

Genetically determined mate choice can be influenced by learning in *Apistogramma cacatuoides* HOEDEMAN, 1951 (Teleostei, Cichlidae)

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Abstract

Mate choice in female *Apistogramma cacatuoides* is genetically determined. Females of the aquarium strain studied have a strong preference for red-coloured males of their own strain, although some deviate from this basic sexual preference, and those which choose red-coloured males in a first mate-choice experiment may subsequently choose males of a different strain. Where fry were raised by parents of a different strain in cross-fostering experiments, the mate choice of females raised in this way differed significantly from that of females raised by their own parents. This indicates a clear influence of learning on the basic genetically determined mate preference. The implications of these findings are discussed in the context of speciation.

Kurzfassung

Die Partnerwahl weiblicher *Apistogramma cacatuoides* ist genetisch präformiert. Weibchen der untersuchten Aquariumpopulation haben eine starke Präferenz für rot gefärbte Männchen des eigenen Stammes, obwohl einige von diesem basalen Wahlmuster abweichen und diejenigen, die im ersten Experiment rote Männchen wählen, später auch Männchen anderer Formen wählen können. Wenn Nachkommen in Adoptionsexperimenten von den Eltern eines anderen Stammes aufgezogen wurden, wich die Partnerwahl der so aufgezogenen Weibchen von der durch die eigenen Eltern aufgezogener Weibchen signifikant ab. Dies kann als klarer Hinweis darauf gewertet werden, dass Lernprozesse die grundlegend genetisch fixierte Partnerpräferenz beeinflussen können. Die Konsequenzen dieser Befunde werden im Zusammenhang mit Artbildungsprozessen diskutiert.

Key words

Colour preference, evolutionary traits, Neotropics, sexual selection, speciation in sympatry.

Introduction

Mate choice in cichlid reproductive systems is often based on conspicuous morphological traits. Males develop these traits as a result of mutation and sexual selection by female mate choice (ANDERSSON, 1994; ANDERSSON & SIMMONS, 2006). Thus, female mate preference may

reflect an inherent bias (BARLOW *et al.*, 1990) indicating a co-evolutionary process in female preference and male sexual characteristics (FISHER, 1958; KIRKPATRICK, 1982, 1985; HOEDE, 1987; RYAN, 1998; COTTON *et al.*, 2006; MAAN *et al.*, 2010). The morphological traits of

males of related cichlid species – especially within the Neotropical genus *Apistogramma* – are similar in some cases (KULLANDER, 1980, 1986; RÖMER, 2000, 2006; BEISENHERZ & RÖMER, 2003; BEISENHERZ *et al.*, 2006). Hence, the female species recognition system may be in conflict with the mate assessment mechanism (BOAKE *et al.*, 1997; PFENNIG, 1998; McPECK & GAVRILETS, 2006).

Females of polygamous cichlid species, for instance *Apistogramma cacatuoides* HOEDEMAN 1951, are frequently courted by males of closely related species as well as by males of their own species, as has been reported several times from observations in the aquarium (SCHMETTKAMP, 1978; LINKE, 1985). In mate choice experiments RÖMER & BEISENHERZ (2005) have shown that female *Apistogramma cacatuoides* strongly discriminate against heterospecific males, and it has been possible to demonstrate that they clearly discriminate between variants of their own species of different geographical origin (ENGELKING *et al.*, 2010). Preference of females for males of their own population or the colour type of their own father has been found in other cichlid species (McKAYE, 1991; BARLOW *et al.*, 1990; REDDY *et al.*, 2006; HAESLER & SEEHAUSEN, 2005). This could not be demonstrated for species of the genus *Apistogramma* until now.

The mating preferences of females, as well as the corresponding sexual characters of males, have been shown to be heritable and genetically determined (HOUDE & ENDLER, 1990; BAKKER & POMIANKOWSKI, 1995; HOUDE, 1997; MARLER & RYAN, 1997; HAESLER & SEEHAUSEN, 2005) and can contribute to the evolution of sexually-selected traits if they are beneficial or neutral for survival (FISHER, 1930, 1958; LANDE, 1980, 1981; KIRKPATRICK, 1982; ANDERSSON, 1994). As a result of this mechanism female mate preference influences the genetic variability of male characteristics (ENDLER & HOUDE, 1995; GODIN & DUGATKIN, 1995; BAKKER & POMIANKOWSKI, 1995; RYAN, 1998; COTTON *et al.*, 2006), and thus may be the starting point for the evolution of new species, including in sympatry (MAYNARD SMITH, 1966; ENDLER, 1977; WHITE, 1978; SEEHAUSEN, 1997).

Theory predicts that female preference for conspicuous male traits is a driving force of diversification within cichlid species (BARLOW, 2000; SEEHAUSEN, 2000; BARLUENGA & MEYER, 2004) and significantly contributes to the rapid speciation of cichlids (RÖMER & HAHN, 2000; SEEHAUSEN, 2000; VAN DER SLUIJS *et al.*, 2010). As most cichlid species practise extended parental care (BAERENDS & BAERENDS-VAN ROON, 1950; KEENLEYSIDE, 1991; BARLOW, 2000), there is a likelihood of parental influence on mating preferences (NOAKES, 1991). Given the importance of mating preferences and sexually selected traits in mate selection, learning (in this context) could turn out to be an important factor in the speciation process (MAGURRAN & RAMNARINE, 2004; VERZIJDEN *et al.*, 2008; KOZAK & BOUGHMAN, 2009; KOZAK *et al.*, 2011).

In this study we have tested how far mating preferences in female *Apistogramma cacatuoides* may actually be influenced by social experience.

Materials and methods

A red colour strain of the dwarf cichlid *Apistogramma cacatuoides* was used to demonstrate social influences on female sexual preference (Fig. 1). Females raised by their own parents or by adoptive parents of an inconspicuously coloured wild strain (Fig. 2) or raised without parents were examined for their mate preference using standardised dichotomous mate choice experiments, which have been described in detail by RÖMER & BEISENHERZ (2005) and ENGELKING *et al.* (2010).

KULLANDER (1980) and RÖMER (2000, 2006) have published detailed descriptions of the cichlid genus *Apistogramma* and the species investigated, *Apistogramma cacatuoides*. This represents one of the cichlid species with distinctive sexual dimorphism. Adult males are significantly larger than females, and have longer lappets in the dorsal fin and a lyrate caudal fin (fig. 1). During reproduction *Apistogramma* females show typical yellowish nuptial coloration with contrasting black markings (fig. 2). They attach their eggs to the upper interior surface of cave-like shelters and perform most of the brood care [for further information compare RÖMER (2000, 2006)].

In the mate-choice experiments we used a red strain of *Apistogramma cacatuoides* [for background data on the origin see HOHL (2010 a & b)]. Males of this red strain were tested against males of a wild colour morph in which males are slightly bluish with the same exaggerated morphological sexual characteristics as males of the red strain. However males of the red strain are much more colourful than the wild males and exhibit large red dots or speckles on their dorsal and caudal fins [fig. in RÖMER (2000), p. 118]. The dorsal and caudal fin in females of this strain may also exhibit red dots or speckles.

Adoption experiments were conducted in order to evaluate the degree of parental influence on the mating preferences of the offspring. Clutches from breeding females of the red strain were transferred to breeding wild-strain females, replacing their own clutches. These females adopted the replacement clutches and reared the stranger fry like their own, without problems. In a series of experiments, designed to exclude potential parental influence on the mating preferences of the offspring, red-morph clutches were removed and raised artificially until the sexes could be identified. In each experiment, females and males were separated as soon as the first sexual traits were visible (see RÖMER, 2001).

As sex determination in *Apistogramma* species may be manipulated by temperature (from 0 to 35 days after spawning) and pH, the temperature was reduced after fertilisation from 26° C (yielding a balanced sex ratio) to 24° C to obtain a higher proportion of females for our experiments (RÖMER & BEISENHERZ, 1996; RÖMER, 2000, 2001; BEISENHERZ & RÖMER, 2003).

In mate-choice experiments to test the sexual preferences of females, each female was offered two males,



Fig. 1. *Apistogramma cacauioides* HODEMANN, 1951, red strain male bred by N. WILHELM. Foto: Frank Martin WARZEL / copyright: Warzel-Archive Uwe RÖMER.



Fig. 2. *Apistogramma cacauioides*, pair. Results from the mate choice experiments in this study indicate, that juveniles females may learn the image of their future mate by imprinting by observing the brood-caring male, which should usually represent their own father. Specimens collected 2012 north of Pacaya Samira National Parc, Peru. Foto: Uwe RÖMER.

one of each of the two different colour strains, as potential reproductive partners.

For this we used experimental tanks (60 × 30 × 30cm) which were divided into three unequal subunits by two glass dividers siliconed towards the left- and right-hand

ends (compare BEISENHERZ *et al.*, 2006; RÖMER & BEISENHERZ, 2005). Any influence of scent on fish behaviour during the experiments could thus be excluded. Our experimental set-ups also excluded acoustic information to a certain extent, as permanent external and internal

noise was generated by air blowers and bubbling water. We therefore postulate that acoustic information, which may be of importance in mate choice in cichlid fishes (SLABBEKOORN *et al.*, 2010; VERZIJDEN *et al.*, 2010), probably had no decisive influence on the experimental results.

A female was placed in the larger, central compartment of each aquarium (27 litres, 30 × 30 × 30cm), and a male in each of the smaller lateral compartments (13.5 litres, 15 × 30 × 30cm). Two plastic canisters (the type used for photographic films, without lid) were placed in the female's section of each experimental tank to act as caves, one close to each of the lateral compartments housing the males. To exclude habituation or general preference by females for a particular end of a tank during the experiments, males of different colour strains were randomly placed into the left- or right-hand compartments of the experimental tanks. To exclude size preferences (here taken as total length) as a choice-modifying factor, only males of similar size and condition were offered to a female. [In a previous study influence of size versus colour had been tested to a certain extent (data UR)]. Females were placed in the larger, central compartments of the experimental aquaria at least one day after males had been placed in the smaller lateral compartments. Displaying males were visible to females in the adjacent tank compartments. Females chose a male by spawning next to it. This provides irrefutable evidence of their mate-choice behaviour [for detailed description see RÖMER & BEISENHERZ (2005), BEISENHERZ *et al.* (2006), and ENGELKING *et al.* (2010)].

Differences in preferences were tested using Chi-squared test and Fisher's exact tests. Analyses were processed using the program STATISTICA Version 6.0 (STATSOFT, Tulsa, USA). In the case of dependence we calculated using McNemar Chi-square.

Results

In mating experiments female *Apistogramma cacatuoides* of the red aquarium strain, raised by their own parents, showed a high degree of preference for males of their own strain instead of for inconspicuous wild-caught males. Seven out of 74 females chose males of the different strain, i.e. 9.5 % of all mates (Table 1).

Thirty females were tested for a second time, and of these 16 out of the 19 that had chosen red-strain males in the first experiment repeated that choice. Thus individual repeatability in mate choice did not vary significantly (Table 2). Of those females that had chosen wild-strain males in the first experiment, only four out of 11 repeated their first choice, indicating a generally higher preference for red males.

Where females of *Apistogramma cacatuoides* of the red aquarium strain had been raised without parents, their

mating preferences did not differ significantly from those of females raised by their own parents (Table 1).

However, in mate choice experiments involving the female offspring of red strain *Apistogramma cacatuoides*, raised by parents of the inconspicuous wild strain, about one third (32.8 %) chose males of the adoptive parents' strain (table 1). Mate choice in these females was significantly different from that of females raised by their own or without parents (table I).

Discussion

In our experiments, females of the red strain showed a significant sexual preference for red-strain males, that is males of their own strain. This preference was maintained when the mate choice was repeated. Even females that chose males of the inconspicuously coloured wild strain during the first experiment, showed a significant preference for red-strain males during the second. This suggests that these females generally preferred red males, that is, males of their own colour morph. Even if the fry were raised without parents, females preferred males of their own red colour strain. However, earlier experiments suggest that there is no general preference of female *Apistogramma cacatuoides* for red colour elements in their mates (RÖMER & BEISENHERZ, 2005; ENGELKING *et al.*, 2010). These findings were still valid if females were offered males of different sizes: they preferred the red males even if the alternative partner offered was larger or had larger fins (UR, unpublished data from different earlier studies). This leads to the conclusion that in our experimental setting colour was probably the key factor in mate choice in the case of *Apistogramma cacatuoides*.

If the fry were raised without parents, even these females developing from these, preferred males of their own red colour strain. The mate preferences of these females did not differ significantly from those of females raised by their original parents. Thus our results show a genetic predisposition in mate choice in female *Apistogramma cacatuoides*. Earlier studies have shown that females of various *Apistogramma* species strongly prefer males of their own species and (colour) morph (RÖMER & BEISENHERZ, 2005; READY *et al.*, 2006). In a recent study, females from different *Apistogramma cacatuoides* populations demonstrated preferences for red coloured males following a geographical cline (ENGELKING *et al.*, 2010) indicating that the sexual preference for special coloured males may be variable in different populations of the species.

Mate choice can be genetically determined in cichlid fishes. In behavioural mating experiments HAESLER & SEEHAUSEN (2005) found an inheritance of female mating preference in a sibling species pair of mouth-brooding cichlids, *Pundamilia pundamilia* SEEHAUSEN & BOUTON 1998 and *Pundamilia nyererei* WITTE-MAAS & WITTE

Table 1. Results of mate choice experiments in red strain female *A. cactuoides*. Influence of parental colour strain on female mating preference. Offspring females raised by their own or without parents preferred red males; offspring females of red strain raised by wild strain parents did show reduced preference to red males. Differences between female preferences were analysed by Chi-squared test (χ^2) (with Yate's correction). Significance levels are marked by * (= significant, $p < 0.05$), or ** ($p < 0.005$).

	females	female chose male of			differences (p-values):	
females tested were raised	n	red strain	wild strain	red strain (%)	raised by adoptive parents (wild strain)	raised without parents
by own parents (red strain)	74	67	7	90.5	$p = 0.002$ **	$p = 0.786$
without parents	47	41	6	87.2	$p = 0.029$ *	
by adoptive parents (wild strain)	61	41	20	67.2		

Table 2. Stability of mate choice in red strain female *A. cactuoides*. Females that had chosen red strain males did not differ in the repetition experiment from their first individual choice, whereas those that had originally chosen wild strain males changed significantly to prefer males of their own red strain. Data were analysed by Fisher's exact test (STATISTICA) and McNemar χ^2 (χ^2) ($\alpha = 0.05$; $df = 1$) (with Yate's correction). Significance levels are marked by * (= significant, $p < 0.05$).

	first choice	second choice		differences (p-values):	
red strain females		females repeating first choice:			
preferred male of	(n)	(n)	(%)	Fisher's exact	McNemar
red strain	19	16	84.2	$p = 0.421$	$\chi^2 = 2.083$
wild strain	11	4	36.4	$p = 0.032$ *	$\chi^2 = 6.036$ *

1985, and characterised the genetic basis of the divergent female mating preferences for red and blue male nuptial coloration. In spite of the fact that our results indicate a genetic component to mate preference, some female *Apistogramma cactuoides* deviate from the basic preference pattern, as some females of the red strain chose males of the inconspicuous wild form. This sometimes occurred even in cases where the female's first choice was for its own strain. Obviously female choice is not fixed completely. This leads to the question of whether learning may be of some importance in determining mate preferences in females. The results of our cross-fostering experiments clearly demonstrate that females of *Apistogramma cactuoides* can be influenced by social experience such as the presence of the father.

Most actual literature dealing with genetic determination and learning in mate choice in cichlid fishes is based on research on African lacustrine species such as the haplochromines (e.g. CRAPON DE CAPRONA, 1982; HAESLER & SEEHAUSEN, 2005; VERZIJDEN & TEN CATE, 2007; PIEROTTI *et al.*, 2008; VERZIJDEN *et al.*, 2008). There is, however, a fundamental difference between the studies cited and our own research, namely the completely different life history of the model species used: In contrast to the haplochromine cichlids of Africa, the species of the Neotropical genus *Apistogramma* are polygamous species in which males usually take part in brood care to a certain extent. Brood care in mouth-brooding haplochromines is entirely the task of females, and males are not involved in raising the fry. Hence any type of learning or imprinting of male patterns is restricted, if not impossible. In *Apistogramma*, by contrast, the fry are in

more or less frequent contact with the male dominating the territory, which, on the basis of field observations, will usually be the father (RÖMER, 1992, 1993, 1998, 2000, 2001). They therefore have clear opportunities to learn the male sexual traits of their own (form of their) species (Fig. 2).

Studies of mate preference influenced by social experience, and even some studies in which learned mate preferences override genetic preferences, have been summarised by WITTE (2006) and WITTE & NÖBEL (2011). But most of these studies were performed using species of poeciliids, and none with cichlids of the genus *Apistogramma*. Female preference for conspecific males based on non-visual cues such as olfactory signals has been shown for various cichlid species (CRAPON DE CAPRONA, 1982; PLENDERLEITH *et al.*, 2005; BLAIS *et al.*, 2009), while in other species multiple cues may be used in mate choice (KODRIC-BROWN, 1993; CANDOLIN, 2003). Our experimental design excludes factors other than sight as traits for mate choice (*cf.* BEISENHERZ & RÖMER, 2003; RÖMER & BEISENHERZ, 2005) in clear contrast to the experiments described in READY *et al.* (2006).

In species with promiscuous males, as in the genus *Apistogramma*, females may frequently be courted by both conspecific and heterospecific males [RÖMER & BEISENHERZ, 2005; McPEEK & Gavrillets, 2006; own field observations (UR)]. According to a theoretical model constructed by PFENNIG (1998), males exhibit traits that enable females to separate conspecific from heterospecific, and high-quality males exhibit traits promising fitness that may be beneficial to females or their offspring. Females making mate choice decisions may be unable to

distinguish effectively between high-quality conspecific males and similar heterospecific males. This problem may be even more evident in polygamous species living in sympatry. RÖMER & BEISENHERZ (2005) have previously demonstrated accurate identification of conspecific males by females of different *Apistogramma* species, and recently ENGELKING *et al.* (2010) have done the same for different morphs of conspecific males. In this study we have, again, demonstrated that PFENNIG's assumptions are not valid in *Apistogramma*: Female *Apistogramma* may choose their mates according to a basic, genetically fixed preference for primary traits, that may be critical for partner and / or species recognition. Preference for secondary sexual traits, which may be important for choosing the right mate, can apparently be modified by learning. As mate preference is not totally genetically fixed in *Apistogramma cacauioides* an element of gene flow between different forms should be possible, but on the other hand observation of the paternal phenotype favours mate preference for that phenotype if the offspring are raised by their parents.

"Kidnapping" of fry occurs frequently in most species of *Apistogramma* in captivity (BURCHARD, 1965; DIEKE, 1993; LORENZEN, 1989; RÖMER, 2000, 2001, 2006) and has also been demonstrated for wild populations of some species (RÖMER, 2000, 2001). The kidnapping of fry by breeding females or pairs of fish has usually been regarded as a strategy for reducing the predation risk to their own fry (McKAYE & McKAYE, 1977; LORENZEN, 1989). But a side effect of the kidnapping of conspecific fry by a different colour form may be that "learning" the male phenotype of the adopting form influences mate choice and thus maintains gene flow between different morphs. But females not strictly determined for a certain morph may have a more significant impact on the population genetics.

If, as a result of learning, the offspring – deviating from their genetically fixed preference – prefer males of a different phenotype to those of their own form, it is possible that gene introgressions within the different colour forms may occur more or less frequently. This may lead to a reduction in morphological variation within a given population, or even initiate a process of regressive speciation if species hybridisation is involved. In the genus *Apistogramma* both effects may be realised, as we can observe a number of mainly Amazonian species which have been reported to show extreme colour polymorphism in a small distribution area (e.g. nearly all species of the *Apistogramma agassizii* STEINDACHNER, 1875 and *Apistogramma cacauioides* complexes *sensu stricto*, nomenclature following RÖMER (2006), as well as a number of almost monomorphic species (such as *Apistogramma commbrae* REGAN, 1906, *Apistogramma gossei* KULLANDER, 1982, *Apistogramma hippolytae* KULLANDER, 1982, or *Apistogramma rupununi* FOWLER, 1914) with a comparatively wide distribution. To the best of our knowledge, mate choice preferences have not yet been tested in the latter group of species, which may be a good test case for our conclusions.

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