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A sex-specific trade-off between mating preferences for genetic compatibility and body size in a cichlid fish with mutual mate choice

Timo Thünken^{1,*}, Denis Meuthen¹, Theo C. M. Bakker¹
and Sebastian A. Baldauf^{1,2}

¹*Institute for Evolutionary Biology and Ecology, University of Bonn, An der Immenburg 1, 53121 Bonn, Germany*

²*Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands*

Mating preferences for genetic compatibility strictly depend on the interplay of the genotypes of potential partners and are therein fundamentally different from directional preferences for ornamental secondary sexual traits. Thus, the most compatible partner is on average not the one with most pronounced ornaments and vice versa. Hence, mating preferences may often conflict. Here, we present a solution to this problem while investigating the interplay of mating preferences for relatedness (a compatibility criterion) and large body size (an ornamental or quality trait). In previous experiments, both sexes of *Pelvicachromis taeniatus*, a cichlid fish with mutual mate choice, showed preferences for kin and large partners when these criteria were tested separately. In the present study, test fish were given a conflicting choice between two potential mating partners differing in relatedness as well as in body size in such a way that preferences for both criteria could not simultaneously be satisfied. We show that a sex-specific trade-off occurs between mating preferences for body size and relatedness. For females, relatedness gained greater importance than body size, whereas the opposite was true for males. We discuss the potential role of the interplay between mating preferences for relatedness and body size for the evolution of inbreeding preference.

Keywords: inbreeding; fish; kin selection

1. INTRODUCTION

Mating preferences for secondary sexual traits indicating the intrinsic quality of an individual (ornamental or quality traits) can be distinguished from mating preferences for genetic compatibility [1–4]. On the one hand, it is assumed that individuals developing extravagant secondary sexual traits are uniformly preferred by the choosing individuals of a population over individuals with lower character values and, thus, that the evolution of such ornamental traits underlie directional selection [5,6]. On the other hand, the most compatible mating partner differs between individuals of a population because genetic compatibility depends on the interaction between the genotypes of mating partners [7].

Owing to this fundamental difference, mating preferences for compatibility and highly ornamented partners are often difficult to reconcile simultaneously: a mating partner with pronounced ornaments is not necessarily the most compatible one and vice versa [8–12]. Thus, individuals may face a conflict between preferences for genetic compatibility and preferences for ornamental traits. Individuals might trade off between both criteria to solve the conflict and such trade-offs may have important evolutionary implications because they contribute to the generation or maintenance of genetic variation in

mating preferences as well as in secondary sexual characters [10,13].

Mate choice based on compatibility criteria and ornamental criteria have been studied extensively, particularly concerning female mate choice, although studies on male mate choice have gained ground recently (see [5,6,14]). Examples for compatibility choice comprise a variety of phenomena ranging from inbreeding avoidance [15,16], optimal outbreeding/inbreeding [17,18] to active inbreeding [19] and MHC-polymorphism [20,21]. The evolution by mate choice of ornamental traits such as conspicuous body coloration [22], exaggerated body extensions [23] or body size has concerned evolutionary biologists since Darwin [5,24]. Although several species (such as three-spined sticklebacks [16,25–28] or mice [8,20,29] but also humans [30,31]) are known to use both compatibility and quality criteria, the interplay between preferences for ornamental traits and compatibility has received relatively little attention in experimental research (but see [8]).

The aim of the present study was to examine potential trade-offs between mating preferences for ornamental traits and genetic compatibility in the fish *Pelvicachromis taeniatus*, a socially monogamous cichlid from West Africa with intense biparental brood care and mutual mate choice [19,32]. Previous experiments revealed that males and females of *P. taeniatus* use body size (an ornamental trait) as well as genetic relatedness (a compatibility criterion) in mate choice, when these criteria were tested

* Author for correspondence (tthuenken@evolution.uni-bonn.de).

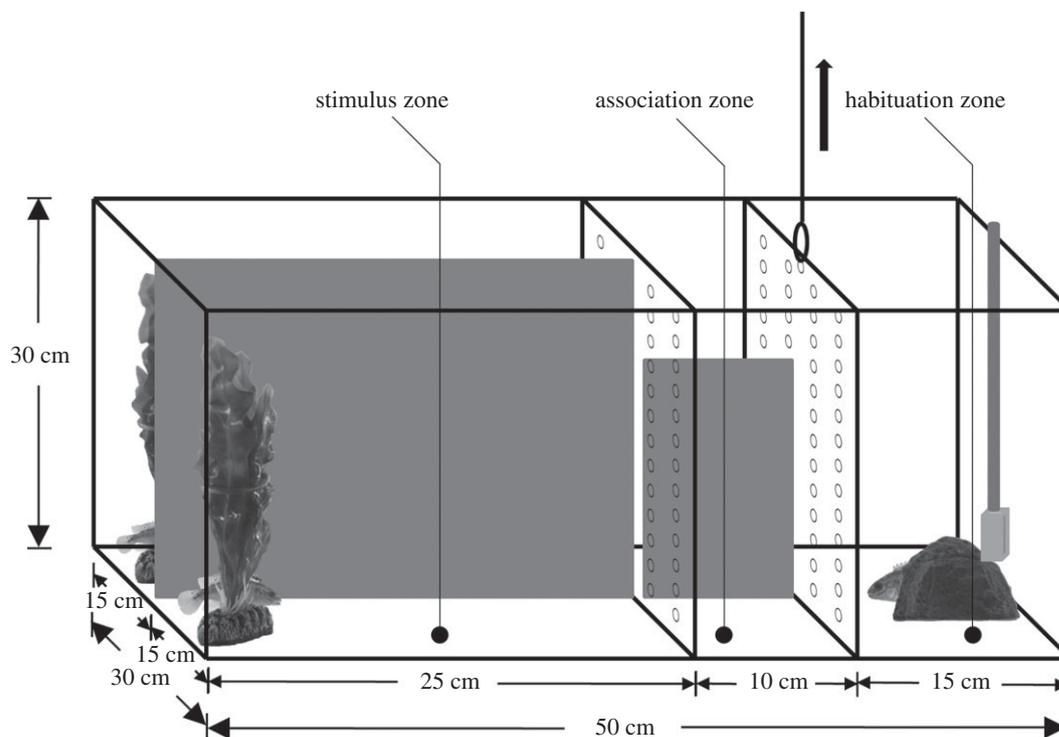


Figure 1. Experimental set-up. A reproductively active individual (male in this case) was given the conflicting choice between a small, related and a large, unrelated stimulus fish of the opposite sex. After removing the transparent, perforated plate (see arrow), the focal fish was able to enter the association zones in front of the stimulus fish (see main text for details).

independently from each other: as in other cichlids [33–37], both sexes preferred large individuals [32]. Mating with large individuals provides several indirect and direct benefits in biparental cichlids, e.g. high fecundity (in females) or increased ability to defend a brood [36]. Furthermore, close kin were preferred as mating partners [19,38,39]. The unusual kin mating preferences appear to be adaptive in *P. taeniatus* because of increased cooperation between siblings during costly brood care and can be traced back to the natural population that is highly inbred [40]. In the present experiments, males and females were forced to weigh their preferences for large body size and relatedness by giving them a choice between a related (favoured), but small (unfavoured) and a large (favoured), but unrelated (unfavoured) stimulus fish of the opposite sex.

2. MATERIAL AND METHODS

(a) *Experimental fish*

Pelvicachromis taeniatus is distributed in rivers and streams of western Africa. The sexes are brightly coloured [22,41] and show a conspicuous size dimorphism, with males being larger than females [32]. Reproductively active males occupy territories with appropriate breeding caves and defend them against rivals [39]. Females compete among each other for access to males with caves [22]. After mutual mate choice, breeding pairs are formed. Both sexes show active courtship and defend the territory against intruders. After spawning, mainly the female cares for the eggs and wrigglers in the cave by fanning them and removing dead eggs and larvae. Meanwhile, the male protects the territory. After about one week, the free swimming fry leave the cave and are then guarded by both parents for a few weeks. Parents often show coordinated behaviour by guiding their young [42].

Fish used in the experiments were descendants of wild-caught *P. taeniatus* that were collected in June 2007 from the

Moliwe River near Limbe, Cameroon (04°04' N, 09°16' E). Prior to the experiments, the fish were kept in 60 × 45 × 30 cm tanks in sibling groups comprising between 10 and 50 fish each at a 12 L : 12 D regime and a water temperature of approximately 25°C. Fish originating from 19 different families were used in the experiments. Experimental fish were reproductively active and showed typical courtship coloration.

(b) *Experimental set-up*

Mate choice experiments were conducted in parallel in three tanks (50 × 30 × 30 cm; figure 1) which were visually separated from each other by opaque plates. Additionally, the whole setup was encased with plates of 1 m height to avoid disturbance from the surrounding environment. Each experimental tank was divided into three compartments (figure 1), two for the stimulus fish (25 × 15 × 30 cm each) and one for the focal fish (25 × 30 × 30 cm). The stimulus fish compartments were separated by an opaque plastic sheet to prevent interaction. Focal and stimulus fish compartments were separated by a fixed, transparent, perforated Plexiglas sheet (28 × 29 cm) to allow visual and chemical communication. The focal fish compartment was further subdivided into a habituation zone (15 × 30 × 30 cm) and two association zones (10 × 15 × 30 cm each) in front of the stimulus fish compartments. Access to the association zones was enabled only during the experiment by removing a retractable, transparent, perforated Plexiglas sheet. The test tank was filled with substrate-treated water, enhancing the acclimation of fish to experimental conditions [43]. Oxygen supply was provided by an air stone centred at the back of the focal fish area.

(c) *Experimental procedure*

In the experiments, focal fish were given the choice between a small, related (i.e. full sibling) and a large unrelated, stimulus fish of the opposite sex. Prior to the experiments, the focal and the stimulus fish were carefully captured from the

family tanks. In order to minimize stress for the animals, we estimated the size differences between stimulus fish before the experiments and measured them accurately afterwards. At first, the focal fish was introduced into the habituation zone and, afterwards, the two stimulus fish were placed in their compartments; fish could acclimatize overnight. Experiments were initiated the next morning, 1 h after the beginning of the light period (approx. 10.00), by lifting the retractable sheet in the focal fish's compartment, so that it was able to enter the association zones. Focal fish's behaviour was then recorded from above for 2 h using an USB web camera (QuickCam Pro 9000, Logitech). Video records were analysed with the BIOOBSERVE VIEWER v. 2.2.0.151 software (Bonn, Germany) to ensure naive observation. Mating preferences were estimated by measuring the time the focal fish spent in the association zone of the corresponding stimulus fish over the experimental period of 2 h. We analysed only the trials in which the focal fish had entered both association zones in order to ensure that the focal fish has perceived both stimulus fish. As in other cichlids [44,45], the association time reliably predicts mating decisions in *P. taeniatus* ([19]; T.T., T.C.M.B., N. Henning & H. Kullmann, 2009, unpublished data).

(d) Statistical analysis

All analyses were conducted using R v. 2.9.1 (R Development Core Team, Austria, Vienna). In order to investigate potential trade-offs between preferences for relatedness and body size, we examined the effect of stimulus fish status ('stimulus status', small kin/large non-kin) on the mating preference of the focal fish (time spent in the association zones) using linear mixed-effect models (R function 'lme' in library 'nlme'), with the individual nested in the family as the random factor to control for the multiple use of families. In order to analyse whether the sexes responded differentially to the stimuli, we added the sex of the focal fish ('sex', male/female) as a factor and examined its interaction with the stimulus fish status (sex \times stimulus status). To investigate whether potential trade-offs between relatedness and body size vary between stimulus pairs of different size, we conducted an additional model, with the body size of each stimulus fish ('stimulus size') as covariate. Generally, we assessed whether the removal of a variable caused a significant decrease in the model fit. Reported *p*-values of models refer to the increase in deviance when the respective variable was removed. Tests of statistical significance were based on likelihood ratio tests (LRTs), which follow a χ^2 -distribution. Hence, the degrees of freedom always differ by one. These routines use maximum-likelihood parameter estimation. Non-significant factors and interactions were removed from the analysis [46]. Model residuals were tested with Shapiro–Wilk tests to confirm that they reached normality.

3. RESULTS

In the female mate-choice experiments, the mean body size of the large, unrelated stimulus males ($n = 19$) was 7.82 ± 0.84 cm s.d., while the small, related stimulus males ($n = 19$) measured on average 6.17 ± 0.71 cm s.d. The mean size difference between the stimulus males was 1.85 ± 0.41 cm s.d. In the male mate-choice experiments, the mean body size of the large, unrelated stimulus females ($n = 16$) was 5.24 ± 0.36 cm s.d. and that of the small, related stimulus females ($n = 16$) was

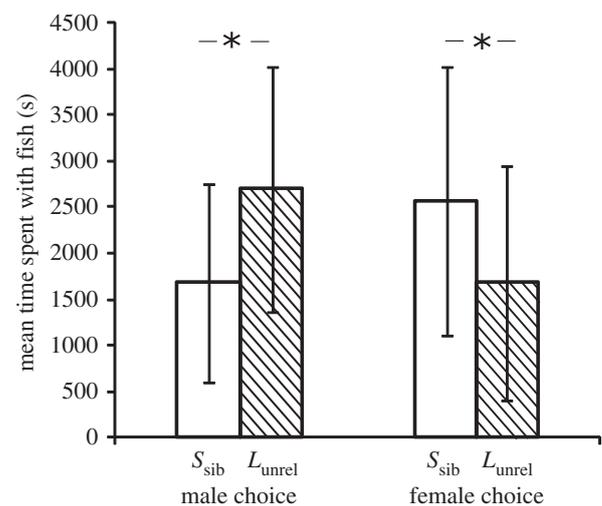


Figure 2. The mean time (s \pm s.d.) males and females spent with the small sibling (S_{sib}) and large, unrelated fish (L_{unrel}), respectively. $p < 0.01$ for the sex \times stimulus status interaction; asterisks indicate $p < 0.05$.

4.36 ± 0.29 cm; the size difference between stimulus females was on average 0.89 ± 0.28 cm s.d. Neither the relative nor the absolute size difference between fish of a stimulus pair correlated significantly with the mean stimulus fish size of a stimulus pair (Pearson correlations, male stimulus pairs: $n = 19$, $r = 0.056$, $p = 0.820$ and $n = 19$, $r = 0.310$, $p = 0.197$, respectively; female stimulus pairs: $n = 16$, $r = -0.107$, $p = 0.693$ and $n = 16$, $r = 0.274$, $p = 0.304$, respectively), indicating that the size differences within pairs were similar over the trials.

The sexes differed significantly in their mate choice trade-off (sex \times stimulus status: LRT, d.f. = 1, $\chi^2 = 9.218$, $p = 0.002$). Females preferred the small, related male over the large, unrelated male (LRT, d.f. = 1, $\chi^2 = 4.001$, $p = 0.046$; figure 2), whereas males preferred the large, unrelated female over the small, related one (LRT, d.f. = 1, $\chi^2 = 5.537$, $p = 0.019$; figure 2).

Furthermore, the preference of females for the small, related males was significantly negatively correlated with male stimulus pair size (stimulus size \times stimulus status: LRT, d.f. = 1, $\chi^2 = 5.675$, $p = 0.017$; figure 3a), i.e. the kin preference was particularly pronounced when the stimulus pairs were relatively small. Male preference did not significantly correlate with female pair stimulus size (stimulus size \times stimulus status: LRT, d.f. = 1, $\chi^2 < 0.001$, $p = 0.991$; figure 3b).

4. DISCUSSION

Here, we provided one of the few experimental studies that address the interplay of compatibility and ornamental mate-choice criteria. Our study gave evidence for a sex-specific trade-off between mating preferences for body size and genetic relatedness in the cichlid *P. taeniatus*. Females weighed genetic relatedness of the potential partner stronger than body size, whereas the opposite was true for males.

Roberts & Gosling [8] reported that in mice, genetic compatibility as well as quality traits play a role in female mate choice. However, genetic compatibility was important only when the potential mating partners were of similar ornamental quality. In Chinook salmon, *Oncorhynchus*

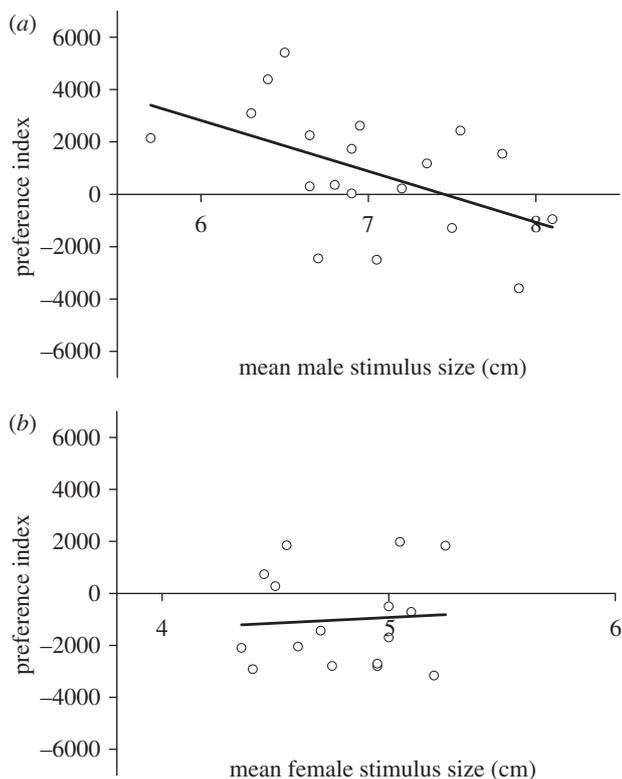


Figure 3. Correlation between focal (a) female and (b) male preference index and mean body size of the two stimulus fish of a stimulus pair. The index is calculated by subtracting the time (seconds) the focal fish spent with the large, unrelated stimulus fish from the time the focal fish spent with small, related stimulus fish. Thus, positive values indicate a preference for the small, related stimulus fish, whereas negative values a preference for the large, unrelated stimulus fish. The lines are the least-squares regression lines.

tshawytscha, Neff *et al.* [47] also found that male body size (but not genetic relatedness to a female) predicts male mating success. In contrast, a study of Garner & Schmidt [48] suggests that relatedness between potential partners rather than male body size influenced paternity in the alpine newt, *Triturus alpestris*. In conclusion, these studies indicate that the relative importance of these choice criteria differ between species. Variation in realized mate choice may reflect variation in the obtained benefits concerning different choice decisions [49–51].

The sex-specificity of the trade-off in the present study adds a new aspect and suggests that the benefits associated with the choice of a related or large partner are different for males and females. Although in *P. taeniatus* males greatly contribute to brood care, females still seem to have higher reproductive expenditure [42]. As a consequence, although both sexes may benefit from reduced sexual conflict over care by kin mating [19], females seem to benefit in particular. Indeed, in sibling pairs, males invested more in the offspring than males in unrelated pairs and were less aggressive against the female kin partner [19]. In the present study, female's relative kin preference decreased with increasing stimulus pair size (figure 3a), suggesting that the relative importance of relatedness and body size continuously varies and depends on the males' absolute size. This context-dependent trade-off might be adaptive. Females may gain direct and indirect benefits by selecting large males, e.g. male body size predicts intra-sexual

competitiveness in *P. taeniatus* [39]. However, size-related benefits might only emerge when males are large enough because small males are inferior to average-sized or large males. Thus, in the case of small males, females appear to gain more by choosing a related and thus more cooperative partner.

In contrast to females, for males the benefits of choosing a large partner seem to exceed those of choosing a related partner. The result confirms the immense role of female body size as the mate choice criterion in male *P. taeniatus* found in a previous study [32]. Body size is correlated with female fecundity in *P. taeniatus* ([32]; T.T., T.C.M.B., N. Henning & H. Kullmann, 2009, unpublished data), and thus closely related to fitness. The particular importance of female body size in male mate choice is therefore not surprising. Males preferred the large, unrelated females over the small, related female irrespective of females' size. Previous studies using *P. taeniatus* revealed that sisters were preferred by males over unrelated females when female quality was matched [19,38]. The present results indicate that sisters are rejected as mating partners when their quality, as indicated by body size, is low.

The interplay of preferences for quality traits and kin mating preferences might be an important mechanism for the maintenance of kin mating preferences [19]. Although inbreeding can increase the inclusive fitness of an individual [11,52], it may also increase the probability that recessive deleterious alleles are expressed, often resulting in short-term reduction of fitness-related traits (inbreeding depression [53]) such as fecundity [54]. 'Purging'—i.e. selection against deleterious alleles—is [55,56], however, in the long term an opportunity to get rid of the genetic load and thus the costs of inbreeding depression may be reduced after a few generations [11]. Thus, the evolution of kin mating preferences critically relies on effective purging. The presented results suggest that related females, when of low quality, are rejected against unrelated, high-quality females as partners. Such purging by sexual selection might support purging by natural selection. Furthermore, by occasional outbreeding with high-quality partners individuals can enhance the genetic quality/variability of their offspring. In conclusion, the interplay of mating preferences for quality traits and kin may contribute to effective purging of deleterious alleles and contribute to the maintenance of genetic variability of an inbreeding population.

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