Chapter 5

Learning and Mate Choice

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5.1 Introduction

One of the most fascinating questions within the field of sexual selection is why and how females and males choose particular conspecifics as mates. Sexual selection theories provide different explanations for the origin and evolution of ornamental traits and mate preferences for such traits (overview in Andersson 1994; Jennions *et al.* 2001; Kokko *et al.* 2003; Kokko & Jennions 2008; Clutton-Brock 2009). Genes for the ornamental trait and those for the concomitant preference can co-evolve as a result of a genetic linkage between those genes as a result of the Fisherian runaway process (Fisher 1930; Lande 1981; Kirkpatrick 1982; Brooks 2000) or as a result of selection for mates advertising 'good genes' (indicator models; Zahavi 1975; Møller & Alatalo 1999). These models generally assume that mate preferences are genetically based (Bakker 1999; Iwasa & Pomiankowski 1999; Andersson & Simmons 2006). Mate preferences can be highly variable within populations. Part of this variation is owing to flexibility in mating preferences expressed by individuals during their lifetime (Jennions & Petrie 1997). Of increasing interest is the potential influence of the social environment on mate-choice decisions (e.g. Gibson & Höglund 1992; Dugatkin 1996a, 1996b; Witte 2006). Forming mate preferences is a complex process involving not only genetic factors but also non-genetic factors. Increasing evidence suggests that the social environment (Dugatkin 1996a; Westneat *et al.* 2000) and learning are important factors in forming mate preferences. The mate choice of conspecifics influences the mate-choice decisions of an individual, who can alter mate preferences through learning processes. Therefore, social learning and using public information (Danchin *et al.* 2004; Dall *et al.* 2005; Bonnie & Earley 2007; and see Chapter 11) and other kinds of learning significantly influence the process of sexual selection. Forms of social learning have now been recognised as meaningful mechanisms for the non-genetic inheritance (i.e. cultural transmission) of mate preferences (Brooks 1998), leading to cultural evolution of mate preferences. This chapter illustrates how learning is involved in the mate choices of fishes and emphasises the important roles that different kinds of learning, particularly social learning, play in sexual selection. It focuses on four different kinds of learning: (1) sexual imprinting; (2) learning

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after reaching maturity; (3) eavesdropping including audience-effect; (4) and mate-choice copying.

5.2 Sexual imprinting

Sexual imprinting is a learning process restricted to a specific period during early development (the sensitive phase), which influences mate preferences later on in life (Immelmann 1972). A prerequisite for sexual imprinting is that at least one parent, a genetic or social parent, cares for the young to ensure that young have intense contact with the parent(s) and get the opportunity to learn specific traits of the parent(s). Mate preferences learned by sexual imprinting can be transmitted from one generation to the next generation in a socially inherited way. Thus, sexual imprinting is assumed to be a powerful mechanism for the cultural evolution of mate preferences. Theoretical models show that sexual imprinting potentially plays an important role in sexual selection (Aoki *et al.* 2001) and in sympatric speciation (Laland 1994a).

5.2.1 Does sexual imprinting promote sympatric speciation in fishes?

Sexual imprinting in cichlids, which was studied intensively in the 1970s and 1980s (Fernö & Sjölander 1976; Siepen & Capron de Caprona 1986; more details in Witte 2006), has begun to receive attention within behavioural ecology again, largely because sexual imprinting is thought to be a meaningful mechanism for promoting sympatric speciation. Verzijden & ten Cate (2007) investigated the effect of sexual imprinting on the mother's phenotype in two sister species of African mouth-breeding cichlids (*Pundamilia nyererei, P. pundamilia*, Cichlidae) living in sympatry in the Lake Victoria, Africa. In both species, only females provide brood care to young. In a cross-fostering experiment, Verzijden & ten Cate (2007) exchanged eggs between breeding females of the two different species. Results show that cross-fostering influenced the mate-choice decisions of females in these species. Thus, female offspring sexually imprinted on the mother's phenotype and preferred heterospecific males over conspecific males when reared by a heterospecific foster mother. In these species sexual imprinting on the mother's phenotype forms mate preferences of young females and can promote reproductive isolation in sympatry.

In 2009, Verzijden *et al.* repeated the cross-fostering experiment mentioned above with males of *P. pundamilia* and *P. nyererei* and investigated male–male aggression behaviour and male mate preferences. Males raised by conspecific and heterospecific foster mothers showed no differences in mate preferences and preferred conspecific females as mates. Males of both species directed aggression in territorial defence primarily towards conspecific intruders. Thus, there is no evidence for sexual imprinting in males in these two species. Both studies together show that there is a sex difference in the potential of sexual imprinting in these cichlid species as has been shown in bird species (Witte & Sawka 2003; Witte & Caspers 2006).

Sexual imprinting might also play a role in forming mate preferences in the three-spined stickleback (*Gasterosteus aculeatus*, Gasteroidae), a species in which males care intensively for the young. In several lakes in British Columbia, Canada, three-spined sticklebacks occur in sympatric species pairs. These pairs consist of a large-bodied invertebrate-feeding benthic species and a small-bodied zooplankton-feeding limnetic species (Schluter & McPhail 1992). In the same species-pair of sticklebacks, Kozak & Boughman (2009) showed that both sexes enhance conspecific mate preferences through experience with them, but in opposite directions. Female limnetic sticklebacks learned to prefer conspecific males if they were raised with them. However, limnetic and benthic males learned to court conspecifc females less when reared with conspecifics. It was the experience with heterospecific females that enhances discrimination against heterospecifics. Thus, males learn to discriminate against heterospecific females via sexual imprinting, whereas limnetic females learn to prefer conspecifics by imprinting on siblings.

Sexual imprinting can potentially be an important learning process in fishes for forming mate preferences. It may be worth investigating which factors facilitate the occurrence of sexual imprinting in a species and its potential role in sympatric speciation.

5.3 Learning after reaching maturity

Whereas sexual imprinting is a learning process that is restricted to a specific sensitive period during early development, there are other learning processes that are not restricted to a specific sensitive period and occur in sexually mature individuals. Learning processes exhibited later on in life that affect mate choice are observed in a wide range of fish species, including those without any parental care, like livebearing fishes. In an early study, Haskins & Haskins (1950) showed that when guppy (*Poecilia reticulata*, Poeciliidae) males were reared in isolation until sexual maturity and then exposed to females of a specific colour variant, which differed from their own colour variant, for a month or longer, males preferred females of the other colour variant with which males were reared after reaching sexual maturity. Liley (1966) investigated species recognition in four sympatric species within the family Poeciliidae. Guppy males with female experience restricted to conspecifics did not show a preference for conspecific females when females of three other species were present. He concluded that males must require experience with females of their own species, as well as with females of other species, to learn to discriminate between conspecific and heterospecific females. Haskins & Haskins (1949) investigated whether male guppies learn to discriminate between conspecific and heterospecific females by experience. They presented guppy males with females of three related species *(P. reticulata, P. picta* and *P. vivipara*). Male guppies that had had no experience with heterospecifics, initially directed most of their courtship displays towards swamp guppy females (*P. picta*). However, after about a week males courted mostly conspecific females (*P. reticulata*). Magurran & Ramnarine (2004) investigated sexually mature Trinidadian guppy (*P. reticulata*) males and swamp guppy (*P. picta*) males living in either sympatry or allopatry. In a baseline mate-choice test, two *P. reticulata* males, collected from the same locality, or two *P. picta* males, could physically interact with one *P. reticulata* female and one *P. picta* female, matched for size. One of the two males was the focal male and the authors recorded the number of sneaky matings of that male. Males of both species living in allopatry attempted matings with heterospecific females and conspecific females at random. However, males living in sympatry with the other species preferred to attempt matings with females of their own species. In a test for learned preferences, two males, both from the same localities, were housed together with two size-matched females, one of each species. Trinidadian guppy males with no experience with *P. picta* females learned to discriminate between heterospecific and conspecific females and preferred conspecific females within a few days. Thus, learning may modify mate preferences in guppy males and may help to prevent them from mating with the wrong species. Such modification of choice via learning may be mediated via feedback emanating from potential mates. Several other studies have shown that male preferences in guppy females are also altered by experience (Breden *et al.* 1995; Rosenqvist & Houde 1997; Jirotkul 1999).

5.4 Eavesdropping

Eavesdropping is defined as the act of extracting information from signalling interactions between conspecifics (McGregor & Dabelsteen 1996). Eavesdropping occurs when information from an animal transmitting a signal to another individual is picked up by one or more bystanders towards whom the signal was not directed (McGregor 2005). Eavesdropping is now recognised as representing an important component of animal communication, particularly communication in a network, and has been studied intensively in songbirds and fishes (Peake 2005). Females can gain information about potential males by assessing their quality on the basis of morphological cues (Endler & Houde 1995; Houde 1997). In addition, by observing two males interacting (e.g. fighting) with each other, females gather further reliable information about these males that they can then use to guide mate-choice decisions. Eavesdropping can be an effective way for females to evaluate potential males.

5.4.1 Eavesdropping and mate choice

Doutrelant & McGregor (2000) investigated whether female Siamese fighting fish (*Betta splendens*, Osphronemidae) monitor aggressive interactions between two males and whether the information gained by eavesdropping is used to guide mate-choice decisions. In a well-controlled experimental set-up, they found that females that had the opportunity to watch two displaying males subsequently first visited the winner significantly more often, spent significantly more time with the winner and displaying to the winner, than to other male. Females that had not seen the interaction between two males visited the loser first more often than females under other conditions, and did not behave differently to winner and loser. This experiment shows that females use the information gained from an aggressive interaction between two males in their mate-choice decision. In the sexually role-reversed pipefish *Syngnathus typhle* males that have observed fighting females preferred to associate with the more dominant female than with the more attractive female (Berglund & Rosenqvist 2001).

5.4.2 Benefits of eavesdropping

What are the benefits of eavesdropping? As eavesdroppers are not engaged in conspicuous, probably risky communication, eavesdropping could constitute an easy, rapid and safe way to acquire information on conspecifics and should be rather common (McGregor 1993). In general, mate choice is costly for females because it requires them to devote to evaluating males and may expose them to enhanced predation risk (Andersson 1994). Additionally, mate-sampling females may be injured in aggressive courtship displays by males or even suffer from harassment by males (Schlupp *et al.* 2001). Plath *et al.* (2007) performed a comparative approach with nine species of livebearing fish and examined costs of male sexual harassment for females as reduced feeding time. In all species females spent significantly less time feeding in the presence of a male. Ojanguren & Magurran (2007) could show that in guppies (*P. reticulata*) male harassment causes a direct reduction in female short-term fitness by significantly reducing the number of offspring produced. Eavesdropping females can avoid some of these costs, gaining information about male quality without being directly involved in an interaction with conspecifics. Moreover, they may be able to watch interactions between several conspecifics at the same time, thus providing direct comparisons. Females can then use this information about male quality gained from eavesdropping to supplement direct information gained on the basis of male morphological cues. Eavesdropping females gain information on the relative quality of males at little cost and/or risk (McGregor & Peake 2000). Information gained by observing an aggressive interaction between two individuals is assumed to be reliable and not subject to cheating. From this perspective, eavesdropping may be more reliable than mate-choice copying (see below), where a female may copy a 'wrong' choice of the model female. While eavesdropping seems to be a good strategy for mate choice, as yet there is no quantitative evidence for any fitness advantages based on this strategy.

5.4.3 The audience effect

The individual that eavesdrops not only gains information about the two interacting individuals, but the presence of the eavesdropper may also influence the nature of the interaction. This so-called 'audience effect' or 'bystander effect' has been intensively investigated in Siamese fighting fish, but recently also in the livebearers (Poeciliidae).

Doutrelant *et al.* (2001) tested whether the presence of a female or male changed the intrasexual interaction between two fighting males. In the experiments, the two fighting males could interact with each other through clear partitions, over two trials. In one trial, both males saw a female prior to interacting with the other male. In the other trial, the same males did not see a female before the interaction started. A similar experiment was performed with a male as an audience. Results clearly show that a female audience changes the male–male interactions. With a female audience males performed more tail beats, spent more time with gill cover erected, interacted farther away from the other male and performed aggressive displays that are used only in male–male interactions and more of the displays that are considered more conspicuous used in the presence of both sexes. Conversely, whether a male audience was previously present or not did not significantly change the characteristics of the male–male interaction. A similar result was found by Matos & McGregor (2002) in the same species. When a male audience was present prior to encounter, males attempted significantly more bites and spent less time near the opponent than when a female audience was observed prior to the encounter.

Due to the fact that female *B. splendens* eavesdrop on male contests, Herb *et al*. (2003) tested mate-choice decisions of male fighting fish after losing or winning a contest. They conducted two sets of trials: in one set-up they tested the losers' courting preference for eavesdropping females or naïve females (females which had no opportunity to observe the contestants). In the other set-up they tested the winners' courting preference for eavesdropping females or naïve females. The loser male preferentially courted a naïve female, while the winner showed no preference for either female type. This suggests that loser males are able to assess the effect of their subordinate status on their attractiveness to females. By courting naïve females, loser males may increase their chance of being accepted by that female, and reducing the costs of courting a female with a high probability of being rejected by her. These results suggest that *B. splendens* males moderate their behaviour in response to an audience in ways more complex than previously thought.

Similar to Siamese fighting fish, males of the northern swordtail (*Xiphophorus birchmanni*, Poeciliidae) perform courtship display with an audience 'in mind' (Fisher & Rosenthal 2007). Male northern swordtails display large, sail-like dorsal fins. Dorsal fin raising is a dynamic component in both courtship displays and male–male aggression displays. In this species typically males with large dorsal fins are more dominant and more aggressive than other males. Fisher & Rosenthal (2007) showed that males, together with a mate, raise their dorsal fin more frequently when an audience male is present than with an audience female or no audience. They assume that male swordtails have not evolved courtship behaviour involving dorsal fin raising in response to exploit a pre-existing preference in females, but rather as a competitive signal to male bystanders. This assumption is supported by the fact that females reject males with large fins, possibly due to their general high aggressiveness.

Recently, the audience effect has been investigated in the Atlantic molly (*P. mexicana*) (Plath *et al*. 2008a). The authors tested males in two mate-choice situations. Males could choose between a conspecific *P. mexicana* female and a heterospecific *P. formosa* female (experiment 1) or between a large conspecific female and a small conspecific female (experiment 2). Each experiment had two trials: first trials without an audience male and the second trial with an audience male. In both experiments, males spent significantly less time near the initially preferred female (a conspecific female or the larger of the two females) and spent significantly more time near the initially non-preferred female when a conspecific audience male was present. In a control Plath *et al.* (2008a) showed that males choose consistently without the presence of an audience male. This study highlights that the social environment has an important influence on male mate-choice decisions, and that visual presence of a conspecific competitor alone can affect mate-choice decisions.

In another study (Plath *et al.* 2008b) *P. mexicana* males could physically interact both with a large conspecific female and a small conspecific female or with two size-matched females, one a conspecific *P. mexicana* female and the other a heterospecific *P. formosa* female. After the initial preference test, an audience male was presented to the focal male. In the presence of the audience male, focal males reduced their mating activity and preferred no longer one of the two females. Rather focal males directed their first sexual interaction toward the initially non-preferred female when an audience male was present. Plath *et al.* (2008b) suggest that focal males tried to deceive the audience male about their mating preferences to avoid sperm competition because surrounding males may use public information and copy the focal male's mate choice (see Section 5.5).

In 2009, Plath *et al*. performed a similar study with *P. mexicana* females. However, females interacted with the audience female and their mate-choice decisions were not affected by the audience female. We have now evidence that *P. mexicana* females also respond to an audience female and change their mate preferences in the presence of an audience female (Nöbel *et al*. submitted).

But why does a male audience affect male mate choice? One potential benefit of changing mate-choice decisions in the presence of a male audience is reducing sperm competition risk. Sperm competition can be reduced if the audience male copy the 'deceived' choice of the focal male. Ziege *et al.* (2009) investigated this aspect in *P. mexicana* males. They gave *P. mexicana* males the opportunity to choose between two different females (large vs. small) under five conditions. Results indicated that focal males showed weaker expression of mating preferences when being observed by a rival. This suggests that focal males tried to deceive surrounding males so that they will copy the false mate-choice decision. Focal males seem to gain benefits from concealing their original mating preferences. However, to understand the complex social information network in *P. mexicana* males in the context of mate choice, it is necessary to investigate whether *P. mexicana* males copy the mate choice of other males. There is now evidence that this is the case (Nöbel *et al.* submitted).

Whether an individual acts as an eavesdropper or an audience makes a big difference for the information he or she can gather. In the case of an eavesdropper this individual is not recognised by the two interacting individuals and can get reliable information on the basis of signals transmitted back and forth between the two interacting individuals, i.e. on signals that are not directed to the eavesdropper. However, when two interacting individuals are aware of an audience, these individuals will change their behaviour in reaction to the audience. Fighting males might change their behaviour to 'impress' a watching female. However, males during mate choice might conceal their real mate preference and the audience male will receive false information. This shows that these small social networks are already highly complex. Further research might focus on benefits and costs for individuals that are eavesdropped and those individuals that make up the audience.

5.5 Mate-choice copying

Models of sexual selection assume that females and males choose among potential mates independently of other conspecifics and on the basis of their genetically determined preferences. However, there is strong evidence that females and males choose a mate non-independently of other conspecifics and on the basis of social information. A sophisticated form of inadvertent social information (ISI) arises as a by-product of performance activities of individuals. When this by-product provides information about the quality of any environmental parameter, including conspecifics and heterospecifics, it is called public information (Valone 1989). Public information is gained by an individual observing the performance of others and used to estimate the quality of environmental parameters or by noting the behavioural decisions of other individuals and gain information about the quality of conspecifics (Valone 2007). Performance-based public information has been observed in the context of assessing the quality of potential mates (Danchin *et al.* 2004; Valone 2007). Mate-choice copying occurs when an observation of a sexual interaction between a male and a female influences the subsequent mate-choice decision of the observing individual, biasing his or her decision to favour the observed mating individual. Mate-choice copying is a form of social learning in which individuals gain information and learn about potential mates by observing conspecifics (see Chapter 11 for a review of social learning in fishes). Mate-choice copying is an important mate-choice strategy demonstrating that individuals gather and use social and public information (Danchin *et al.* 2004; Dall *et al.* 2005). The first prerequisite and necessary condition for mate-choice copying to occur is that individuals must be able to observe the mate choices of others (Losey *et al.* 1986). To qualify as mate-choice copying, it must be the sexual interaction, and not the consequence of the choice of a female or a male, that influences the mating decision of another (Pruett-Jones 1992). Thus, it is not mate-choice copying when females prefer to lay their eggs in nests that already contain eggs, as in the Bullhead goby (*Cottus gobio*, Cottidae; Marconato & Bisazza 1986), fathead minnow (*Pimephales promelas*, Cyprinidae; Unger & Sargent 1988), fantail darter (*Ethiostoma flabellare*, Percidae; Knapp & Sargent 1989), and three-spined sticklebacks (Ridley & Rechten 1981; Goldschmidt *et al.* 1993). This behaviour can be explained by dilution of the risk of egg predation or egg cannibalism (Rohwer 1978), or as resulting when male sticklebacks that have eggs in their nests court more vigorously and are, therefore, preferred by females (Jamieson & Colgan 1989). Mate-choice copying is most likely to occur in polygynous and promiscuous mating systems with no parental care or with maternal care only.

Several theoretical models have investigated how mate-choice copying could evolve and be maintained in a population (Losey *et al.* 1986; Gibson & Höglund 1992; Pruett-Jones 1992; Laland 1994b; Nordell & Valone 1998; Stöhr 1998; Sirot 2001; Uehara *et al.* 2005; Brennan *et al.* 2008). Wade & Pruett-Jones (1990) showed that copying is likely to increase the variance in mating success among males, and thus intensify sexual selection. Servedio & Kirkpatrick (1996) showed theoretically that an allele for copying can spread through a population even when there is mild selection against it.

5.5.1 Mate-choice copying – first experimental evidence and consequence

The first experimental evidence for mate-choice copying came from Dugatkin *et al.*'s (1992) study with Trinidadian guppies (*P. reticulata*, Poeciliidae). Following his study, several other studies regarding mate-choice copying in fishes have been published (see Subsection 5.5.2) and research on this topic is continuing (Amlacher & Dugatkin 2005; Godin *et al.* 2005; Goulet & Goulet 2006; Hill & Ryan 2006; Widemo 2006; Witte 2006; Vukomanovic & Rodd 2007; Heubel *et al*. 2008; Frommen *et al*. 2009; Godin & Hair 2009; Witte & Godin 2010).

At present there is good evidence for mate-choice copying in guppies (Dugatkin & Godin 1992, 1993; Dugatkin 1996a, 1996b, 1998a, 1998b; Amlacher & Dugatkin 2005; Godin *et al.* 2005; Vukomanovic & Rodd 2007; Godin & Hair 2009), and in other fish species like the sailfin molly (*P. latipinna*, Poeciliidae; Schlupp *et al.* 1994; Schlupp & Ryan 1997; Witte & Ryan 1998, 2002; Witte & Noltemeier 2002; Witte & Massmann 2003; Witte & Ueding 2003; Hill & Ryan 2006; Witte 2006; Heubel *et al.* 2008), the humpback limia (*Limia nigrofasciata*, Poeciliidae; Munger *et al.* 2004), the Japanese medaka

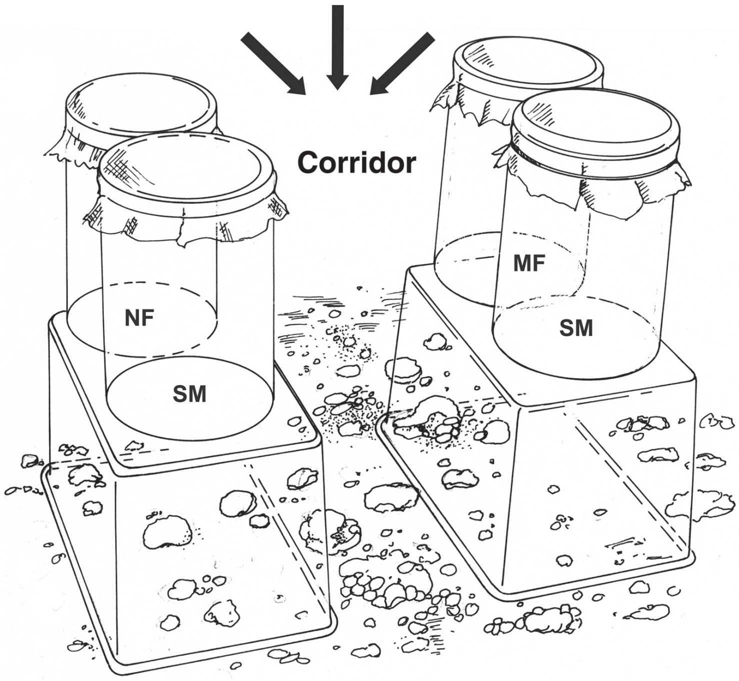
(*Oryzias latipes*, Adrianichthyidae; Grant & Green 1996, but see Howard *et al.* 1998), three-spined sticklebacks (*G. aculeatus,* Gasterosteidae; Frommen *et al.* 2009), white belly damselfish (*Amblyglyphidodon leucogaster*, Pomacentridae; Goulet & Goulet 2006), ocellated wrasse (*Symphodus ocellatus*, Labridae; Alonzo 2008) and deep-snouted pipefish (*S. typhle*, Syngnathidae; Widemo 2006).

However, there are a few studies that failed to detect mate-choice copying in fish species. Brooks (1996) could not detect mate-choice copying in guppies from a feral South African population; Lafleur *et al.* (1997) found no indication for mate-choice copying in pet store guppies (but see Dugatkin 1998a for a comment on this study); and Patriquin-Meldrum & Godin (1998) found no evidence for mate-choice copying in the three-spined stickleback (but see Frommen *et al.* 2009). Ambiguous results for the Perugia's limia (*L. perugiae*, Poeciliidae) were reported by Applebaum & Cruz (2000). It is currently unclear why mate-choice copying should be observed in some populations and not in others.

According to the definition of Pruett-Jones (1992), female mate-choice copying occurs when 'the conditional probability of choice of a given male by a female is either greater or less than the absolute probability of choice depending whether that male mated previously or was avoided, respectively. The outcome of the female is that if one female mates with or avoids a specific male successively choosing females will be accordingly more or less likely to mate with that male than they would otherwise have been' (Pruett-Jones 1992, pp. 1001–1002). Thus, mate-choice copying may decrease the probability that a female mates with a particular male when the female has observed that another female has rejected that male. This idea was investigated experimentally by Witte & Ueding (2003). They showed that female sailfin mollies rejected a previously preferred male, after observing another female escaping from that male. So far this is the only study for copying mate rejection.

5.5.2 Mate-choice copying – evidence from the wild

There is convincing evidence that females and males copy the mate choice of other conspecifics in several fish species. Although most studies have been performed in the laboratory, there are an increasing number of studies demonstrating the occurrence of mate-choice copying in fish species in their natural environment. These studies emphasise the biological relevance of this fascinating mate-choice strategy and its prevalence and generality for using social information in the context of mate choice. The first experimental evidence that mate-choice copying exists in wild populations of a fish species comes from the sailfin molly *P. latipinna* (Witte & Ryan 2002). They performed experiments for male mate-choice copying, female mate-choice copying (Fig. 5.1a) and a control for schooling behaviour in each sex (Fig. 5.1b). In the case of female mate-choice copying, they presented focal females with two stimulus males in a river. Next to a stimulus male was a jar containing a model female or no fish for a symmetrical set-up. The two pairs of jars formed a corridor. Witte & Ryan (2002) counted the number of females swimming into this corridor and interacting with the stimulus male next to the model female or with the lone stimulus male. In the case of male mate-choice, they presented stimulus females and a model male in the same manner and counted the number of males swimming into this corridor and interacting with the stimulus females. These experiments indicated that males and females copy the choices of others, i.e. females preferred to associate with the male next to a model female

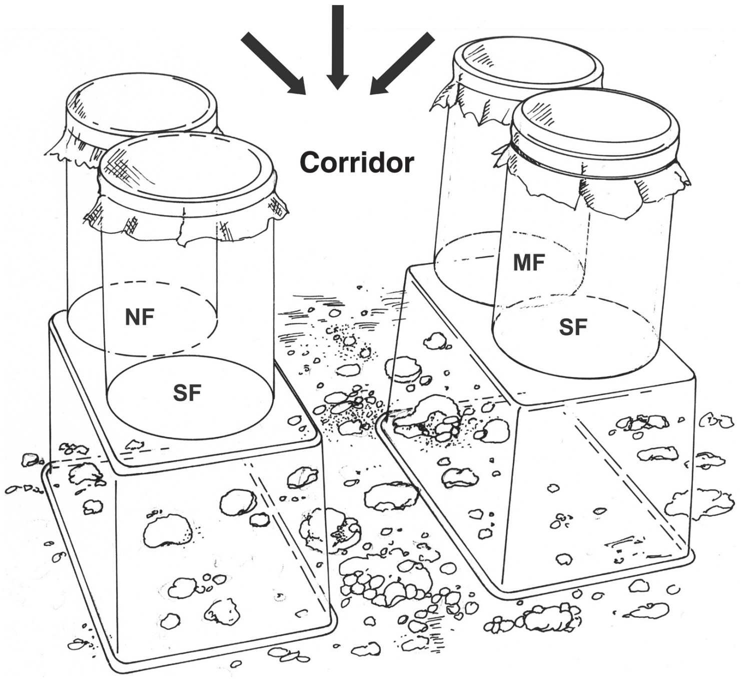


(a)

Fig. 5.1(a) Top view of the set-up of the female mate-choice test in the sailfin molly in a river. Two jars stood on two upside-down plastic tanks. Each jar had a net on top and was filled with water from the river. In the female mate-choice tests, Witte & Ryan (2002) presented stimulus males (SM) in two jars, in one jar next to a stimulus male was the model female (MF), the fourth jar had no fish (NF). Only females were counted when they entered the set-up from the side with the empty jar and the model female (indicated by the arrows) came through the 'corridor' and stopped within body length of the jar containing the stimulus males. For the male mate-choice test, stimulus females replaced stimulus males and a model male the model female. Only males were counted, when they entered the set-up from the side with the empty jar and the model male (indicated by the arrows) came through the 'corridor' and stopped at the jar within one body length of the jar with the stimulus females.

rather than the lone male, and males preferred to associate with a female next to a model male rather than next to a lone female. Neither sex showed shoaling behaviour in this experimental set-up.

This field experiment is a convincing indication that mate-choice copying is a biologically relevant mate-choice strategy in sailfin mollies. Witte & Ryan (2002) provide a practicable design for mate-choice copying studies in the natural habitat of a fish species. This design was recently used and significantly advanced by Godin & Hair (2009) to investigate whether female Trinidadian guppies copy the mate choice of others in the natural riverine environment in the Quaré River. The authors showed convincingly that female guppies copy the mate choice of others in the natural environment. To date there exist two other studies on mate-choice copying in the natural environment. Goulet & Goulet (2006) showed that females of the coral reef white belly damselfish, *A. leucogaster*, copy the mate choice and prefer to spawn with males that have recently mated. With an egg-switching experiment, they could exclude the hypothesis that females base their mate choice on the presence of eggs in the nest of a male. Alonzo (2008) demonstrated that female ocellated



(b)

Fig. 5.1 (*Continued*) **(b)** Top view of the set-up of the female control test for shoaling in the river. In the set-up of the female control for shoaling there was a stimulus female (SF) and a jar with a model female (MF) on one tank and a stimulus female next to a jar with no fish (NF) on the other tank. Females were counted only when they entered the set-up from the side with the empty jar and the extra female (indicated by the arrows) came through the 'corridor' and stopped within one body length of the jar with a stimulus female. In the male control for shoaling, Witte & Ryan (2002) presented two stimulus males and an extra male.

wrasse *S. ocellatus* copy the mate choice of others in the wild. Female ocellated wrasses are more likely to spawn with a male when another spawning female is present than with a male that is alone. She could show that females copy the mating behaviour of other females directly. These studies give strong evidence that mate-choice copying is a biologically relevant mate-choice strategy, which can be demonstrated in the natural environment as well. The next step would be now to investigate the ecological factors in the natural environment, which facilitate or complicate the evolution of mate-choice copying in different model systems.

5.5.3 Mate-choice copying when living in sympatry or allopatry

The Amazon molly (*P. formosa*) is an all female gynogen hybrid species originated by natural hybridisation between the sailfin molly *P. latipinna* and the Atlantic molly *P. mexicana.* It occurs in diverse freshwater habitats from the lower Rio Grande Valley (USA) to Tuxpan in Northeast Mexico. Most of these populations live in sympatry with one of their parental species. Amazon mollies reproduce through a sperm-dependent parthenogenesis (gynogenesis). The sperm of the host species only triggers embryogenesis and do not contribute any genetic information to offspring (Schlupp *et al.* 2007). Gabor & Ryan (2001) have demonstrated that sailfin molly males from populations sympatric with Amazon mollies have significantly stronger mating preferences for conspecific females than have males from populations allopatric with Amazon mollies. Male sailfin mollies cannot increase their fitness by mating with Amazon mollies because male genes are not transferred to offspring. However, males gain some benefits when conspecific females see them courting and copulating with heterospecific Amazon molly females. These males become more attractive to conspecific females because female sailfin mollies copy the mate choice of Amazon mollies (Schlupp *et al.* 1994). This study provides first evidence that it might be adaptive for males to serve as sperm donors for heterospecific females. So far this is the only species system for heterospecific mate-choice copying. Recently, Heubel *et al.* (2008) demonstrated that both *P. latipinna* and *P. mexicana* females and also the asexual Amazon molly females copy each other's mate-choice decisions when they live in sympatry, but females from allopatric populations do not show heterospecific mate-choice copying. This supports the hypothesis that heterospecific mate-choice copying is beneficial for sailfin molly males in sympatric populations. The absence of heterospecific mate-choice copying in females from allopatric populations suggests that mate-choice copying is a population-specific response (Heubel *et al.* 2008).

In sympatric populations of *P. formosa* and *P. latipinna*, males show high seasonal variation in association patterns. They spent less time with the asexual *P. formosa* females at times that may coincide with reproductive peaks of their own species (Heubel & Schlupp 2008). So males may gain some benefits from mating with the heterospecific *P. formosa* females, but prefer conspecific females in times of reproductive peaks in spring. By this strategy males maximise their own fitness and stabilise this sexual/asexual species complex.

5.5.4 Mate-choice copying – the role of the early environment

Mate-choice copying has been successfully investigated in many fish species. So far, little is known about the influence of the early environment on the decision of an observer fish to copy the mate choice of others when mature. Dugatkin (2007) showed that early environmental conditions have indeed an influence on copying behaviour later on in life. He tested whether certain social environments favour the use of social information in the context of mate choice later on in life. Groups of fifteen 1- to 2-day-old guppies were raised in individual pools for 35 days under five different 'social environments'. After 35 days fishes were removed from pools and kept individually for 14 days. During that period they underwent sexual maturity. Females were then tested for their tendency to copy the mate choice of others in a standardised mate-choice copying experiment (Dugatkin 2007). Dugatkin showed that guppy females copy the choice of other females when they were raised without adults and when they were raised with adult males and sexually receptive females. These two conditions correspond to the natural social environment of young guppies. During their first week of life, young guppies swim together with other young guppies. Later on they join shoals with adult males and sexually receptive females (simulated by exchanging virgin females every 14 days). Dugatkin assumed that the natural developmental environment primes the guppies for using social information. His study is a first stimulation to further investigate the role of early environment on mate-choice copying to understand developmental processes potentially involved in mate-choice copying which might explain variation in mate-choice copying between populations and species.

5.5.5 Quality of the model fish

In a typical mate-choice copying situation the observer (copier) female can potentially assess the quality of the male, the quality of the model female or both, and use this information subsequently in her mate-choice decisions (Westneat *et al.* 2000; Witte 2006; Witte & Godin 2010). Thus, the observer (copier) female can obtain social information about the quality of a prospective mate by observing a sexual interaction between that male and another (model) female. In this chapter, we focus on the essential role of the model female within the social information network in mate-choice copying and take into account the quality of the model, i.e. different cues of the model female like size, colour, age, experience, condition, behaviour, etc. Dugatkin & Godin (1993) have investigated the role of the model female in mate-choice copying in guppies. They presented (copier) female guppies with two males consorting with model females of different quality – either a small (young) female that was probably inexperienced in mate choice or a large (older) female that was likely experienced in mate choice. Observer females copied only the choice of larger (presumably higher quality) model females. Amlacher & Dugatkin (2005) investigated the role of the quality of the model female in guppies. They presented an observer young guppy female two males matched for colour and body size. But this time each male was together with a model female, one male with a smaller (younger) model female, and the other interacted with a larger (older) model female. Test females preferred to associate with the male they have seen together with an older female. Similarly, Vukomanovic & Rodd (2007) repeated and extended the study by Dugatkin & Godin (1993) by testing four model/copier female combinations (i.e. large/large, small/small, large/small and small/large) in the guppy. Their results corroborate those of Dugatkin & Godin (1993) and, additionally, they found that large female guppies copy the choice of large model females, but small guppy females did not copy the choice of small model females. Vukomanovic & Rodd (2007) concluded that females are more likely to copy when they perceive that there is an imbalance between their assessment ability and that of another female. Thus, females used the quality of the model female as a cue in mate-choice copying. In the sailfin molly, Hill & Ryan (2006) showed that the quality of the model female indeed matters in mate-choice copying. In their study, Hill and Ryan gave (observer) sailfin molly females (*P. latipinna*) a binary choice between two conspecific males as potential mates. Thereafter, females could observe the previously preferred male interacting with a heterospecific female (a low-quality model), the gynogenetic hybrid species, the Amazon molly (*P. formosa*). The previously non-preferred male was together with a conspecific female (a high-quality model). Subsequently, sailfin molly females significantly increased the time spent with the males they have previously seen interacting with a conspecific model female and they significantly decreased the association time with males they have seen interacting with a heterospecific model female. Thus, again the phenotypic quality of the model female influenced the mate-choice copying behaviour in females. Age and correlated experience in mate choice and the species type of the model female are only two possible qualities for model females. To get a better understanding how information and what information of the model females influences mate-choice copying behaviour in the observer female, one should manipulate other modes of the model female qualities in future studies.

Not only the quality of a model female influences the mate-choice copying behaviour of observing individuals, but also the number of model females has an impact on the mate-choice decision. Dugatkin (1998b) showed that there is a significant stronger copying effect in female guppies when the copier female observes two model females interacting one after another with a drab coloured male for 5 minutes each. In this situation 13 of 20 females copied the choice for a drabber male, which is in contrast to their genetically based mate preference (see Section 5.6). A similar result was found in the sailfin molly. When females have a choice between a larger male and a smaller male they prefer the larger male. In mate-choice copying experiments females do not copy the choice for a smaller male if only one model female is presented next to the smaller male for 10 minutes. However, when two model females are interacting with a smaller male, each for 5 minutes, females copy the choice for the smaller male (Witte & Noltemeier 2002, see also Chapter 6). These studies emphasise the role of the model female in the context of mate-choice copying.

5.6 Social mate preferences overriding genetic preferences

5.6.1 Indications from guppies

The evolution of mate preference is a complex process in which genetic and non-genetic factors are involved. Several models indicate how genetic factors influence mate choice, and we know how social cues and environment can influence the mate-choice decision. However, it is less clear how genetic and social factors interact and how this interaction can influence a female's mate-choice decision. Two studies show how a genetically based mate preference is influenced by social learning, i.e. by mate-choice copying.

Guppy females generally exhibited a genetically based preference for males with a higher amount of orange-coloured body surface (Houde 1988, 1992, 1997; Endler & Houde 1995). Guppy females also copy the mate choice of another female when both males presented in a test are matched for size and body colouration, and this is true for guppies of different populations (Dugatkin 1992, 1996a; Dugatkin & Godin 1992; Briggs *et al.* 1996). How do guppy females respond when they are challenged with a conflict between their genetically based mate preference and a socially based mate preference? Dugatkin (1996b) presented guppy females with this conflict in a mate-choice copying experiment. He varied the difference in male body colouration between males presented in a test. The two males presented simultaneously in a binary choice situation differed by 10%, 25% or 40% in total orange body colouration. In all cases, test females observed model females next to and interacting with the less colourful male. Afterwards, the test female was allowed to choose between the two males. When males differed in only 10% or 25% of the amount of orange body colouration, females copied the choice of the model female and preferred to associate with the paler of two males, despite a strong genetic preference for more colourful males. However, when males differed by 40% in orange body colour, test females always preferred the more colourful male, although they observed an interaction between the model female and the paler male. Thus, in this case, the genetic preferences seem to have a stronger influence on the mate-choice decision than the social cues.

In a later study, Dugatkin (1998b) further explored the interaction between genetic and social factors with regard to a preference for orange-coloured males in guppies. In this study, he presented two males simultaneously to females and these males always differed in the amount of orange by an average of 40%. In different experiments, test females could observe either no model female, one model female interacting with the drabber male for 5 minutes, two different model females interacting with the drabber male each for 5 minutes or one model female interacting with the drabber male for 10 minutes. When females observed no model female or one model female next to the drabber male, they did not copy the choice and preferred the more colourful male, thus females followed their genetic preferences. These results were consistent with the previous findings (Dugatkin 1996b). When females observed two different model females next to the drabber male, 12 of 20 females preferred the drabber male and 13 of 20 females that had observed one model female next to the drabber male for 10 minutes preferred the drabber male.

Thus, in these two experiments, social cues were shown to override the genetic predisposition and had a stronger influence on mate-choice decision than genetic factors. Therefore, it seems that the amount of information a female can gain by observing the sexual interaction between a male and the model female lowers the threshold in favour of social cues having a stronger influence on the mate-choice decision than genetic factors. In these cases, social preference overrides the genetic preference in guppy females.

5.6.2 Indications from sailfin mollies

Sailfin mollies also provide evidence for an interaction between genetic and social factors influencing mate-choice decisions. Sailfin molly females show a strong preference for larger over smaller males, which had been documented in different populations of sailfin mollies (Schlupp *et al.* 1994; Marler & Ryan 1997; Ptacek & Travis 1997; Witte & Ryan 1998; Gabor 1999; Witte & Noltemeier 2002; MacLaren *et al.* 2004). Marler & Ryan (1997) provide strong evidence that the preference for larger males in sailfin molly females is genetically based. Witte & Noltemeier (2002) investigated the relative importance of genetic and social cues regarding the female preference for larger males. In a standard mate-choice copying experiment, females could first independently choose between a smaller and a larger male. In the first mate-choice test, all females preferred the larger male over the smaller male. After this independent mate choice, females had the opportunity to observe a sexual interaction between a model female and the smaller male. Afterwards, females were allowed to choose between the same larger and smaller males again. The authors varied the situation during the observing period in three experiments. In the first experiment, females could observe one model female next to the smaller male for 10 minutes. Afterwards, as predicted by previous experiments (Witte & Ryan 1998), females did not copy and still preferred the larger male over the smaller male. In a second experiment, females were allowed to observe two different females interacting with the smaller male each for 5 minutes. Thereafter, seven of 15 females reversed their initial preference for the larger of two males and spent significantly more time with the smaller male. The strongest effect was in the experiment in which females could observe one model female interacting with the smaller of two males for 20 minutes. Here, 13 of 15 females reversed their mate choice in favour of smaller males. Thus, social preference overrides the genetic preference in favour of smaller males. In several control conditions where there was no opportunity to copy, Witte & Noltemeier (2002) found that females consistently preferred larger males over smaller males, while females in other control conditions exposed solely to stimulus females did not show shoaling behaviour that might explain the experimental findings. This study suggests that genetic factors interact with social cues during mate choice. Depending on the amount of social information received, females may be more influenced by their genetically determined mate preference or social cues. These experiments demonstrate the significance of social learning for mate choice and emphasise the potential of mate-choice copying to precipitate sexual selection.

5.7 Cultural evolution through mate-choice copying

Several studies have demonstrated that females change their initial mate preferences as a result of mate-choice copying. However, for mate-choice copying to be a meaningful mechanism for the cultural inheritance of mate preferences, it is necessary to show that females do not only copy the choice of a particular male, but also acquire and maintain a preference for a particular male phenotype (Brooks 1998). We now have evidence from two studies in fishes that mate-choice copying achieves these criteria for cultural inheritance of female mate preferences.

Female sailfin mollies that had previously copied the mate choice of a smaller male after observing one model female interacting with the smaller of two males for 20 minutes were retested by Witte & Noltemeier (2002) for a preference for smaller males up to 36 days after copying. Females that had previously reversed their mate preference in favour of smaller males through mate-choice copying maintained this preference for smaller males in binary mate-choice tests. This was the first evidence in fishes that females copied a mate choice for a male phenotype and that females maintain a mate preference learned by mate-choice copying for a considerable period of time. These females may serve as models for other females and may induce a new mate preference in favour of smaller males within a population. Thus, the prerequisites for mate-choice copying as a mechanism for the cultural inheritance of mate preferences were fulfilled. Godin *et al.* (2005) have presented further evidence that guppy females copy the choice for a male phenotype and not just a choice for an individual male and that females maintained their copied mate preference. The authors showed that guppy females copied the choice of other females for less colourful males and that these females still preferred less colourful males the next day when different males were presented in a mate-choice experiment. These two studies provide good evidence that cultural transmission of mate preferences via mate-choice copying is possible in fishes even when the socially induced mate choice conflicts with the genetically based mate preference. Therefore, these studies emphasise mate-choice copying as a powerful mechanism in sexual selection.

5.8 Does mate-choice copying support the evolution of a novel male trait?

How secondary sexual traits have evolved in males is one of the most fascinating questions in sexual selection. The sensory exploitation hypothesis (Ryan & Keddy-Hector 1992;

Ryan 1998) states that females have latent preferences for particular male traits before the evolutionary appearances of these traits in males. These latent mate preferences are shaped by natural selection, mostly acting in the context of foraging behaviour, through pleiotropic effects of genes expressed in both foraging and mate choice. Guppy females prefer males with a higher amount of orange colouration on the body surface (Houde 1988, 1992, 1997; Endler & Houde 1995). Rodd *et al.* (2002) showed that this mate preference probably originated as an innate preference for orange as a cue for rare and high quality food sources in both sexes. Therefore, males that developed orange spots exploited the pre-existing preference for orange in females and are preferred as mates by females. However, in a later study Grether *et al.* (2005) interpreted the female preference for orange in males as a correlated effect of selection on mate preferences.

5.8.1 Theoretical approaches

Although the sensory exploitation hypothesis explains how a female preference for male traits has originated, it does not explain how a novel male trait can spread within a population. Therefore, an interesting question is whether mate-choice copying can support the spread of a novel male trait within a population. This fascinating question has been examined theoretically by Kirkpatrick & Dugatkin (1994). They assumed that female mate preferences evolve only through cultural evolution, whereas the male trait on which they act is inherited via a haploid autosomal or a Y-linked locus. In their model, they simulated two different copying situations: 'single mate copying', in which younger females copy the choice of only one older female, and 'mass copying', in which younger females have the opportunity to copy the choices of a large number of older females. Thus, copying females strengthen their mate preference towards the male type they have observed mating. As a result of frequency dependence, females in the 'mass copying' scenario have a stronger preference for the male type they have seen mating most frequently. On the one hand, Kirkpatrick and Dugatkin's model shows that copying can lead to a rapid exaggeration of the male trait and female preference for it. On the other hand, copying seems to make it more difficult for a rare male trait to become established and does not maintain a polymorphism for that trait. Only under specific conditions can copying lead to two alternative evolutionary equilibria for the male trait. Female preference and the male trait can rapidly co-evolve, with a positive frequency-dependent advantage to the more common male trait allele. This is true even for a male trait that lowers male viability, when it has reached a certain threshold in frequency. Both scenarios lead to a positive frequency-dependent advantage to males: the more common a male type, the stronger is the female preference for it. This effect of frequency dependence is stronger in the 'mass copying' scenario than in the 'single copying' scenario. Thus, according to the model of (Kirkpatrick & Dugatkin 1994), mate-choice copying does not favour the spread of a novel male trait within a population. Similar conclusions were reached by Laland (1994b).

Agrawal (2001) has developed another model on evolutionary consequences of mate-choice copying on male traits. In contrast to Kirkpatrick & Dugatkin's model (1994), Agrawal's model shows that mate-choice copying can cause positive or negative directional selection on male traits, or positive or negative frequency-dependent selection on male traits. Whereas Kirkpatrick & Dugatkin (1994) assume that each copying event influenced the mate-choice decision of the observing female equally, Agrawal (2001) assumed in his model that different observations have differing degrees of influence on the mate-choice decision. Agrawal assumed that females are influenced by the extent to which the male-observed mating successfully differs from the population mean regarding the focal male trait. He concluded from his model that mate-choice copying can, first, facilitate the spread of a novel male type through a population, even if there is no inherent preference for the novel male trait, and second, that mate-choice copying can maintain genetic variation for sexually selected male traits. When a female observes males of different phenotypes successfully mating in proportion to their frequency in the population, her mating preferences are not altered by social cues like mate-choice copying. When a female observes a particular male phenotype mating disproportionately more often than other male phenotypes, her preference is biased towards this type of male. Thus, a female that observes a rare male type mating is more strongly biased towards this rare male phenotype than a female that observes a common male phenotype successfully mating. This assumption is based on the notion that unusual or unexpected stimuli affect individuals more strongly than common stimuli (Cohen 1984). The legitimacy of this assumption has yet to be evaluated within the context of mate-choice behaviour, although see Subsection 5.8.2. Nonetheless, the model of Agrawal (2001) provides some indications that mate-choice copying may favour the spread of a novel rare male trait within a population.

5.8.2 Experimental approaches

Is there any experimental evidence for mate-choice copying supporting or preventing the spread of a novel male trait? Sailfin molly females from the Comal River, Texas, USA, have no pre-existing preference for males with an artificial sword imitating the natural sword of male green swordtails (Witte & Klink 2005), and several previous experiments have demonstrated that sailfin molly females copy the choice of other females (Witte & Ryan 1998, 2002; Witte & Noltemeier 2002; Witte & Massmann 2003). To investigate this question, Witte (2006) attached an artificial yellow plastic sword with a black border or a transparent plastic sword to the base of the male tail fin and created video playbacks of courting males bearing the yellow sword or the transparent sword. In copying experiments, females could first choose between the two male videos presented on television monitors at each end of the female test tank. They quantified the time the female spent within a preference zone at each end of the test tank. After this first preference test, females had the opportunity to observe the male with the yellow sword courting another female on a video, whereas the male with the transparent sword was alone. In the second preference test, females were allowed to choose between the two males, one with the coloured sword and the male with the transparent sword, a second time. Fourteen of 23 females that had rejected the male with the coloured sword in the first preference test preferred that male in the second preference test after having observed the male courting another female (McNemar's test, $P = 0.001$). This result seems to indicate that mate-choice copying can support the spread of a novel male trait, because females copy the choice for that novel male type. However, ten of 17 females, which had preferred the male with the coloured sword in the first preference test, changed their preference and preferred the male with the transparent sword in the second preference test (McNemar, $P = 0.031$). Thus, in this situation mate-choice copying prevented the spread of a novel male trait. These experiments at least support Agrawal's (2001) assumption that different observations have differing degrees of influence on the female mate-choice decision. The observation of an unattractive male interacting with a female seems to increase the probability that females copy the mate choice, whereas the observation of an attractive male interacting with another female decreases the probability that females copy the mate choice of others. An alternative explanation might be that fishes adopt a 'copy when uncertain' strategy (Laland 2004). An attractive male with familiar characteristics evokes a clear preference and leaves little uncertainty as to courtship behaviour. Conversely, a strange-looking male generates uncertainly as to whether he is an appropriate mate, so fishes look to the behaviour of others for guidance. There is good evidence for this strategy being utilised by fishes (van Bergen *et al.* 2004). Further experiments are necessary to estimate the evolutionary consequences of mate-choice copying for the evolution of novel traits in males.

5.9 Is mate-choice copying an adaptive mate-choice strategy?

So far we have provided strong evidence that mate-choice copying exists in several fish species and that mate-choice copying is a biologically meaningful mate-choice strategy. Unfortunately, it is still not clear what the adaptive value of this mate-choice strategy is. What are the benefits and what are the costs of this socially driven mate preference?

5.9.1 Benefits of mate-choice copying

Pruett-Jones (1992) demonstrated in a game-theoretical model that the adaptive significance of mate-choice copying depends on the ratio of costs to benefits of independent mate choice. Gibson & Höglund (1992) proposed two important benefits resulting from copying. Copying can serve to increase the accuracy of mate assessment and reduce the costs of mate choice. Increasing the accuracy of mate assessment through mate-choice copying (Losey *et al.* 1986) is especially valid for females inexperienced in mate choice. Dugatkin & Godin (1993) found in guppies that young females, which are assumed to be relatively inexperienced in mate choice, copy the choice of older, presumably more experienced, females in mate choice, but not the reverse. Inexperienced females can learn to recognise a male or male phenotype of good quality by copying the choice of experienced females. Another example of copying facilitating the learning of mate assessment is provided by the sailfin molly. Sailfin molly females copy the choice of others when both males presented in a test are similar in colour and body size. Females do not copy the choice for a smaller male when both males presented in a test differed obviously in size. In the latter case, females prefer the larger of two males, even though a model female is placed next to the smaller male (Witte & Ryan 1998). Thus, when it is difficult to distinguish between males, females are more likely to copy than in a situation when males clearly differ in quality, i.e. females are more likely to copy when they are uncertain in their mating strategy.

Another benefit of mate-choice copying is that the observing female is not physically involved in courtship displays with a prospective mate. In some species, courting males behave aggressively towards females, or even harass females, during courtship displays

(Schlupp *et al.* 2001; Ojanguren & Magurran 2007; Plath *et al.* 2007). A female that observes how a male courts another female gains information about this male, and may reject an aggressive male, without being physically involved (Witte & Ueding 2003).

Mate-choice copying is assumed to reduce the time costs of searching for a mate. Females often visit several males before they choose one (Forsgren 1997). By observing others' mate-choice decisions, copying females may save time for their own mate choice. Copying females can decrease the time spent on directly assessing potential mates by copying the mate choice of others, and thus can minimise the 'opportunity costs' associated with the assessment of males. Briggs *et al.* (1996) tested this hypothesis. They investigated whether female guppies show a higher tendency for mate-choice copying when a predator is present than with no predator around. Mate-choice copying should reduce the time for mate inspection, and thus should increase the time available for predator vigilance and, therefore, reduce the risk of predation. In both situations, with predator present and predator absent, females copied the mate choice of others, but the authors found no indication of a higher mate-choice copying tendency in females when a predator was present. Copying females may be able to reduce the time for mate assessment and, therefore, increase the time for foraging activities. Hungry females should show a higher tendency to copy the mate choice of others than satiated females. Dugatkin & Godin (1998) tested this assumption in guppy females. However, their results contradicted the expectation; only the well-fed females copied the mate choice of others significantly more often than expected by chance.

5.9.2 Costs of mate-choice copying

Mate-choice copying is also likely to entail some costs. Copying females might risk a reduced fertility as a result of sperm depletion in males when the copying female immediately copulates with that male after he has already copulated with several females. Male courtship display is a highly conspicuous behaviour not only to conspecifics but also to predators (Houde 1997); therefore, it might be risky for a copying female to mate with a male immediately after that male has courted another female and might have attracted the attention of a predator. However, both disadvantages would be reduced when copying females do not have to copulate with a particular male immediately after observing a sexual interaction between another female and that male. Witte & Massmann (2003) showed that sailfin molly females are able to memorise an observed interaction between a male and a female for at least 1 day. Thus, copying females may copy the choice of others not immediately but rather later, when the male has replenished his sperm supply and at a safer time. Godin *et al.* (2005) showed that guppy females copy the choice for a male phenotype 1 day after they have seen another female interacting with such a male phenotype. It is also possible that the female may acquire outdated, inappropriate or inaccurate information about mate quality through mate-choice copying. Thus, females always have to decide whether to base their mate choice on social or private information. Nordell & Valone (1998) showed that females do better when copying the choice of another female. Even if the other female has no good discrimination abilities regarding the quality of males, the copying female will not be worse than choosing independently. Due to the fact that females can assess the quality of other females and use this information for mate-choice decision, females that copy the choice of a 'good' model will be on the safer side.

5.10 Outlook

Learning in mate choice is a highly dynamic research field in behavioural ecology with an enormous increase in experimental and theoretical work in recent years. Different types of learning have a specific potential as a driving force in sexual selection. Cultural evolution, i.e. inheritance of mate preferences based on and inherited through social learning provides a faster and a more dynamic potential for evolution of mate preferences than genetically determined mechanisms and can even overwrite genetically based mate preferences. In future researchers should focus on how widespread cultural evolution via social learning is and what factors facilitate or complicate cultural evolution, specifically the evolution of novel mate preferences. Sexual imprinting is an efficient mechanism to promote sympatric speciation. It may be worth investigating which specific factors facilitate the occurrence of sexual imprinting in a species and its potential role in sympatric speciation.

The social environment provides additional information for 'networkers' using such public information about potential mates. Studies on eavesdropping, the audience effect and mate-choice copying showed that individuals use this public information, but they are also a part of the complex information network and they can be manipulated by others as well. Future studies should investigate costs and benefits for individuals taking part in the social network. The social environment plays an interesting role in forming mate-choice decisions in all stages of life. To get a better understanding on mate-choice decisions in adult fish, one should focus on the social environment individuals have experienced early in life. This aspect might help to understand variation in mate-choice decisions between populations and species.

In spite of good progress in understanding mate-choice copying, there is still little indication that mate-choice copying is an adaptive mate-choice strategy. It would be valuable if future experiments focus on this question to aid understanding of the function of mate-choice copying. It is also important for future studies to investigate the relative reproductive success of copying and non-copying females. Answers to these questions would strengthen the claim that mate-choice copying plays an important role in sexual selection. Although the typical mate-choice copying situation involves only three players, the male, the model female and the focal female, these players are connected in a complex social information network. The focal female can gain information about the male via the male itself, the interaction of the male with the model female and the quality of the model female itself. The question what is the portion of each of the components that results in the mate-choice decision of the focal female is still open. Future research might focus on these interesting questions.

Although mate-choice copying has been studied experimentally in many fish species, there is no clear experimental evidence that mate-choice copying increases the fitness of a copying individual. In other words, there is no experimental indication that mate-choice copying is an evolutionary adaptive strategy. In theory, there are several benefits but also some costs associated with mate-choice copying. It should be the focus for experimental studies to investigate the adaptive value of mate-choice copying in the next years.

5.11 Conclusions

Learning has an enormous influence on mate choice in fishes and is, therefore, potentially an important influence on sexual selection. Learning during an early phase of development (sexual imprinting) can shape mate preferences later on in life when the individual has reached sexual maturity. Other forms of learning, which involve experience with conspecifics, occur during all phases of life and can form and change mate preferences in adults. Social learning, which includes observing conspecifics, is arguably the most fascinating kind of learning. Individuals can gather ISI from conspecifics about the quality of potential mates and use this information for their own mate-choice decision. The evolutionary consequences for social learning by using ISI is a new expanding research field in evolutionary biology and will provide novel aspects for the intriguing role of socially induced mate preferences in sexual selection.

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