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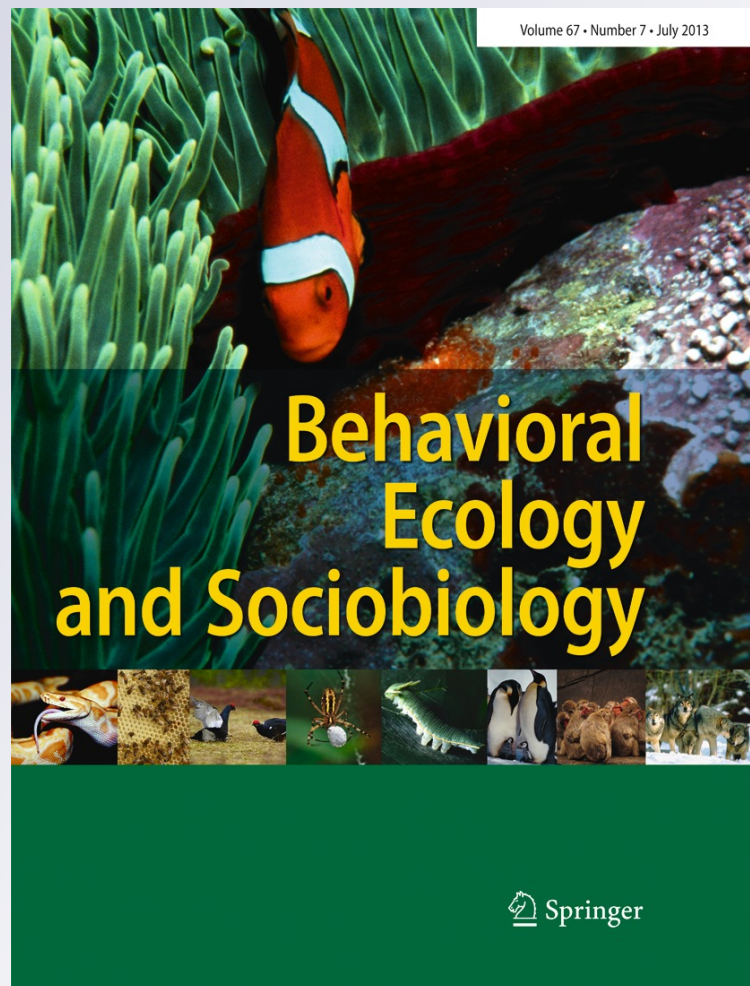
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Sex-specific conditional mating preferences in a cichlid fish: implications for sexual conflict

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Abstract Conditional mating strategies enable individuals to modulate their mating behaviour depending on 'individual status' to maximise fitness. Theory predicts that variation in individual quality can lead to differences in mating preferences. However, empirical evidence is scarce particular in terms of variation in male and female strategies. Here, we experimentally investigated quality-dependent variation in mating preferences concerning reliable quality indicators in *Pelvicachromis taeniatus*, a colourful cichlid fish with mutual mate choice and ornamentation. Males as well as females were artificially manipulated in phenotypic quality by different feeding regimes. Ornamentation was connected to individual quality in both sexes. Males and females showed conditional mating strategies in different directions. Males showed prudent choice by preferring females of similar quality. In contrast to males, low-quality females preferred highly ornamented males, whereas high-quality females showed neither preferences for high- nor for low-quality males. The results suggest that individuals aim for specific benefits depending on individual quality. Furthermore, the conflicting conditional mating preferences of males and females might lead to sexual conflict, implicating a highly dynamical mating system that evolves even in absence of environmental changes.

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Introduction

Theory suggests that variation in quality of the choosing individuals can lead to a range of potentially evolutionarily stable mate choice strategies (ESS) (Härdling and Kokko 2005), instead of a general preference for the mate of highest quality that is available on the mating market (Jennions and Petrie 1997; Widemo and Saether 1999). Especially in species in which reproduction is associated with high costs, e.g. due to strong competition over mates (Fawcett and Johnstone 2003), intense brood care (Kokko and Monaghan 2001) or viability costs connected to the development of the sensory apparatus (Cotton et al. 2006a), phenotypic variation may lead to conditional mating strategies that depend on individual quality (Cotton et al. 2006b). The resulting ESS may differ depending on the mating system or the benefits of choice.

Recent studies provided the first empirical evidence that quality-related mating preferences exist in females (Bakker et al. 1999; Holveck and Riebel 2010; Holveck et al. 2011). For instance, preferences for mates of similar quality can evolve, resulting in assortative mating patterns (e.g. Franceschi et al. 2010), i.e. that high-quality individuals prefer high-quality individuals, whereas low-quality individuals show preference

for low-quality ones (Härdling and Kokko 2005). These studies largely support the theoretical predictions that females optimally balance their costs and benefits of mate acquisition. High-quality females may indeed prefer high-quality males that offer the highest benefits, whereas low-quality females prefer low-quality males (Holveck and Riebel 2010) or show no mating preferences at all to optimally outweigh the costs connected with choosiness (Cotton et al. 2006b) .

However, sexual selection is a complex co-evolutionary process in which the mating strategies of males and females interact. For example, in species with mutual mate choice conflicting preferences between the sexes might lead to sexual conflict over mating which, however, can be resolved in assortative mating patterns (Parker 2006; Baldauf et al. 2009a), or female preferences for high-quality individuals may conflict with the outcomes of male intrasexual competition. Striking examples are species with antagonistic co-evolution in which highly competitive males impose costs for females (e.g. Friberg and Arnqvist 2003), or species where different male morphs exists due to environmental conditions (Tomkins et al. 2011). However, knowledge about variation of male and female condition-dependent mating preferences still remains poorly explored, particularly in species with mutual mate choice, which we will address in this study. In biparental species with mutual mate choice, both sexes should show co-evolving mating strategies (that might be related to individual quality) (Burley 1986; Kokko and Johnstone 2002), thus making them ideal model systems to investigate the variation between male and female strategies.

Here, we investigated quality-dependent mating preferences of both sexes and their interaction in the cichlid fish *Pelvicachromis taeniatus*, a socially monogamous fish with biparental brood-care and mutual mate choice (Thünken et al. 2007a). Both sexes develop a distinct nuptial belly coloration that underlies sexual selection (Baldauf et al. 2009b; Baldauf et al. 2011). Females prefer males that show yellow belly coloration over dull males (Baldauf et al. 2009b), whereas males prefer females that show a large extent of their belly coloration (Baldauf et al. 2011). Female belly ornamentation predicts female fecundity as well as maternal quality, suggesting that body coloration is a reliable indicator of female quality (Baldauf et al. 2011). Body size and genetic relatedness are further important mate choice criteria in *P. taeniatus*: the largest potential mating partner is preferred independent from own body size (Baldauf et al. 2009a), and kin is preferred over non-kin (Thünken et al. 2007a, b). Both sexes face high costs of reproduction: after intrasexual competition (Baldauf et al. 2011; Thünken et al. 2011) and mutual mate choice the female cares for the eggs in the breeding cave, while the male attempts long-range defence against intruders. After hatching, the fry are guarded by both parents for a period of several weeks (Thünken et al. 2010). Since both males and females greatly invest in the offspring, both sexes are expected to be choosy according to variation in quality of mating partners (Johnstone et al. 1996). However, mating preferences may further depend on own quality.

We investigated variation in mating preferences of male and female *P. taeniatus* for high- and low-quality partners with test fish that varied in phenotypic quality. To this end, we manipulated body condition of the focal individuals by keeping fish under different feeding regimes, i.e. high or low energy intake. Individual body condition is an effective proxy to estimate individual quality in fishes (see Bolger and Connolly 1989 for review; Schütz and Taborsky 2005; Taborsky et al. 2007; Lehtonen 2012), especially when changing nutritional balance during food supply. We tested whether ornamentation of both sexes was related to body condition, thus representing reliable indicators of quality in both sexes. Subsequently, we used the variation in condition-dependent colour ornaments identified in the diet manipulation experiment in mate choice experiments under highly controlled conditions. To achieve a high degree of standardisation between stimuli during mate choice experiments, virtual computer animations of fish were developed and were used in dichotomous choice experiments. A set of two virtual stimuli that imitated a high- or low-quality mating partner with respect to the honest visual ornament was presented to each test fish. We would expect that males as well as females show conditional mating preferences depending on their own quality, suggesting quality-assortative mating.

Methods

Experimental animals

Experimental fish were the F1 and F2 generation of fish that were collected in 2007 from the Moliwe river, Cameroon (04°04′N/09°16′E). Fish from 14 different families were housed in family tanks prior to the start of the feeding regimes. Mean offspring sex ratio of *P. taeniatus* is at 1:1 (SAB, TT, personal observation), and reproduction was prevented due to missing breeding spots. All fish started experimental treatments at the age of 300±10 days as adult virgins and were haphazardly chosen from family tanks. Fish that showed no courtship coloration were replaced with a reproductively active family member. All experiments were conducted between January and June 2010.

Feeding regimes

In order to manipulate phenotypic quality and to identify costly indicator ornaments, fish were randomly assigned into a high (7% of body mass/day) or low (3% of body

mass/day) feeding regime over a period of 43 days prior to the mate choice experiments. Whenever possible, four males and four females were taken from a family; however, two families allowed only three reproductive animals per sex. Thus, in each feeding regime 27 males and 27 females were present ($n = 108$). Two males and two females were introduced in a single aquarium ($50 \times 30 \times 30$ cm) that was divided in four parts (25×15 cm) by transparent, perforated plastic sheets, thus allowing visual and olfactory communication between the fish. Fish within a single tank originated from the same family and received the same feeding regime. Fish were fed with a standardised mixture of defrosted *Chironomus* larvae and *Artemia*.

Fish mass (g) and standard length (mm) of each individual were measured before and after the feeding regime. Subsequently, body condition was calculated as a function of mass and standard length [$(100 \times \text{mass})/\text{standard length}^3$], following Bolger and Connolly (1989).

Quantification of male and female ornamentation

Photospectrometrical readings between 300 and 700 nm (Avantes AVS-USB2000 spectrometer, connected to an Avantes DH-2000 light source) of each individual were taken before and after the feeding regime in a dark room. Prior to photospectrometrical measurements, each fish was gently captured and remaining water on lateral side was removed. Subsequently, scans were collected under standardised conditions from the lateral side were the nuptial coloration is located. Spectra were measured after dark calibration relative to a 98 % Spectralon white standard with a bifurcated 200-μm small-tip fibre optic that was held at a 90° angle to the body surface. For each individual, 15 measurements were recorded with Spectrawin 5.1 (Avantes) and imported into Microsoft Excel in which the measurements of each individual were averaged. The procedure was carried out within 1 min in order to minimise stress and changes in colour. Additionally, we took digital photographs (camera—Nikon D70s) of each individual prior to mate choice experiments in order to measure the area of the female belly ornamentation. Photographs were taken under standardised conditions (light source—two Somikon LP001 lights illuminating the lateral side), including a Munsell white standard within the scene. The pictures were saved in RAW format and were white balanced during import into Photoshop CS2. For image processing, they were saved in TIF format without compression to avoid the loss of coloration data due to compression algorithms. Images were analysed using SigmaScan Pro 5.0. We selected the number of pixels of the blue colour component (SigmaScan hue blue, 128–192/hue) as well as the number of pixels forming the body area (excluding the fins) to calculate the relative extent of the nuptially coloured area.

Mate choice experiments

Manipulated males and females were habituated individually in a tank ($30 \times 20 \times 20$ cm) for the period of mate choice experiments in which a breeding cave (males) or a plastic plant (females) was installed. Each fish continued to receive an amount of food according to its feeding regime. Males and females performed mating preference experiments in a dichotomous design in which they were given the choice between a computer-animated high- and a low-quality stimulus of the opposite sex. Experimental procedure followed the protocol described in Baldauf et al. (2011). Previous studies showed that *P. taeniatus* reliably responds to computer stimuli (Baldauf et al. 2009b). We calibrated monitors ensuring that they emitted light that corresponded to spectral data of the nuptial area using a digital colorimeter (Quato Silver Haze pro). To achieve moving animations of the models, we used 'The GIMP 2.2.17 with animation package' (http://www.gimp.org/). A neutral grey background ($1,024 \times 400$ px) was shown (RGB = 238, 238 and 238) including a plant as a size reference object in the middle of the image. Each animation consisted of 30 frames per second, which is an established method to present artificial stimuli to fishes (Künzler and Bakker 1998; Baldauf et al. 2009b). Models were constructed from digital photographs of five males or females, respectively. By creating such an artificially mixed phenotype, we aimed to reduce the probability (or theoretical possibility) that the elicited response arises only because the manipulated trait were presented with a single specific natural phenotype (McGregor 2000). Subsequently, we virtually manipulated the quality traits using Adobe Photoshop CS4 in RGB colour mode. Males received a pair of female stimuli that differed only in their extent of the nuptial coloured belly area, whereas virtual male stimuli of different yellow belly brightness were presented to the females. By using computer-animated stimuli, other confounding variables were ruled out, e.g. behavioural interactions with live stimuli or differences in body size that play an important role in mate choice of this species since individuals prefer the largest mating partner independent from own body size (Baldauf et al. 2009a). Both stimuli moved synchronously from one side of the monitor to the other within a period of 15 s, including a 2-s stop in the middle of each screen. After that, stimuli moved their pathway back in the same time frame. Each fish was tested twice with reversed position of the stimuli, thereby controlling for potential side biases. Fish behaviour was recorded with a camera and the mean relative time over both trials spent in the association zone in front of the virtual stimuli was quantified by a naïve observer. Association time with live stimulus fish reliably predicts mating decisions in *P. taeniatus* (Thünken et al. 2007a).

Although the feeding regime had a significant impact on the body condition of the fish (see results), there was still a

large overlap between treatment groups (e.g. because some individuals with an initially high body condition that got the low feeding regime maintained a relative high condition, or individuals with initially low condition in the high feeding regime maintained a relative low condition). For such individuals, food manipulation did not seem to notably affect the phenotypic quality and thus might have an ambiguous impact on their mating preferences. Because our main interest was on the effect of condition-related preferences (and not the effect of food manipulation per se), we only included individuals above the mean body condition in the high-quality feeding regime ('high-quality individuals') and vice versa individuals below the mean body condition of the low-quality feeding regime ('low-quality individuals'), i.e. individuals of definitive high or low phenotypic quality into the statistical analysis. Two females that showed the lowest body condition and thus a body coloration below 5 % of the body area were considered as not reproductively active and were removed from the analysis, thus leading to a total number of n_{males}=25 from 13 different families (10 per feeding regime) and $n_{females}$=23 from 12 different families (10 different families in the high-quality group and eight in the low-quality group). Post hoc selected males were significantly different in body condition prior to food manipulation (LRT, χ^2=4.24, p=0.04), whereas females were not (LRT, χ^2=0.624, p=0.43). However, in each sub-group of both sexes body condition after food manipulation was not significantly explained by initial body condition (males, LRT, χ^2=2.436, p=0.12; females, LRT, χ^2=0.65, p=0.42) but by feeding regime (all p<0.001). Furthermore, initial as well as final body condition did not differ significantly between families of the post hoc selected subgroups (all p>0.6), suggesting that the variation in the post hoc selected males is caused by the food manipulation rather than by intrinsic genetic differences.

Statistical analysis

All analyses were performed using R 2.11.0 for Windows (R Development Core Team 2009). Linear mixed-effect models (LME) with family as random factor were fitted using maximum likelihood (Pinheiro et al. 2009). We assessed whether the removal of a variable or interaction term caused a significant decrease in the model fit (Zuur et al. 2009) using likelihood ratio tests (LRT). Reported p values of models thus refer to the increase in deviance when the respective variable was removed. Thus, degrees of freedom differ by one. QQ plots of model residuals were inspected visually for deviations from normality and were additionally tested with Kolmogorov–Smirnov test with Lilliefors correction.

In order to examine the effect of the feeding regime on body condition, we fitted models with 'body condition' as dependent variable, 'feeding regime' (high/ low) as explanatory factor and 'family' as random factor. Similarly, we analysed the relationship between ornaments and body condition after the feeding regime. In this case, the male or female ornament, respectively, was the dependent variable, body condition the explanatory term and family as random factor. Initially, there were no significant differences between treatment groups concerning body condition or ornamentation of each sex (all p>0.2).

The main aim of the study was to test potential differences in conditional strategies between the sexes. To achieve this, we first calculated a preference index for each individual as response variable (mean relative time a test fish spent with the high-quality stimulus minus that spent with a low-quality stimulus). We then examined the interactive effect between 'sex' (male/female) and 'feeding regime' (high/low) on the mating preferences.

Additionally, we investigated the nature of the conditional strategies in detail. First, we tested—for each sex separately—if males and females exhibit conditional preferences when facing mating partners of different quality. Here, the mean relative time each individual spent in front of a stimulus type over both trials was the dependent variable, stimulus quality (high/low quality) and feeding regime (high/low) were explanatory variables, and individual ID nested in family was the random factor. We then tested the interaction between feeding regime and stimulus quality to see whether the preference for a certain stimulus quality depends on own quality. Subsequently, we analysed separately whether high- or low-quality individuals discriminated between both stimuli.

The post hoc selected subsamples were furthermore analysed to disentangle the effects of manipulation and initial quality (see above). Here, the final 'body condition' was the dependent variable, 'feeding regime' (high/low) and 'initial body condition' explanatory factors, and 'family' was the random factor.

Results

Condition dependence of individual quality

The feeding regime had a significant impact on body condition of males (LRT, n_{high}=27, n_{low}=27, χ^2=9.418, p=0.002) as well as females (LRT, n_{high}=27, n_{low}=27, χ^2=9.598, p=0.002). Ornamentation of both sexes was significantly related to the manipulated body condition (male brightness, LRT, χ^2=4.447, p=0.03, Fig. 1a; female extent of belly ornament area, LRT, χ^2=13.259, p<0.001, Fig. 1b).

Quality-dependent mating preferences

The strategies of males and females differed significantly (interaction between 'feeding regime' and 'sex', LRT, n_{males}=25, $n_{females}$=23, χ^2=8.182, p=0.004; Fig. 2). Males preferred
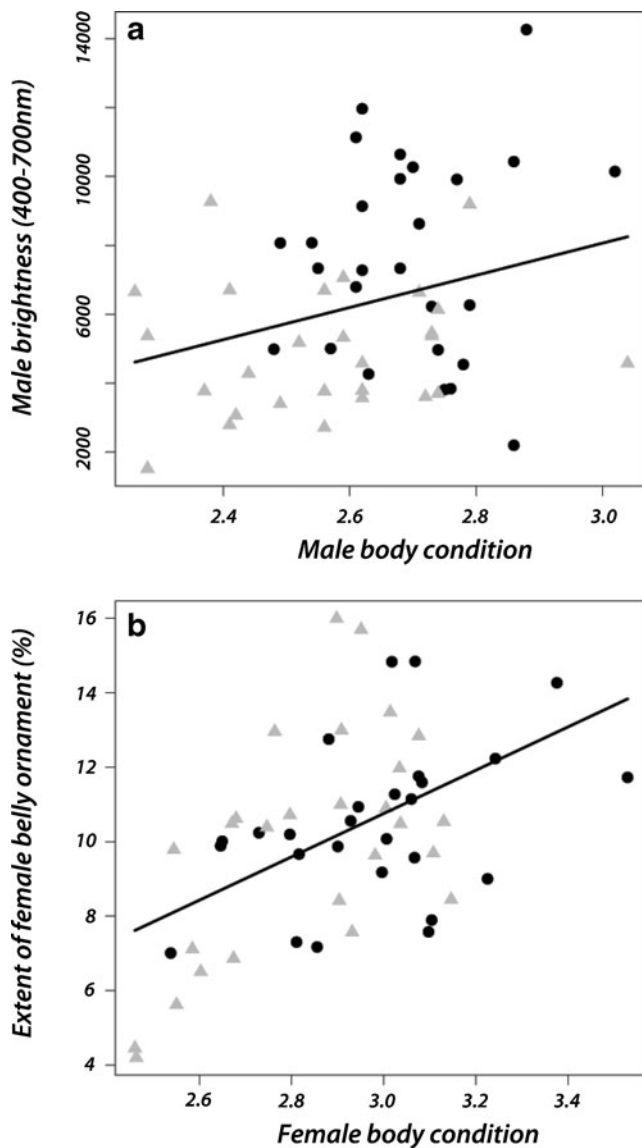
Fig. 1 Condition-dependent expression of the ornamental traits. *P. taeniatus* develops a sex-specific belly coloration. The male yellow brightness was related to male body condition (**a**), and the extent of the area of the female belly coloration was related to female body condition (**b**), thus rendering the ornaments of both sexes a reliable indicator of individual quality. *Grey triangles* indicate individuals in the low feeding regime, and *black circles* show individuals in the high feeding regime

females of similar quality (interaction between 'feeding regime' and 'stimulus quality', LRT, $\chi^2=8.444$, $p=0.003$; Fig. 2). Low-quality males preferred low-quality females (LRT, $\chi^2=4.277$, $p=0.04$, Fig. 2) whereas high-quality males preferred high-quality females (LRT, $\chi^2=4.134$, $p=0.04$, Fig. 2).

Females also showed conditional mating preferences (interaction between 'feeding regime' and 'stimulus quality', LRT, $\chi^2=8.711$, $p=0.003$, Fig. 2). However, the low-quality females preferred high-quality males (LRT, $\chi^2=$ 7.198, $p=0.007$, Fig. 2), whereas females of high quality showed no significant preferences (LRT, $\chi^2=0.276$, $p=0.6$, Fig. 2).

Discussion

Both sexes showed conditional mating preferences. Males adjusted their mating preferences depending on individual quality suggesting positive assortment. The male strategy is in accordance with theory and empirical work that previously dealt with conditional strategies (Härdling and Kokko 2005; Bel-Venner et al. 2008; Venner et al. 2010). Although low-quality males would largely benefit when mating with a high-quality female, e.g. in terms of number of offspring and maternal care, the costs to gain access to such females may be high. The potential costs of developing the sensory apparatus did not seem to be significantly affected by the feeding regime since in both sexes low-quality individuals were able to discriminate between the two stimuli. Instead, in nature searching for a high-quality mate might be time and energy consuming, and intrasexual competition to gain access to high-quality females is expected to be strong in many species (Venner et al. 2010) which is also true for males of *P. taeniatus* (Thünken et al. 2011). Hence, it could be adaptive for low-quality males to show conditional preference for low-quality females in order to increase their mating chances on the mating market by directing their mating efforts towards a female which is more likely to accept their courtship and to avoid direct competition with males in better condition (see below). In contrast, high-quality males should be expected to prefer high-quality females since such males are most likely successful in both intra- and intersexual competition. The viability costs associated with conspicuous ornamentation (Pomiankowski 1987) should be compensated by the direct and indirect benefit of mating with high-quality females (Andersson 1994) since female ornamentation is a reliable indicator that reflects fecundity and maternal quality in *P. taeniatus* (Baldauf et al. 2011).

Surprisingly, though, females exhibited a different conditional strategy than males by preferring high-quality males only when their own quality was low. Variation in female choice has recently been found by Griggio and Hoi (2010), who reported that in house sparrows, *Passer domesticus*, only low-quality females were selective but showed preference for males of average quality, whereas high-quality females were not choosy. Such female strategies contradict the common hypothesis that only high-quality females should be able to show the strongest mate preference, whereas low-quality females should not be able to pay the costs associated with choosiness (Cotton et al. 2006b). The current results might suggest that females seek specific

Fig. 2 Conflicting conditional mating preferences of both sexes. Males as well as females showed conditional strategies depending on own quality but in opposite directions. The *Y*-axis shows the mean relative amount of time+SE over both trials that individuals spent in front of high-quality (*black bars*) and low-quality stimuli fish (*white bars*) of the opposite sex. For levels of significance, see "Results" section
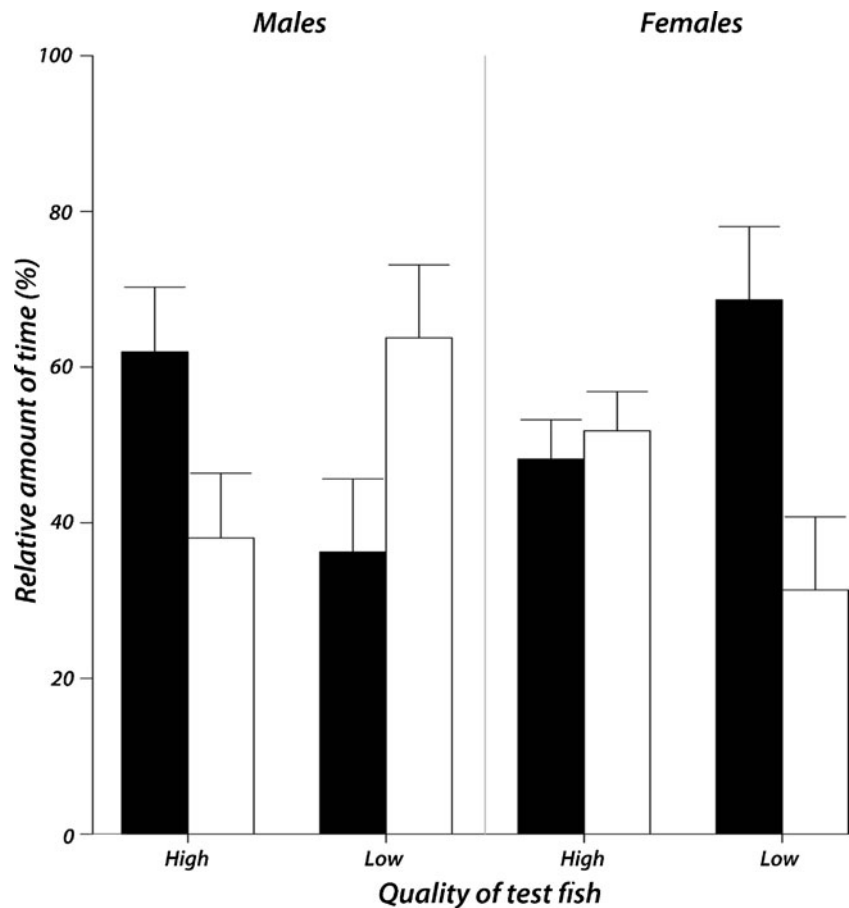
benefits depending on individual quality. Low-quality females might aim at indirect benefits according to good genes or sexy son hypotheses (Weatherhead and Robertson 1979; Hamilton and Zuk 1982), whereas high-quality females might seek for direct benefits that may not be indicated by the investigated ornament. Mate choice in *P. taeniatus* is based on several criteria [ornamental traits like body coloration, exaggerated body extensions, body size and compatibility, i.e. genetic relatedness (Thünken et al. 2007a; Baldauf et al. 2009a, 2010, 2011)], whose relative importance seems to be sex specific (Thünken et al. 2012). Furthermore, multiple and multimodal cues may play a role in mate choice by interacting one with each other (e.g. visual and olfactory cues as in Thünken et al. 2011). Although it is not known whether the different ornaments signal different benefits, high-quality females may focus in mate choice on other indicator traits or criteria than investigated in the present study. For instance, the genetic relatedness to a male seems to be a more important criteria in female mate choice than male body size (Thünken et al. 2012), suggesting that the ornamental trait might be less important compared to other traits not investigated in our study.

In *P. taeniatus* as well as other fish species, female belly coloration has been shown to signal both readiness to spawn and relative fecundity (Massironi et al. 2005; Baldauf et al.

2011). Thus, a possible explanation for the lack of preference in high-quality females may be due to their urgency to mate. In contrast, low-quality females may be less close to spawn and thus could increase their choosiness by conducting a finer mate assessment. Female choosiness is expected to increase with higher levels of benefits and decrease with costs of choice (Jennions and Petrie 1997). Consequently, females from the high feeding regime may have higher costs of choice when choosiness would delay their reproduction, whereas low-quality females might not pay this cost because they have more time before reproduction. Alternatively, high-quality females might not need to show any preference since they will be preferred by high-quality males anyway. However, the lack of preference of high-quality females is puzzling but might reflect results from the dynamics and complexity of systems with mutual mate choice.

Here, we only tested for conditional mating preferences for a relatively short experimental period. Hence, not all potential costs such as intrasexual competition were present during the trials, which have been shown to affect or even reverse initial mating preferences in other species (e.g. Plath et al. 2008; Jeswiet et al. 2012). Possibly, low-quality females of *P. taeniatus* might reverse their preference towards less preferred males in presence of high-quality competitors (Mautz and Jennions 2011; Wada et al. 2011). Although this

possibility cannot be ruled out, prior to the start of the experiments fish were raised in mixed-sex family tanks in which intrasexual competition was allowed, thus rendering fish not naïve to potential competitive costs. Intrasexual competition is expected to be strong within family tanks since *P. taeniatus* prefers to mate with related individuals (Thünken et al. 2007a).

Our main focus was on condition-dependent mating preferences which we were able to demonstrate. However, it remains unsolved whether the variation in mating preference between high- and low-quality males is a consequence of the feeding regime since males of the analysed sub-group were different in body condition before entering the experimental manipulation. Nevertheless, the feeding regime had a stronger impact on final male body condition than initial body condition, suggesting that the diet manipulation had a stronger impact than other factors, such as genetic effects.

Several consequences of the conflicting preferences of males and females could be outlined. High-quality individuals are expected to easily find a mating partner, whereas low-quality individuals may be rejected, and thus remain unmated at first. However, as males are expected to have higher potential reproductive rates than females, high-quality males could abandon the current brood, which is often observed in biparental cichlids (Keenleyside 1983; Jennions and Polakow 2001) and try to attract additional females including low-quality females who are still available on the mating market. Under this scenario, the low-quality females' preference for high-quality males makes sense because competition with high-quality females is reduced if the latter have already mated. Low-quality females may also receive a relatively high fitness gain from an attractive father that would provide indirect benefits to the offspring. Hence, the strongest selective pressure lies upon low-quality males, which show indeed 'prudent' mating preferences, but might receive no or low fitness benefits.

The conflicting preferences of males and females may lead to a sexual conflict resulting from conflicting reproductive interests, which is especially expected to emerge in biparental species (Chapman et al. 2003). In the case of interlocus sexual conflict, it might indeed be in the interest of an allele in a low-quality female that the female mates with a high-quality male to increase the female's fitness. However, such a female strategy is initially not in the male's interest since it would reduce fitness of high-quality males. Thus, the expected rejection of low-quality females should generate direct negative selection on female preference for high-quality males.

Still, it remains unknown whether the observed mating strategies represent an evolutionary equilibrium, implicating that high-quality males may aim to mate with multiple females or whether we observe a certain phase of an co-evolutionary arms race in the evolutionary cycle. Nevertheless, the current results suggest that in a species with conventional sex roles the conditional mating strategies implicate highly evolutionary dynamics that might involve antagonistic co-evolution (Chapman et al. 2003; Chapman 2006) or Red-Queen processes in the evolution of the mating system (Parker 2006). Such highly dynamic mating systems are expected to evolve even in absence of environmental changes (Chapman et al. 2003), suggesting that the observed results might contribute to the understanding of the role of sexual selection and rapid speciation (Salzburger 2009).

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