most intuitive method by which mate preferences are expected to evolve is by direct selection on females (Andersson & Simmons 2006). The benefits females gain by being choosy can include mating with a male that has a high-quality territory or one that provides females with nutrition, parental care, or protection from harassment.

While most of these benefits are uncommon in livebearing poeciliid fishes, evidence from the mosquitofish (*Gambusia holbrooki*) suggests that females gain direct benefits from proximity preference in the form of reduced sexual harassment (Pilastro et al. 2003; Dadda et al. 2005; Agrillo et al. 2006; Dadda et al. 2008). Females that choose males that provide more sperm or more viable sperm would also be under direct selection, although there is currently no evidence for this in poeciliids (Pilastro et al. 2008). In addition, direct benefits can include a reduction in search costs. Female preference for larger males (*Heterandria formosa*, *P. reticulata*, and *X. nigrensis*) (Ryan et al. 1990; Houde 1997; Aspbury & Basolo 2002; Magellan et al. 2005) and more conspicuously pigmented males (*P. reticulata* and *X. cortezi*) (Endler 1980, 1983; Morris et al. 2001) could have evolved due to direct selection on females to reduce search costs.

Distinguishing between the current function of a trait such as female mate preference and the context in which the trait initially evolved requires the use of comparative studies. The first clear evidence that a female mating preference initially evolved in a context other than preference for the preferred male trait (a preexisting bias) came from a study of *Xiphophorus* fishes (Basolo 1990). This now classic work, in which Basolo attached artificial swords to *Xiphophorus maculatus* males, a species in which males have no swords, and found a significant female preference for the sword, led to numerous studies across diverse taxa demonstrating similar preexisting biases. Further work by Basolo (1996, 1998) has provided additional support for this preexisting bias in poeciliid fishes. The context in which the preference initially evolved, however, is still unclear. There is some evidence to suggest that the preference for swords may have initially evolved due to female preference for large male size (Rosenthal & Evans 1998). The detection of preferences for specific components of the sword that would not increase the male's apparent size suggests that, at the very least, there has been subsequent evolution of the preference after the sword evolved (Basolo & Trainor 2002).

Female mate preferences for males that have good genes could provide females with indirect benefits and could therefore evolve through direct selection on the females' preference (Kokko et al. 2003; but see Kirkpatrick & Ryan 1991 for an example of female preferences for good genes evolving due to indirect selection, described below). Demonstrating that the expression of the preferred male trait is condition dependent has often been considered evidence for "good genes" models (e.g., Nicoletto 1993). However, a study by Nicoletto on guppies (1995) revealed no significant differences between the offspring of preferred and nonpreferred males with respect to constitution (e.g., criti-

cal swimming speed), ornamentation, or sexual behaviors. One possible explanation for these results is that the best traits for a female to provide to her offspring may vary depending on her age, the sex ratio of her brood, or even the time of year. This is also true for the "sexy son" hypothesis, which predicts that females can have indirect benefits by producing males that are better at attracting females (but see Kirkpatrick 1985). Here we see that increasing our understanding of why female preferences vary helps increase our understanding of the benefits females gain from their mate preferences. At the same time, a better understanding of selection on male traits is needed before assuming that we understand the benefits females gain from mating with particular males. For example, Reynolds and Gross (1992) suggested that in guppies, female preference for large male size indirectly benefited females due to heritable benefits to their offspring. Larger guppy fathers produce both larger male and female offspring with higher growth rates and higher daughter fecundity due to their larger size. While the benefit of producing larger female offspring seems to some extent inarguable, recent work with the green swordtail *Xiphophorus hellerii* suggests that increased growth rate may not necessarily be beneficial in all situations (Walling et al. 2007). When considering the evolution of female preference for large male size, trade-offs with functions other than mating success are too seldom considered.

A recent example of direct selection on female mating preferences comes from work by Fernandez and Morris (2008) on female preference for males with the spotted caudal pigment pattern (Sc; see fig. 17.1), which is always associated with the oncogene *xmrk* (see also Scharl & Meierjohann, chapter 26). They suggest that direct selection against preferring males with Sc could explain why females from a population of *X. cortezi* with high frequencies of *xmrk* prefer males without Sc, compared with other populations of this species where females prefer males with this pigment pattern. When *xmrk* is overexpressed, the macromelanophore pattern Sc can form melanomas in natural populations of *X. cortezi*, reducing an adult's reproductive life span by approximately half (A. Scharl et al.



Figure 17.1 *Xiphophorus cortezi* male with vertical bars and spotted caudal fin. Photo by K. de Queiroz.

1995; Weis & Schartl 1998). In addition, there is evidence to suggest that offspring with two copies of *xmrk* are unviable (Kallman 1971). In the population where females prefer males without Sc, the frequency of females with Sc is much higher, which means that if females were to prefer males with Sc, they would increase the probability of producing offspring with two copies of *xmrk*.

Indirect selection on female mating preferences relies on a genetic correlation between preference and preferred traits (Kirkpatrick & Ryan 1991). These correlations form when mating is nonrandom and there is sufficient genetic variation in preference and trait (Fisher 1958; Lande 1981). Two different types of study have tested the hypothesis that preference and trait are genetically correlated in poeciliid fishes. The first involves selection experiments, in which one determines whether, by selecting on the male trait, female preference evolves as a correlated response. Using this approach, Houde (1994) demonstrated that female guppies from lines in which males were selected for increased orange tended to show stronger preferences for orange than females from lines where males were selected for decreased orange. However, evidence from Houde's study also suggested that such genetic correlations may break down over time in laboratory conditions, possibly due to situations that are not favorable to continued nonrandom mating.

Another way to test for genetic correlations between preference and trait is to examine the congruence between female preferences and male traits (both trait and preference present or absent in a taxon) across populations or species in a phylogenetic context. If genetic correlations can explain the evolution of diverse preferences across taxa, these correlations should result in the loss of preferences when the trait is lost and should persist over speciation events. Morris and Ryan (1992) compared the congruence of a male trait and female preference with congruence of the same male trait and male response to the trait in the sister species *X. nigrensis* and *X. multilineatus*. They found that while male response was congruent (*X. multilineatus* with vertical bars had male response to the bars, *X. nigrensis* without vertical bars had no male response to the bars), female preference was not (females preferred the bars in both species). These results suggest that any genetic correlation between preference and trait was lost when the bars were lost in *X. nigrensis*. Further studies of both male (Moretz & Morris 2006) and female (Morris et al. 2007) responses to vertical bars in the northern swordtail clade confirmed this earlier conclusion. Over the same evolutionary events (loss of vertical bars and speciation), male response remained correlated with the trait in every case (three out of three changes once male response evolved), while female preference was incongruent in three out of six changes in bar state (once female response had evolved; fig. 17.2). Lack of sufficient genetic variation could be responsible for the

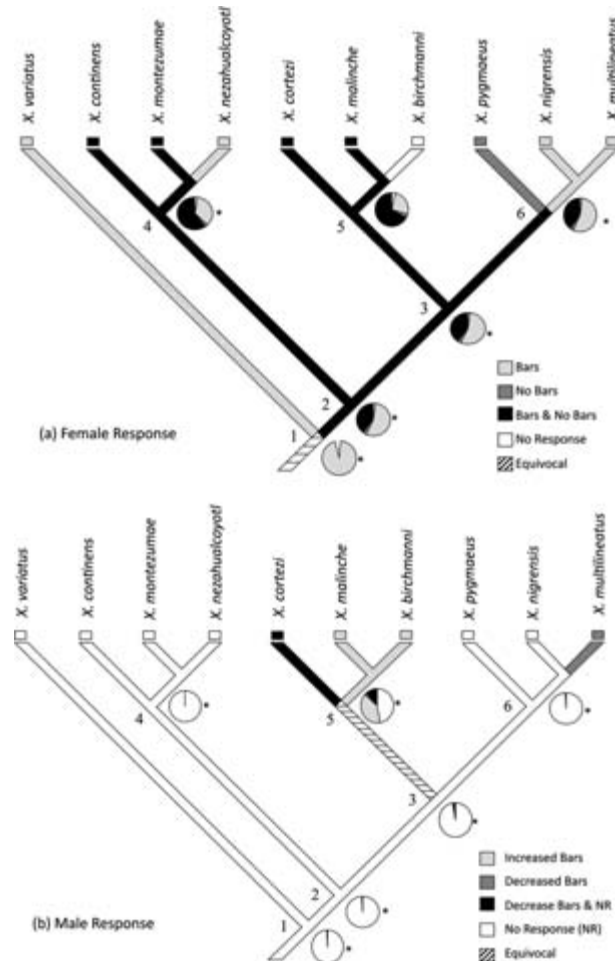


Figure 17.2 Reconstruction of ancestral states of both female and male response to vertical bars using maximum parsimony and maximum likelihood and using the Rauchenberger et al. (1990) phylogeny. Branches are shaded based on maximum-parsimony reconstruction. Area of pies indicates relative support for different ancestor states using maximum likelihood. Likelihood decision threshold was $T = 2$ (* next to pie indicates one or more significant states). (a) Ancestral states for female response to bars; (b) ancestral states for male response to bars. Modified from Morris et al. 2007.

loss of the genetic correlation, especially if speciation resulted from dispersal and involved population bottlenecks. However, if this were the case, one might expect the same pattern of congruence for male response as for female response, and this does not appear to be the case. While the difference in the coevolution of female and male response with the trait has not yet been explained, one possibility that is currently being explored is a potential sexual difference in phenotypic plasticity of the response to the bars.

17.3 Competition for mates

This section will focus on direct competition for mates in the narrow sense (i.e., mechanisms that increase access to mates through contests or fights). Contests between mem-

bers of the same sex over access to mates is very common in nature, and when fighting and ritualized contests are involved, such contests can be the most dramatic and obvious form of sexual selection. Among poeciliids, it has been suggested that male-male competition is more important in species that defend territories, as well as in species lacking courtship where males inseminate females without cooperation (Bisazza 1993a). Here we review the recent literature on competition for mates in poeciliids.

17.3.1 Traits used by males to determine the outcome of male-male contests

Precopulatory intrasexual selection should favor sexual differences in body size and shape, strength, and traits that can serve the bearer as weapons for defense or to threaten opponents (Darwin 1871). Nevertheless, it has been suggested that male contests over mates can select not only for traits that serve as physical weapons but also for conspicuous signals that serve as either indicators of strength or indicators of aggressiveness (e.g., as badges of status; Fisher 1958). Male traits that indicate strength and aggressiveness may be under selection if they help males win aggressive interactions and also if they make good fighters recognizable and memorable (Andersson 1994). Among poeciliids, dorsal fins have significance in both courtship and male-male competition: examples are the sailfin mollies *Poecilia velifera* (Bildsøe 1988) and *Poecilia mexicana* (MacLaren & Rowland 2006) and the swordtail fish *Xiphophorus birchmanni* (Robinson et al., forthcoming; Fisher & Rosenthal 2007). In the green swordtail *X. hellerii* the sword serves to attract females but is also used during male-male competition. Males with longer swords win more contests (Benson & Basolo 2006) and also do so more quickly (Prenter et al. 2008). These recent studies suggest that in the green swordtail, both male-male competition and female choice (see above) play a role in the evolution of longer swords.

A similar phenomenon occurs with pigment patterns. An example of this situation occurs in the Jalapa population of *X. hellerii*, which has two types of male: those with a black or dark brownish midlateral stripe (black males) and those with a red or brownish midlateral stripe (red males). In addition to a strong female preference for the red males in this population (which are, on average, larger), red males are dominant over black males, even when red males are smaller (Franck et al. 2003).

In some species of the northern swordtail clade (including *X. cortezi*, *X. multilineatus*, *X. nigrensis*, and *X. birchmanni*), the vertical-bar pigment pattern functions as a signal of aggressive intent, as males have the ability to intensify the expression of the bars at the onset of aggression (prior to the first bite), and the subordinate male suppresses expression of the bars at the end of the contest (Moretz &

Morris 2003). The males of *X. cortezi* are polymorphic for vertical bars, and barred males respond to the expression of the bars with reduced aggression. In this species aggression and fighting ability are correlated; barless males are more aggressive and dominant over their barred counterparts, and they seem to have a higher resource-holding potential (RHP) than barred males of the same size (Moretz 2005). Finally, further comparative studies that included the remaining members of the northern swordtails (*X. pygmaeus*, *X. nezahualcoyotl*, *X. montezumae*, and *X. malinche*), as well as a platyfish (*X. variatus*), have suggested that because the ability to vary the expression of the bars evolved before the male response (either reduced or increased aggression toward the expression of the bars), the bar's function as a sexually selected trait seems to have evolved first in the context of female mate preference and later as an honest signal of aggressive intent in male-male competition (Moretz & Morris 2006; Morris et al. 2007).

In the guppy, the contribution of male-male competition to the overall pattern of sexual selection is probably minor relative to other poeciliid species (but see Luyten & Liley 1991; Bruce & White 1995; Houde 1997). However, studies with guppies have shown that aggressive interactions that occur during competition for mates may have important consequences in the maintenance of pigmentation patterns that are not necessarily preferred by females. In this species, despite strong female preference for visually attractive males, visually unattractive but behaviorally dominant males were able to obtain a substantial proportion of matings by restricting mating opportunities and suppressing the courtship of subordinate males (Kodric-Brown 1992, 1993). Similarly, in the mosquitofish *G. holbrooki*, a melanic (black) body coloration is correlated with aggressive mating behavior, and it has been suggested that the persistence of this melanic morph in nature may be related to its advantage in male-male competition (Horth 2003).

Although prior experience contributes to the outcome of fights in *X. hellerii* (Franck & Ribowski 1987, 1989; Beaugrand et al. 1991), as in many animal species body size is usually a good indicator of RHP in poeciliid fishes in general (Farr 1989; Bisazza 1993b) and in *Xiphophorus* fishes in particular (Beaugrand & Zayan 1985; Ribowski & Franck 1993). Male-male competition contributes to the greater reproductive success of large males than small males in *X. nigrensis*; both field and laboratory experiments showed that large males exclude smaller males from access to females (Morris et al. 1992). Further studies showed that in both *X. nigrensis* and *X. multilineatus*, aggressive motivation in addition to body size seems to influence the outcome of contests (Morris et al. 1995). In *X. cortezi* body size is a moderate predictor of RHP (but see above and Moretz 2005 for the effect of the presence or absence of bars); however, contrary to predictions, smaller

males are more likely to initiate a conflict than larger males (Moretz 2003).

17.3.2 Alternative male mating strategies

In the past, with the exception of sex and age differences, individuals within populations were traditionally regarded as similar in ecology and ethology. However, a few decades ago a new emphasis on individual selection made clear that many populations had large, discontinuous differences in mating behaviors and morphology among individuals (Gross 1996; Shuster & Wade 2003). We now realize that such within-population variation has important ecological and evolutionary consequences and also that this variation seems to be strongly influenced by sexual selection in the form of competition for mates (Shuster & Wade 2003). Alternative reproductive phenotypes may be categorized as “real” alternative strategies (*sensu* Gross 1996) or conditional strategies, depending on the degree of genetic variation underlying the phenotypic variation (Gross 1996). In this section we review studies where alternative ways of achieving fertilization have evolved; generally, this implies using different strategies or tactics such as sneaky matings or female mimicry. Some of the early descriptions of alternative male reproductive matings in poeciliids included guppies (Liley 1966; see Magurran 2005 for a recent review). Here we focus on the species where most research has been done (table 17.2), but for a comprehensive list we refer the reader to the reviews by Bisazza (1993b) and Taborsky (1994, 2008).

Male guppies have two methods to achieve fertilization: they can either perform a sigmoid display to attract females (courtiers), or they can use a sneaky mating attempt, also termed a gonopodial thrust (sneakers) (Liley 1966). Males from populations with different predation regimes vary in their use of these tactics (Luyten & Liley 1985, 1991; Endler 1995). Furthermore, these differences among populations relate to the male’s ability to switch from conspicuous displays to sneaky mating attempts in the presence of a predator. Fish from predator-safe streams performed sigmoid displays, even when exposed to predators; alternatively, fish from predator-rich sites seem risk sensitive (but see below), as they decrease the rate of sigmoid displays while increasing the rate of sneaky matings when exposed to predators (Endler 1987; Magurran & Seghers 1990b; Magurran & Nowak 1991; Godin 1995). In the case of the guppy, sneaking is not adopted by inferior competitors since this behavior is preferentially adopted by larger males under predation risk (Reynolds et al. 1993). Finally, Evans et al. (2002a) report that males do not switch their mating behavior to avoid risk to themselves but instead switch to exploit changes in female behaviors brought on by the presence of predators.

Alternative strategies have never been rigorously demonstrated because it has proven extremely difficult to simultaneously show that the alternatives are the result of a genetic polymorphism, that the strategies have equal average fitness, and that this equality is maintained through negative frequency-dependent selection. However, some of the best evidence demonstrating the existence of this type of strat-

Table 17.2 Poeciliid species where alternative reproductive matings have been well described

Common name	Species	References
Mosquitofishes	<i>Gambusia affinis</i>	Hughes 1985
	<i>G. holbrooki</i>	Pilastro et al. 1997
	<i>Limia perugiae</i>	Erbelding-Denk et al. 1994
Sailfin mollies	<i>Poecilia latipinna</i>	Travis & Woodward 1989
	<i>P. velifera</i>	Oliveira, Gonçalves, & Schlupp, unpublished data
Guppy	<i>Poecilia reticulata</i>	Liley 1966; Farr 1980b; Bisazza 1993a
Gila topminnow	<i>Poeciliopsis occidentalis</i>	Constantz 1975
Platy	<i>Xiphophorus maculatus</i>	Halpern-Sebold et al. 1986
Northern swordtails	<i>Xiphophorus montezumae</i>	Kallman 1983
	<i>X. nezahualcoyotl</i>	Morris et al. 2008; Rios-Cardenas et al. 2010
	<i>X. multilineatus</i>	Zimmerer & Kallman 1989; Rios-Cardenas et al. 2007
	<i>X. nigrensis</i>	Zimmerer & Kallman 1989; Ryan et al. 1990

Note: In all cases differences between males are size correlated (small males tend to sneak, while large males tend to court). About 40% of poeciliid species practice alternative matings, about 55% only sneak, and about 5% only court (Bisazza 1993b; Bisazza & Pilastro 1997).

egy comes from poeciliids, and in particular the swordtails. In the pygmy swordtail, *X. nigrensis*, and the high-backed pygmy swordtail, *X. multilineatus*, maturation age and hence adult male size are under genetic control, and in the presence of large males, small males adopt sneaky matings (Zimmerer & Kallman 1989; Ryan et al. 1990). In the former species Ryan et al. (1992) presented evidence to suggest that courters and sneakers have equal fitness due to a mating advantage for the courters and a higher probability of reaching sexual maturity for the sneakers. Current studies of *X. multilineatus* (fig. 17.3) are evaluating the same prediction as well as other possible mechanisms (besides negative frequency-dependent selection; see section 17.2.1) that could be maintaining both strategies in natural populations (Bono et al., forthcoming).

Mank and Avise (2006a, 2006b) considered the evolution of alternative male mating strategies of ray-finned fishes (Actinopterygii) in a phylogenetic context and showed that the evolution of alternative mating behaviors was significantly correlated with the presence of sexually selected traits in bourgeois males (see Taborsky 1997). They focused on the effect of male-male competition on producing alternative behaviors (bourgeois, parasitic, and cooperative; Taborsky 1997) but did not consider the role of female mate choice. To determine how and when coercive behaviors evolved in relation to coaxing behaviors or to evaluate the relative roles of male-male competition and female mate choice in driving the evolution of alternative mating tactics, alternative tactics should be considered not only in the context of circumventing male-male competition but also in relation to circumventing female mate choice. For example, adding or removing male competitors did not always affect the mating behaviors used by *X. nezahualcoyotl* males. When

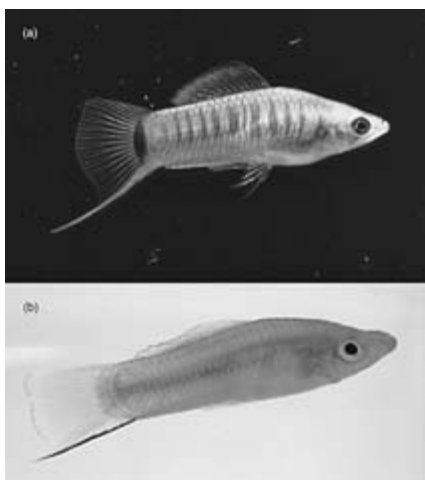


Figure 17.3 *Xiphophorus multilineatus* males. (a) Large courting male photo by K. de Queiroz. (b) Small sneaker male photo by Lisa Bono.

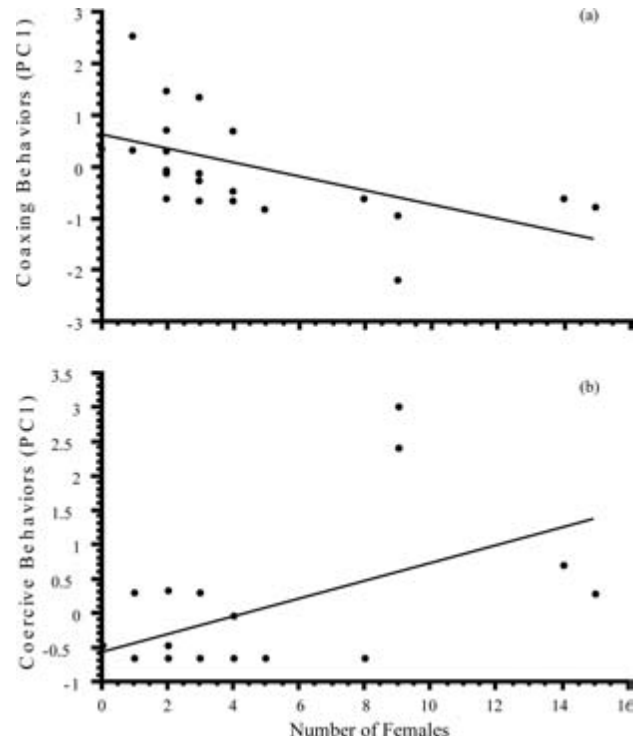


Figure 17.4 Relationship of the number of *Xiphophorus nezahualcoyotl* females and the rate of mating behaviors that males directed toward them. The number of females around focal males was significantly correlated with the mating behaviors that males directed toward those females, with (a) the rate of coaxing behaviors (first principal component shown; PC1) decreasing with the number of females; (b) in contrast, the rate of coercive behaviors (first principal component shown; PC1) increased with the number of females.

the behavior of males with and without larger competitors was examined in the laboratory, the largest males never used fast chase (a coercive behavior) even when a larger competitor was present, and the smallest males never performed headstands (a coaxing behavior) even when alone with a female. However, analysis of field data suggests that the number of females available plays an important role in the mating behaviors employed by *X. nezahualcoyotl* males (fig. 17.4). In this particular case, female mate choice rather than male-male competition appears to determine the tactic adopted by males. Further studies in other systems should also consider this possibility.

17.4 Interaction between mate preference and male-male competition

It was previously thought that female mate choice played little to no role in the mating system in which males do not court (Farr 1989; Bisazza & Marin 1995; Kolluru & Joyner 1997). The assumption was that males either coax females to mate through courtship, in which case females would have the opportunity to choose their mates, or co-

erces females to mate, in which case females would not be able to exercise mate choice. We now know that the situation is not so clear-cut, and that the interactions among the diversity of male and female mating behaviors can be complex. For example, female mate choice is expected to diminish as male-male competition increases, especially when the operational sex ratio (OSR) becomes male biased. However, Jirotkul (1999) demonstrated that both modes of sexual selection (female mate choice and male-male competition) became more intense in guppies when they experimentally shifted the OSR toward males. Finally, although it had initially been suggested that traits that function in both male-male competition and female mate choice evolved in the context of male-male competition and were co-opted by females (Berglund et al. 1996), this does not appear to be the case for all dual-functioning traits. Morris et al. (2007) found that female preference for vertical bars was present before male response to the bars in the context of male-male competition evolved (see fig. 17.2), suggesting that males may co-opt courtship signals for use in male-male competition.

17.5 Future directions

We hope that this chapter has made evident how the study of sexual selection using poeciliids as model systems has greatly advanced our understanding of sexual selection and evolution over the past 20 years. Most studies have focused on just a few representatives of the clade (mainly guppies, swordtails, platies, mollies, and mosquitofish). It is important to continue to investigate these model systems, as

building on what is known will facilitate the next wave of investigations into the interactions among different female and male preferences, between preference and competition, and the interactions between environmental and genetic influences.

Throughout the chapter we have identified several areas where future research on precopulatory sexual selection within these model species could take sexual selection research to the next level, which we view as providing us with a more integrative perspective on the different components of sexual selection, as well as incorporating the interaction between environmental and genetic influences on these traits. In particular, by incorporating multivariate analyses of multiple mating preferences and interactions between female and male mating preferences, we will gain a more integrative perspective on the evolution of mating preferences within each species. Nevertheless, we also suggest that future research should expand to include other members of the family. Information about the mating systems and sexual selection patterns of additional species will provide a more general and comparative perspective on the important factors that have shaped the evolution of the multiple mating systems that exist among the poeciliid fishes. With more information on the mating systems of all the species in this group, comparative phylogenetic studies could be used to determine if plasticity of mating behaviors is ancestral or derived, why courtship behavior evolved in some species and not others, and the factors that promote and maintain alternative mating behaviors, to name a few of the many questions that could be addressed with comparative studies in this group.