

Mate Choice

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INTRODUCTION

Among the myriad of reproductive decisions that individuals must confront, few have as direct a bearing on individual fitness as choosing the right mate. Indeed, as we have seen already (Chapter 8 'Variation in Sexual Selection in Fishes' by Ahnesjö *et al.*, this book), mate choice by any given sex can be a potent evolutionary force, resulting in the elaboration of spectacular ornaments in members of the opposite sex.

Like most animal groups studied to date, research on mate choice in fishes has tended to focus on female mating preferences because females are often regarded as the choosier sex. Naturally, given the vast sexual selection literature on female mating preferences, many of the examples we will be using are taken from studies of female choice. It is worth noting, however, that males too can benefit from being choosy (Sandvik *et al.* 2000; Kokko and Johnstone, 2002; Werner and Lotem, 2003; Wong

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et al., 2004) and that many of the issues addressed in this chapter are just as applicable to male mating preferences as they are to females. Thus, wherever possible, a concerted effort has been made to highlight examples of mate choice in both sexes.

It is also important to understand that mate choice is not always inevitable: both the existence and extent of choice can depend on the life history. With few exceptions, fertilizations in most species of fish occur externally. Spawning, in this regard, can take place in large aggregations, involving considerable numbers of participants, broadcasting their gametes into open water and, as such, there may be few opportunities for mate choice. Whether individuals spawn in groups or pairs has implications for offspring care. In fishes, care of offspring is rare. When it does occur, however, offspring care differs dramatically from most other taxa: paternal care, it seems, is the rule, rather than the exception (for an in-depth discussion, see Chapter 10 'Parental Care and Sexual Selection' by Lindström and St Mary, this book). Factors such as these can all play a role in determining, first of all, whether mate choice occurs at all; and secondly, the degree of choice that may be exercised.

We begin this chapter by asking a fundamental question: Why should individuals be choosy? Here, we will discuss the suite of benefits— both direct and indirect—that individuals can acquire from being selective about their mates. After describing the benefits of choice, we will proceed to explore how individuals might actually go about the task of sampling and choosing among a bevy of potential suitors. Of course, like any other behavioural decision, mate choice is not without its costs and, in this regard, we will be outlining some of the factors that can restrict the mate choice process. In a world facing increasing pressures from anthropogenic disturbance, we will also be examining how environmental change might impinge on the mate choice process. Finally, in our conclusion, we offer researchers some suggestions of potentially exciting and rewarding avenues for future study.

WHY BE CHOOSY?

Why should an individual spend time and energy on choosing a mate instead of mating with the first suitor that he/she encounters? Choice almost invariably incurs some form of cost. Mate choice, for example, can be energetically demanding and time consuming. By being choosy, individuals may also heighten their vulnerability to predators and/or risk the possibility of missing out on fertilizations altogether (for a detailed discussion of how costs influence choice, see 'Restrictions on choice'

below). Thus, for individuals to derive a net fitness gain from being choosy, the benefits of mate choice should outweigh the costs. The benefits that individuals may receive are mostly concerned with helping them maximize the number and/or quality of offspring, and can largely be divided into two main groups: direct and indirect benefits. Direct benefits are those that have an immediate bearing on fitness and may include such gains as access to superior parental care of offspring, provisioning of high-quality resources, or improved fertilization success. Indirect benefits, on the other hand, enhance offspring fitness by increasing their viability and/or attractiveness through the inheritance of 'good' genes. We now proceed to discuss each group of benefits in more detail.

Direct Benefits

(a) Parental care

In many species of fish, males alone are responsible for taking care of the offspring (see Chapter 10 'Parental Care and Sexual Selection', by Lindström and St Mary, this book). Females, in those species, can maximize their own fitness by choosing males with superior parental abilities. Indeed, based on a recent meta-analysis, direct benefits in the form of higher egg-hatching success appear to be especially important in guiding the female mate preferences of fishes with parental care (Møller and Jennions, 2001). Evidence for this is seen, for example, in the sand goby *Pomatoschistus minutus*, a European inhabitant of shallow, coastal waters (Forsgren, 1997a). Male sand gobies build nests under empty mussel shells and care for the eggs they receive by actively fanning the brood and defending them against potential egg predators. When female gobies were allowed to choose between two nesting males, females preferred good fathers that brought more of their eggs to the hatching stage (Forsgren, 1997a). Moreover, females preferred to spawn with males that already had eggs in their nests (Forsgren *et al.*, 1996). Females, in this regard, probably benefit because, for males, the payoff from paternal effort increases with egg number and, as a consequence, males tend to invest more care in larger broods (see Chapter 10 'Parental Care and Sexual Selection', by Lindström and St Mary, this book). Evidence suggests that females may also gain by spawning with such males through the diluting effects of increased egg number, which reduces the risk that the eggs of any given female will be lost to filial cannibalism or predation (Forsgren *et al.*, 1996).

Male parenting ability is often advertised through a broad range of behavioural and morphological characteristics, which are correlated with

different components of parenting ability and/or the level of male investment into parental care. In the bicour damselfish, *Stegastes paritus*, for example, males provide exclusive care of eggs, and females discriminate among males based on the males' courtship efforts (Knapp and Kovach, 1991). Experimental manipulation of egg number in nests showed that courtship rate is an honest indicator of male parental quality. Specifically, males that courted vigorously brought a greater proportion of their eggs to the hatching stage than did males, which courted at reduced rates (Knapp and Kovach, 1991). The latter also had lower energy reserves and, as such, were more likely to cannibalize the females' clutch, thus making them especially undesirable as potential mates.

(b) Resources

Resources defended by males can have a considerable impact on female fitness, particularly in species with male parental care. The characteristics of the territory, the nest site, or the nest itself, may determine the level of predation risk, the likelihood of the nest being destroyed by predators or competitors, or the availability of food for the parents and newly hatched offspring. In a coral reef fish, the beaugregory damsel, *Stegastes leucosticus*, males defend permanent all-purpose territories around pieces of rubble that serve as egg-deposition sites (Itzkowitz and Koch, 1991; Itzkowitz *et al.*, 1995). Males that were given new artificial nest sites enjoyed higher reproductive success than did males that remained on natural sites and those that had been left with an artificial site for an extended time (Itzkowitz *et al.*, 1995). This was most likely due to the lower number of egg predators (e.g., brittle stars) present on the newer sites, which made these territories more desirable to females (Itzkowitz and Koch, 1991).

The structure of the nest site itself can also influence the probability of nest raids and sneak fertilizations by other males. In the three-spined stickleback, *Gasterosteus aculeatus*, for example, vegetation structure around the territory can have a significant impact on reproductive success, since it affects the probability that both the male and the nest will disappear due to predation (Kraak *et al.*, 1999), the number of nest intrusions by other males, the time that the male spends fanning the eggs, and subsequent egg-hatching success (Sargent and Gebler, 1980). Females may gain information on the quality of the territory and the nest either by direct assessment of the site, or by inspection of the males. The latter is likely if males compete vehemently for high-quality sites and this, in turn, results in high-quality males occupying the best territories, as seen, for example, in sticklebacks occupying densely populated habitats (Candolin and Voigt, 2001).

(c) Fertilizations

Based on the above examples, it would seem that female mate choice is heavily influenced by the material resources provided by the males. Female choice for direct benefits, however, can also occur in resource-free mating systems if the traits used by females to assess male quality covary with the size or quality of the male's ejaculation (Sheldon, 1994). The male with the most exaggerated secondary sexual traits, under these circumstances, would also be the most virile and, as such, benefit the female by increasing her fecundity through higher fertilization success. A positive correlation between the number of sperm transferred and male phenotype has been found in the guppy, *Poecilia reticulata*, a tropical fish species with internal insemination, where females copulate with several males. Males with attractive colour phenotypes transfer more sperm to females during solicited copulations than their less-ornamented counterparts (Pilastro *et al.*, 2002a). This is true irrespective of the size of their initial sperm stores. The relationship breaks down, however, during coercive copulations, which suggests that females exert at least partial control over the number of sperm inseminated during cooperative mating. The possibility that male phenotype can influence fertilization success indirectly through cryptic female choice, will be discussed in greater detail later in this chapter.

A further way that females may be able to improve their fertilization success is to spawn with a male when sneaker males are present, since the increased number of individuals that attempt to mate with a female can boost the number of sperm released and, hence, increase the proportion of eggs that are fertilized. This is seen, for example, in the European bitterling *Rhodeus amarus* (Candolin and Reynolds, 2002b). Male bitterling defend territories around several living mussels and attract females which, in turn, deposit their eggs onto the gills of a mussel with the help of a long ovipositor (Fig. 9.1). Males then fertilize the eggs by releasing sperm over the mussel. In an experiment that manipulated the number of males present during a spawning event, Candolin and Reynolds (2002b) showed that females preferred to spawn in the presence of several males. By contemporaneously releasing their sperm over the mussel, the presence of multiple males increases the proportion of eggs that are fertilized (Smith and Reichard, 2005) (Fig. 9.1).

(d) Male choice for fecundity or fertilizations

Although males have traditionally been viewed as being less discriminating than females, recent studies suggest that under certain circumstances,

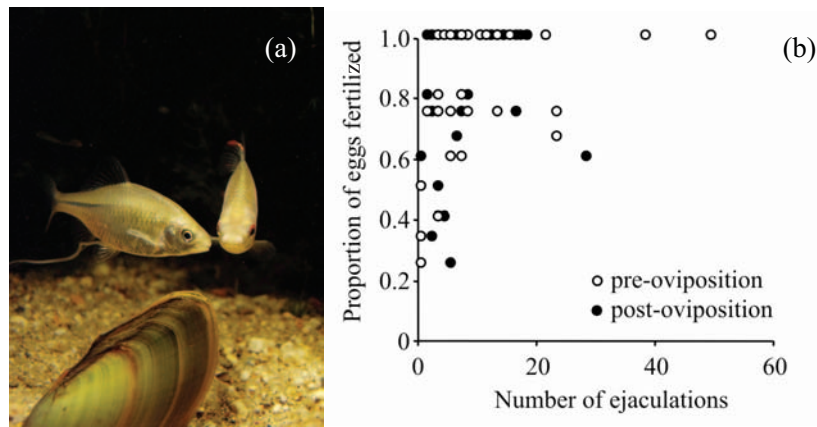


Fig. 9.1 (a) A female, with an ovipositor, and a male bitterling, *Rhodeus amarus*, attempting to spawn in a mussel. (b) The proportion of eggs fertilized increases with the number of ejaculations in bitterling. Adapted from Smith and Reichard (2005). Photograph: Carl Smith.

males can be just as fastidious about their mates as females. In this regard, several studies have shown that males may often exercise mate choice for fecund females. An example of this is seen in the two-spotted goby, *Gobiusculus flavescens* (Amundsen and Forsgren, 2001, Pelabon *et al.*, 2003). Male two-spotted gobies take up nests in empty mussel shells or in crevices, and take exclusive care of the eggs. Males prefer females that have bright yellow-orange bellies (Amundsen and Forsgren, 2001). The colour displayed by female gobies comes from the pigmented eggs that are visible through the semi-transparent abdominal skin and also the pigments present in the skin itself. Thus, by paying close attention to the females' colour, choosy males are able to acquire pivotal information about female fecundity and the carotenoid content of her eggs (Svensson *et al.*, 2006) which, in turn, may be important in signalling egg quality. However, the preference for large, more fecund females found in the male two-spotted gobies were weak, which was suggested to depend on a low variation in fecundity in this species (Pelabon *et al.*, 2003). Male mate choice has also been documented in the Banggai cardinalfish, *Pterapogon kauderni* (Kolm, 2004), a coastal marine species from Sulawesi. Parental care in this paternal mouthbrooder involves considerable investment, with males incubating the eggs for as long as 30 days without feeding. The courtship display of females, in this case, is correlated with fecundity and how close the female is to spawning. As a consequence, courtship provides male cardinalfish with important information about the maturity of the females' eggs (Kolm, 2004).

Male mate choice for fecund females is by no means restricted to species that invest heavily in male parental care. In a species of lek-forming cichlid, *Astatotilapia flavijosephi*, females visit male aggregations solely for the purpose of having their eggs fertilized. The females are then left with the onerous task of mouthbrooding the eggs. Werner and Lotem (2003, 2006), found that although male, *A. flavijosephi*, contribute little more than sperm, they nevertheless show a preference for larger and more fecund females. Constraints on fertilizing multiple females in this case, are likely to be responsible for strategic allocation of male mating effort.

Males may also choose to maximize their reproductive value through increased fertilization success. Generally, males prefer to spawn with females that have not mated with other males because, by exerting such a preference, males can increase the probability of successfully siring the female's clutch. In this regard, Dosen and Montgomerie (2004) showed that guppy males spend more time with—and direct more courtship towards—females that they have seen alone, compared to females that they have seen receiving forced copulations from rival males. This is most likely a strategy to reduce sperm expenditure when the risk of sperm competition is high and the pay-offs from sperm investment is low. In some species, sensitivity to the risk of sperm competition is so great that male mating behaviours can be affected even if the males themselves do not actually see potential mates copulating with other males, but gain information about the probability of sperm competition from the operational sex ratio (Evans and Magurran 1999). The probability of foregoing spawning opportunities can also depend on future spawning opportunities. For example, large male rainbow darters *Etheostoma caeruleum* with greater prospects of future mating opportunities tend to forego their chance to spawn in the presence of sperm competition more often than do smaller males (Fuller, 1998). In some species, males are also able to adjust the number of sperm released in response to the risk of sperm competition. Such a strategy is seen, for example, in guppies (Pilastro *et al.*, 2002b), bitterlings (Candolin and Reynolds, 2002a), and sticklebacks (Zbinden *et al.*, 2003) (see also Chapter 11 'Alternative Reproductive Tactics' by Knapp and Neff this book).

(e) Species recognition

Apart from allowing individuals to select a high quality suitor, mate choice also plays an important role in species recognition. In this regard, different cues such as body size, colour and courtship behaviour may help females

to distinguish between conspecifics and heterospecifics. A classic example of this is seen amongst the cichlid fishes that inhabit the Great Lakes of East Africa. Different cichlid species living in the same area often display considerable differences in colour patterns that appear to be important as cues in female mate choice. Divergent colour patterns in these cichlids reduce the risk of hybridization by playing a key role in pre-mating reproductive isolation (Knight and Turner, 2004).

In some cases, however, mate preferences may actually increase the risk of heterospecific mating. This can occur if preferred traits overlap with those found in heterospecifics, and/or if heterospecifics actually exhibit traits that are more attractive than those displayed by conspecifics. An example of this is seen in sailfin mollies, *Poecilia latipinna* (Gumm and Gabor, 2005). Male sailfin mollies, due to a positive female size-fecundity relationship, prefer to associate with and produce more sperm in the presence of, larger conspecific females (Gumm and Gabor, 2005). In populations sympatric with the larger unisexual, gynogenetic Amazon mollies, *Poecilia formosa*, male preference for large females occasionally results in male sailfin mollies mating with female Amazon mollies (Gumm and Gabor, 2005).

Among the swordtails and platyfishes, *Xiphophorus* spp., females often show strong preferences for the visual cues of heterospecifics (Ryan and Wagner, 1987; Crapon de Caprona and Ryan, 1990; Basolo, 1995; Hankison and Morris, 2003). For instance, in one species, *X. pygmaeus*, females prefer larger males (Hankison and Morris, 2003). This results in a mating preference that favours males of a larger, coexisting species, *X. cortezi* (Hankison and Morris, 2003). Nonetheless, despite a preference for the visual cues of heterospecifics, female swordtails often show robust preferences for the odour cues of conspecifics (Crapon de Caprona and Ryan, 1990; McLennan and Ryan, 1997, 1999; Hankison and Morris, 2003; Fisher *et al.*, 2006). The same, however, cannot be said of males. In one swordtail species, *X. birchmanni*, males actually preferred the female odour cues of a closely related heterospecific, *X. malinche*, over those of conspecific females (Wong *et al.*, 2005).

Indirect Benefits

As we have already indicated at the start of this section, mate preferences may also evolve for indirect genetic benefits (i.e., the passing on of genes that enhance offspring fitness). Such benefits may occur in both resource-based and resource-free mating systems but their importance is generally

assumed to be greater in resource-free systems where direct benefits are of lesser value (Jennions and Petrie, 2000). Generally, however, studies demonstrating the existence of indirect genetic benefits are far fewer than those in support of direct benefits, since the strength of indirect benefits is generally weaker than that associated with direct fitness gains (Fisher *et al.*, 2006). As a consequence, large sample sizes and extensive breeding designs are often required to demonstrate the existence of indirect benefits. Moreover, in cases where females or males may differentially invest resources into reproduction (i.e., according to the attractiveness of their mate), maternal and paternal effects may have to be accounted for and controlled (Sheldon, 2000).

(a) Condition and size

The genetic quality of a male may, at least to some extent, be reflected in his physical condition and advertised by exaggerated sexual signals, with high quality suitors in superior condition expressing larger signals than those of poor quality (Tomkins *et al.*, 2004). This relationship can arise if high quality individuals have either a higher resource intake or lower resource requirements and, as such, can better afford to allocate more of their resources into sexual signalling. Body size, in this regard, can be an important cue to females. Reynolds and Gross (1992) showed, for instance, that large male guppies are preferred by females and sire offspring that grow faster and have a higher fecundity than those sired by small males. This suggests that female guppies acquire genetic benefits by mating with larger partners.

The reliability of condition as a signal of genetic quality may also depend on the degree of food limitation. An interesting example of this is mate choice in the Atlantic molly, *Poecilia mexicana* (Plath *et al.*, 2005). In populations from nutritionally poor areas, such as caves, where there is large variation in male condition, the females show a strong preference for males in good condition (Plath *et al.*, 2005). However, in populations from nutrient-rich areas, such as rivers, where most males are well-nourished, the preference is less pronounced (Plath *et al.*, 2005). It is likely that the body condition reflects fitness, and possibly high genetic quality, only in environments where food supplies are limited. This suggests that female preference for males in good condition evolve relative to the indicator value of male condition. More recently, a preference for well-fed males has also been uncovered in another poeciliid, the swordtail fish *X. birchmanni* (Fisher and Rosenthal, 2006a, b).

(b) Parasite resistance

Parasite resistance is an important component of viability. Several studies indicate that females attempt to maximize the parasite resistance of their offspring through mate choice for compatible genes, where genetic quality reflects interactions between maternal and paternal genes, i.e., non-additive genetic effects (Landry *et al.*, 2001; Neff and Pitcher, 2005; Rudolfson *et al.*, 2005). Research on three-spined sticklebacks has shown, for example, that females seek to achieve an optimal level of MHC diversity in their offspring by using an odour-based mate selection strategy (Reusch *et al.*, 2001). This, in turn, gives offspring optimal resistance toward pathogens and parasites. Males signal their MHC composition through MHC peptide ligands which females are able to smell in the water (Milinski *et al.*, 2005).

Parasite resistance is also advertised by visual cues in the three-spined stickleback (Barber *et al.*, 2001). To investigate if male red coloration indicates, in this case, good genes (i.e., additive genetic effects), Barber and co-workers (2001) used *in vitro* fertilizations to generate maternal half-siblings that were raised without parental care. The offspring sired by brightly coloured males turned out to have higher counts of white blood cells and were also more resistant to a cestode parasite. However, they suffered a cost in terms of reduced growth rate. Thus, highly ornamented males confer disease resistance to their offspring, but an apparent trade-off appears to exist between parasite resistance and early growth rate, which suggests a mechanism for the maintenance of heritable variation in both disease resistance and male sexual coloration (Barber *et al.*, 2001).

A maternal half-sibling study by Wedekind and co-workers (2001) on whitefish *Coregonus* sp. similarly suggests strong genetic effects of parental sexual advertisement on offspring viability. When 10 females and 10 males were crossed to generate 100 sibling groups, strong maternal and paternal effects on egg mortality were found. Male breeding ornamentation, measured as the size of breeding tubercles, predicted egg mortality from bacterial infection, with more strongly ornamented males siring offspring that better survived epidemics during egg development.

(c) Predator avoidance

Bright colours often make a fish more susceptible to predators. The ability to bear the cost of displaying gaudy colouration may, therefore, indicate important genetic information about the quality of potential suitors. To

determine whether the orange colour variation reflects predator avoidance in guppies and whether this, in turn, is heritable, Evans and co-workers (2004) artificially inseminated guppy females with sperm from males that exhibited high variation in the area of orange pigmentation. When they subsequently exposed the offspring to a simulated predator attack, they found that sire coloration predicted the ability of newborn offspring to evade capture. Sire attractiveness, however, was not correlated with other components of anti-predator behaviour, such as swimming speed and schooling behaviour. These were probably determined by maternal effects. Still, the results of their study suggest that, by mating with bright males, females are, at the very least, able to benefit by producing offspring that are more proficient at dodging predators.

(d) Attractive sons

In a half-sibling laboratory study on guppies, Brooks (2000) found a negative genetic correlation between sire attractiveness, measured as orange coloration, and the survival of the male offspring. This could have arisen through the genetic hitch-hiking of deleterious genes with attractiveness genes. However, despite the undesirable survival cost to offspring, females may gain a genetic benefit from their preference for colourful males, if attractive males sire attractive sons that have a high mating success. Thus, although the trait—in this case—correlates negatively with offspring viability, the genetic benefit of attractive sons could outweigh the viability cost and result in a net benefit of mating with sexy males.

HOW TO CHOOSE A MATE?

Direct and Indirect Mate Choice

There are two main ways in which individuals may choose their mate. They may actively compare and choose among a suite of potential suitors, or they may, instead, take a more passive role and set the conditions for competition among individuals of the opposite sex (Wong and Candolin, 2004). In most species, at least some degree of direct choice occurs, with females inspecting several males before making a decision (see section on 'Mate sampling' below). In the garibaldi damselfish, *Hypsypops rubicundus*, for example, females defend permanent feeding and shelter territories and must leave these to search for, and spawn with, nesting males. Females usually make multiple trips, each separated by a return to

the nest to reduce the amount of food lost to competitors that enter the territory. During these forays, females can end up inspecting the nests of up to 15 males more than 200 m from their territory, before finally deciding with whom they will eventually spawn (Sikkel, 1998).

In indirect mate choice, 'choosy' individuals restrict the set of potential suitors available for mating by deliberately promoting competition in the opposite sex. This can be achieved, for example, by advertising fertility, by loitering in specific locations, or through evasive behaviour. Such tactics reduce the costs of choice to the female, since part of the work is done by the opposite sex. Fertility or fecundity is commonly advertised through visual cues. Examples of this include the head-up posture of the female three-spined stickleback, which exposes the belly to the male (Wootton, 1976), and the orange belly coloration of the two-spotted goby (Amundsen and Forsgren, 2001). Odour cues, however, can also play a critical role in signalling fertility, as demonstrated, for example, in sailfin mollies, *Poecilia latipinna* (Farr and Travis, 1986), and gouramies, *Trichogaster* spp. (McKinnon and Liley, 1987). Odour cues can also be valuable in signalling the release of eggs, which in rose bitterlings, *Rhodeus ocellatus*, induce males to release their sperm (Kawabata, 1993). Such cues can serve two important purposes: they can enhance competition among males for access to females, and also ensure that males court and spawn with females that are actually receptive and, in doing so, play an important role in male mate choice as well.

In species where a territory or a nest site is needed for reproduction and these sites are in short supply, male-male competition for attractive sites determines which males will be available for mating. On coral reefs in the Caribbean, bluehead wrasses, *Thalassoma bifasciatum*, typically spawn at specific locations so that their offspring can safely drift away from predators on the reef (Warner, 1988). Females generally remain faithful to particular spawning sites and male-male competition for these sites determines mating success (Warner, 1988). As a consequence, territory quality in this species is correlated both with the male body length and the relative length of his pectoral fin (Warner and Schultz, 1992). Females are, therefore, assured of mating with a high quality suitor simply by choosing a good mating site.

Cryptic Choice

In recent years, considerable interest has been gathering around the phenomenon of cryptic mate choice (i.e., choice that occurs after mating).

Such choices are exercised by females in an attempt to bias the fertilization of their eggs in favour of particular males and/or their sperm. Pilastro and co-workers (2004) were able to show, for instance, that guppy females are capable of adjusting the number of sperm transferred during solicited copulations, and that this choice depends to a great extent on the colour and attractiveness of the male (Fig. 9.2). The mechanism that allows females to make this kind of adjustment is unknown, but females may be able to either selectively eject the sperm of males that are perceived to

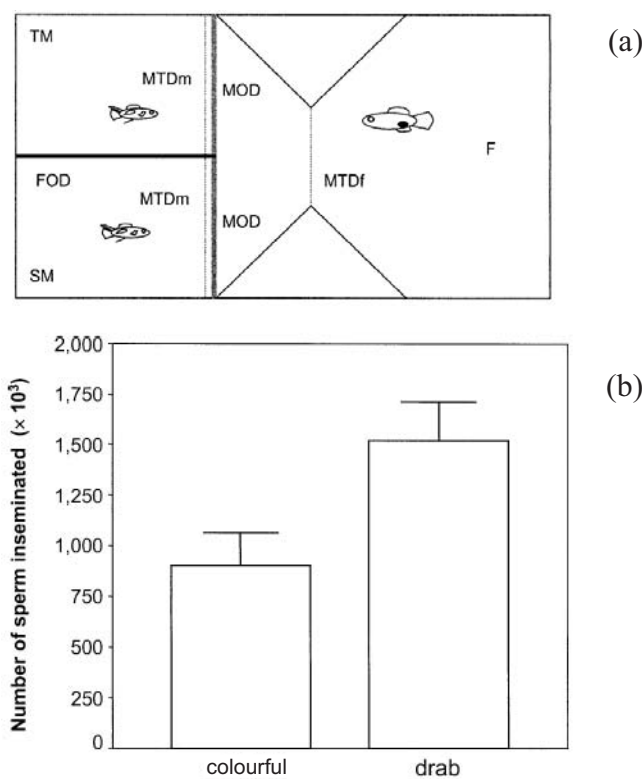


Fig. 9.2 Cryptic female preference for colourful males in guppies, *Poecilia reticulata*. (a) During initial mating, a sexually receptive virgin female (F) was allowed to observe a test male (TM) and a stimulus male (SM) that could not see each other. Test males had intermediate levels of body coloration with respect to two stimulus groups. After the assessment period, the test male was allowed to enter the female compartment, while the stimulus male's mobile opaque divider (MOD) was lowered, preventing visual access into his compartment. (b) During the consequent mating, the number of sperm inseminated depended on the colour of the stimulus male, with males inseminating more sperm when the other male was drab. Adapted from Pilastro *et al.* (2004).

be unattractive or, alternatively, manipulate the duration of copulation and, hence, the direct transfer of sperm by different males. Regardless of what mechanism might actually be involved, the results of the study carried out by Pilastro *et al.* (2004) demonstrate that the cryptic choice in this case reinforces pre-copulatory female preferences for colourful males.

Non-random gamete fusion is another potential mechanism of cryptic choice. In a recent study involving Arctic charr, *Salvelinus alpinus*, Skarstein and co-workers (2005) exposed the eggs of individual females to the sperm of different males. The researchers found that MHC-heterozygous males enjoyed higher fertilization success than MHC-homozygous males, suggesting that eggs may be selecting sperm based on MHC. Wedekind and co-workers (2004), however, found no evidence for MHC-linked gamete fusion in whitefish (*Coregonus* sp.). More research is clearly needed to ascertain the prevalence of this phenomenon in fishes.

Mate Choice Copying

Mate choice can also be influenced by the social environment and the decisions of conspecifics. Females, for example, may be more likely to mate with a male that they had previously seen consorting with another female. This phenomenon is known as mate choice copying. In these cases, females apparently gain useful information about potential suitors by keeping a close watch on the behaviour of other females and this, in turn, influences their own mating decisions. Mate choice copying may be advantageous if the females are inept at discriminating between males of different qualities (Nordell and Valone, 1998), or if copying reduces the costs associated with mate search and discrimination (Gibson and Höglund, 1992; Stohr, 1998).

Evidence for mate choice copying has been found in several fish species, such as guppies (Dugatkin, 1992; but see also Brooks, 1999), sailfin mollies (Schlupp *et al.*, 1994), Japanese medaka, *Oryzias latipes* (Grant and Green, 1996), Perugia's lima, *Limia oerugiae* (Applebaum and Cruz, 2000) and pipefish, *Syngnathus typhle* (Widemo, 2006). A multitude of factors can apparently influence the degree of copying, such as experience (Dugatkin and Godin, 1993), predation risk (Briggs *et al.*, 1996), hunger levels (Dugatkin and Godin, 1998), age (Uehara *et al.* 2005) and sex (Widemo 2006). Dugatkin and Godin (1993), for instance, found that small female guppies copy the choice of larger females, but not vice versa. Smaller individuals, in this case, are likely to be younger and less experienced

and, as such, appear to be guided by the preferences of older and more learned counterparts.

Mate choice copying can lead to the cultural transmission or 'cultural inheritance' of female mating preferences, if the females copy the preference of other females and then repeat this behaviour by generalizing their mating preferences for a particular male to other males that share his distinctive characteristics. Such a possibility has been experimentally demonstrated in guppies. Specifically, Godin *et al.* (2005) showed that individual females not only copy the observed mating preferences of other females, but that this preference is subsequently repeated and generalized to other males possessing a similar phenotype.

Sampling Methods

Individuals can carry out the task of mate sampling by making a direct comparison between two or more prospective suitors that are encountered simultaneously or, by remembering and comparing mates encountered in a sequential manner. Evidence suggests that preferences are generally stronger under simultaneous comparisons. When female sailfin mollies were presented with five 'dummy' males in sequence, they showed a much weaker preference for large males than when presented simultaneously with a series of dummy male pairs (MacLaren and Rowland, 2006).

In nature, the possibility of simultaneous comparison of potential mates is often limited, and fish must, instead, sequentially visit the potential mates. Several different search methods are possible under a sequential mate choice scenario. These can largely be divided into five main tactics: (1) random mating, where females have no mate preferences, (2) fixed threshold tactic, where females inspect males in a sequence and choose the first to meet some minimum specification, (3) sequential-comparison tactic, where females always compare the two most recently encountered males, according to some rule, (4) one-step-decision tactic, where females decide at each encounter whether to accept or reject a male, depending on the costs and benefits of continuing searching and (5) best-of-N tactic, where females assess a number of potential mates and then choose the best one among the lot (Janetos, 1980).

Mate search behaviour has been investigated in only a few species of fish. In the sand goby, female mate sampling behaviour was examined in the field by releasing and following gravid females (Forsgren, 1997b). The search strategy adopted by female gobies turned out to be the most

consistent with a threshold criterion tactic (Forsgren, 1997b), which is expected when search costs are important. In sticklebacks, evidence of a 'previous male effect' meant that a female's assessment of any given male was strongly influenced by the attractiveness of the male that was encountered previously (Bakker and Milinski, 1991). This suggests that females may be able to rely on an adjustable internal ranking of what is attractive to guide their reproductive decisions as they continuously gather information on variation in male quality (see also Pitcher *et al.*, 2003). According to Milinski (2001), this is likely to be adaptive because a female insensitive to the local distribution of male quality can end up choosing a poor quality suitor in a population teeming with males of higher quality.

There is also evidence to suggest that males, like females, may be capable of exercising sequential mate choice (Wong *et al.*, 2004; Werner and Lotem, 2006). Wong and co-workers (2004) investigated sequential male mate choice in the Pacific blue-eye fish, *Pseudomugil signifier*, by presenting males sequentially with large and small females. Male blue-eyes ended up investing more effort courting large females. However, this appeared to be due to an absolute preference for large females, since the time spent courting did not depend on the size of the female encountered previously. In other words, in contrast to the results obtained from studies of sequential female choice, there does not appear to be any evidence of a 'previous female effect' guiding the sequential mate choice decisions of males. One possibility for this apparent sex difference is that, for male blue-eyes, the cost of missing out on mating with any given female, irrespective of quality, outweighs the benefits that may come from fine-tuning any internal standard of attractiveness during sequential mate assessment.

The Use of Multiple Cues

Mate choice is often based on multiple cues. This may be advantageous if the use of supplementary cues provides additional, or more precise, information about the quality of prospective mates. Evidence also suggests, however, that extra cues may, in some instances, be unreliable indicators of mate quality but, nonetheless, facilitate detection or signal assessment, or are simply remnants from past selection (Candolin, 2003). The preference for multiple cues may even be maladaptive if the sender takes advantage of the existing preference to manipulate mating resistance (Candolin, 2003). Broadly, informative cues can be divided into several

different categories: (1) multiple messages, where different traits reflect different qualities, (2) back up cues, where different traits reflect the same quality, (3) species recognition cues that facilitate species recognition and (4) Fisherian cues that indicate heritable attractiveness.

The role of multiple cues in conveying multiple messages appears to be well supported by studies involving fish (Brooks and Caithness, 1995; Kraak *et al.*, 1999; Candolin and Reynolds, 2001; Fisher and Rosenthal 2007). This is seen, for example, in male roach, *Rutilus rutilus*, which develop breeding tubercles on the head and on the lateral sides of their body during the breeding season. The number and height of these tubercles—depending on where they appear on the body—seem to give quite detailed information to females about parasite loads, resistance, as well as overall male condition (Wedekind, 1992; Taskinen and Kortet, 2002; Kortet and Taskinen, 2004). Further support for the multiple messages hypothesis comes from the observation that mate choices frequently changes when a cue is added or removed. Female guppies, for instance, choose differently, depending on whether they receive only visual or olfactory cues, suggesting that the cues provide different information to females about male quality (Shohet and Watt, 2004).

In contrast to the multiple messages hypothesis, the back-up hypothesis for the evolution of preferences for multiple cues has received far less attention. One notable exception comes from a study involving pygmy swordtails, *Xiphophorus pygmaeus* (Hankison and Morris, 2003). In this species, female preference for large males results in heterospecific mating with large bodied, sympatric males of another species, *X. cortezi*. The addition of chemical cues did not appear to be enough to reverse this preference. However, when females had access to both chemical cues and visual access to the vertical bars displayed by conspecific males, they more readily preferred males of their own species (Fig. 9.3). Thus the existence of two species-specific cues increases the accuracy with which females are able to avoid heterospecific males. In this way, multiple cues operate through a process of reinforcement.

Odour cues often appear to play an important role in species recognition. In *Pseudotropheus emmiltos*, a species of Mbuna cichlid from Lake Malawi, females are unable to distinguish between the visual cues of conspecific males and those of a closely related species, *P. fainzilberi* (Plenderleith *et al.*, 2005). However, the addition of olfactory cues induces a female preference for conspecific males (Plenderleith *et al.*, 2005).

The use of different cues can depend on the social and physical environment. In guppies, females decrease the attention paid to

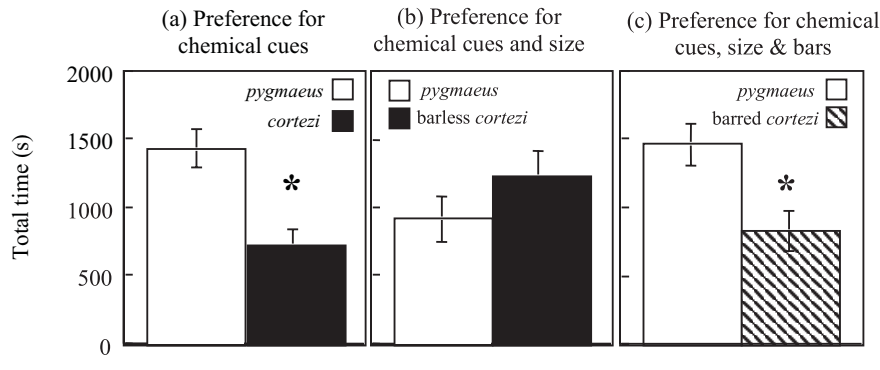


Fig. 9.3 The use of multiple cues in mate choice to prevent heterospecific matings. Female of *Xiphophorus pygmaeus* prefer larger males and two species specific cues are needed to avoid to mate with heterospecific *X. cortezi* males, which are larger. (a) Preference when only chemical cues are allowed, (b) when chemical cues and one visual cue (size) are present and (c) when chemical, and two visual cues (size and bars) are present. Data shown are mean time(s) spent with males \pm 1 SE. * $p < .05$. From Hankison and Morris (2003).

ornamental traits when agonistic interactions among males are rife. Instead, behavioural traits that indicate dominance become increasingly important (Kodric-Brown, 1993). Multiple cues may also be used in different environments (Reynolds, 1993; Endler, 1995) at different distances (Candolin and Reynolds, 2001) or at different stages of the courtship ritual (Luttbeg *et al.*, 2001). The use of multiple cues may then be a way of mitigating the costs and errors of mate choice by allowing choosy individuals to use different cues, depending on the context. The use of multiple cues may also enable the chooser to quickly eliminate the worst candidates from the pool of potential mates, by first using a cue that is easily assessed, and then concentrating on inspecting the best mates more closely by using another cue that is more difficult to assess.

The Honesty of Sexual Signals

Theoretical and empirical evidence suggest that some degree of dishonesty is permitted in an honest signalling system; signals need only be honest, on an average, to be evolutionarily stable (Johnstone and Grafen, 1993; Kokko, 1997). If the frequency of cheating becomes pervasive, however, the signalling system becomes unstable. If this occurs, cues that were once important in mate choice will become ineffective and, in time, may be replaced by other cues that more reliably communicate the quality of the bearer.

It is traditionally assumed that honest signalling is guaranteed by the differential fitness cost of developing or expressing the sexual trait, which prevents low quality males from signalling at the same level as high quality males (Zahavi, 1975; Grafen, 1990). In this regard, a number of studies have identified a range of cues that accurately reflect some aspect of mate quality, such as parenting ability (Knapp and Kovach, 1991) or condition (Milinski and Bakker, 1990; Knapp, 1995; Östlund-Nilsson, 2001). Moreover, studies show that signalling can, indeed, incur fitness costs: the expression of sexual traits can heighten the risk of predation, as in Amarillo fish, *Girardinichthys multiradiatus* (Marcías Garcías *et al.*, 1998), and increase energy expenditure, as demonstrated, for instance, in *Tilapia zilli* (Neat *et al.*, 1998) and Montezuma swordtails, *Xiphophorus montezumae* (Basolo and Alcaraz, 2003).

Dishonest signalling may occur, however, if signallers differ in the costs or benefits of signalling, or in their relatedness to the receiver (Johnstone and Grafen, 1993), or if the expression of the trait is subject to a life history trade-off between present and future signalling effort (Kokko, 1997). An example of dishonest signalling due to life-history trade-offs is seen in three-spined sticklebacks. Male sticklebacks increase the expression of red nuptial coloration when the condition deteriorates and future reproductive opportunities decrease (Candolin, 1999). Most likely, the lower cost of signalling, in terms of loss of future reproductive opportunities, allows an increase in signalling as a terminal effort. Such males make poor choices for females because they are less successful at bringing her brood to the hatching stage (Candolin, 2000a, b). Similarly, male sand gobies displaying more intensity were afterwards found to be in a worse condition than those having displayed less vigorously (Svensson *et al.*, 2004). However, whether this was due to increased energy expenditure or to poor survival prospects increasing signalling effort is unknown.

There are a number of ways by which females can overcome dishonesty. To avoid cheaters females may, for example, base their mate choice on multiple cues. Other factors, like the social environment, may also prevent cheating. For example, in the three-spined stickleback, male competition ensures that poor condition males cannot afford to signal at the same level as males in good condition. This, in turn, reduces the level of dishonest signalling (Candolin, 2000a, b).

The honesty of traits may also change over evolutionary time. For example, traits that attract females because they exploit receiver biases, may initially incur fitness costs to the female. However, with time, they

may evolve to become honest indicators of mate quality if the sexual and non-sexual response to the trait becomes separated. An example of this is the terminal yellow bands found on the caudal fins of several Goodeinae species, which evoke both feeding and sexual responses. Macías Garcia and Ramirez (2005) recently showed that sexual responsiveness predates the expression of the trait, but that feeding responsiveness decreases with more ostentatious trait elaboration. Since displaying the yellow bands is costly, the traits have evolved into an honest signal even though they initially arose as a sensory trap.

RESTRICTIONS ON CHOICE

Mate choice is seldom, if ever, free from constraints. Having discussed the benefits of being choosy, we now turn to some of the factors that may restrict individuals in their quest to select a mate.

Male Competition and Sneaking

Earlier, in this chapter, we canvassed circumstances where choosy individuals are able to benefit from the competitive antics of prospective suitors. We discussed, for example, the value of competition in ensuring that signals of quality are conveyed honestly. We also examined situations of indirect choice, where females advertise their fertility, or deliberately incite competition, so as to try to secure a mating outcome that is biased towards the preferred males. Competition, under these circumstances, often favours the dominant males because it gives them a significant mating advantage by excluding rivals and increasing their access to females. Thus, if the females prefer dominant males, competition may help the mate choice process by reinforcing female preferences as seen, for example, in Japanese medaka (Howard *et al.*, 1998). Evidence suggests that competitive interactions may also facilitate choice by excluding inferior males from establishing desirable territories, as in three-spined sticklebacks (Candolin and Voigt, 2001). Moreover, since competitive interactions are often conspicuous, choosy individuals may also be able to gain by 'eavesdropping' on aggressive encounters and, in so doing, obtain pivotal information about the quality of potential suitors. Female Siamese fighting fish, *Betta splendens*, for instance, eavesdrop on the competitive interactions of rival males and subsequently spend more time associating with the winner of the contest (Doutrelant and McGregor, 2000). Similarly, in sex-role-reversed pipefish, *Syngnathus typhle*, choosy males use the B-shaped markings displayed by competing females to choose

their mates instead of relying on potentially more attractive markings displayed in the absence of competition (Berglund and Rosenqvist, 2001).

Recent insights from the field of sexual conflict, however, suggest that intrasexual competition need not always facilitate intersexual mate choice (Arnqvist and Rowe, 2005; Wong and Candolin, 2005). In seeking to maximize their own reproductive fitness, males can engage in behaviours that increase their access to mating opportunities, and this can occur even if their actions end up having deleterious consequences for females and female mate choice (reviewed in Wong and Candolin, 2005). Under those circumstances, competition is more likely to be a hindrance than a help. This is especially true in species where fitness benefits sought by females are either unrelated to, or even negatively correlated with, male fighting ability. For example, in trout, *Salmo trutta*, females prefer males with a larger adipose fin, a trait that is unrelated to male dominance (Petersson *et al.*, 1999). Dominant male trout, however, override female preferences by excluding more attractive subordinates. Apart from usurping female mating preferences, dominant male trout are also undesirable because they tend to be more aggressive to females.

Apart from preventing females from gaining access to potentially more attractive suitors, male competition can also restrict mate choice by interfering with the ability of females to accurately assess prospective mates. As discussed earlier, courtship seems to play a particularly important role in communicating male parental qualities in fish. In at least two species—the sand goby and the Pacific blue-eye—courtship appears to be unrelated to male competitive ability (Forsgren, 1997a; Wong, 2004). Indeed, experimental studies in both species show that dominant males were no better at raising the females' clutch than subordinate individuals (Forsgren, 1997a; Wong, 2004). However, under competition, dominant males prevent subordinates from communicating accurately to females (Kangas and Lindström, 2001; Wong, 2004). In a study on sticklebacks, Östlund-Nilsson and Nilsson (2000) found that when females and males are allowed to freely interact with one another, mating were skewed in favour of dominant males. This was attributed directly to interference by dominant males which prevented females from interacting with subordinates: when males were tethered, dominant individuals no longer enjoyed a mating advantage. Interference may not always be as overt as those seen in sticklebacks. Male guppies, for example, do not display any obvious signs of aggression; nor do they appear to establish dominance hierarchies (Houde, 1997). Males do, however, jockey with one another in an attempt to court receptive females. Kodric-

Brown (1992) showed that this behaviour can restrict the mating opportunities of more attractive suitors by interfering with the ability of females to assess potential mates.

Alternative mating strategies can also have important consequences for female choice. We have earlier discussed the possibility of females benefiting from the presence of sneaker males by deliberately spawning in their company in order to increase the likelihood of high fertilization success. In some situations, however, alternative male strategies can actually circumvent female choice. In bluegill sunfish, *Lepomis macrochirus*, sneakers not only steal fertilizations but parental males that are cuckolded subsequently reduce their level of care (Neff, 2003). In so doing, the antics of sneaker males ameliorate the benefits that are otherwise gained by female sunfish from choosing males with good parental qualities. In pygmy swordtails, *X. pygmaeus*, males are polymorphic with respect to body coloration and the two male colour morphs appear to differ in their strategies for securing mating (Kingston *et al.*, 2003). Gold males are dominant over blue males during agonistic encounters and are also more aggressive in pursuing mating opportunities from females. Female pygmy swordtails, however, prefer blue over gold males. As such, the behavioural tactics of the gold colour morph can stifle mate choice by preventing females from gaining access to preferred suitors.

Predation Risk

Being choosy might result in extensive mate searching activity and this, in turn, could expose individuals to a heightened risk of encountering a predator. According to theoretical predictions, choosy individuals should respond adaptively to the cost of choosing (Sutherland, 1985; Hubbell and Johnson, 1987; Crowley *et al.*, 1991). In this regard, if choosiness is expensive in terms of predator-induced mortality, individuals are expected to become less choosy and mate indiscriminately with increasing predation risk. Several empirical studies on fish appear to be concordant with these predictions. For example, female tailspot wrasse, *Halichoeres melanurus*, living under higher predation pressure changed mates less often and conducted shorter spawning trips than did those from a lower predation site (Karino *et al.*, 2000). In sand gobies, females prefer large, colourful males in the absence of predators but are far less discerning in the presence of a piscivorous cod (Forsgren, 1992).

In some species, females do not appear to become any less choosy under predation risk but exhibit a switch in the males normally preferred. This

can occur if males with the most exaggerated ornaments are also more conspicuous to predators (Rosenthal *et al.*, 2001), and increases the females' risk of being eaten by associating with such males. In green swordtails, *Xiphophorus helleri*, for instance, females shown a video of a cichlid consuming a male with a conspicuous sword ornament subsequently reversed their preference for males with swords and, instead, chose males without swords (Johnson and Basolo, 2003). Similarly, female guppies under predation risk preferentially associate with less colourful males (Godin and Briggs, 1996; Gong and Gibson, 1996; Gong, 1997) probably because, in that species, females are actually more likely to be eaten than are the colourful males (Pocklington and Dill, 1995). This is likely due to the fact that in guppies, as in many poeciliids, females are actually larger than males, and may represent a more profitable prey item to would-be predators.

Predation risk can also have important consequences for male mate choice, with evidence suggesting that males are also capable of responding adaptively to predation pressure. In the Panamanian bishop, *Brachyrhaphis episcopi*, a small, promiscuous live-bearing fish, males from populations with predators were only choosy when light levels were dim (Simcox *et al.*, 2005). In contrast, males from populations without predators were choosy when light levels were brighter. Presumably, shifts in choosiness under different light conditions help reduce the risk of being detected by visually-oriented predators. In pipefishes, *S. typhle*, male preference for large females disappears under the threat of predation (Berglund, 1993). A reduction in the opportunity to choose has important implications in this species because large females are known to carry larger eggs (Berglund *et al.*, 1986a, b) which, in turn, results in heavier and higher quality offspring (Ahnesjö, 1992a, b). From a life-history perspective, a decrease in choosiness with increased predation risk may allow male pipefishes to trade current fecundity with an increase in the probability of future survival and reproduction.

Time and Energy Costs

Time and energy costs are also known to constrain mate choice and, like predation, are predicted by theoretical models to result in a decrease in choosiness (Real, 1990). In this regard, some of the most compelling empirical evidence comes from experimental work on sticklebacks. In nature, female sticklebacks move between territories, inspecting and assessing prospective suitors in a sequential manner. In a classic study,

Milinski and Bakker (1992) found that female sticklebacks were highly selective in their sequential choice between dull and bright males when costs were low. However, with increasing time and energy costs between encounters, females became less choosy and more readily accepted dull males as mates. A similar situation has also been reported for male mate choice in the Pacific blue-eye fish. Male blue-eyes more readily chose to court a less preferred suitor in still water than to continue courting a preferred mate whilst having to swim against a water current (Wong and Jennions, 2003) (Fig. 9.4).

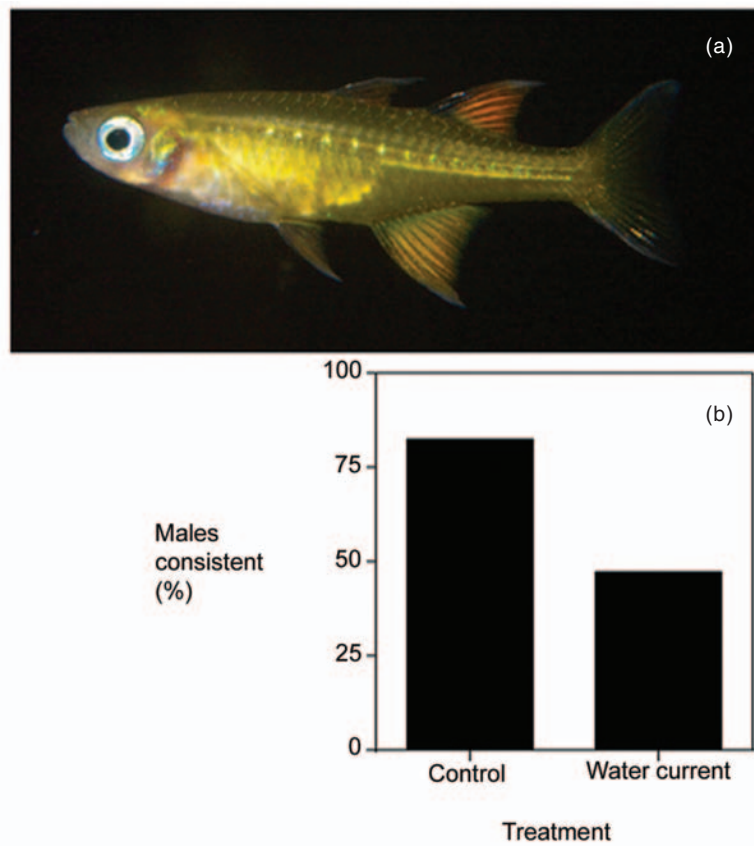


Fig. 9.4 (a) Male Pacific blue-eye, *Pseudomugil signifer*. (b) Males are highly consistent in their choice of females in the control treatment (i.e., still water) when the costs of associating with prospective suitors are equal. By contrast, males were far less consistent when forced to swim against a current to remain with their initially preferred mate. Graph based on data in Wong and Jennions (2003). Photograph: David Nelson.

Another compelling example of time and energy costs come from field studies of peacock wrasse, *Symphodus tinca*, a Mediterranean inhabitant of shallow rocky habitat (Warner *et al.*, 1995). Females of this species adopt one of two possible spawning strategies: they can either deposit their eggs in a nest under the care of a male or otherwise disperse their eggs so that they receive no protection. Survival and hatching success are higher for eggs that are placed in nests. This is especially true around the middle of the mating season when egg predation is high and the hatching time of the embryos are long. Yet, despite this, between 30-80% of females actually place their eggs outside nests. Why? In a model incorporating search time for nests, Warner *et al.* (1995) correctly predicted tendency for females to choose care versus no care over the course of the breeding season. During the middle of the breeding season, for example, females are likely to sample more nests because, at this time, the advantages of care are highest and the travel time between nests are low.

Depleted energy reserves associated with parasitic infestations can also constrain mate choice. Poulin (1994) investigated the mate choice decisions of female upland bullies, *Gobiomorphus breviceps*, infected with trematode cysts and found that heavily parasitized females made fewer mate inspections and were more likely to settle for lower quality males than were lightly parasitized females. Similarly, female guppies infected with the monogenean parasite, *Gyrodactylus turnbulli*, were less discriminatory than healthy females (Lopez, 1999). An energetic constraint imposed by the parasite was seen in a reduction in the level of activity displayed by female guppies with increasing parasite loads (Lopez, 1999). Interestingly, in pipefishes, *Syngnathus typhle*, males infested with the trematode parasite *Cryptocotyle* sp. become less choosy and failed to discriminate against infected females as potential mates (Mazzi, 2004). This can have important implications for male reproductive success because of an inverse relationship between female fecundity and parasite loads.

Opportunities for Mate Choice and Fish Density

Although several theoretical studies have underscored the importance of density on mate choice (Parker, 1983; Hammerstein and Parker, 1987; Real, 1990; Crowley *et al.*, 1991), actual empirical tests are surprisingly scant (Kokko and Rankin, 2006). In pipefishes, males are less choosy when mate density is low and, as a consequence, are more likely to mate with smaller females (Berglund, 1995). Aside from density-dependent

effects, however, the operational sex ratio also appears to be important in that species. Specifically, when the operational sex ratio was female biased, male pipefishes preferred larger females but when the operational sex ratio was male biased, males became less discerning and mated more randomly (Berglund, 1994). In sticklebacks, females more readily accepted a dull male when the time between the sequential presentation of males was lengthy (Milinski and Bakker, 1992). This length of time presumably simulated a low encounter rate which appears, in sticklebacks, to lower the net benefits of being picky through increased search costs (Milinski and Bakker, 1992). Similarly, female sailfin mollies are less choosy when presented with males in sequence compared to when they are presented with males simultaneously (MacLaren and Rowland, 2006). A shift in female choosiness in response to density is not, however, inevitable. In a study on the effects of density in guppies, Jirotkul (1999) showed that female preference for males with a higher percentage of orange colouration was similar regardless of density. More recently, Head and Brooks (2006) examined the effects of operational sex ratio on sexually coercive behaviour in guppies. They showed that the net rate of coercive behaviours were higher presenting the presence of more males. However, increased sexual coercion did not affect direct fitness components nor the proportion of courtships to which females responded positively (see also Jirotkul, 1999a, b).

Constraints Imposed by the Physical Environment

The signalling environment can have a profound impact on mate choice by affecting the efficacy of communication systems and this, in turn, can influence the ability of individuals to detect potential mates and/or discriminate between prospective suitors. Male sailfin mollies, for example, spend less time associating with females in turbid waters than they do in clear waters, presumably because females are harder to detect under turbid conditions (Heubel and Schlupp, 2006).

Attractiveness of different male phenotypes may also shift with changes in the signalling environment. Gamble *et al.* (2003) recently investigated the effects of spatial and temporal variation in lighting conditions on mating behaviour in guppies. They found that female preferences were influenced by the ambient light spectrum. Females tested under lighting conditions that mimicked midday woodland shade preferred the same males as those preferred under conditions that simulated early morning/late afternoon light. However, the attractiveness of males under those

conditions was unrelated to attractiveness of males under lights that mimicked midday forest shade. Variation in female preferences reflected differences in visual acuity under different light spectra and could be important in explaining the maintenance of colour polymorphism in this species.

MATE CHOICE IN A CHANGING WORLD

The world is in a constant state of flux. How, then, do changes to the aquatic environment influence mate choice? In this section, we begin by examining how mate choice can be adjusted to natural environmental variation. We then proceed to discuss the more recent impact wrought by anthropogenic disturbance to aquatic systems. As a result of human-induced processes, aquatic habitats are being altered at an unprecedented rate and scale. Such changes, based on a small but growing number of studies, appear to be having a drastic impact on mate choice in fishes, resulting in a reduction in population viability, a break-down in species isolation mechanisms and, ultimately, a loss of biodiversity.

Adjustment to Natural Environmental Variation

As discussed earlier in this chapter, several studies show that fishes are able to adjust their mate choice behaviours and sexual signalling in response to variation in environmental conditions. Some of the most compelling evidence, in this regard, comes from studies where individuals have been transferred from one environment to another, and from comparison of closely related populations living in different environments. Endler (1978), for instance, found that male guppies from streams with high levels of predation have fewer and smaller colour spots than do males from streams with lower predation risk. He suggested that this was due to a balance between female preference for brightly coloured males and selection by predators for more modestly coloured males. A comprehensive study on guppies from 11 different localities in nine rivers in Trinidad provide further evidence in support of the notion that female preferences for male traits are often finely attuned to local environmental conditions (Endler and Houde, 1995). Mate-preference criteria varied among localities in intensity, sign and the number of traits used, with large variation found in preferences for colour pattern parameters depending on water colour and predation intensity. On average, females were more attracted to males from their own population than from alien populations (Endler and Houde, 1995).

Colonization of new environments can also affect cues used in mate choice. Atlantic mollies are widespread in freshwater streams across Central America. At least one population, however, has colonized a limestone cave where they live in complete darkness. Plath and co-workers (2005) compared this cave population with two other populations living in light, and found that the population living in darkness had maintained a preference for large males despite the lack of visual communication. Most likely, information about male body size had been taken over by other, non-visual cues, such as the lateral line.

A species that is well-known for having colonized and adapted to a range of different habitats is the three-spined stickleback. Boughman (2001) investigated male red colour expression and female preferences for red in sticklebacks in four lakes in coastal British Columbia, Canada, that differed in light conditions. She found female perceptual sensitivity to red light varied with the extent of the shift in the visibility of red in the light environment. Intriguingly, male nuptial colour also varied with the environment and appeared to be tuned to female perceptual sensitivity (Boughman, 2001). This suggests that both traits are adjusted to local environmental conditions.

Human-induced Environmental Changes

Within species, anthropogenic disturbance of the physical environment—by impinging upon the mate choice process—can have important consequences for the success of particular phenotypes and the viability of the population as a whole. Eutrophication, in this regard, interferes with mate choice by promoting the rampant growth of filamentous algae and phytoplankton, which diminishes visibility in the water column. Järvenpää and Lindström (2004) experimentally increased algal turbidity in aquaria to investigate the effects of diminished visibility on the opportunity for sexual selection in sand gobies. They found that increased turbidity equalized the distribution of eggs among males and reduced the skew in mating success towards large males, which suggests that the intensity of sexual selection on male size was reduced. Most likely, increased algal turbidity influences the opportunity for selection through negative effects on the ability of individuals to properly evaluate mates using visual cues. For example, in order to capture the attention of females, three-spined stickleback males are forced to increase their courtship activity in turbid water (Engström-Öst and Candolin, in press). Reduced visibility due to phytoplankton blooms has also been shown to undermine

the honesty of sexual signalling in three-spined sticklebacks. Specifically, Wong and co-workers (in press) recently found that algal turbidity compromised socially enforced signals of male quality and, in so doing, allowed males in poor physical condition to signal dishonestly.

Similarly, increased growth of filamentous algae due to eutrophication can affect mate choice and the strength of sexual selection by impinging upon mate preferences based on visual cues. When stickleback males were allowed to court females in open habitats and in habitats overrun with dense algal vegetation, the latter increased the time and energy that males had to spend on courtship and mate choice (Candolin *et al.*, 2007). This increase, however, was not followed by a concomitant increase in mate attraction. Instead the strength of selection on male red nuptial coloration and courtship activity was relaxed when visibility deteriorated (Candolin *et al.*, 2007). Further evidence for a negative effect of heightened growth of filamentous algae on the opportunity for sexual selection comes from the field, where the distribution of eggs among nests of sticklebacks is more uniform in more densely vegetated areas (Candolin, 2004). This suggests that the opportunity for mate choice and sexual selection decreases when the growth of filamentous algae becomes too dense, probably due to reduced visibility making it more difficult for females to detect and compare males.

When the ability to properly assess mates is compromised, the consequences for biodiversity can be quite severe. In the cichlid fishes of the Great Lakes of Africa, mate choice is largely based on interspecific differences in male colour patterns. Strong assortative mating is common and appears to have led to sexual isolation of colour morphs and given rise to the diversification of cichlids found in the rift valley lakes (Seehausen *et al.*, 1997). In support of the importance of visual cues in speciation, the lakes where haplochromine cichlids have formed endemic species flocks have distinctively clearer water than lakes in which they have not (Seehausen *et al.*, 1997). Due to human activities, the Great lakes of Africa and Lake Victoria in particular, have been plagued by increased eutrophication in the last few decades resulting in heightened water turbidity. This, in turn, appears to interfere with colour communication by causing a decrease in light penetration and a narrowing of the light spectrum due to strong loss of shortwave light. In a now classic study documenting an insidious case of environmental deterioration, Seehausen and co-workers (1997) were able to show that increased turbidity constrains colour vision and interferes with mate choice based on visual cues. This results in a break down of reproductive

barriers which, in turn, is likely to have led to the erosion of species diversity documented in these lakes.

More recent work suggests that it is not only visual systems that are susceptible. Influx of untreated sewage and agricultural waste is disturbing many water bodies by changing the chemical environment. Such changes have been implicated as a possible cause of hybridization between two swordtail species in a Mexican stream that has seen the replacement of both parental species by a hybrid 'swarm' (Fisher *et al.*, 2006; Fig. 9.5). Fisher and co-workers (2006) found that swordtail females, *Xiphophorus birchmanni*, prefer the odour cues of conspecific males over the congener, *X. malinche*, in clear water, but fail to show a preference when tested in waters subject to sewage effluent and agricultural runoff. Moreover, they found that exposure to concentrations of humic acid, a natural product that is elevated to high levels by anthropogenic processes,

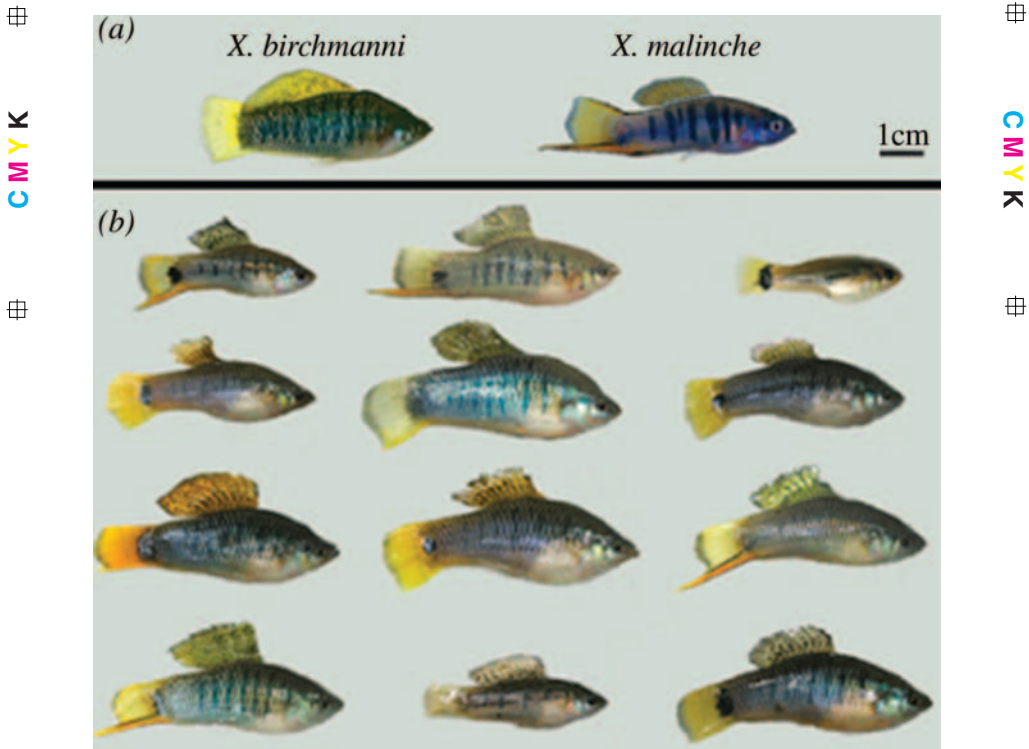


Fig. 9.5 Anthropogenic disturbance has been touted as a possible cause of hybridization in swordtail fishes. (a) The parental species, *X. birchmanni* and *X. malinche* and (b) hybrids collected from the Rio Calnali, Mexico. After H.S. Fisher *et al.* (2006).

causes females to lose their preference for the odour cues of conspecific males (Fisher *et al.*, 2006). Thus, anthropogenic disturbances to the signalling environment hinder chemically mediated species recognition in swordtail fish.

Conclusions

Fish studies have provided compelling insights into the processes involved in sampling and selecting mates. In this chapter we have illustrated, through examples, a myriad of direct and indirect benefits that individuals can acquire from being choosy. So far, most of the work that has been carried out on this topic have tended to focus on material gains, with evidence suggesting that direct benefits can play a key role in guiding mate choice decisions. Although indirect fitness gains are also important they are less well studied. Future research might wish to redress this deficit and, more generally, place greater emphasis on how different benefits might be traded against each other as individuals try to achieve a mating outcome that results in net gains that maximizes total fitness (Kokko *et al.*, 2003). How an individual goes about the task of choosing a mate also offers tremendous research possibilities. For instance, despite evidence suggesting that certain species of fish are capable of exercising cryptic mate choice, very little is currently known about the mechanisms that are actually involved (Pilaastro *et al.*, 2004). Another topical area of research centers around the role of multiple cues: only a handful of fish studies have specifically sought to examine the utility and function of different traits, how they interact, and how they are used by choosy individuals to select a potential mate (reviewed in Candolin, 2003). Signal honesty also deserves closer attention. For signals to reliably indicate the desired fitness gains to choosy individuals, theory suggests that they must be costly to produce and/or maintain (Zahavi, 1975). However, as we have discussed earlier, recent theoretical and empirical evidence indicate that sexual signals are not always reliably conveyed (see also Wong and Candolin, 2005). What are the circumstances that lead to signal dishonesty? And what consequences might this have for adaptive mate choice? Finally, incisive researchers should not overlook the impact of environmental change on mate choice. This topic is likely to gain greater research focus as fish habitat continues to be altered at an ever-increasing pace and scale. How mate choice decisions are adjusted to this change (if at all), has implications for the evolutionary potential of sexual selection, the viability of populations, the integrity of species, and the maintenance of biodiversity.

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