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Mate choice in fish: a review

Hannah Gardner

Project Advisor: [Pete Cotton](#), School of Marine Science & Engineering, University of Plymouth, Drake Circus, Plymouth, PL4 8AA

Introduction

The gemmeous dragonet *Callionymus lyra* displays conspicuous sexual dimorphism with the male displaying an elongated dorsal fin and brighter colouration than the female; it was through observations of this amongst other species that Darwin (1871) first began to develop his theory of sexual selection. Sexual selection theories today which have stemmed from the original concepts put forward by Darwin tend to recognise two main areas of sexual selection. Intrasexual selection which is usually direct competition between members of one sex over a member of the opposite sex and intersexual selection which is choice based on one sexes individual preference for a particular trait of the opposite sex (Andersson, 1994). It is the second of the two that shall be reviewed in this paper. Intersexual selection, otherwise known as mate choice has been widely studied in many fish species and it is through a combination of some key concepts, theories and models that much of today's study around the area has been allowed to develop. As defined by Heisler et al (1987) mate choice is the process leading to the tendency of members of one sex to mate non-randomly with respect to one or more varying traits in members of the opposite sex. In a large proportion of species it is the female that is choosy as it is in her advantage to mate with a male of high fitness, with good genes or who can offer her plentiful resources, as she invests a high proportion of energy into reproduction.

One of the simplest concepts of mate choice and female preference that was originally put forward is that certain male traits have been selected for and so evolved simply to make it easier for females to find/recognise their own species, though this is unlikely to explain more conspicuous male secondary sex traits (Andersson, 1994). A model put forward by Parker (1982) called the Game theory model explains many aspects of animal behaviour but in relation to mate choice states that comparisons between mates are not always necessary and that a male may attract more mates based upon the fact he has a stronger signal or trait that is noticed more quickly or from further away. He believed that such direct attraction can lead to conspicuous male traits where there is no genetic variation in female preference. Two contrasting ideas for explaining mate choice are the Fisherian process theory and indicator mechanisms model.

The first as quoted by Fisher (1930) is that 'a sexual preference of a particular kind may confer a selective advantage and therefore become established in a species'. So the general idea of this theory being that a genetic variation that is favoured by natural selection and is also favoured by female choice, creates a higher frequency of the trait in question which then creates a 'runaway process' up until the point where the trait significantly begins to reduce survival. The indicator mechanism model as initially suggested by Wallace (1889) favours the idea that conspicuous, costly male traits are favoured by female choice as they indicate high heritable viability. This received little attention when first published but was redeveloped 50 years later to specify that it is in the female's advantage to pick the fittest male to father her offspring and pass on those fitness qualities. So a male who is fit enough to fully develop secondary sexual characteristics and show courtship behaviour is likely to be genetically fit (Williams, 1966).

The last two theories that will be considered in looking at influential, preliminary ideas about mate choice are direct phenotypic benefits and sensory bias. The first, based on genetic models is that non-heritable variation in parental ability may lead to the evolution of male traits that advertise high parental quality such as shown by courtship feeding in birds (Heywood, 1989 & Hoelzer, 1989). Sensory bias or sensory exploitation as referred to by Ryan (1990) is based upon the observation that responses of organisms for things already selected for in other contexts, e.g. high sensitivity to a certain colour in foraging, if appearing in mates (e.g. by mutation) may be selected for. This review aims to give a comprehensive account of evidence for how mate choice has shaped the variety within and between species of fish to see if current studies are supporting the key theories and models described above that much of the past literature has been based upon. It also aims once reviewed to suggest new research directions in the future.

Female preference of male colouration

There is a vast amount of literature supporting the idea of female mate choice in fish from a variety of different species, with one male being chosen over another due to more pronounced conspicuous traits. One such trait that has been shown to be particularly important in fish is colouration. This has been demonstrated with key species such as the three-spined stickleback (*Gasterosteus aculeatus*) in which it has been shown that females prefer males that develop a stronger red colouration on their undersides during the breeding season. This has been demonstrated using choice experiments in natural light and then again under green light (which causes the red colouration to be indistinguishable to females) in the latter condition she shows no preference (Milinski & Bakker, 1990). It is thought in this species at least, the preference for stronger red colouration is related to the fact it indicates good health and parasite resistance. This not only has implications in passing on good genes to her offspring but is also related to the fact that male sticklebacks play an important part in parental care and so it will benefit her offspring to have a healthy male to play this role (Heywood 1989). The findings were further supported in a more recent investigation of the three-spined stickleback by Luttbeg et al (2001) which in addition focuses on how exactly the mate is chosen by the female and the observation that females become less choosy when her time or energy is reduced. This is thought to be due to her being less thorough in assessing her options before choosing a mate and lowering her standards when she does. This was shown through manipulation of how long they were held away from the males (allowing less time to choose) and how long they were forced to swim against a current which used up their energy reserves. This study also highlights mate choice is not just a single

decision but more of a series of steps from courtship initiation to entering the nest of a male, the mate-choice behaviour being quantified as the probability of transitions between these steps. Therefore in the case of this species at least there appears to be support for the indicator mechanism model but that it is less applicable in certain situations.

Support comes from an investigation looking at two closely related species of cichlid in Lake Victoria in East Africa that differ in colouration, with one species being blue and the other red. A similar method was used as that of Milinski & Bakker (1990), viewing female choice under different lighting in which the males' difference in colouration was either visible or masked. This brought up findings that females discriminate which male is from their own species using colour and show a preference towards them. However under lighting where the colour of the two males appeared the same, females from both species preferred blue males. This was thought to be due to the fact they were larger and displayed more frequently to the females, (Seehausen & Van Alphen, 1998) thus in this case providing support for the game theory model. Probably one of the most well known cases of mate choice based on differing colouration of males is in guppies. Here it has been suggested that females will prefer a male who is conspicuous against his background and shows bright orange colouration. This is due to the fact it indicates high carotenoids, a major component in their diet therefore giving the female a direct indication of his food finding ability, a heritable trait that can be passed on to her own young (Endler, 1983).

Selection of multiple traits

An interesting observation that has been shown in recent studies is that it is not always just a single factor that determines which male will be chosen when a female fish has multiple options. This has been suggested from a study of the two line pupfish (*Cyprinodon bifasciatus*); a species that has a resource based breeding system where males defend a patch of territory, in which if they are successful females will lay their eggs within. It has been found that females will assess more than one independent trait of a male when deciding whether to choose him as a mate. Firstly his size, where in this case the larger males are preferred as it is seen as a good predictor of competitive ability. By this what is meant is that a larger male will be better equipped to defend a female from interference from other males during mating and to her eggs. The second trait that has been shown to affect female choice is the substrate type of the males chosen territory, usually being on either rock or sand. Rock is the preferred substrate, thought to be related to the fact the eggs adhere to it better and that it contains more crevices in which they can be laid (Ludlow et al, 2001). It was also suggested that it could be due to sensory bias on the females' behalf, known also as the 'sensory exploitation' hypothesis; it predicts the male evolved this trait to take advantage of the females pre-existing preference for it, so the preference evolved prior to the trait (Ryan & Keddy-Hector, 1992). It was shown in Ludlow's study that these two traits were of equal importance to the female.

Female mate choice and preference in fish is not always consistent throughout a population, such as in the clear cut case of the three-spined stickleback and this can lead to variation in male phenotypes. This has been demonstrated in the swordtail fish (*Xiphorus cortezi*), in which males show polymorphism in colouration pattern, having either vertical bars along their body or no barring. Females of the species also appear to differ in their preference for the trait. When this was investigated using

live test subjects there was significant variation in the female's preference for barring which led to differing mate choice. So this phenotypic variation in mating preference may be acting to maintain variation in male traits through frequency dependent sexual selection (Morris, Nicoletto & Hesselman, 2003).

Electric Organ Discharge and courtship songs as mate choice cues

Differences in external morphology, such as pigmentation and size, although the most frequently observed and studied mate choice preferences in fish, are not the only factors of the male that the female will have differing preferences towards. From the observation that many electric fish possess strong sexual dimorphism in their electric signals and electricity producing structures, it is thought sexual selection, mate choice in particular may be an underlying factor that caused this. This has come from early work showing electric fish such as Gymnotiformes and mormyrids can distinguish between male and female electric organ discharges (EODs) (Kramer 1999). A study on one such Gymnotiform, the pintail knifefish, *Brachyhypopomus pinnicaudatus*, suggests preference leading to mate choice shown through successful spawning to larger males with a greater EOD discharge, a trait also shown in the bulldog fish, *Marcusenius pongolensis*. It is the female knifefish' choice as courtship will not begin until she has approached the males but it is not totally clear which of these characters is the one being preferred. Despite this it is unlikely that male size was being assessed visually as the experimental set up compromised of the males being behind a dark divider and in the lack of any light source. Indication of size through electric sense or lateral line is also unlikely as this would require difficult, parallel swimming. Therefore EOD amplitude in this case, is thought to be the most likely cue used in mate choice as she is able to assess this without direct contact. This cannot be generalised to their natural environment however as here there are many more contributing factors that may affect behaviour and mate choice (Curtis & Stoddard, 2003).

The case of the South African bulldog fish, *M.pongolensis*, in which a correlation between female preference and male EOD duration has been shown, it demonstrates that this preference is not just limited to one species. Hanika and Kramer (2005) had previously thought the evolution of EOD in sexual selection had come about through intrasexual selection only, with EOD pulse duration signalling strength and fighting ability to contenders for territories or access to females. However there has now been significant evidence to suggest that mate choice also has an important role with females of the species when given a choice between short and long EOD pulse durations, showing significantly more courtship behaviour (head butts, association time and circling) towards the longer duration call backs. It has been proposed female sensory bias in *M.pongolensis* may be part of the reason for this. The female possess ampullary organs which are tuned to low frequencies, these help in detecting the presence of objects in their environment and helping them find live prey items etc. These ampullary organs respond to the low-frequency component of EODs given out by males and thus a longer EOD represents a stronger stimulus for the female (Machnik and Kramer, 2008) suggesting that the preference for stronger and longer duration EODs may be as a result of sensory bias as suggested by Ryan (1990).

Lamml & Kramer (2006) presented a case in which differential mate choice was observed in male courtship songs in two parapatric sibling species of dwarf stonebasher, *Pollimyrus castelnaui* found in the Okavango River and its inland delta and *Pollimyrus marianne* from the Upper Zambezi River. The investigation showed

several lines of evidence that the differing calls may be serving a purpose in mate recognition during the breeding season. Firstly the two species songs differed with *P.castelnaui* having a husky quality consisting of 3-4 broadband formats and longer moan and grunt durations. *P.marianne* on the other hand, had a single spectral line that was much more tonal. This high between but low within variability in mating call is thought to be contributing factor in individual recognition and intersexual selection. Secondly males are shown only to begin their courtship songs when they are ready to reproduce and not at other times of the year and it seem unlikely that they would carry out this costly (in terms of attracting predators) presentation if it were not worth it. This case demonstrates that courtship calls are not just restricted to birds, insects and amphibians and that fish can show a variety of differences that serve to function female preferences accordingly. A similar situation is found in EOD of another pair of closely related sympatric species, *Campylomormyrus compressirostris* and *Campylomormyrus rhynchophorus* with these species specific changes in EOD being linked to female preference acting as mechanism of divergence through assortive mating (Feulner et al, 2008).

Male mate choice

So far the literature reviewed has focused on mate choice that involves females choosing males, as predicted by the original theories and models however this is not always the case such as in sex role reversed species such as some of the Syngnathidae family where it is the males who are choosy and provide post-zygotic care of offspring by brooding embryos on their ventral surfaces (Jones & Avise, 2001). In some pipefish species such as *S.typhle*, although there is some degree of mate choice by the female, with her preferring larger males who can offer better parental care than a smaller male could to her offspring (Berglund et al, 1986a), the degree of male choosiness for larger size in females is greater. In another species of pipefish, *N.ophidion*, males once again showed preferences for larger females, but also independent of size, preferred females that displayed larger areas of blue colouration along their heads and those with larger skin folds along their body. All of these secondary sexual characteristics correlate with female fecundity so it benefits a male to mate with a female possessing these characters, as for him it means he will get more and larger eggs to brood (Berglund et al 1986a & Rosenqvist, 1990). Some of the more recent combined work by Berglund & Rosenqvist still supports these early findings but with some additional ones too. They looked once again at *Syngnathus typhle*, the females of which present a temporary, just one minute long, striped pattern to males and in female-female interactions. When males were given the choice between females displaying the ornament or not and in both field and lab experiments the females with stripes were preferred. It is thought the ornament indicates high female and egg quality (Berglund & Rosenqvist, 2001) the striped pattern has now also been shown to have a dual function of not only attracting males but also having an intimidating effect to deter rival females (Berglund & Rosenqvist, 2009).

Mate choice by the male is not just limited to sex role reversed species, however, this has been shown in studies on the sockeye salmon (*Oncorhynchus nerka*), a species that occurs in two genetically distinct and usually reproductively isolated life history morphs, the anadromous sockeye and the smaller nonanadromous kokanee. Foote et al (2004) studied the male behaviour towards females of differing colours, focusing in particular on the brightness and purity of reds displayed by females. They found that males when given the choice, preferentially spawned with females that exhibited a general red hue and maximum reflection in long (red) wavelengths. It

was also revealed that although males showed the strongest preference for the brightest, purest reds they also displayed a strong attraction towards a broader range of darker, less saturated reds. This suggests what is being viewed here is more than just species recognition. The most likely reason for the preference of males towards bright red females is that it shows good carotenoid acquisition (a heritable trait) and condition. The nonanadromous kokanee have inherited the preference for red, which is likely to be innate due to the semelparous lifestyle of the salmon, but often lack the ability to turn the same degree of red due to the carotenoid poor freshwaters they live in. The preference for red however may have increased the genetic ability to utilise carotenoids in some cases. Therefore it is thought that sexual selection (mate choice) and sensory drive are the driving evolutionary forces behind the phenotypic and genetic differentiation of populations (Craig & Foote, 2001).

Conclusions

This review brings together some of the main areas of mate choice in fish that have recently been researched. Showing that the initial ideas proposed by some of the key theories on mate choice still stand, with choosy females preferring males that show indicators of fitness such as within key species as the three-spined stickleback and the guppy therefore in accordance with the indicator mechanism theory. There is even support for Andersson's early ideas of mate choice functioning in mate recognition suggested through Seehausen & Van Alphen's (1998) work on cichlids and work done on the parapatric sibling species of dwarf stonebasher. However this review has highlighted that mate choice is not always as clear cut as the early theories predicted and that while in some cases aspects of one theory may be relevant in others they are not. Firstly that it is not always just one trait that a certain sex may prefer and in fact that it can be a whole range of preferences that ultimately lead to mate choice which can also differ between individuals of a species' population. The original theories presented all put forward that in most cases it is males who show intra-sexual selection and females that show intersexual selection. This review however has highlighted that much current literature is presenting cases where it is the females that compete over the males and the males who are choosy, or in some cases with both sexes showing a degree of both inter and intra sexual selection. What this highlights is that perhaps future research should not set out to look for evidence for one process or theory only but try to investigate the idea that there may be a combination of factors and processes shaping the evolutionary history of a species.

Finally the sensory bias theory is one that makes recurrent appearances in recent literature and it seems all the time that new mate choice cues that are less obvious perhaps to humans, such as EOD seem to be functioning as important cues to fish on top of the cues that are more obvious to ourselves, such as colouration, that researchers were focusing on originally. Subsequently an important direction for mate choice research in fish may be to still work within the sensory bias theory but try and see whether fish possess pre-existing preferences for aspects of their mates we may not have previously expected them to use as mate choice cues such as pheromones, alarm substance or other subtle differences in their physiology or biochemistry.

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