

Intraspecific colour preference in mate choice by female *Apistogramma cacatuoides* HOEDEMAN, 1951 (Teleostei: Perciformes: Cichlidae)

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> Abstract

In mate-choice experiments females of the Neotropical cichlid *Apistogramma cacatuoides* unerringly differentiate between males of different populations and a red aquarium strain. Females use male colour traits to choose their mates. The preference of wild females for red-coloured males varies from 3 % to 69 % dependent on geographical origin, whereas aquarium-strain females prefer their own bright-coloured males in about 90 % of cases. The preferences of wild females show significant differences depending on their origin and following a geographical gradient. The high degree of stability in assortative mating behaviour in female *A. cacatuoides* may indicate incipient speciation processes.

> Kurzfassung

In Zweifachwahlversuchen differenzieren Weibchen des neotropischen Cichliden *Apistogramma cacatuoides* eindeutig zwischen Männchen verschiedener Populationen und denen eines roten Aquarienstammes. Weibchen nutzen die Farbmerkmale um ihren Partner zu wählen. Die Wahl durch Wildfangweibchen variiert abhängig von ihrem Fundort zwischen 3 % und 69 %, während Weibchen des Aquarienstammes zu etwa 90 % Männchen der eigenen Farbvariante bevorzugen. Das Wahlverhalten der Wildfangweibchen zeigt abhängig von ihrer Herkunft signifikante Unterschiede entlang einer geographischen Kline. Die hohe Stabilität und Selektivität des Wahlverhaltens weiblicher *A. cacatuoides* könnte auf einsetzende Speziationsprozesse schließen lassen.

> Resumen

En experimentos de selección de parejas, las hembras del cichlido neotropical *Apistogramma cacatuoides* logran diferenciar de manera inconfundible entre machos de diferentes poblaciones y machos de una variedad roja cultivada en acuarios. Las hembras usan las características de la coloración para elegir a sus parejas. La preferencia de las hembras capturadas en la naturaleza por los machos de color rojo varía entre 3 % y 69 % dependiendo del origen geográfico, mientras que las hembras cultivadas en acuarios prefieren machos de su mismo color en un 90 % de los casos. La preferencia de las hembras capturadas en la naturaleza varía dependiendo del sitio de origen y sigue un gradiente geográfico. La alta estabilidad y selectividad en la conducta discriminatoria de las hembras de *A. cacatuoides* podría indicar un proceso de especiación insipiente.

> Key words

Speciation, behaviour, reproductive biology, assortative mating, sexual selection, cichlids, Neotropics, Peru.

Prefatory remarks

The Neotropical cichlid *Apistogramma cacatuoides* HOEDEMAN, 1951 is a highly polychromatic species. The species' range is basically restricted to the River

Ucayali basin in the northern half of Cis-Andean Peru and neighbouring Brazil, downriver to the Amazon drainage near Tefé (KULLANDER, 1986; RÖMER, 2000, 2006). In the laboratory wild fish of different origins

as well as domestic strains of variable colour are available. HOHL (2010a & b) presents background data on the origin of various aquarium-hobby colour morphs of *A. cactuoides*.

In mate-choice experiments wild-caught females from the río Algodón (150 km to the north of Iquitos) prefer inconspicuous males of their own morph with high statistical confidence instead of conspicuous males of a red-coloured aquarium strain (RÖMER & BEISENHERZ, 2005). This contradicts the widespread assumption of a general preference for mates with exaggerated traits as signals (DARWIN, 1871; BISCHOFF *et al.*, 1985; BRADBURY & ANDERSSON, 1987; ANDERSSON, 1994; HOUDE, 1997). On the other hand, phylogenetic studies of different animal taxa indicate that secondary sexual characteristics can be lost due to environmental, social, and random factors (reviewed by WIENS, 2001). Hence mate-choice preference for conspicuous traits in different fish species may decrease (FORSGREN, 1992; ENDLER & HOUDE, 1995; GODIN & BRIGGS, 1996), reverse (JOHNSON & BASOLO, 2003), or even disappear (KINGSTON *et al.*, 2003) so that mating happens at random (BERGLUND, 1993; BREDEN & STONER, 1987) and thus deviate from theoretical expectations.

The availability of wild specimens of different origin and coloration as well as of domestic strains offers an opportunity to monitor the way in which female *A. cactuoides* choose their mates.

The importance of colour in communication within and between the sexes of *Apistogramma* species has been demonstrated by RÖMER (2000) and RODRIGUES *et al.* (2009). BEISENHERZ & RÖMER (2005) provide data supporting the influence of colour in inter- and intraspecific mate choice. READY *et al.* (2006) examined the specific status of allopatric *Apistogramma* populations with a similar habitus but differences in coloration.

Allopatric populations may practise assortative mating by colour and thus may have to be seen as different distinct biological species (READY *et al.*, 2006). We will test on *A. cactuoides* whether a preference for inconspicuously-coloured males confirms this general concept or is simply a matter of geographical variation.

Materials and methods

The dwarf cichlid *Apistogramma cactuoides* was used for our standardised dichotomous mate-choice experiments. A detailed description of the cichlid genus *Apistogramma* and the investigated species *A. cactuoides* has been given elsewhere (KULLANDER, 1980; RÖMER, 2000, 2006).

Females and males of *A. cactuoides* are sexually dimorphic and dichromatic. Adult males are significantly larger than females. Additionally they have longer lappets in the dorsal fin and a lyrate caudal fin (Fig. 1). Courting and breeding female *Apistogramma* show a yellowish body with contrasting black markings (Fig. 2).

The diagrams show the correlation between female preference for red-coloured males (red) and the proportion of wild males with red-coloured ornamentation on the caudal fin.

A. cactuoides prefer richly structured areas with scattered driftwood and branches and a thick leaf layer where they can hide and establish their breeding territories (see RÖMER, 2000). Females of most *Apistogramma* species attach their eggs to the upper interior surface of cave-like shelters and perform most of the brood care (for further information see RÖMER, 2000).

In experiments for intraspecific mate choice, wild-caught males and their first and second generation (F₁, F₂) descendants from random spawns with wild-caught females were tested against males from a red-coloured aquarium strain (fig. 3). Males of this captive strain are much more colourful than wild males and exhibit large red or yellow dots or speckles on their dorsal and caudal fins (Fig. in RÖMER, 2000, p. 118). We used wild-stock *A. cactuoides* from different importations and locations, obtained by commercial collectors from four different collecting sites. Wild stock I originated from the río Algodón (150 km to the north of Iquitos) (RÖMER & BEISENHERZ, 2005). Two further wild stocks were collected near Iquitos: wild stock II derived from the río Itaya 20 km northwest of Iquitos, and wild stock III from the río Nanay 3.6 km southwest of Iquitos; specimens of wild stock IV were captured in small tributaries of the río Huallaga about 500 km west of Iquitos.

All fish were kept in the laboratory in water with matching parameters. Temperature, pH, and water hardness were measured electronically. The water was purified by filtration and regular weekly water changes. All fish were fed *ad libitum* with *Artemia* nauplii.

In mate-choice experiments females of *A. cactuoides* were offered two males as potential reproductive partners in experimental tanks (60 × 30 × 30 cm) which were divided into three unequal subunits by two separating glass dividers siliconed in at 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



Fig. 1. *Apistogramma cacatuoides*: typical adult wild male without any red markings on the unpaired fins, collected in the vicinity of Iquitós, Peru.



Fig. 2. *Apistogramma cacatuoides*: typical adult wild female in incipient brood-care coloration. Imported from Iquitós, Peru.

acoustic information, which may be of importance in mate choice in cichlid fishes (SLABBEKOORN *et al.*, 2010), probably had no decisive influence on the experimental results. One female was placed in the larger, central compartment of each aquarium (27 litres, 30 × 30 × 30 cm), and a male in each of the smaller lateral compartments (13.5 litres, 15 × 30 × 30 cm). 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 wild stocks and the domestic strain were randomly placed into the left- or right-hand compartments of the experimental tanks. To exclude size



Fig. 3. *Apistogramma cacatuoides*: typical adult male of the red aquarium strain used in the experiments, with clearly expressed red dots and ocelli in the unpaired fins.

preferences (here taken as total length) as a choice-modifying factor, only males of similar size were offered to a female. Females were randomly 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 with him; this provides irrefutable evidence of their mate-choice behaviour (for detailed description see BEISENHERZ & RÖMER (2006)).

During the experiments all but two females laid their eggs in one of the “caves” next to the glass pane close to one of the displaying males. Therefore a choice was considered made as soon as a female had spawned close to one of the available males. The two exceptions split their clutches between the two caves adjacent to each of the available males.

After spawning, females were transferred from the experimental tanks to other aquaria where they were kept for several days before being retested with different males.

67 females of wild stock I, 44 of wild stock II, 34 of wild stock III, and 13 of wild stock IV were tested in mate-choice experiments. The females chose between males of their own population and males of the

red aquarium strain. In addition, 74 females of the red aquarium strain were tested using males of their own strain and wild stock I.

Differences in preferences between wild-stock and aquarium-stock females, as well as between the wild populations, were tested using Chi-Square and Fisher’s exact tests. Repeated female choice was analysed by McNemar’s Chi-Square for dependent samples.

The frequency of colour ornamentation in male finnage in each wild stock was noted to permit checking for correlation with preferences for red-coloured aquarium-strain males. The coefficient of determination (R^2) and Spearman’s rank correlation coefficient were used to estimate probability of future results. All analyses were processed using the program STATISTICA Version 6.0 (STATSOFT, Tulsa, USA).

Results

Different preferences for red- versus inconspicuously-coloured males were detected in our experiments (Fig 4, Tab. 1). Whereas 97 % of females of wild population I preferred inconspicuously-coloured males of

Tab. 1. Intraspecific mate-choice experiments in female *Apistogramma cacatuoides*. Results for wild populations I–IV and a red aquarium strain (V). Significant differences between female preferences analysed by Chi² (with Yate's correction) and Fisher's exact test (if frequency of choices lower than 6) marked *) (= significant) or **) (= not significant).

females of	choice of male of			choice of out-group male (%)	males with fin ornamentation (in %)	differences in female choice (p-values) to population			
	n	red aquarium population strain	wild population			II	III	IV	aquarium strain
population I	67	2	65	3	3	0.000 *)	0.000 *)	0.000 *)	0.000 *)
population II	45	15	30	33.3	1.1		0.161 **)	0.023 *)	0.000 *)
population III	35	18	17	51.4	12.2			0.220 **)	0.000 *)
population IV	13	9	4	69.2	10.6				0.056 **)
aquarium strain (V)	74	67	7	9.5	100				

Tab. 2. Repeatability of female mate choice in *Apistogramma cacatuoides* of wild populations II and III. Differences were analysed by Chi² test (with Yate's correction) and Fisher's exact test (if frequency of choices lower than 6). Comparison of repeatability of choices between population II and III shows no difference (p = 0.526) (Chi² and Fisher's exact test). Analyses of first and repeated choices by McNemar's Chi² marked *) (= significant difference) or **) (= no significance).

female of	first choice colour preference for	females mate choice for male of					differences in female choice (p-values)	
		n	aquarium strain	wild population	individual repeatability	%	individual repeatability	1 st and 2 nd choice
population II	wild male	21	4	17	17	81		0.000 *)
	aquarium-strain male	10	9	1	9	90		0.023 *)
	∑ =	31	13	8	26	83.9	0.4720 **)	0.749 **) 0,677 **)
population III	wild male	14	3	11	11	78.6		0.000 *)
	aquarium-strain male	14	13	1	13	92.6		
	∑ =	28	16	12	24	85.7	0.2978 **)	0.855 **) 0,845 **)

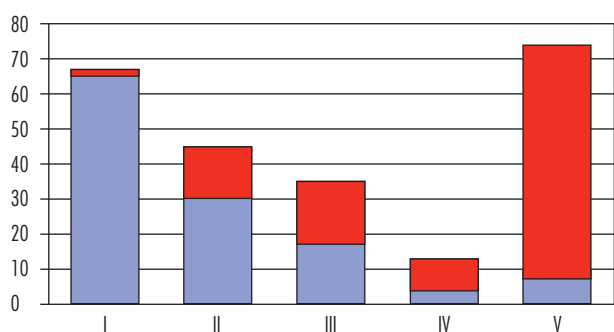


Fig. 4. Intraspecific colour preference of female *Apistogramma cacatuoides*. Results of female mate choice in laboratory experiments using females of four wild populations (I–IV) and an aquarium strain (V). Differences between groups II and III and between groups III and IV are not significant (Chi²-test and Fisher's exact test).

their own population, about 90 % of red aquarium-stock females chose males of their own strain (see also RÖMER & BEISENHERZ, 2005). Females of wild populations II, III, and IV showed a preference for red-coloured males in about 33 %, 51 %, and 69 % cases, respectively (Tab.1).

Individual repeatability of female colour choice was measured to exclude random mate choices. Preference for inconspicuous wild or red-coloured domestic-strain males was repeated in about 84 % of cases in wild stock II, and about 86 % in wild stock III (Tab. 2). This indicates high but not entirely consistent mate-choice behaviour.

In both populations preference for own inconspicuous males was reduced during the repeat experiments, but the differences were not significant (Tab. 2); how-

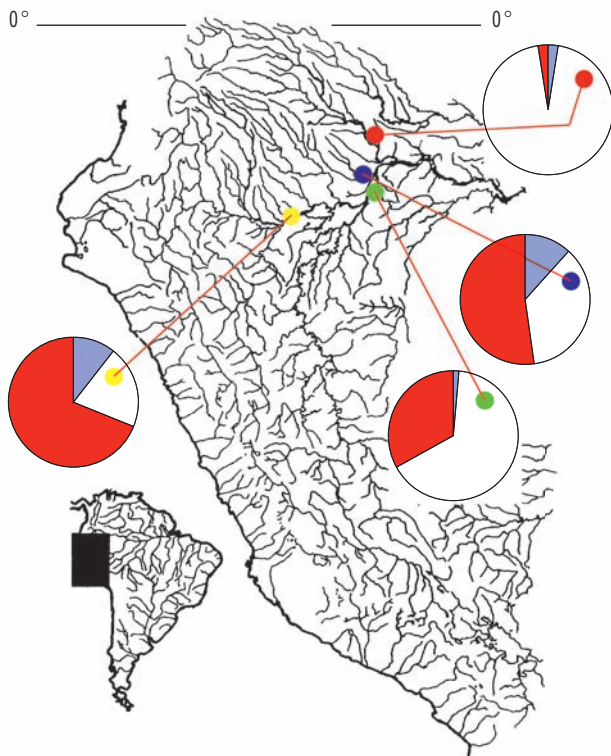


Fig. 5. Origin of *Apistogramma cacatuoides* populations I–IV in the Peruvian Amazon basin (Loreto): red dot: population I; green dot: population II; blue dot: population III; yellow dot: population IV. Red: amount of females choosing outgroup male; light blue: amount of males showing fin ornamentation.

ever, this may simply reflect the comparatively small data set.

Females of the two populations tested increased their preference for red-coloured males by a corresponding amount. In these choice-repetition experiments the preference for red males increased to about 57 % in females of population II, and was about the same as previously at 58 % in females of population III.

There was weak (but not significant) correlation between female choice of brightly-coloured males and frequency of red ornamentation on the caudal fin of own-population males (Fig. 5).

Discussion

In our experiments female *A. cacatuoides* chose their mates on the basis of shape and colour pattern through a glass pane acting as a physical barrier. Thus other signals than visual for mate choice were not available to the females. They laid their eggs next to the preferred male. This experimental design excludes direct male interaction – especially aggression – which may

influence female behaviour (*cf.* BEISENHERZ & RÖMER (2006) and READY *et al.* (2006)).

Our results suggest that different strains and populations of *A. cacatuoides* have different preferences in relation to male colour.

Wild females of different geographical populations showed different degrees of preference for conspicuous red-coloured males; however, only a few wild males in the populations we used in our experiments exhibited red fin ornamentation. The results of experiments with two *A. cacatuoides* populations were consistent on repetition.

While females of wild population I almost exclusively chose their own inconspicuous males, those of populations II, III, and IV showed higher degrees of preference for red-coloured males.

Sexually selected secondary sexual characteristics are genetically determined and vary within and between populations (LANDE, 1981; KIRKPATRICK & RYAN, 1991; BAKKER & POMIANKOWSKI, 1995; BAKKER, 1999; NORRIS & BRADLEY, 1999; BROOKS, 2002; CARVALHO, 2005). Females often prefer males with bright and colourful signals because these signals are indicators of male quality (FISHER, 1915, 1930; WEATHERHEAD & ROBERTSON, 1979; ZAHAVI, 1977, 1975; RYAN, 1990; ANDERSSON, 1994; SARGENT *et al.*, 1998).

The sexes have different investments in reproductive activities. Females usually invest more energy in direct reproduction than do males, as, for example, production of eggs is generally more costly than production of sperm (ANDERSSON, 1994; JENNIONS & PETRIE, 1997; POMIANKOWSKI, 1987). Thus females need to be more selective in their choice of a potential mate. They probably use secondary sexual traits indicating the genetic quality of males, for example colour, size, etc. (KODRIC-BROWN & BROWN, 1984; ANDERSSON, 1994; JENNIONS & PETRIE, 1997; BROOKS & ENDLER, 2001; STEIN & UY, 2006).

Furthermore, the criteria for mate choice may be dependent on geographically determined differences in the environment, which may also influence the direction and intensity of sexual selection (ENDLER & HOUDE, 1995; HOUDE, 1997; JENNIONS & PETRIE, 1997). Thus the different degrees of preference for red-coloured males between populations tested in our experiments may be explained by differences in selective ecofactors, determined by geographical distance.

Different studies indicate that sexually-selected secondary sexual characteristics can be lost (reviewed in WIENS, 2001). In many animal taxa there is a discernible discrepancy between the frequency of female preferences and conspicuous male traits. This indicates that environmental, sociobiological, and random factors may influence the appearance of sexually-selected secondary sexual characteristics differently in females and males (reviewed in WIENS, 2001).

Depending on morphological and/or environmental factors female mate choice may lead to alternative reproductive strategies (ALONZO & SINERVO, 2001; BARLOW, 1973, 2000; BROOKS & ENDLER, 2001; HURTADO-GONZALES *et al.*, 2010; KINGSTON *et al.*, 2003; RIOS-CARDENAS *et al.*, 2007). For instance, heavy predation on conspicuous males may reduce female preference for conspicuous males in a given population. If susceptibility to visual predators reduces the advantages of mating with conspicuous males, this may indirectly lead to reduction of conspicuousness in males (HOUDE & ENDLER, 1990). Alternative mating strategies may be triggered by this type of interaction between female mating preferences and susceptibility to predation within populations (BOND & KAMIL, 2006; GAMBLE *et al.*, 2003; HURTADO-GONZALES *et al.*, 2010). A secondary effect of this interaction may be the stable occurrence of certain secondary sexual traits and colour morphs in given fish populations (HURTADO-GONZALES *et al.*, 2010). HURTADO-GONZALES *et al.* (2010) and LINDHOLM *et al.* (2004) found the same frequency patterns of such traits and morphs across the geographical distribution of the cyprinodont fish species *Poecilia parae*.

The situation is completely different in the polychromatic cichlid species *Apistogramma cacatuoides*: in this species the occurrence of certain colour morphs, especially that involving red blotches in the caudal and the soft portion of the dorsal fin, apparently follows a geographical cline (Fig. 5). In general there is a lack of systematically collected field data on variation in male coloration in *Apistogramma* populations (RÖMER, 2000; RÖMER & BEISENHERZ, 2005; HOHL, 2010), but we have taken data relating to our test populations from numerous imported specimens and have interviewed Peruvian and US-American collectors (*cf.* RÖMER & BEISENHERZ, 2005).

Relating this data to female choice in our experimental fish, differences in preference apparently follow a geographical cline (Fig. 5). Nevertheless, the correlation between female choice and occurrence of fin ornamentation in wild populations is still weak owing to the small sample size.

Mate choice based on colour is important in cichlid fish evolution. Many cichlid radiations, at least in part, involve the evolution through mate choice of secondary sexual characteristics based on colour (BARLOW, 2000; DOMINEY, 1984), in other words female colour preference is responsible for the development and maintenance of colour morphs through mate choice (SALZBURGER *et al.*, 2006).

Various species of the genus *Apistogramma* are widespread throughout the entire neotropical region east of the Andes and are often found sympatric (KULLANDER, 1980, 1986; RÖMER, 2000; 2006). Many *Apistogramma* species exist in various colour morphs, and

on closer examination may turn out to be different genotypic clusters or biological species (READY *et al.*, 2006).

Earlier experiments by RÖMER & BEISENHERZ (2005) have shown that female *Apistogramma* of different species are able clearly to distinguish between conspecific and heterospecific mates. Interestingly they make mistakes regarding potential mates only when potential mates are males of allopatric species. This indicates that mate choice by females may be the key factor in preventing hybridisation and for stabilising genotypic clusters in the wild (KOCHER, 2004; STELKENS *et al.*, 2008; VAN DER SLUIJS *et al.*, 2008a), even if hybridisation has been shown to be a possible mechanism triggering speciation in some African cichlids (EGGER *et al.*, 2007; RÜBER *et al.*, 2001; SALZBURGER *et al.*, 2002; SCHILTHUIZEN *et al.*, 2004; SEEHAUSEN, 2004; SEEHAUSEN *et al.*, 2007; SMITH *et al.*, 2003; STAUFFER *et al.*, 1996; STELKENS *et al.*, 2009; VAN DER SLUIJS *et al.*, 2008b). In our case the clear geographical cline seen in the distribution of males with coloured fin ornamentation and in female assortative mating may indicate the beginning of speciation in *Apistogramma cacatuoides*.

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