OXFORD

Article

Male mate choice in livebearing fishes: an overview

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Handling editor: Zhi-Yun Jia

Abstract

Although the majority of studies on mate choice focus on female mate choice, there is growing recognition of the role of male mate choice too. Male mate choice is tightly linked to 2 other phenomena: female competition for males and ornamentation in females. In the current article, I review the existing literature on this in a group of fishes, Poeciliidae. In this group, male mate choice appears to be based on differences in female quality, especially female size, which is a proxy for fecundity. Some males also have to choose between heterospecific and conspecific females in the unusual mating system of the Amazon molly. In this case, they typically show a preference for conspecific females. Whereas male mate choice is relatively well documented for this family, female ornamentation and female competition are not.

Key words: binary choice test, fecundity, female choice, female size, *Gambusia*, guppy, *Poecilia*, preference function, sexual selection, *Xiphophorus*.

Introduction

Within sexual selection, mate choice is especially important. Selecting a mating partner might be the most critical decision any individual makes. Mate choice is thought to drive the evolution of ornamental traits, including courtship, and can induce competition for mates in the opposite sex. Based on work by Darwin (1859, 1871), Bateman (1948), Trivers (1972), and Lehtonen et al. (2016), it is generally agreed that the sex that invests more into the offspring evolves to be the more selective one. In the majority of species this is the female, which invests strongly into eggs, as compared with a very small investment of males into sperms. This ecological differential in investment sets the stage for sexual selection and the 2 mechanisms proposed by Darwin: typically females choose partners and males compete over reproductive opportunities. In species with post-copulatory paternal investment into offspring, males can compensate for the lack of early investment, sometimes leading to a reversal in roles and the evolution of male mate choice and female competition for males. This is well understood in some of the few species that show this pattern, like pipefish (Vincent et al. 1992) and

Jacanas (Temrin and Sillentullberg 1994). In the vast majority of species, however, the pattern is much more subtle, and one question arising from male compensatory investment is whether this can lead to the evolution of choosiness in males (Edward and Chapman 2011). In addition to male investment, environmental stochasticity may flip the balance between limiting and limited sex, for example, when males become exceedingly rare locally (Heubel et al. 2009), thus potentially increasing their choosiness. More importantly, can choosiness evolve in species where there is no compensatory investment? Essentially, we have to ask what the adaptive benefits, the mechanisms, and the evolutionary consequences of male mate choice might be for such males. We need to explore if male mate choice could induce the evolution of female ornaments, and also lead to female competition over males (Figure 1).

To investigate this, I am reviewing our knowledge of a group of fishes that are on one extreme of the continuum of male investment. Males of livebearing fishes of the family Poeciliidae show no paternal investment into offspring after copulation. They only invest into ejaculates, pre-copulatory behavior, including courtship, as well as
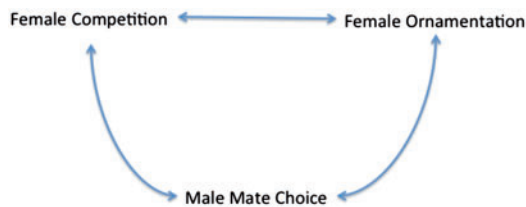
Figure 1. Hypothesized relationship between male mate choice, female competition, and female ornamentation.

sexually selected ornaments. Although clearly unlikely to evolve due to male investment, empirically, male preferences have been documented in several species within this family. However, even males that invest very little can be selected to respond to differences in female quality (Edward and Chapman 2011) and most authors assume that male preferences in this group evolved due to significant differences in female fecundity. Alternatively, this may simply be the easiest hypothesis to test, with other ideas still awaiting attention. Also, males should be able to distinguish between females of different quality, but preferences can also be based on sensory or cognitive bias (Rosenthal 2017). Furthermore, choosiness is typically expressed with the cost of foregoing some mating opportunities.

Fecundity is tightly linked to size in most fishes (Helfman et al. 2009). In livebearing fishes, male growth rates slow down once they reach maturity (Snelson 1984; Morris and Ryan 1990). Females, however, continue to grow throughout their lives. Because larger females typically can carry more eggs, males that prefer larger females should have increased fitness. To my knowledge this direct link has not been experimentally demonstrated, although many studies have found male preferences for larger females. However, in Poeciliids a few factors complicate the picture. First, females store sperm and can use stored sperm for several months to fertilize eggs (Greven 2011). It is not clear that males can directly assess how many eggs a female carries (although in a related family, Goodeidae, a male preference for females with wider bellies was reported [Méndez-Janovitz and Macías Garcia 2017], and in 2 Livebearers, females are known to prefer well-fed males with an extended belly [Fisher and Rosenthal 2006, Plath et al. 2005]) or how many may be available for fertilization. Second, in most species, females cannot conceal pregnancies due to a significant change in body shape. Hence, body shape is probably not an ornament, and it is not clear if females evolved to honestly advertise fecundity. Third, females go through a sexual cycle of roughly 30 days and appear to be fully capable of receiving sperm from males only during a few days during the cycle, or right after parturition (Parzefall 1973). This means that the operational sex ratio is almost always male biased, with many more males available to inseminate females than females being receptive for males. Fourth, the relationship between female body size and fecundity is not uniform across all species. In other words, the slope of the regression line describing the relationship between fecundity and size is not the same for all species. How this might influence the evolution and potentially the strength of male preference is not well understood (Arriaga and Schlupp 2013). In addition, this relationship of fecundity and size can be confounded by superfetation (Pollux and Reznick 2011), which evolved several times independently within the family. Superfetation means that females carry broods of different stages at any given time. This provides a fertile ground for asking how males actually judge female fecundity based on female size. Finally, very large females may not be of high value to males because they may be senescing, and not reproducing

anymore. Senescence in fishes in general (Reznick et al. 2002), and livebearing fishes in particular, is well documented (Reznick et al. 2006), but any effect this may have on male choice is unknown.

Nonetheless, almost all studies that looked at male preferences for size did find a preference for larger females (Dosen and Montgomerie 2004b), with a notable exception in the Least Killifish, *Heterandria formosa* (Ala-Honkola et al. 2010). This study seems to be the only one that found a preference for smaller males in a binary choice test, and a lack of preference in an open field test. The authors suggest that the absence of a preference may be driven by the strong first male precedence found in sperm competition. It is also possible, however, that publication bias exists and that studies reporting no preference are less likely to be published (e.g., Scherer U., Tiedemann R., Schlupp I., submitted for publication). A majority of studies did document a clear preference for larger females in multiple taxa (Herdman et al. 2004; Guevara-Fiore et al. 2010; Arriaga and Schlupp 2013; Head et al. 2015). Fundamentally, this predominance of male preference for larger females is matched with similar preferences in females, in other taxa (Ryan and Keddy-Hector 1992) beyond livebearing fishes. As we discuss the potential evolution of male mate choice in response to differences in female quality (e.g., as differential fecundity) or via other pathways (Edward and Chapman 2011), a very commonly invoked explanation is that male preferences are expressed via pleiotropy and may simply be due to the existence of evolved female preferences. They would not have evolved independently and might not even be adaptive. Interestingly, males and females can show preferences—seemingly for the same trait—body size, but likely for very different reasons. Male preferences seem to be related to a direct benefit, via increased fecundity (although a *direct* link to fitness remains to be shown [Dosen and Montgomerie 2004a, 2004b]), whereas female preferences for large males are thought to be due to indirect genetic benefits (Reynolds and Gross 1992).

Relevant Theoretical Treatment of Male Mate Choice

As male mate choice has moved more into the mainstream of sexual selection research (Clutton-Brock 2007; Edward and Chapman 2011), additional theoretical analysis of male mate choice has been published (for a recent review, see Fitzpatrick and Servedio, this volume; Fitzpatrick and Servedio 2018; Servedio 2007; Fitzpatrick and Servedio 2017). In a somewhat simplified view, male mate choice can evolve when mate availability is larger than the capacity to mate with, due to which there is recognizable variation in female quality and the benefit of choice is larger than the cost (Edward and Chapman 2011). A classical view in population ecology was that males did not matter much, but this has been corrected (Rankin and Kokko 2007). It needs to be acknowledged, again, that male mate choice (just like female ornaments; see Section on Female ornaments), might not be adaptive, but may be expressed due to pleiotropy. Recently, relative searching time (RST), the proportion of lifetime invested into mate search has been suggested as an important factor shaping the evolution of choosiness (Etienne et al. 2014; Courtiol et al. 2016). This approach emphasizes the role of direct benefits in the evolution of mate choice. For example, one study (Head et al. 2015) argues that males should be choosier when encountering females simultaneously, as compared with sequential encounters, because there is no opportunity cost. Empirically, preferences were indeed—as predicted—stronger during simultaneous encounters, but the number of sperms transferred and insemination success were unaffected. Theory also predicts that male

mate choice will not easily evolve under sequential mate choice conditions (Barry and Kokko 2010). These authors rightly call for rigorous tests of male mate choice, going beyond just describing the existence of male preferences.

Overall, one could argue that there is still a mismatch between theoretical predictions and empirical evidence, as models often argue that male mate choice will evolve only under a limited set of conditions (Barry and Kokko 2010), yet, empirically, an increasing number of studies in a variety of taxa other than fishes (e.g., insects [Bonduriansky 2001] or amphibians [Krupa 1995]) do report the widespread presence of male mate choice.

Natural History of Livebearing Fishes

Species in the family Poeciliidae are ideally suited to test the fecundity hypothesis of male mate choice as outlined above. As there are likely no or few benefits to male mate choice other than increased fecundity, this seems to be the default explanation for the existence of male mate choice. Poeciliids are generally small, freshwater fishes that tend to be ecological generalists. The family is widespread from the United States of America to South America, with a center of diversity in Mexico. Roughly 200 species in 29 genera are currently recognized (Hrbek et al. 2007, Meredith et al. 2010). Members of the family are widely used in biological research, including ecology, evolution, and animal behavior, but also genetics, genomics, and cancer research (Evans et al. 2011). The group is characterized by internal fertilization and ovoviviparity, where females give live birth to a relatively small number of offspring that have developed in the female. Males have a modified anal fin, called the gonopodium, which is used to transfer sperm (Greven 2011) and plays a role in evolution and speciation (Langerhans et al. 2005, 2007). Other important traits, however, like superfetation or courtship, have evolved several times within the family (Parenti and Rauchenberger 1989; Meredith et al. 2011). Females show lifelong growth, while male growth slows down significantly after they mature (Snelson 1984). Consequently, females are often larger than males (Bisazza and Pilastro 1997). It is not entirely clear what the evolutionary benefit of this is, but females might grow too big for some of their gape-limited predators. Generally, the mating system is characterized by promiscuity, with males either trying to court females or force copulations. Courtship evolved multiple times independently within the family, and genera can be polymorphic for this trait (Plath et al. 2007). Even within some species, such as sailfin mollies (Travis and Woodward 1989), males can be polymorphic and some size classes will show courtship whereas others may not (Rios-Cardenas and Morris 2011). Courtship displays usually involve males presenting themselves in front of a female, or showing elaborate motion patterns either in front or sideways of the female (Rios-Cardenas and Morris 2011). Coloration and courtship has been implicated in increased mortality rates for males (Garcia et al. 1998, Godin and McDonough 2003), but males from non-courting species can also experience high sex-specific mortality (Tobler et al. 2008), so that not only courtship can be blamed for this pattern. Females, especially because they are larger and more profitable prey, may also be at higher risk by size-selective predators (Trexler et al. 1994). Generally, it should be taken into account that most of our knowledge of mating behavior in Poeciliids stems from relatively few, well-studied species, such as the guppy Poecilia reticulata, some swordtails Xiphophorus sp., and several mollies Poecilia sp., while other genera and species are far less well studied.

In the sailfin molly Poecilia latipinna, for example, males of intermediate size can show courtship behavior when accompanied by small males and sneaky copulation attempts when accompanied by large males (Travis and Woodward 1989). These sneaky copulation attempts and the associated sexual harassment (Magurran and Seghers 1994a, 1994b; Clutton-Brock and Parker 1995) are very common and can be the only male mating behavior in some species (Plath et al. 2007). They are best understood as male strategies to circumvent female choice in the context of sexual conflict. Males in some species can switch from courtship to sneaking dynamically; in other species, the trait is genetically fixed. Often larger males show courtship (and other ornamentation), whereas smaller males rely on sneaky copulation attempts, and consequently being around larger males is less costly for females (Schlupp et al. 2001; Makowicz and Schlupp 2013). Probably the best understood example is a swordtail, Xiphophorus nigrensis, where a balanced polymorphism for 2 male morphs has been documented (Ryan et al. 1992).

Also, in many species males can be very colorful. Many colors are in the red and orange, but black spots are known from many species. The red and orange ornaments are produced by carotenoids or pteridines in chromatophores (Grether 2001). Black spots are generated by melanocytes, and are thought of as enhancers (Brooks 1996). Interestingly, there is a widespread parasitic disease, named Black Spot Disease that also results in black spots (Tobler and Schlupp 2008a, 2008b). Occasionally, white ornaments are observed, for example, in Poecilia gillii. Finally, males and females can have structural colors, often as iridescent blues. In many species, males have exaggerated dorsal fins, which are often displayed to females during courtship (MacLaren and Rowland 2006). In one group, swordtails of the genus Xiphopohorus, males of some species have evolved extended rays of the tail fin (Rosenthal and Evans 1998), in at least one species Xiphophorus montezumae, exceeding the length of the body of the male. These appendages are thought to mimic large male body size (Rosenthal 2017). Color and black spots are found in females of many species (see Section on Female ornaments for a discussion), but no exaggerated fins (MacLaren and Fontaine 2013). It might be worthwhile to point out here that color and spotting patterns may arise also under natural selection, not just by sexual selection.

Definitions

Before I begin to review male mate choice in livebearing fishes, I want to provide an operational definition of "mate choice." I am using the definition recently suggested by Rosenthal (2017): "Mate choice can be defined as any aspect of an animal's phenotype that leads to it being more likely to engage in sexual activity with certain individuals than with others." Note that this definition parts elegantly from the problematic traditional usage of sex roles (Ah-King and Ahnesjö 2013). Consequently, Rosenthal (2017) replaces female and male with the terms chooser and courter, which can be of any sex. I fully agree with this definition, but for the purpose of this review I retain the usage of male and female as a heuristic tool, to reflect the existing difference in the ecology of early investment into gametes, without acknowledging specific sex roles. I think that we eventually have to realize that mate choice is best understood as a continuum with the traditional sex roles of male and female confined to the extreme ends. I suggest that in reality in most mating systems, females and males both have preferences, exercise choice, and resolve the underlying sexual conflict in some form of mutual mate choice.

Another term that needs to be defined is "preference." Again, I use a definition by Rosenthal (2017): "a chooser's internal

representation of courter traits that predisposes it to mate with some phenotypes over others." The difference between choice and preference is that we can assess choice by measuring actual sexual behaviors, while preferences can also be measured indirectly, for example, using association times (Wagner 1998). One thing that can dictate how we measure preference or choice is the obviously interactive nature of actual mating, which involves behaviors from both individuals. Ironically, this sometimes requires that we separate individuals in a choice test, because we are interested in their "pure" preferences, not the outcome of an interaction between 2 partners.

Finally, an ornament is a trait that is likely to have arisen via sexual or social selection, and plays a role in mate choice by making the bearer attractive to choosers, often at a cost to survival. Ornaments are often sexually dimorphic, but they do not have to be. They do not have to have a function outside of social interactions.

Historical Studies on Interspecific Male Choice

In the 1960s and 1970s, the seminal papers by Hamilton (1964a, 1964b), triggered a Kuhnian paradigm shift (Kuhn 1962), which led to recognizing the gene as unit of selection in biology providing a new framework for biology, including mate choice. However, there was already considerable interest in male mate choice, including in livebearing fishes prior to this paradigm shift. Consequently, very early, livebearing fishes emerged as important model organisms in the study of mate choice. This early work was focused on questions of species recognition and isolating mechanisms; historically, female choice had not yet been recognized as very important (Milam 2010). Very importantly, with more female scientists conducting and publishing research on Sexual Selection beginning in the 1990s, more studies on female choice appeared (Zuk 1993). In a broader context, this provides a cautionary tale of how societal conditions influence and often hinder scientific work. Early on, Haskins and Haskins (1949, 1950) published their studies of male mate choice in guppies and some close relatives and reported evidence for male preferences for conspecific females and also provided a first comment on the role of size in male mate choice: "It is well known that males of *Lebistes*, when exposed to several females of their own species, tend to pay most attention to the largest individuals …" [note: *Lebistes reticulatus* was the recognized name for the guppy at the time] (Haskins and Haskins 1949). Another early account of male mate choice in the context of species recognition was offered by Hubbs and Delco (1960). In this article, the authors describe a conspecific preference in 4 species of *Gambusia*. They conclude that most species indeed show the predicted species preference, but that *G. affinis* does not. They note that this may explain why *G. affinis* is involved in many interspecific hybridization events. A recent study revisits this topic and found strong male preferences for conspecifics (Espinedo et al. 2010) in sympatric *G. affinis* and *G. geiseri*.

Male Choice within Populations

Generally based on the notion that larger females would provide a direct fecundity benefit to males, later studies started investigating male choice. Virtually all studies used binary choice tests. In such a test, a male is simultaneously exposed to (typically) 2 females that differ in the trait under investigation and can reveal his preference by approaching the females. The measured variable is typically association time, which is generally a good proxy for preference (Bischoff et al. 1985; Berglund 1993; Kodric-Brown 1993; Witte 2006), especially in male mate choice (Jeswiet and Godin 2011). Very few published studies

have used preference functions (Wagner 1998), in which 2 or more females are presented singly in random order (Arriaga and Schlupp 2013, Spikes and Schlupp, manuscript in preparation).

One of the few studies directly comparing male and female choice was conducted by Ptacek and Travis (1997) looking at mate preferences in sailfin mollies *P. latipinna*. The study also stands out because it used multiple populations, investigating population variation in the traits under consideration. This seems especially relevant in species that have a wide range. This is the case in the sailfin molly, which occurs from Wilmington, NC southward to roughly Tuxpan in Mexico (Schlupp et al. 2002). The study by Ptacek and Travis (1997) reported that both males and females generally prefer larger partners and that, larger males showed stronger preferences for female size.

Male mate choice is particularly well researched in guppies, often combined with studying the role of social influences on mate choice (Auld and Godin 2015; Auld et al. 2015, 2016, 2017; Jeswiet et al. 2011, 2012) (see also Section on Male mate choice and social information). In general, male preferences for larger females have been found many times (Dosen and Montgomerie 2004b; Herdman et al. 2004), often, but not always, using just visual information. In a study by Herdman et al. (2004), visual information was not sufficient for males to show a preference, but males did show a preference when allowed to access other information as well. Another study using guppies documented that results from open field tests and binary choice tests are correlated and yield comparable results (Jeswiet and Godin 2011). Mosquitofish, *G. holbrooki*, were also found to have a preference for larger females (Hoysak and Godin 2007).

Females can differ in quality in many different ways, and virgin females might be of very high value, especially in systems with first male sperm precedence. In this case, mating with a virgin female might secure a large number of offspring for the male that inseminates a female first. In guppies, males do not distinguish visually between virgin and mated females, but in an open field test, where males and females could fully interact, males directed more sexual behaviors toward virgin females. However, they showed more coercive, sneaky copulations toward previously mated females (Guevara-Fiore et al. 2009). Males also invested more effort into mating with females that were in the receptive phase of their sexual cycle (Guevara-Fiore et al. 2010). Finally, males of *Brachyrhaphis episcopi*, a species from Panama, preferred familiar females, but this preference was modulated by predation risk (Simcox et al. 2005). Another trait that may be used in male choice is a brood spot (or gravid spot) that is found in many livebearing fishes. A recent study found that size and intensity of the gravid spot are correlated with clutch size (Norazmi-Lokman et al. 2016), which may potentially be used by males in mate choice.

Cave mollies are a special population of the Atlantic molly, which has colonized a hydrogensulfide (H_2S) rich, toxic cave in Tabasco, Mexico (Tobler and Plath 2011). This population is widely used to study effects of both toxicity and darkness on mollies, often addressing ecological speciation (Riesch et al. 2011). Cave mollies are capable of mate choice both in darkness and in light. One study found that males of both the surface and cave form have a preference for larger females, but only cave mollies show the preference in darkness (Plath et al. 2006). Males of the surface form, but not males of the cave form can deceive other males relative to their mate choice (Plath et al. 2010; see also Section on Male mate choice and social information).

Mechanisms of Male Mate Choice

Documenting male mate choice would be incomplete without looking at the mechanisms (see Section on Male mate choice and social

information) that are used in male mate choice. Turbidity, for example, was found to slow down decision-making in sailfin mollies *P. latipinna* (Heubel and Schlupp 2006). A separate study found that male choice is also affected by seasonality (Heubel and Schlupp 2008). A study using *G. affinis* documented that males rejected females that were parasitized with nematodes, presumably because the infection reduces fecundity (Deaton 2009; Cureton et al. 2011). Furthermore, in the Atlantic molly, personality affects male mate choice and bolder males respond more strongly to the presence of an audience (Bierbach et al. 2015). Interestingly, in *G. holbrooki*, dominant females were preferred by males, whereas size had no significant effect (Chen et al. 2011). This is an important finding, because it shows that other factors—not only size—likely play an important role in male mate choice. MacLaren and Fontaine (2013) explored a potential female ornament in *X. variatus*, a species of swordtail without a sword. They found that males preferred larger body size in females, but not larger fins. Larger fins in males are often preferred by females and could serve as an indicator trait for females (McLaren et al. 2004). Apparently this is not the case for males. Finally, a general concern with mate choice studies is how reliable the data collected are. This has been addressed in a few studies investigating how repeatable male mate choice is, finding very low repeatability (Gabor and Aspbury 2008). By contrast, a study on guppies (Godin and Auld 2013) reported that male mate choice is fairly consistent, and a study on the swordtail *X. nigrensis* also found relatively good repeatability (Cummings and Mollaghan 2006). Clearly more studies on this topic are needed. Low repeatability between individuals may reflect many different things, including problematic experimental design. But it may also reflect true changes in a chooser's preferences, especially when responding to conditional traits.

Very little is known about the many other factors that are recognized in female choice, including preferences for Major Histocompatibility Complex (MHC) compatibility and inbreeding avoidance. It is well known that learning plays a role in mate choice (Verzijden et al. 2012) (see Section on Male mate choice and social information for discussion of social influences), and that there are sex differences in learning. In guppies, for example, females are twice as efficient in reversal learning (Petrazzini et al. 2017), possibly indicating that females have a generally higher cognitive flexibility.

Cost to Males and Cryptic Male Choice

Females make strong investments into their eggs. By comparison, sperm and mating are less costly. It is important to realize, however, that sperm is not free. There is growing evidence that males can be sperm depleted and that the costs of mating (viewed inclusively, and counting, e.g. cost for sperm, ejaculates, courtship behavior, predation risk, and lost opportunities) can be high for some males as compared with other males (Anthes et al. 2014, Hardling et al. 2008). Consequently, males may evolve mechanisms to exercise cryptic mate choice and allocate ejaculates and sperm strategically (Matthews et al. 1997; Schlupp and Plath 2005; Riesch et al. 2008; Robinson et al. 2008, 2011), and also prime sperm relative to species identity (Aspbury and Gabor 2004b) and female size (Aspbury and Gabor 2004a). Sperm priming is a mechanism that makes sperm ready to be ejaculated. Furthermore, there is growing evidence—at least in guppies—that males differ in sperm and ejaculate characteristics based on age (Gasparini et al. 2010), and that they can adjust to changes in the social environment very quickly (Boschetto et al. 2011; Barrett et al. 2014; Cattelan et al. 2016). Females appear to respond to these

changes by modulating the environment for sperm in their ovaries (Gasparini and Pilastro 2011; Gasparini et al. 2012). These interactions seem to reflect an ongoing sexual conflict (Parker 2006).

Clearly, mating in livebearing fishes is often characterized by intense sexual conflict (Chapman et al. 2003, Schärer et al. 2012) in which male or female preferences may be undermined or thwarted by the behavior of their mate. Forced copulations (Magurran 2001) and sexual harassment (Plath et al. 2007; Heubel and Plath 2008) are common throughout the family and probably lead to significant differences between measurable mate preferences and actual reproductive outcomes (Rosenthal 2017).

Male Choice for Correct Female Species: The Amazon Molly as an Example

The ecology of male investment relative to the mating value of the female can drive the evolution of male mate choice. In pipefish, male investment is very high and they have evolved to be selective. In other cases, the mating value of certain females may be so low that males evolve to reject them. The latter is the case in males facing a choice between heterospecific Amazon mollies *P. formosa* and their conspecific females. Amazon mollies are an all-female, clonal species of fish of hybrid origin (Hubbs and Hubbs 1932, Schlupp and Riesch 2011). The maternal ancestor is the Atlantic molly *P. mexicana* and the paternal ancestor is the sailfin molly *P. latipinna*. The single, original hybridization apparently took place about 100,000 generations ago in an area near present-day Tampico (Stöck et al. 2010; Warren et al. 2018), but see Alberici da Barbiano et al. (2013). Amazon mollies reproduce by gynogenesis, where sperm simply serves as stimulus for embryonic development, but is typically not incorporated into the offspring (Schlupp 2005). Based on this, the sperm-providing males are generally predicted to prefer conspecifics to heterospecifics. The Amazon molly uses at least 3 species as sperm donors: its 2 parental species, *P. latipinna* and *P. mexicana*, and *P. latipunctata* (Tamesi molly), an endemic species found near Ciudad Mante. Sailfin and Atlantic mollies not only show populations that occur in sympatry with Amazon mollies, but also populations that occur in allopatry. This creates an opportunity for work comparing characters, including male mate choice between allopatric and sympatric populations (Gabor and Ryan 2001, Gabor et al. 2005).

More importantly, this situation can be used to make very clear predictions relative to male mate choice. For males the fitness return for mating with Amazon mollies is very low. Even if the cost of mating is low or moderate, males should evolve to prefer conspecific females, or lower their cost by investing less into heterospecific copulations. Via mate copying, a process of using social information in mate choice (Witte et al. 2015; Varela et al. 2018), males gain an indirect fitness benefit offsetting some of the cost of heterospecific matings: the interactions of a sexual male and an Amazon molly are observed by conspecific females and make that male more attractive to conspecific females. Interestingly, males have also been shown to copy the mate choice of other males (Schlupp and Ryan 1997; Bierbach et al. 2011).

Male mate choice in this complex has been intensively studied (reviewed in Schlupp 2009; Schlupp and Riesch 2011). Often the "wrong" mating decisions are viewed as mistakes, and several studies looked into potential mechanisms for the mistakes. Interestingly, theory does not predict the evolution of perfect male choice (Heubel et al. 2009), and it seems that evolving very strong preferences is costly to the sexual males. Nonetheless, an older study, for example, found that male Atlantic mollies show species recognition when

choosing between visually presented conspecific and Amazon molly females, but that females undermine this probably with chemical signals when they are post-partum (Schlupp et al. 1991). In this case, females seem to win the underlying evolutionary arm-race. Chemical information alone, however, is insufficient for species recognition (Aspbury et al. 2010). A study of sailfin mollies (Muraco et al. 2014), documented the existence of distinct male behavioral phenotypes or personalities, but found no strong correlation with male preferences. A unique feature of this mating system highlights the complexity of mating interactions: Amazon mollies are known to actively intervene in conspecific mating attempts (Schlupp et al. 1991; Foran and Ryan 1994). They sometimes approach mating pairs of sailfin mollies and maneuver themselves into the position of the sexual female, thereby redirecting the mating to them.

Most importantly, in this system, male mate choice has been hypothesized to drive the system and play an important role in the apparent ecological stability of the coexistence of Amazon mollies and its hosts (Schlupp 2009), essentially via frequency-dependent male mate choice. This coexistence is an ecological puzzle because the Amazon mollies should quickly outcompete their sexual host. The role of male mate choice in the stability has been explored in a series of papers presenting evidence that both in the laboratory and in the field, female Amazon mollies receive fewer sperm from males of one of their hosts, the sailfin molly (Aspbury and Gabor 2004b; schlupp and Plath 2005; Riesch et al. 2008, 2012; Robinson et al. 2008. Furthermore, male mate choice changes over the season, potentially in response to changing frequencies of Amazon mollies in nature (Heubel and Schlupp 2008).

Male Mate Choice and Social Information

Mating is by nature an interactive process. Mating decisions are increasingly viewed as interactions that take in a public realm, and often other individuals observe these interactions (Danchin et al. 2004). Male mosquitofish *G. holbrooki*, for example, are attracted to all-female groups (Agrillo et al. 2008) and the authors conclude that males are capable of recognizing important properties of the presented groups.

The general question of how an audience (known to the focal individual) or eavesdropping (audience unknown to the focal individual) might alter sexual preferences is a relatively young line of inquiry. It should be noted that for social species, a situation where mating happens in public is more likely to be the default, not a more private situation, which is often assumed in laboratory choice tests. In addition to studying effects on female choice, there is also a strong emerging literature on social influences on male mate choice. This includes mate copying (see above for examples using the Amazon molly system) in guppies (Auld and Godin 2015), but also general audience effects (Jordan et al. 2006; Plath et al. 2008a; Auld et al. 2015). Responses by males to another male as an audience are surprisingly fine-tuned. For example, several studies documented that the response of a focal male guppy is influenced by the size of the audience male, potentially minimizing sperm-competition risk (Jeswiet et al. 2012; Nöbel and Witte 2013; Auld et al. 2017). One mechanism for mediating this might be to manipulate their chances of obtaining copulations by selectively associating with less attractive individuals and also reduce sperm competition this way. This is indeed what a study on guppies found: males preferred females that were surrounded by drab males, presumably because those pose a lesser threat in sperm competition (Gasparini et al. 2013).

In guppies, male mate choice can also be modified based on the perceived difference between self and the value of an opponent

(Yoshikawa et al. 2016): dull males abandoned approaches to females in the presence of bright males. This shows the importance of including information about the tested subjects into our interpretation of male mate choice. In this context, more studies on the role of learning in male mate choice would be very useful.

Finally, deceptive behavior is relatively rare. Therefore, one of the more striking recent findings is that males of the Atlantic molly seem to be able to deceive other males by interacting with females they initially did not prefer in the presence of other males. This was documented in the surface form of the Atlantic mollies (Plath et al. 2008b), but not in the Cave molly (Plath et al. 2010) or in guppies (Makowicz et al. 2010). A theoretical model of this process (Castellano et al. 2016) indicated that this kind of deceptive behavior is not very likely to evolve.

Female Competition

Another important question in this context is if males are choosy, do females start competing over males? Female competition is probably widespread, but documentation of direct female competition over males is relatively rare (Rosvall 2013; Cain and Rosvall 2014). Most female competition seems to be relative to resources other than males (Scharnweber et al. 2011a, 2011b), but at least 2 studies (Schlupp et al. 1991; Foran and Ryan 1994), found that Amazon molly females will actively compete for males. Furthermore, female sailfin mollies appear to be suppressing the feeding efficiency of Amazon mollies (Alberici da Barbiano et al. 2010). A field study in Atlantic mollies (Heubel and Plath 2008), pointed toward intensive between species competition over males and other resources. This view is supported by recent experimental work on female aggression and competition (Makowicz and Schlupp 2013, 2015, Makowicz et al. 2016). This research can be a template for more work on within species competition, as we seem to know relatively little about within species female competition. Theoretically, females might compete over males if they show signs of sperm depletion.

Female Ornaments

In parallel to the effects of female choice on males, does male choice have the potential to drive the evolution of female ornaments? Logically, if males are choosy this could induce sexual selection on females and lead to female ornamentation. It should be noted, however, that traits that are detrimental to female fitness are not likely to evolve under male mate choice (Fitzpatrick and Servedio 2018). Male ornaments are typically under selection by females, which have preferences for elaborate, and often costly, ornaments (Andersson 1994). Whether preferring ornamented males confers a fitness advantage to females is not always clear, especially when indirect benefits are invoked. One also has to keep in mind that not all dimorphic traits are automatically ornamental and under sexual selection. To complicate things further, we are very likely to miss important traits because they are difficult for humans to assess. Recent work has highlighted the role of visual ornaments that are in the UV wavelengths that we can measure, but not see, in mate choice and predation avoidance (Cummings et al. 2003, 2006). Beyond that there are aspects of chemical communication, or lateral line communication that we cannot fathom. Even acoustical communication, although very unlikely (Schulz-Mirbach et al. 2010; Schulz-Mirbach et al. 2011), should not be completely ruled out. One example would be the role of chemical information in species recognition and female mate preference (McLennan and Ryan 1997; Fisher et al.

2006; Plath and Tobler 2007; Rosenthal et al. 2011; Rüschenbaum and Schlupp 2013).

Based on this, it is not clear if female Poeciliids have ornaments. Restricting my argument to coloration, clearly females in many species have color, but I am not aware of any coloration that would be easily interpreted as a female ornament. In all cases the males seem to have similar coloration, which means the trait is either not an ornament and has evolved under natural selection (e.g., black spots might contribute to crypsis) or could be expressed due to pleiotropy as a result of a genetic correlation with males. One example would be the black spots and orange coloration in the Cuban Limia, *Limia vittata*. Both sexes seem to have equal amounts of black spotting, but orange is less common in females than in males. The black spots could make the fishes cryptic in their environment by dissolving the body outline, and the expression of orange could be some form of evolutionary byproduct, due to pleiotropie, or beneficial to females due to the general advantages often ascribed to carotenoids, such as anti-parasite properties (Olson and Owens 1998; Martin and Johnsen 2007). In the black-finned goodeid, *Girardinichthys viviparus*, a preference for orange hue in females was described (Méndez-Janovitz and Macías Garcia 2017), but interestingly, female coloration was not associated with fecundity and negatively associated with offspring survival. Furthermore, in Salmon, male preferences for red have been documented (Foote et al. 2004) and extensive studies in birds on the species level have recently shown that the degree of ornamentation in females is often correlated to the ornamentation found in males, but that sexual selection and also life-history characteristics can influence the degree of dimorphism (Rubenstein and Lovette 2009; Dale et al. 2015). In livebearing fishes, a similar analysis would be very useful.

For the green swordtail *X. hellerii*, a very interesting potential female signal has been suggested. Females of that species (and others) are known to perform "headstands" and males prefer this behavior to females showing regular swimming (Fernandez et al. 2008). Without further investigation, it is difficult to say if this behavior is any kind of advertisement, but the possibility is intriguing. In other groups of fishes, female ornaments have been suggested, such as female eye color, which can indicate readiness to spawn (Olsson et al. 2017) in sand gobies.

Same-sex Behavior

Many species show same-sex behavior, but almost nothing is known about this in livebearing fishes. Yet, clearly if we discuss mate choice in general, and male mate choice in particular, potential preferences for members of the same sex needs to be considered (Poiani 2010). In one study (Field and Waite 2004), using guppies, the authors found that males can show same-sex behavior after long times of isolation from females. Interestingly, male sexual behaviors toward males persisted even after exposure to females. Another study, conducted on Atlantic mollies, suggests that same-sex behavior is beneficial to males as it makes them more attractive to females via the use of social information (Bierbach et al. 2013). It is apparent from the lack of studies that much more work is needed on this topic.

Conclusion

Intuitively, the evolution of male mate choice in livebearing fishes seems an unlikely proposition: males make no investment into their offspring after copulation, and most mating systems seem to be strongly characterized by sexual conflict. Nonetheless, male mate

choice has been documented in several species within the family, mainly for female size, but also for female species.

Outlook

1. Male mate choice, female competition, and female ornamentation are tightly connected. While male mate choice has been surprisingly well documented in livebearing fishes, the other 2 elements are poorly understood. Nonetheless, this provides an excellent basis for future research.
2. More work is needed to document and understand female competition for males. Right now it is not very clear if this even exists.
3. Females have a number of traits that might be considered ornamental, but how they evolved and if they are preferred by males, is less studied.
4. More interaction between theoretical and empirical studies would be beneficial.
5. So far, variability in female fecundity is viewed as the driver of male mate choice, but there might be many more traits in which females differ and that might be used in male mate choice.
6. Better evidence for the adaptive benefit of choosing larger females is needed. The large variability in fecundity found in livebearing fishes, should allow for comparative tests.
7. In recent decades, much progress has been made understanding the perceptual and cognitive aspects of female mate choice (Ryan and Cummings 2013), without similar attention to male mate choice.
8. Finally, there is significant taxonomic bias, even within the livebearing fishes. A majority of studies conducted use guppies; clearly more diversity would be important.

Acknowledgments

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