SEXUAL SELECTION AND SOCIAL HIERARCHY IN FISHES

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ABSTRACT

Sexual selection is a crucial element to understand behavioral evolution. Teleost fish have been considered as good models for research on sexual selection in the last decades due to their variety of sexual behavior. Female fish can choose males based on body and behavioral traits, such as body size, body color, ornaments, territorial quality, nest size and courtship behavior. Choices are based upon several types of sensorial inputs, such as visual, chemical, sonorous and electrical signals. Intrasexual selection also acts on females because they can mate with a dominant individual in male-male competitions. For both approaches, there is an expectation regarding the benefits of sexual selection by means of female choice. However, in several cases females do not choose the dominant male. In this mini-review, we present and discuss both intersexual and intrasexual mechanisms of sexual selection in fish and point out that females do not always choose a male for mating.
Key-words: Courtship, communication, morphological traits, Teleost, reproductive behavior.

RESUMO

SELEÇÃO SEXUAL E HIERARQUIA SOCIAL EM PEIXES. A seleção sexual é um assunto de amplo interesse para entendimento da evolução comportamental. Os Teleósteos têm sido considerados bons modelos para pesquisas em seleção sexual nas últimas décadas devido à sua variedade de comportamentos sexuais. As fêmeas podem escolher os machos com base em características corporais e comportamentais, como tamanho corporal, coloração, ornamentos, qualidade do território, tamanho do ninho e corte. Tal escolha ocorre por meio de várias informações sensoriais, como sinais visuais, químicos, sonoros e elétricos. A seleção intra-sexual também atua sobre as fêmeas porque elas podem selecionar um dominante para acasalar em situação de competição entre machos. Nas duas abordagens, há uma expectativa relacionada aos benefícios oriundos da seleção sexual por meio da escolha da fêmea. No entanto, em vários casos, a fêmea não escolhe o macho dominante. Nesta mini revisão, nós apresentamos e discutimos os mecanismos da seleção inter e intra-sexual em peixes e destacamos que as fêmeas nem sempre escolhem o macho com quem acasalar.
Palavras-chave: Corte, características morfológicas, teleósteos, comportamento reprodutivo.

RESUMEN

SELECCIÓN SEXUAL Y JERARQUIA SOCIAL EN PECES. La selección sexual es un asunto de amplio interés para el entendimiento de la evolución del comportamiento. En las últimas décadas los peces Teleósteos han sido considerados buenos modelos para investigaciones sobre selección sexual debida su amplia variedad de comportamientos sexuales. Las hembras pueden escoger a los machos basándose en características corporales y comportamientos, tales como tamaño corporal, coloración, ornamentos, calidad del territorio, tamaño del nido y cortejo. Tal escogencia ocurre a través de diversas informaciones sensoriales, como señales visuales, químicas, sonoras y eléctricas. La selección intra-sexual también actúa sobre las hembras porque ellas pueden seleccionar un macho dominante para aparearse en una situación de competencia entre machos. En ambos casos, hay una expectativa relacionada a los beneficios naturales de la selección sexual por medio de la escogencia de la hembra. Sin embargo, en algunos casos, la hembra no escoge el macho dominante. En esta mini-revisión, presentamos y discutimos los mecanismos de la selección inter e intra-sexual en peces y destacamos que las hembras no siempre escogen el macho con el que se van a aparear.
Palabras clave: Cortejo, características morfológicas, teleósteos, comportamiento reproductivo.

INTRODUCTION

Why do some males or females mate while other mature individuals do not? Why do some individuals obtain a higher reproductive success? Such differences in reproductive ability result from two important mechanisms: male-male competition and female choice (Andersson 1994). Both mechanisms are part of Darwin's theory of sexual selection named, respectively, intrasexual and intersexual selection (Andersson & Iwasa 1996). According to this theory, reproductive decisions may maximize individual fitness. Although males and females contribute equally to the brood's genetic pool, the energetic investment of the female is higher than that of the male (Andersson & Simmons 2006). This explains why mate choice is less pronounced in males than females. In fact, such an explanation was given by Trivers' Parental Investment Theory, which predicts that the sex that invests more heavily in the offspring, at the expense of potential future offspring, should face the least competition (Ahnesjö *et al.* 2008).

Fitness can be enhanced by direct benefits (*e.g.*, by enhancing brood size); or indirect fitness (*e.g.*, by enhancing the lifespan and, indirectly, the reproductive success) (Barbosa & Magurran 2006). Because females spend more energy during reproduction, they should select good mates, or good males in terms of genetic quality for brood survival, in order to enhance fitness (Andersson 1994). By choosing mates, female can acquire direct benefits, such as brood protection, higher fertilization rate and resources; or indirect benefits, such as higher survival rate for broods and parasite resistance (Berglund *et al.* 1996, Barbosa & Magurran 2006, Lailvaux & Irschick 2006, Candolin & Wong 2008).

One important environmental trait related to variations in choice is the operational sex ratio (OSR) (Emlen & Oring 1977). The OSR is the ratio of the number of males to females, in a given population, that are ready to mate at a given time and place (Emlen & Origin 1977, Kvarnemo & Ahnesjö 1996). Thus, when OSR is biased, sexual selection will act more strongly on the more abundant sex (Emlen & Oring 1977). Thus, literature provides us with several hypotheses to explain variability in sexual strategies for mate selection (*e.g.*, Clutton-Brock 2007, Ahnesjö *et al.* 2008). In fishes, mate choice can be modified by operational sex ratio, nest quality and other environmental conditions that cause a sex reversal role (*e.g.*, Andersson & Iwasa 1996, Gonçalves *et al.* 2002a, Forsgren *et al*. 2004, Barlow & Lee 2005). In the cichlid *Astatotilapia flaviijosephi*, males choose larger females because body size is positively associated with number of eggs (Werner & Lotem 2003). Thus, males also acquire reproductive benefits by choosing larger and heavier females (Kraak & Bakker 1998, Dosen & Montgomerie 2004, Herdman *et al.* 2004). Moreover, there are some species with sex role reversal, such as the pipefish, *Syngnathus typhle* (Berglund & Rosenqvist 2003) and bleniid fish, *Salaria pavo* (Gonçalves *et al.* 2002a, 2002b), in which females court males. In some circumstances, the number of males ready to reproduce can be reduced in the population, consequently shifting the OSR towards females which, in turn, increases female-female competition, courtship and aggression (Shibata & Kohda 2006).

When OSR is biased toward males, enhanced competition for females will result (Andersson & Iwasa 1996). Considering intersexual selection, females can choose males based on body and behavioural traits, or they can mate with a winner in male-male competitions. In social fishes, such as cichlids, theory predicts that females should prefer larger and also more aggressive males that could better hold territories and defend offspring against predators (Barlow 1998). In this mini-review, we discuss the main mechanisms of sexual selection of fishes and also discuss why females do not always choose males. This suggests female choice is sometimes obscured by male social position.

THE WAY TO CHOOSE – COMMUNICATION

Selection of a mate depends on signals displayed by males and females. Such signals are displayed by different sensory channels, depending on the environment and the sensorial input-output adaptations. The studies related to sex communication are essentially those linked to visual signs, probably because these are the first ones to attract our attention. In fact, vision is only one input channel for fish communication and not the most important one (Giaquinto & Volpato 1997, Rosenthal & Lobel 2006). Moreover, the opposite sex usually evaluates

more than one sensorial cue coordinated in a set of sensorial information. Visual communication can be useful to evaluate body colour, body size, nest, territory quality, and courtship movements. In the three-spined stickleback, for example, the more red and bright the male's belly, the stronger stimulus to attract females (Bakker & Milinski 1993). Moreover, Poecilidae females prefer the intensity of orange in the male body. Iridescent spots in the male's body are attractive to females and enhance the male mating success (Kodric-Brown 1993).

Courtship is one of the most potent visual signals to the opposite sex. In the sex role reversed fish *S. pavo*, female courtship behaviour is elicited exclusively by male visual features (Gonçalves *et al.* 2002b). In Nile tilapia, *Oreochromis niloticus*, spawning occurs even when males are separated from the female by a transparent glass, without chemical or physical contact (Castro *et al.* 2009 *in press*). In this study, male visual contact with the female enhanced the courtship rate and also the gonadossomatic index, thus reinforcing the importance of visual stimulus to courtship and also to control reproduction in fish (Castro *et al.* 2009 *in press)*.

Chemicals are involved in fish behaviour in several ways (*e.g.*, Giaquinto & Volpato 1997, 2005, Gonçalves-de-Freitas *et al*. 2008), and reproduction is obviously one of them (*e.g*. Volpato *et al.* 2006, Barata *et al.* 2008, Serrano *et al*. 2008). In fact, Almeida *et al.* (2005) showed that male *Oreochromis mossambicus* urinates in the presence of females. Since urine is a way of communication in reproductive behaviour, it is assumed to be used during mate choice. Fisher & Rosenthal (2006) found that female swordtail fish, *Xiphophorus birchmanni*, prefer the chemical cues from well-fed males than from food-deprived males. Moreover, the authors found no consistent female discrimination regarding the nutritional state of other females, showing that the preference is sex-specific. In addition, McLennan & Ryan (2008) found that the olfactory cues in other *Xiphophorus* spp. transmit complex information about species identification and sexual status (sneaker males and courting males).

Sound production is another way of signalling reproductive traits in fishes. Although studies on fish sound production are incipient, a few studies are devoted to reproductive traits and sexual selection. Recent studies on the African cichlids *Pseudotropheus* spp. show that male sound is emitted during the courtship displays, and the sound rate increases significantly with courtship (Amorim *et al.* 2004, 2008). Additionally, Phillips & Johnston (2008) also demonstrated the role of sound production in agonistic and courtship interactions in the fish *Cyprinella galactura*.

Electric cues are restricted to electric fishes and also have a role in sexual communication. The function of electric pulses in courtship behaviour has been studied in gymnotid *Sternopygus macrurus* (Hopkins 1974) and *Apteronotus leptorhynchus* (Triefenbach & Zakon 2003). African mormyrid species also show specific self-generated electric pulses and electroreceptive abilities for orientation, communication, territorial interactions and for courtship (Terleph & Moller 2003, Wong & Hopkins 2007, Baier & Kramer 2007). In the mormyrid *Marcosenius pongolensis*, the male's reproductive success is enhanced by longer and more attractive electric organ discharges (Machnik & Kramer 2008).

WHAT DO FEMALES CHOOSE

Females can choose male phenotypic traits, including courtship displays, nuptial coloration, ornaments, pheromones, body size, and territory quality (Andersson 1994, Barbosa & Magurran 2006, Fagundes *et al*. 2007, Ahnesjö *et al*. 2008, Labonne *et al*. 2009). All these traits are sources of information about male quality that attract females and that can enhance female reproductive success. Table I summarizes some of these traits in several species of fish. Indirect benefits are provided by choosing "good genes" (Andersson 1994) and "sexy sons" (Weatherhead & Robertson 1979). In both mechanisms, the male traits are inherited by broods, and enhance either the chance of survival (good genes theory) or the chance to reproduce (sexy sons theory) (Barbosa & Magurran 2006). In the three-spined stickleback (*Gasterosteus aculeatus*), for example, mate choice is positively correlated to female reproductive success (Kraak *et al.* 1999), thus supporting the predictions of sexual selection.

Female choice implies several types of benefits. In species with parental care, females may enhance reproductive success by choosing good fathers that can help to improve egg hatching and brood survival

(Forsgren 1997, Östlund & Ahnesjö 1998, Takahashi & Kohda 2004, Wong 2004). Female brown trout (*Salmo trutta*) choose less aggressive males, thus avoiding losses due to male attacks (Petersson *et al.* 1999). In *G. aculeatus*, the most colourful males have broods more resistant to parasites (Barber *et al.* 2001), which is in accordance to Hamilton's & Zuck's hypothesis (Krebs & Davies 1993). Moreover, male *G. aculeatus* build nests with algae and females prefer sticks and spangles nests (Östlund-Nilsson & Holmlund 2003). By ornamenting their nests, males show their paternal qualities (Östlund-Nilsson & Holmlund 2003). In fact, as illustrated by this species, female can choose several male signals that, together, give more complete information about male quality (Kunzler & Bakker 2001, Hankison & Morris 2003). Female choice, however, can be affected by environmental conditions. Increased predation risk, for instance, can change male body colour preference in guppies (Godin & Briggs 1996, Locatello *et al.* 2006). Female choice is also affected by food availability, competition, habitat quality and other factors that affect fertility, growing and survival of a population (Charnov 2001).

MALE DOMINANCE AND FEMALE CHOICE

Although female choice can be based on several male traits, another mechanism involved in sexual selection is mating through resource competition. Thus, intrasexual selection, usually more strong among males, will select for fighting ability (Halliday 1994). Because male-male competition is an honest signal, females can easily detect male abilities (Sargent *et al.* 1998, Candolin 2000), and choose dominant males.

The most common type of competition among fish involves aggressive interactions, and a hierarchical rank can arise. Dominance hierarchy is part of social behaviour where the winner in a contest is the dominant, and the loser, the subordinate (Ridley 1995). Dominants have priority access to resources such as food, shelter, nest sites and mates (Huntingford & Turner 1987, Ridley 1995). Moreover, dominants usually grow faster than subordinates, as seen for example in the Nile tilapia, *O. niloticus* (Volpato & Fernandes 1994) and *Haplochromis burtoni* (Hofmann *et al.* 1999). As a result, dominant males are preferred by females because of the resources needed or because of their good genes (Qvarnström & Forsgren 1998).

Table I. Examples of male's traits chosen by females in several fish species.

Species	Traits of preferred males	References
Poecilia mexicana	Larger dorsal fins.	Jordan *et al.* (2006)
Xiphophorus birchmanni	Well-fed mates (chemical cues).	Fisher & Rosenthal (2006)
Rhinogobius brunneus	Males that courted in the faster water streams.	Takahashi & Kohda (2004)
Pseudotropheus zebra	Longer pelvic fins and larger number of eggspots in anal fins.	Couldridge & Alexander (2001)
Astatotilapia burtoni	Territorial males over non-territorial males; more active territorial males.	Clement *et al.* (2004)
Pomatoschistus minutus	Courtship intensity .	Forsgren (1997)
Poecilia reticulata	High display rates, more complex ornamentation, more orange ornamentation and prolonged swimming performance.	Nicoletto (1993)
Spinachia spinachia	More frequent body shakes during courtship.	Östlund & Ahnesjö (1998)
Pterapogon Kauderni	Larger male.	Kolm (2001)
Xiphophorus helleri	Partial swords containing complete black stripes coloration, Longer swords.	Trainor & Basolo (2006)
Salmo trutta	Larger adipose fin.	Petersson *et al.* (1999)
Oreochromis mossambicus	Larger body size and larger spawning pit.	Nelson (1995)
Rhodeus sericeus	Larger body size and more vigorously courting.	Reichard *et al.* (2005)
Pseudomugil signifer	Greater proportion of time engaged in courtship.	Wong (2004)
Gasterosteus aculeatus	Males with decorated nest (colorful sticks and spangles).	Östlund-Nilsson & Holmlund (2003)

In fact, many studies show female choice is based on social rank (Bisazza & Marin 1991, Kodric-Brown 1992, Candolin 1999, Berglund & Rosenqvist 2001) or in traits associated to dominance, such as nest size (McKaye *et al.* 1990, Stauffer *et al*. 2005, Mendonça & Gonçalves-de-Freitas 2008), body size (Santangelo 2005, Gonçalves *et al.* 2002a, Labonne *et al*. 2009), territory quality (Halliday 1994, Dijkstra *et al.* 2008), body colour (Kraak & Bakker 1998, Cubillos & Guderley 2000, Morris *et al.* 2007), courtship frequency (Forsgren 1997, Cubillos & Guderley 2000) and aggressive level (Gozlan *et al.* 2003). Several studies have demonstrated the advantages of being dominant in terms of reproductive success. However, this might be the male's view, as we discuss further.

DO FEMALES FISH REALLY PREFER DOMINANT MALES?

Social dominance requires large investment from males, which in turn could be compensated by enhancing their reproductive success. However, recent studies show that in some fish species females rarely choose the dominant male for mating (Qvarnström & Forsgren 1998, Östlund-Nilsson & Nilsson 2000, Candolin & Wong 2008). In *Pseudomugil signifer*, for example, females prefer males that exhibit more courtship movements and also provide more care to the brood, instead of dominant males (Wong 2004). In the poecilid, *Limia perugia*, fingerprint analysis showed that dominant males had a mating success of 100% in small mating groups, but it dropped to 0% in larger groups (Schartl *et al.* 1993). Thus, it seems that female choice depends on a set of requirements instead of social status alone. On the other hand, male-male competition can reduce the chances for female choice. According to Reichard *et al.* (2005), females of *Rhodeus sericeus,* physically separated from males, choose those males that exhibit more courtship. However, when interacting with them, spawning does not occur with the chosen male (when the chosen one is subordinate) because dominant males do not allow subordinates to approach females (Reichard *et al.* 2005). In another study with *G. aculeatus*, females were allowed to interact and mate with each male, while physical interactions between the males were prevented by leashing them to opposite corners of the aquarium. In such a situation, females did not prefer dominant males; but when the males could freely interact with each other, females chose the dominants (Östlund-Nilsson & Nilsson 2000). In this case the dominant male prevented the female from interacting with the subordinate male (Östlund-Nilsson & Nilsson 2000), a result that reinforces the view that dominants are not always the female's choice, but can be a forceful result of male-male competition. According to Kangas & Lindstrom (2001), female *Pomastoschistus minutus* do not choose dominant males, and neither male aggressive interaction limit a female's possibilities to spawn with a non-dominant male. In the Nile tilapia, nest building is an element for mate choice (Mendonça & Gonçalves-de-Freitas 2008). However, nests are built by dominant males, and provide reproductive advantages (Gonçalves-de-Freitas & Nishida 1998). Although the Nile tilapia is able to reproduce in the absence of a nest, the dominant still reproduces first (Mendonça & Gonçalves-de-Freitas 2008). However, females that view males (separated by glass with no other cue involved), do not choose the dominant males (Castro 2008). In this species, the presence of sneaking behaviour (Gonçalves-de-Freitas & Nishida, 1998) could indicate that females do not prefer dominants, as suggested by Candolin & Wong (2008).

In some poecilids, male-male competition is the extreme threshold for accessing females. Subordinate males *Poecilia reticulata* have their sexual behavior suppressed (Bruce & White 1995). In *Xiphophorus* species, maturation is socially inhibited (Borowsky 1987): dominant's agonistic interactions inhibit subordinate's gonads, thus circumventing female choice. Hence, Birkhead & Møller (1993) suggested that females can be, in some cases, passive subjects relative to decisions about mating. In fact, dominant males that monopolize resources needed by females also monopolize the females themselves, and prevent other males from approaching females. Thus, we conclude that female preference is not always selected in association with a male social trait (social rank) in fish, as predicted by Fisher's Hypothesis (Krebs & Davies 1993). It is possible that dominance is a way to guarantee "good genes" for brood survival independently of selection of preference for traits in females. This is a speculation, but social fish should give us some new direction to understand ultimate causes in sexual selection, and also evolution of social behaviour.

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Submetido em 13/11/2008.
Aceito em 06/12/2008.