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). Genes for the ornamental trait and genes 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 a 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). Forming mate preferences, however, 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. Social learning, and using public information (Danchin *et al.* 2004; and see Chapter 10) and other kinds of learning, therefore, significantly influence the process of sexual selection. Forms of social learning have now been recognized as meaningful mechanisms for the non-genetic inheritance (i.e. cultural transmission) of mate preferences, leading to cultural evolution of mate preferences. This chapter illustrates how learning is involved in the mate choices of fishes and emphasizes the important roles that different kinds of learning, particularly social learning, play in sexual selection. It focuses on four different kinds of learning: sexual imprinting; learning after reaching maturity; eavesdropping; and mate-choice copying.

5.2 Sexual imprinting

Sexual imprinting is a learning process restricted to a specific period during early development, which influences mate preferences later on in life (Immelmann 1972). Sexual imprinting is well studied in many bird species (ten Cate & Vos 1999; Witte & Sawka 2003) and occurs also in mammals (Kendrick *et al.* 1998; Penn & Potts 1998; Owens *et al.* 1999), including human beings (Bereczkei *et al.* 2004). 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 intensive 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 *Sexual imprinting in fish species*

Is there any evidence for sexual imprinting in fishes? This question was investigated 30–50 years ago but has since been subject to reduced attention within behavioural biology. Early studies provided some evidence that phenotypic traits of parents and/or siblings are learnt during early development and that this learning process influences mate preferences later on in life. Ideal candidates for studying sexual imprinting are cichlids. Within the family Cichlidae, at least one parent cares intensively for the young; thus, the main prerequisite for sexual imprinting to occur is satisfied. In an early study, Fernö & Sjölander (1976) used the convict cichlid (*Archocentrus nigrofasciatus*, Cichlidae) to investigate whether the colour of parents influenced the mate-choice decision of siblings later on in life. This species is a typical substrate-spawning cichlid with long-lasting parental care in both parents, and both parents have similar appearance. In a cross-fostering experiment, they used two different colour morphs, a commercially available white morph and the natural greyish-blue morph with vertical black stripes. In a pilot study, Fernö & Sjölander (1976) found the first indication that the colour morph of parents seemed to influence the mate preferences in males later on in life. However, their results provided no information on whether an imprinting process occurred because experience with the other colour morph was not restricted to a particular period during early development. Their study was repeated with a more controlled experimental design by Siepen (1984), in which siblings of *C. nigrofasciatum* (*A. nigrofasciatus*) were cross-fostered within and between the two colour morphs (10 males and 10 females in each design). In 7 of 19 cases, fishes reared by parents of the colour morph different from their own morph later mated with a fish of the parents' colour morph. Fishes cross-fostered within the same colour morph did not pair in any of 20 cases with a prospective mate of the other colour morph (Fisher's exact test $P = 0.014$, added by K. Witte). This result provides some indication, that the parental colour morph influenced mate-choice decision later in life. Thus, sexual imprinting may play an important role in forming mate preferences in the convict cichlid.

5.2.2 *Does sexual imprinting promote sympatric speciation in fishes?*

In recent years, the topic of sexual imprinting in fishes has again begun to receive attention within behavioural ecology, largely because sexual imprinting is thought to be a meaningful mechanism for promoting sympatric speciation. In an ongoing study, M. Verzijden (Verzijden personal communication) is investigating the effect of sexual imprinting on the mother's phenotype in two sister species of African mouth-breeding cichlids (*Pundamilia nyererei*, *P. pundamilla*, Cichlidae) living in sympatry in Lake Victoria, Africa. In both species, only females provide brood care to young. In a cross-fostering experiment, Verzijden exchanged eggs between breeding females of the two different species. After reaching maturity, female offspring were allowed to choose between males of both species. Preliminary results show that cross-fostering influenced the mate choice decisions of females in these species. It seems that female offspring sexually imprinted on the mother's phenotype and preferred heterospecific males over conspecific males when reared by a heterospecific foster mother.

Sexual imprinting might also play a role in forming mate preferences in the three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae), 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). Albert (2005) investigated sexual imprinting in these two species pairs. She created F_1 hybrid females *in vitro* from wild-caught individuals of both species. Six F_1 families were fostered by limnetic males and five F_1 families were fostered by benthic males. After reaching sexual maturity, F_1 females were tested for their mate preferences in two sequential no-choice tests. In one test, the female could inspect a nesting benthic male, in the other test the female could inspect a nesting limnetic male. Results showed that there was no effect of sexual imprinting on forming mate preferences in stickleback F_1 hybrid females. Females that were raised by benthic males were not more likely to inspect benthic males than females raised by limnetic males. Instead females chose males that were similar to themselves in body length. Size-assortative mating seems to be the underlying mechanism for reproductive isolation in these species, but not sexual imprinting.

Nevertheless, 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 may be other learning processes that are not restricted to a specific sensitive period and that occur in sexually mature individuals. Sexual imprinting is limited to species with intense parental care. Learning processes exhibited later on in life that affect mate choice, however, 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 are reared in isolation until sexual maturity and then exposed to females of a specific colour variant, which differs from their own colour variant, for a month or longer, males preferred females of the 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 and 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*). After about a week, however, males courted mostly conspecific females (*P. reticulata*). Learning may, thus, 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).

5.3.1 *Learning when living in sympatry or allopatry*

The early study of Haskins & Haskins (1949) left many questions open. Unfortunately, their sample size was small, data from individual males were combined, and important controls were missing. In a recent study, Magurran & Ramnarine (2004) utilized a more controlled design to investigate the role of learning in mate choice among sexually mature Trinidadian guppy (*Poecilia reticulata*) males and swamp guppy (*P. picta*) males living either in 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 for a period of 15 min. 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. The focal male could interact with different females of both species from day 1 onwards for a further 5 days for 10 min each day. Trinidadian guppy males with no experience with *P. picta* females learnt to discriminate between heterospecific and conspecific females and preferred conspecific females within a few days.

5.3.2 *Learned recognition of colour morphs in mate choice*

Adult learning may also be an important factor influencing male mate choice decisions in the live-bearing platy fish (*Xiphophorus maculatus*, Poeciliidae). Fernö & Sjölander (1973) investigated how experiences in different stages of life influenced the mate choice decisions of male platy fishes for females of red and black colour morphs. In one experiment, young platy fishes were reared either with or without the other colour morph. In another condition, platy males were reared together with both colour morphs until they reached sexual maturity. Afterwards they were kept together with fishes of the colour morph different from their own for 2 months. When males were sexually mature for at least 2 months, they were tested in a four-choice arena for their sexual preference and could choose between both sexes of each colour morph. Male platy fishes preferred females of the colour morph they were exposed to during the 2 months after reaching sexual maturity. Exposure to a colour morph during an early stage of development, that is, before reaching maturity, had no influence on mate choice. Thus, learning after reaching maturity is an important process for forming mate preferences in male platy fishes.

These studies show that learning even after reaching maturity is a significant component in forming mate preferences. Thus, learning is an important factor which should be considered in studies on sexual selection.

5.4 Eavesdropping

Eavesdropping occurs when information from an animal transmitting a signal to another individual is ‘overheard’ by one or more bystanders towards whom the signal was not directed (McGregor 2005). Eavesdropping is now recognized as representing an important component of animal communication, particularly communication in a network, and has been studied intensively in songbirds and fishes (McGregor 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, however, by observing two males interacting (for instance, fighting) with each other, females gather further reliable information about these males that they can then use to guide mate-choice decisions. Eavesdropping is defined as extracting information from signalling interactions between others (McGregor & Dabelsteen 1996), and it 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 spent more time looking at, and displaying to the winner, than the other male. Females that had not seen the interaction between two males visited the loser first more often than females under the 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.

5.4.2 *The audience effect*

The eavesdropper does not only gain information about the two interacting individuals, but the very presence of the eavesdropper may influence the nature of the interaction. This so-called 'audience effect' or 'bystander effect' has also been investigated in Siamese fighting fish. 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 for 3 min. 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. The results clearly show that a female audience changes the male–male interactions. With a female audience, significantly more males performed more tail beats, spent more time with gill cover erected, interacted farther away from the other male, and performed fewer bites than without a female audience. Thus, males performed fewer 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 the encounter, males attempted significantly more bites and spent less time near the opponent than when a female audience was observed prior to the encounter.

5.4.3 *Benefits of eavesdropping*

What are the benefits of eavesdropping? In general, mate choice is costly for females because it requires them to devote time 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). Eavesdropping females can avoid some of these costs, gaining cheap 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. Future experiments may focus on this.

5.5 Mate-choice copying

Models of sexual selection assume that females and males choose among potential mates independently of conspecifics. There is, however, strong evidence that females and males sometimes choose a mate non-independently by copying the choices of conspecifics. Mate-choice copying occurs when observation of a sexual interaction between a male and a female influences the subsequent mate-choice decision making of the observing individual, biasing their 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 10 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). The first prerequisite and necessary condition for mate-choice copying to occur is that individuals must be able to observe the mate choices of other (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). Patriquin-Meldrum & Godin (1998) provide experimental evidence that three-spined stickleback females do not copy the mate choice of others. Mate-choice copying is most likely to occur in polygynous and promiscuous mating systems with no parental care or with maternal care only, and has been studied intensively in polygynous birds (Höglund *et al.* 1995; White & Galef 1999, 2000) and fishes.

Several theoretical models have investigated how 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). 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's (1992) study of Trinidadian guppies (*Poecilia reticulata*, Poeciliidae). The experiment consisted of an observation period and a preference test. During the observation period, a focal female could observe two males, each in a separate end chamber of the test aquarium, with one male courting another female (the so-called 'model female') who was adjacent to the male but separated by glass. After removing the model female, the focal female was allowed to choose between the two males, and the time the focal female spent within the preference zones adjacent to the male chambers was measured as her mate preference. In 17 out of 20 trials the focal females preferred to associate with the male that they had previously observed interacting with the model female. Although convincing, this result could have been explained by alternative hypotheses, which Dugatkin tested in four other experiments:

1 schooling hypothesis: females prefer the side where they have seen the largest group of fishes;
2 no interaction-hypothesis: females prefer the side where they have seen a male and a female but without sexual interaction between the pair;
3 male activity hypothesis: females prefer a more active male;
4 sexual priming hypothesis: females might become sexually primed after observing an interaction between a male and another female and choose males that behaved as though they have just been involved in an interaction with a female.

Results of these additional experiments provided no support for any of these four alternative hypotheses. By excluding these alternative explanations, Dugatkin's experiment provides the first experimental evidence for mate-choice copying in guppies. Following his study, several other studies regarding mate-choice copying in fishes have been published (see below) and research on this topic is continuing (Godin *et al.* 2005; Uehara *et al.* 2005).

At the present time there is good evidence for mate-choice copying in guppies (Dugatkin & Godin 1992, 1993; Dugatkin 1996a, b, 1998a, b; Godin *et al.* 2005), and in other fish species like the sailfin molly (*Poecilia latipinna*, Poeciliidae; Schlupp *et al.* 1994; Schlupp & Ryan 1997; Witte & Ryan 1998, 2002; Witte & Noltemeier 2002; Witte & Massmann 2003; Witte & Ueding 2003), the humpback limia (*Limia nigrofasciata*, Poeciliidae; Munger *et al.* 2004), and the Japanese medaka (*Oryzias latipes*, Adrianichthyidae (Grant & Green 1996, but see Howard *et al.* 1998).

However, there are other studies that failed to detect mate-choice copying in different fish species, including some of the above. 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. Ambiguous results for the Perugia's limia (*Limia perugiae*, Poeciliidae) were reported by Applebaum & Cruz (2000). It is currently unclear why mate-choice copying should be observed in some situations and not others.

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. However, until recently all experiments on mate-choice copying in fish species had been performed in the laboratory, rendering it unclear whether males and females copy the choice of others in their natural habitat, and under natural conditions. To show that mate-choice copying is a biologically relevant mate-choice strategy, it is important to demonstrate that this mate-choice strategy occurs in the wild as well. Witte & Ryan (2002) studied this significant issue in the sailfin molly. The sailfin molly is a good candidate for investigating mate-choice copying in the wild because previous studies have shown that males (Schlupp & Ryan 1997) and females (Witte & Ryan 1998) copy the choice of others under standardized conditions in the laboratory. The field study (Witte & Ryan 2002) was performed in the Comal River, near New Braunfels, Texas, USA, where it was easy to observe free-swimming sailfin mollies in a wild sailfin population. Because it was not possible to perform the complicated design for a mate-choice copying experiment in the laboratory in the river, Witte & Ryan (2002) used a simpler design (Fig. 5.1a,b). They performed experiments for male mate-choice copying, female mate-choice copying, and a control for schooling behaviour in each sex (Fig. 5.1b). In the case of female mate-choice copying (Fig. 5.1a), they presented focal females with two stimulus males, each in a jar with a net on top standing on two upside-down plastic tanks in a natural river. Next to each jar with a stimulus male was a second 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

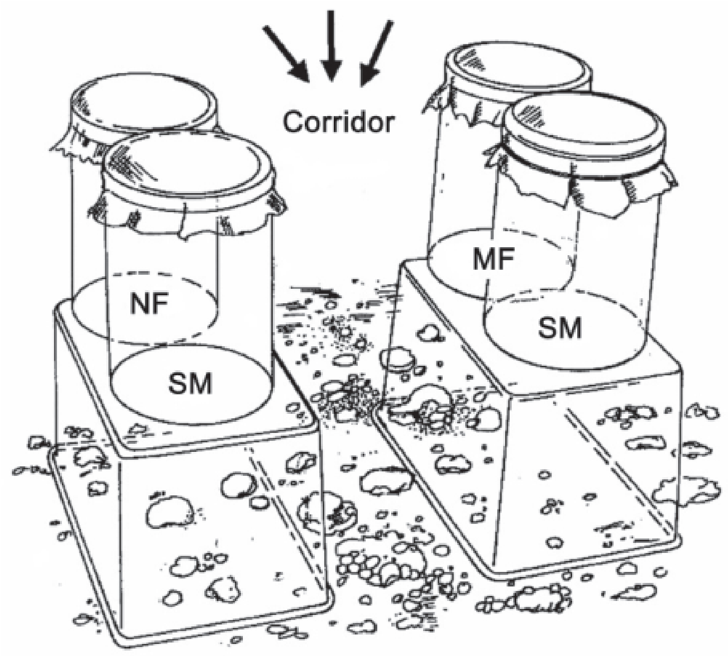

Fig. 5.1 (a) Top view of the set-up of the female mate-choice test in the sailfin molly in a river. Two jars stood on two upside-down plastic tanks. Each jar had a net on top and was filled with the water from the river. In the female mate choice tests, Witte & Ryan (2002) presented stimulus males (SM) 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 (SF) replaced stimulus males and a model male the model female. In the male control for shoaling, Witte & Ryan (2002) presented two stimulus males and an extra male. 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.

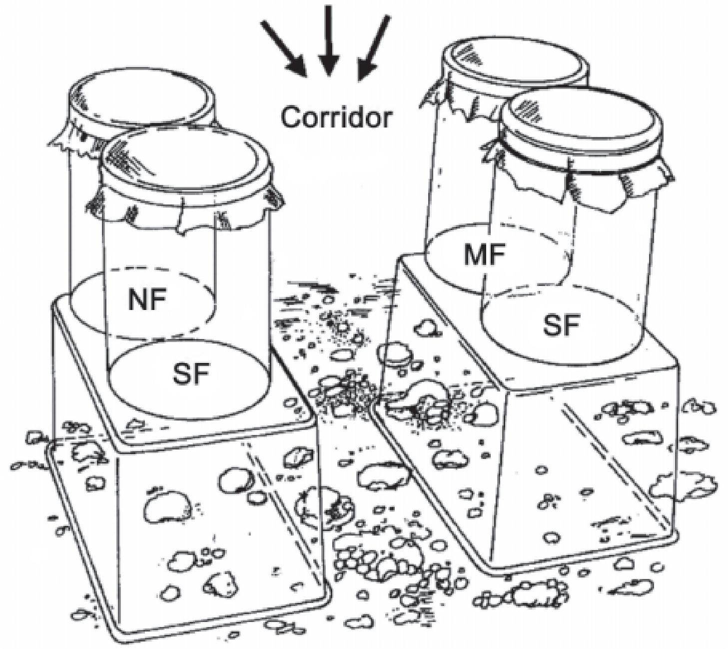

Fig. 5.1 (b) Top view of the set-up of the female control test for shoaling in the river. In the set-up of the female control for shoaling there was a stimulus female (SF) and a jar with a model female (MF)on one tank and a stimulus female next to a jar with no fish (NF) on the other tank. Females were 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.

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; that is, females preferred to associate with the male next to a model female rather than a 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.

To strengthen the significance of mate-choice copying for sexual selection, mate-choice copying under natural conditions should be investigated in other species as well. The Trinidadian guppy, which lives in different river systems under quite different environmental conditions would be an ideal system in which to investigate which environmental conditions facilitate or complicate the evolution of mate-choice copying.

5.5.3 *Copying mate rejection*

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. 1001–2). 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). In their copying experiment, they presented video playbacks of sailfin molly males on two TV monitors, one standing adjacent to each side of the female test tank. First, females were allowed to choose between two male video playbacks and the time females spent within a preference zone in front of the playbacks was used as a measurement of male attractiveness. After the first preference test, females had the opportunity to copy a mate rejection. Females could observe another female escaping from the attractive male when the male tried to court the additional female on one monitor and on the other monitor the previously unattractive male was alone. Afterwards females could choose between the same two single male presentations again. After observing a rejection, females spent significantly less time with the previously attractive male and 8 of 15 females reversed their initial choice and spent more time with the previously unattractive male. In control conditions, sailfin molly females with no opportunity to copy chose consistently. A control condition with the escaping behaviour of a female, but without a male, did not result in females spending less time with the previously attractive male in the second preference test. Thus, it would seem that the females copied the rejection of a male by another female.

What is the advantage of copying a rejection? During the process of mate choice, females may sample several males (Janetos 1982; Real 1990) and may observe several independent choice events by other females. By observing another female rejecting a male, females might also ignore this male and concentrate on other males as potential mates and by so doing they might be able to save time and energy, and reduce exposure to predation. Additionally, by observing the rejection of a male, females might learn which male phenotype is 'bad' as a potential mate. Thus, in copying the mate rejection of other females, females may protect themselves against 'wrong' choices. According to sexual selection theories, the rejection of a male is as important as the acceptance of a male, because females might suffer low reproductive success when mating with poor quality males. Copying not only mate acceptance but also mate rejection will strongly amplify the skew of reproductive success in males within a population. Copying the rejection of a male is, therefore, potentially as important as copying mate attraction for the process of sexual selection.

5.5.4 *The disruption hypothesis – an alternative explanation to mate-choice copying?*

Mate-choice copying as an alternative mate choice strategy to independent mate choice decisions is still under debate, and alternative explanations to some findings have been proposed. Applebaum & Cruz (2000) argued that a disruption effect could better explain mate-choice behaviour in Perugia's limia females than mate-choice copying. They proposed the disruption hypothesis in which 'biotic and/or abiotic events that occur in the perceptible field of a female actively engaged in a mate-choice may disrupt the decision-making and information processing of that female. This may result in a reduction (or increase) in the consistency with which that female selects males with preferred traits'. Applebaum & Cruz stated that previous results showing that guppy females reverse their choices after observing another female interacting with the previously non-preferred male (Dugatkin & Godin 1992) could be interpreted as a disruption effect instead of mate-choice copying. Applebaum & Cruz tested the disruption hypothesis in the live-bearing poeciliid Perugia's limia. They used a design similar to that used by Dugatkin & Godin (1992) and performed three experiments. In each experiment, the focal female could first observe two males placed in the two end chambers of the test tank and separated by glass from the female placed in a clear plastic cylinder. After this observation period, the female was released into the test tank and allowed to choose between the two males. After 30 min with males blocked from view, females could choose a second time between the same males. In Experiment 1, no model females were placed next to a male during the previous observation period. Thus, this experiment tested whether females chose consistently with no opportunity to copy. In Experiment 2, the focal female could view a model female next to the male the focal female had not preferred in the mate choice test before. Afterwards the focal females were allowed to choose a second time between the same males. In Experiment 3, the focal female could view a model female next to her previously preferred male, and was allowed to choose between the same males a second time afterwards. The results indicated that females in Experiment 1 chose consistently when they had not seen a model female next to one male. In Experiment 2, significantly more females than in Experiment 1 reversed their initial preference and preferred the previously non-preferred male in the second mate choice test. In Experiment 3, a similar fraction of females reversed their initial preference, that is, spent less time with the initially preferred male in the second mate choice test. Applebaum and Cruz interpreted this result as an indication of a disruption effect. In both Experiments 2 and 3, females did not choose consistently and the consistency may decline as a result of disruption during mate-choice decision-making by the presence of the model female.

There are, however, at least two factors that imply that the disruption hypothesis is a less likely explanation than mate-choice copying. First, in all three experiments the absolute time females spent with the preferred male did not decrease between the first and second mate-choice test. If females had been disrupted during mate choice, one might expect that they would have lost interest in the males and spent more time outside the preference zones during the mate-choice test, and thus had spent less time with preferred males. Second, the idea that females may become confused by observing another female interacting with a male seems implausible, especially in fish species living in schools in which school members interact with each other all the time and gather and use social information in the context of foraging behaviour (Laland & Reader 1999), mate choice and predator avoidance. Dugatkin (1992) has shown that guppy females can remember males that they have seen interacting with a female before, and additionally Witte & Massmann (2003) have shown that sailfin molly females remember males they have seen interacting with a female after a day. Thus, the ability of individual recognition in females is much better than assumed by the disruption hypothesis (see Chapter 8 for a review of individual recognition in fishes).

Stimulated by the study of Applebaum & Cruz (2000), Dugatkin *et al.* (2003) repeated their experiment with guppies and tested the two contrary predictions of the disruption hypothesis and mate-choice copying when a model female is placed next to the male that was previously preferred by the focal female. When mate-choice copying is operating, focal females would maintain their initial preference as they would be reinforced by the apparent choice of the model female. If disruption is occurring, focal females would be expected to reverse their initial choice and would not choose consistently. Dugatkin *et al.* (2003) showed that guppy females chose consistently when there was no model female present during the observation period, only 6 of 20 females reversed their choices. When the model female was placed next to the previously non-preferred male, 14 of 20 females reversed their choice. When a model female was place next to the previously preferred male, however, only 6 of 20 females reversed their choice and thus females maintained their initial preference. This result strongly supported mate-choice copying in guppies and the hypothesis that disruption plays no role during mate-choice decision-making in guppy females.

Munger *et al.* (2004) performed the same three experiments with humpback limia as performed by Applebaum & Cruz (2000) with guppies. Munger *et al.* (2004) found no evidence for the disruption hypothesis. Humpback limia females chose consistently between two males when they had no opportunity to observe another female interacting with a male. Females reversed their initial choices after observing another female interacting with the male the focal female had initially rejected. Females maintained their initial preference for a male, when they had observed another female interacting with the initially preferred male. Thus, these experiments indicate that humpback limia females copy the mate-choice of others.

In summary, as the evidence currently stands, the disruption hypothesis is not a compelling alternative explanation to mate-choice copying. It might be possible, however, that females may be influenced differently by different observations of mate choice (Agrawal 2001). It could be that a sexual interaction between an attractive male and a female stimulates the female in a different way than an observation of a sexual interaction between a female and an unattractive male, or a sexual interaction between an attractive male and a female may be perceived by the observing female differently from an interaction between an unattractive male and a female. Future research should focus on how females perceive such sexual interactions and what information extracted from this observation is important for mate-choice decision-making.

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 the 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, that is, 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 that 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 dilemma 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, for a period of 5 min. 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. When males differed by 40% in orange body colour, however, 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 on average of 40%. In different experiments, test females could observe either no model female, one model female interacting with the drabber male for 5 min, two different model females interacting with the drabber male each for 5 min, or one model female interacting with the drabber male for 10 min. 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 min 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. Thus, 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 has been documented in different populations of sailfin mollies (Marler & Ryan 1997; Ptacek & Travis 1997; Witte & Ryan 1998; Gabor 1999; Witte & Noltemeier 2002; MacLaren *et al.* 2004; Schlupp *et al.* 1994). 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, which differed in standard body length on average by 12 mm. In the first mate-choice test, all females preferred the larger 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 male 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 min. Afterwards, as predicted by previous experiments (Witte & Ryan 1998), females did not copy and still preferred the larger over the smaller male. In a second experiment, females were allowed to observe two different females interacting with the smaller male each for 5 min. Thereafter, 7 of 15 females reversed their initial preference for the larger of two males and associated significantly more often 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 min. 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 the larger over the 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 emphasize 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.

Females 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 min, were retested by Witte & Noltemeier (2002) for a preference for smaller males up to 36 days after copying. In the intervening period, females were kept isolated from males. In a binary choice situation, females could choose between a smaller and a larger male, both of which were unfamiliar males that had not been used in the copying experiment. Thus, the authors tested whether females still exhibited a preference for a specific male phenotype, and not a preference for an individual male. Females that had previously reversed their mate preference in favour of smaller males through mate-choice copying, maintained this preference for smaller males in the binary mate-choice experiment. 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.

More recently, 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. These studies, therefore, emphasize mate-choice copying as a powerful influence on 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 a pleiotropic effect of a sensory bias for the colour orange, which might have arisen in the context of food detection (e.g. in search of prey items such as crustaceans containing high levels of carotenoids in their exoskeleton). In field and laboratory experiments, Rodd *et al.* (2002) showed that both male and female guppies are more responsive to orange-coloured objects than to objects of other colours, and that was true even outside the reproductive period. The authors assume an innate preference for orange as a cue for rare and high quality food sources in both sexes. Males that developed orange spots, therefore, exploited the pre-existing preference for orange in females and are preferred as mates by females.

5.8.1 *Female preference for swords*

A well known system for a pre-existing sensory bias for a specific male trait has been documented for the genus *Xiphophorus* and the sister group *Priapella*. Male green swordtails (*Xiphophorus helleri*, Poeciliidae) have a yellow-coloured sword with a black border, which is an elongation of certain ventral caudal-fin rays (Basolo 1998), and females base their mate choice largely on the characteristics of this sword (Basolo 1990a). Males of the platyfish (*X. maculatus* and *X. variatus*, Poeciliidae) do not possess a sword. However, females of these species prefer conspecific males with an artificial plastic sword over naturally swordless males (Basolo 1990b, 1995a). A similar preference for artificially sworded males was found in the sister group *Priapella*. Female Olmec priapella (*P. olmaceae*, Poeciliidae) prefer artificially sworded males over naturally non-sworded males (Basolo 1995b). There is, however, no general preference in females of poeciliid fish species for a sword in males. Two-spotted livebearer females (*Heterandria bimaculata*, Poeciliidae) exhibited no pre-existing preference for males with an artificial sword (Basolo 2002a), and results for the sailfin molly regarding a latent preference of females for sworded males are ambiguous. Basolo (2002b) showed a clear preference in sailfin molly females from a Louisiana population for artificially sworded conspecific males of the opposite sex, whereas Witte & Klink (2005) did not find such a preference in sailfin molly females from a Texan population. These population differences in pre-existing biases in females for a sword in males might be explained by differences in female preferences between different populations, and/or by different environmental conditions. The Louisiana sailfin mollies live in murky waters, whereas the Texan sailfin mollies live in clear waters. In murky water, a sword in males would probably enhance the visibility of males for females and also probably enhance their mating success. In clear water, however, a sword may not increase, or may only marginally increase, the visibility of males for females, and may incur high predation risk (Abrahams & Kattenfeld 1997). This may have constrained the evolution of a sword in the Texan male molly and a preference for such a male trait in females.

5.8.2 *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. An interesting question is, therefore, 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 & 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's & 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 1983). The legitimacy of this assumption has yet to be evaluated within the context of mate-choice behaviour, although see below. 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.

5.8.3 *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; Witte & Noltemeier 2002; Witte & Massmann 2003). To investigate this question Witte *et al.* (K. Witte, K. Kotten & K.B. Klink, unpublished data submitted) attached an artificial yellow plastic sword with a black border or a transparent plastic sword to the base of the 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 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, 10 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 uncertainty 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 utilized 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?

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 female. 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.

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 recognize 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, that is, 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). A female that observes how a male courted 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 minimize 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. Both disadvantages, however, 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 memorize 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. 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 rather on social or private information.

5.10 Outlook

In spite of good progress in understanding mate-choice copying, there is, as yet, still little indication that mate-choice copying is an adaptive mate-choice strategy. It would be valuable if future experiments focused 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.

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 reach 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 inadvertent social information 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 inadvertent social information 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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