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Mate choice based on behavioural type: do convict cichlids prefer similar partners?

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In monogamous species that provide biparental care, partners with similar behavioural types generally have a better reproductive success than dissimilar ones. The pattern of assortative mating for behavioural type is thus often interpreted as resulting from a mate choice process. However, an alternative process is also possible when the partners become similar through postpairing adjustments (behavioural convergence). The disentanglement of these two nonexclusive mechanisms is an important evolutionary question. Only sexual selection based on behavioural similarity before pairing can explain the maintenance of the behavioural type variability. In a previous study, we reported the existence of behavioural convergence for aggressiveness between partners in convict cichlids *Amatitlania siquia*, a monogamous tropical fish. We tested herein the assumption of mate choice based on behavioural similarity for aggressiveness using either short-term binary choice or long-term group level pairing. Pairing was not based on behavioural similarity between potential partners. Choosing a behaviourally compatible partner is a complex task because it requires profiling the potential mates. Individuals would thus achieve higher fitness benefits from choosing a partner on more conspicuous criteria (such as size for instance) and then attempt to increase partner similarity by convergence after pairing. Sexual selection does not appear to drive the maintenance of aggressiveness type variability in convict cichlids.

Benefits from choosing a mate can be either direct due to the behaviours of the partner (e.g. its ability to defend a territory, or to provide food or take care of young) or indirect when the genetic contribution of the partner improves the quality of the offspring (Ihle, Kempenaers, & Forstmeier, 2015). Preferences for a given phenotype can be shared by all same-sex individuals because it reflects the absolute quality of the mate. For instance, female guppies, *Poecilia reticulata*, express a directional preference for bolder males because it reflects the viability of the males (Godin & Dugatkin, 1996). However, this preference can also be relative and varies between individuals (Dechaume-Moncharmont, Freychet, Motreuil, & Cézilly, 2013; Ihle et al., 2015). In this case, individuals choose a partner according to a criterion relative to their own genotype or phenotype (Quinard, Dechaume-Moncharmont, & Cézilly, 2014; Schuett, Tregenza, & Dall, 2010). For instance, preference for a dissimilar mate can promote genetic compatibility between mates because it favours heterozygous offspring (Tregenza & Wedell, 2000). Conversely, preference for a behaviourally similar partner could promote cooperation between partners (Gabriel & Black, 2012). This behavioural compatibility seems particularly relevant for monogamous species with biparental care because partners need to efficiently coordinate parental activities in order to achieve high reproductive success (Ihle et al., 2015; Spoon, Millam, & Owings, 2006). For instance, parents can either synchronize their nest defence and feeding behaviours, or they can make joint visits to their offspring which limits nest localization by predators (Bebbington & Hatchwell, 2015; Burtka & Grindstaff, 2015; Mariette & Griffith, 2012).

A key component of reproductive success is the combination of the partners' behavioural type (Schuett et al., 2010). Behavioural types (also named personality or temperament) are defined by the consistency of interindividual differences for behavioural traits across time or context (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Across a wide range of taxa, individuals are frequently distributed alongside the proactive–reactive continuum used to assign each individual to a discrete behavioural type, either proactive (i.e. aggressive and explorative) or reactive (i.e. less aggressive and less explorative)

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(Réale et al., 2007; Sih et al., 2004). It is tempting to consider a priori that within a mate choice context proactive individuals should always be preferred because they appear more competitive and able to defend the nest than reactive individuals. However, this directional preference is not necessarily expected in species with a long-lasting pair bond. First, reactive individuals may prefer similar partners because they cannot cope with the risk of within-pair aggression (Yabuta, 2008). There is a trade-off between the benefits of pairing with a proactive partner that is highly efficient in nest defence and the costs of pairing with this overaggressive partner resulting in chronic stress, injury or even cannibalism for the individual and its young (Dechaume-Moncharmont et al., 2013; Manica, 2002; Yabuta, 2008). Second, the behavioural types can correspond to different strategies of parental care (Réale et al., 2007). Proactive parents may locate and monopolize the best territory more efficiently than reactive individuals which, for their part, could be more flexible in their response to unstable environments and invest more in direct parental care (Bergmüller & Taborsky, 2010; Duckworth, 2006; Koolhaas et al., 1999). Having a similar parental style can thus increase coordination between the parents and the reproductive success of the pair (Both, Dingemanse, Drent, & Tinbergen, 2005; Burtka & Grindstaff, 2015; Gabriel & Black, 2012; Harris & Siefferman, 2014; Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016; Rangassamy, Dalmas, Féron, Gouat, & Rödel, 2015; Schuett, Dall, & Royle, 2011).

The fitness benefits experienced by similar pairs should favour the evolution of relative (also called self-referent or homotypic) preferences leading to a pattern of assortative mating at the population level (Carere, Drent, Privitera, Koolhaas, & Groothuis, 2005; Schuett, Godin, & Dall, 2011; Schuett et al., 2010). Therefore, a preference for a similar partner could be an evolutionary force maintaining the diversity of the behavioural types (Schuett et al., 2010). The persistence of within-population variance in terms of personality traits is a strongly debated question and several mechanisms have been proposed so far (Dall, Houston, & McNamara, 2004; Réale et al., 2007; Schuett et al., 2010). One of these possible mechanisms emphasizes the role of sexual selection based on relative preferences leading to assortative mating (Ingley & Johnson, 2014; Schuett et al., 2010). Such assortative mating may have major evolutionary consequences because it may favour reproductive isolation between phenotypically divergent individuals, and may ultimately lead to speciation (Jiang, Bolnick, & Kirkpatrick, 2013; Rodríguez et al., 2013; Van Doorn, Edelaar, & Weissing, 2009). Note, however, that the observation of a pattern of assortative mating cannot be straightforwardly interpreted as evidence for a relative preference (Galipaud, Bollache, & Dechaume-Moncharmont, 2013; Galipaud, Bollache, Wattier, Dechaume-Moncharmont, & Lagrue, 2015; Taborsky, Guyer, & Taborsky, 2009). An alternative and nonexclusive mechanism is that initially dissimilar partners become similar after pair formation, which has been called behavioural convergence (Burley, 1983; Laubu et al., 2016). The existence of this convergence has been reported in at least one monogamous fish species, the convict cichlid *Amatitlania siquia* (Laubu et al., 2016). Consequently, the maintenance of personality traits by sexual selection cannot be inferred from the sole pattern of assortative mating. Thus, to properly investigate this question it is necessary to distinguish between selection before pairing (mate choice based on consistent heritable traits) and behavioural adjustment after pairing (convergence assuming behavioural flexibility). Only nonrandom pairing, i.e. arising from a relative preference without behavioural convergence after pairing, can account for the maintenance of behavioural type diversity by sexual selection (Schuett et al., 2010).

We investigated the interplay between behavioural type and mate choice in the convict cichlid *A. siquia*, a model species for studies on both sexual selection (Bloch, Estela, Leese, & Itzkowitz, 2016; Galipaud et al., 2013; Lee-Jenkins, Smith, Wisenden, Wong, & Godin, 2015) and personality (Jones & Godin, 2010; Mazue, Dechaume-Moncharmont, & Godin, 2015; Moscicki & Hurd, 2015; Moss et al., 2015; Schweitzer, Motreuil, & Dechaume-Moncharmont, 2015). More specifically, we assessed the relative preference for a similar partner in male and female cichlids.

In this territorial fish, the pair bond lasts several weeks after spawning, and both parents actively care for the offspring from the egg stage to free-swimming fry (Keenleyside, Bailey, & Young, 1990; Snekser, Santangelo, Nyby, & Itzkowitz, 2011). Parents synchronize their behaviours to guard the nest and chase away intruders because the offspring are highly vulnerable to predation and cannibalism from conspecifics (Alonzo, 2001; Gumm & Itzkowitz, 2007; Nicholas Santangelo, 2015; Wisenden, 1994; Wisenden et al., 2016). Parental coordination for defensive behaviours is thus under strong selection (Lamprecht & Rebhan, 1997; Wisenden, 1994). When observed after pairing, partners appeared more similar in terms of behavioural type than expected in the case of random mating, and the more similar partners had a higher reproductive success than dissimilar ones (Budaev & Zworykin, 2002; Budaev, Zworykin, & Mochek, 1999; Laubu et al., 2016). The pattern of assortative mating can, at least partially, be explained by a process of convergence after pairing: dissimilar partners can converge after pair formation to increase their similarity and thus improve their reproductive success (Laubu et al., 2016). Therefore, the mechanism leading to assortative mating in this species is complex and does not necessarily imply a strong relative preference for behaviourally similar partners. It is thus crucial to test whether a strategy involving sexual preference for a similar partner before pairing coexists with convergence after pairing.

We estimated the behavioural type of our fish from measurements of their aggressive behaviour. First, this behaviour is ecologically relevant in a reproductive context as there is strong predation pressure against the fry in this species (Wisenden, 1994). A key component of the pair's reproductive success is their ability to coordinate their nest defence behaviour. The first phase of courtship behaviours is dominated by aggressive displays (Baerends, 1986) which could be a cue for the coordination ability of the potential partners. Second, in previous studies, we validated the aggressiveness score as a relevant proxy for the proactive–reactive score in convict cichlids (Laubu et al., 2016; Schweitzer et al., 2017, 2015). In the present study, mate choice for behavioural type was assessed on two scales. The first experiment assessed the existence of a group level pattern of assortative mating for behavioural type. It was performed in large tanks in which profiled individuals could pair freely based on mutual mate choice. The aim of the second experiment was to evaluate the sexual preference at the individual level in both sexes in the absence of intrasexual competition. It was performed using a standardized binary choice protocol in which one focal individual had to choose between one similar and one dissimilar partner. The preference was assessed in both sexes because mutual mate choice is expected in this monogamous species with prolonged biparental care of the young (Santangelo & Itzkowitz, 2004).

METHODS

Study Animals and Housing Conditions

Individuals came from the breeding stock of the University of Burgundy, France, which originally came from local commercial distributors. All fish were sexually mature and individually marked with passive integrated transponder (PIT) tags. They were housed in same-sex tanks (96 litres, 15–20 fish per tank) at 25 ± 1 °C, under a 12:12 h light:dark cycle. The fish were fed daily with Cichlid XL flakes (Tetra, Berlin, Germany). The sexes were kept separate for at least 6 months before starting the mate choice experiments in order to ensure sexual receptivity. Four to five days before the beginning of the profiling test, fish were isolated in a 20-litre tanks with opaque dividers (40 × 20 cm and 25 cm high). Each tank was equipped with an artificial shelter (a tube that was 8 cm in diameter), an air stone and gravel substrate. Fish were profiled and then returned to their original 96-litre tank with the same conspecifics. The mate choice tests were performed between 30 and 60 days after the profiling phase.

Behavioural Profiling of the Individuals

The aggressiveness scores of 265 adult convict cichlids was assessed in two groups of different fish corresponding to the two experiments described below: the group level experiment (females: $N = 60$, mean standard body length ± SD = 46 ± 4 mm; males: $N = 60$, mean body length ± SD = 60 ± 4 mm) and the individual level experiment (females: $N = 85$, mean body length ± SD = 49 ± 5 mm; males: $N = 60$, mean standard body length ± SD = 61 ± 8 mm). We followed the standard procedure described by Arnott and Elwood (2009), Schweitzer et al. (2015) and Laubu et al. (2016). Briefly, we staged intrasexual agonistic encounters between isolated individuals and suddenly disturbed the agonistic interaction in order to measure the startle response. The test began by pushing two visually isolated adjacent tanks together and removing the opaque divider between them, enabling the focal fish to interact with the stimulus. After the first agonistic interaction, the focal fish was startled by dropping a 4.95 g glass marble on top of the tank. The marble landed behind a narrow opaque tape on the wall separating the two fish in such way that only the focal fish was startled by the marble drop. We recorded the latency to resume an agonistic interaction after the startle and the frequency of agonistic behaviours (extended gills, lateral and frontal displays and attempted bites). Agonistic behaviours were scored with the event-recording program JWatcher (Blumstein & Daniel, 2007). All tests were recorded using a CCD professional 21 series camcorder (The Imaging Source, Bremen, Germany) equipped with a CCTV lens (2.8–12MM, F1.3, Computar, Commack, NY, U.S.A.). We assessed the repeatability of this aggressiveness test after a 1-week interval with another opponent. To limit the number of tests, we only performed this measurement on fish from the second group (60 males and 60 females). The level of repeatability for these tests was high (see Appendix Table A1) and consistent with the values previously reported in the same species (Laubu et al., 2016; Schweitzer et al., 2017, 2015). To limit the risk of type I error, we reduced the dimensionality of these measurements to only one score through a principal component analysis (PCA; see Appendix Table A2). As in previous studies (Laubu et al., 2016; Schweitzer et al., 2017, 2015), the first axis of the PCA was considered as a relevant synthetic score according to the percentage of variance explained (55.1% and 43.7% for the two experiments, respectively, see Appendix Table A2) and because its eigenvalue was greater than 1 (Manly, 2004, p. 103). In addition, this score was the main component of the proactive–reactive syndrome (Laubu et al., 2016; Schweitzer et al., 2017, 2015). Therefore, we used it as a proxy to quickly characterize a large number of individuals ($N = 265$) along the proactive–reactive continuum. Negative values indicate proactive individuals and positive values reactive ones.

Experiment 1: Mutual Mate Choice at the Group Level

The aim of this first experiment was to assess the preference for behavioural traits at the group level based on the measurement of the strength of the assortative mating resulting from mutual choice. Mutual mate choice is expected in species characterized by a long-lasting pair bond (Courtiol, Etienne, Feron, Godelle, & Rousset, 2016). Our experimental set-up was thus designed to let groups of males and females freely interact together over a period of several days (Keenleyside, 1985). The observation of a significant pattern of positive assortative mating could indicate relative preferences (Puebla, Bermingham, & Guichard, 2012). The study was conducted under controlled conditions with fish that were behaviourally profiled before the experiment in order to discern the effect of a preference before pairing from the confounding effect of convergence after pairing. As our experimental facilities could house up to 24 fish in the same tank, we replicated the experiment five times. Previously profiled males and females were randomly sampled from our stock regardless of their body length or behavioural type. We only verified that the sex ratio was balanced and that there was no sibling in a given replicate to avoid any confounding effect due to preferences based on relatedness (Szulkin, Stopher, Pemberton, & Reid, 2013). These constraints limited the group size in each replicate: 12 males and 12 females for replicates A and C, and 10 males and 10 females for replicates B, D and E. These five replicates did not differ in terms of the average behavioural score (see Appendix Fig. A1a; females: $F_{4,49} = 1.872$, $P = 0.130$; males: $F_{4,49} = 0.861$, $P = 0.494$) or body length (see Appendix Fig. A1b; females: $F_{4,49} = 1.349$, $P = 0.265$; males: $F_{4,49} = 1.020$, $P = 0.406$). For each replicate, the individuals were simultaneously introduced into a 450-litre tank (150 × 50 cm and 60 cm high) containing gravel substrate, artificial plants, rocks and air stones. The tank was divided into the same number of territories as females (see Appendix Fig. A2a). Each territory was freely accessible and included an artificial nest. To limit the number of nest defence behaviours and to ease the settlement of the pairs, the territories were separated by opaque partitions (30 × 50 cm) which rose vertically from the bottom of the tank up to the water surface. Individuals were allowed to interact freely with each other and form pairs. A stable pair was defined when partners defended their territory together against conspecifics without partner-oriented agonistic behaviour, stayed close to the nest and performed active nest maintenance. The tank was visually inspected twice a day and the latency to pair was noted. At the end of the 6th day, pairs and single individuals were captured and identified. This duration was determined from unpublished preliminary experiments with different individuals. It was long enough for the majority of fish to form pairs while preventing unsuccessful individuals that were still unpaired after 6 days to finally accept a second-choice partner. Such late choices may result in an underestimation of the strength of assortative mating (Gimelfarb, 1988).

Experiment 2: Binary Choice at the Individual Level

While experiment 1 favoured mutual mate choice and assortative pairing, individual preferences for a behavioural trait may have been underestimated in experiment 1 because pairing at the group level is a complex process that involves multiple cues and the confounding effect of intrasexual competition. In experiment 2, we therefore assessed mate preference at the individual level using a classic binary choice apparatus (Wagner, 1998). The focal individual had to choose between two stimuli of the opposite sex with contrasted behavioural scores, i.e. either a similar or dissimilar fish (Fig. 1). The difference in behavioural scores between the focal individual and the similar stimulus was smaller than half of the standard deviation of the distribution of the behavioural score of all the individuals profiled for this experiment, and the difference between the focal individual and the dissimilar stimulus was larger

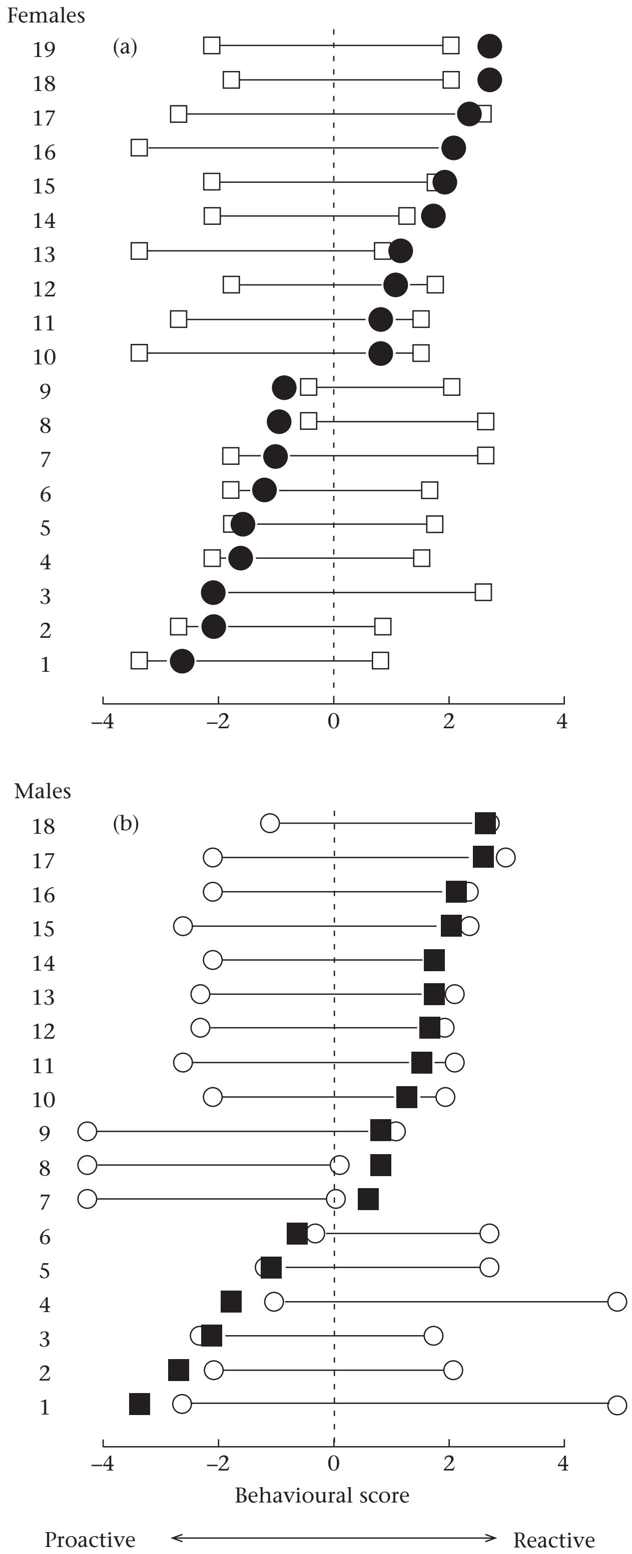

Figure 1. Composition of the triplets (one focal individual and two stimulus individuals of the opposite sex) used in experiment 2 based on their behavioural score. (a) In the female choice experiment ($N = 19$), the focal female (solid circle) had to choose between a similar and dissimilar male (open squares). (b) In the male choice experiment ($N = 18$), the focal male (solid squares) had to choose between a similar and dissimilar female (open circles). The stimuli differed in terms of the behavioural score but not in body length (see details in the text).

than twice the standard deviation. In experiment 1, the strength of assortative mating for body length appeared stronger than for behavioural type (see below), and a marked preference for body length was expected in this species (Alonzo, 2001; Dechaume-Moncharmont et al., 2013). In experiment 2, we therefore decided to carefully control for the body length of the two stimuli in addition to a criterion based on their behavioural score. First, the body length difference between the two stimuli was always smaller than 5 mm. Second, sexual dimorphism was also controlled, where males were 10–50% larger than females, which corresponds to the ideal male/female size range in this species (Dechaume-Moncharmont et al., 2013). Each pair of stimuli was used only once. Owing to the constraining conditions related to the behavioural scores and body lengths of both the focal fish and stimuli, we managed to record the preference of 19 females (nine defined as proactive and 10 as reactive) and 18 males (six proactive and 12 reactive).

The binary choice arena was a 96-litre rectangular tank (80 × 30 cm and 40 cm high) partitioned into four compartments (see Appendix Fig. A2b): one compartment for each stimulus, one compartment for the acclimation of the focal individual and one large compartment. Stimuli were placed in their respective compartments 24 h before the test in order to let them establish their territory. The compartment of each stimulus was equipped with an artificial nest, an air stone and gravel substrate. Opaque partitions avoided any agonistic or dominance behaviour between the stimuli. The focal individual was placed in the acclimation zone for 10 min and then the opaque partition was gently removed from a distance with a pulley system to let the focal individual enter the large compartment where it could move freely in front of each stimulus compartment. The large compartment was virtually delineated into three areas: one association area in front of each stimulus compartment and one neutral area (see Appendix Fig. A2b). The time spent in each association area was recorded for 15 min. We also assessed the mate-sampling strategy of individuals from the number of visits to the stimuli and the proportion of time spent in the neutral area.

Statistical Analysis

All statistical analyses were performed using the R 3.3.1 software (R Core Team, 2016). The strength of the assortative mating (for behaviour or body length) in experiment 1 was estimated with the Pearson correlation coefficient (Arnqvist, Rowe, Krupa, & Sih, 1996; Galipaud et al., 2015; Jiang et al., 2013). This coefficient was calculated separately for each of the five replicates. We also calculated pooled coefficients using DerSimonian and Laird fixed-effect meta-analysis based on Fisher's z-transformation of the correlations (Borenstein, Hedges, Higgins, & Rothstein, 2009, pp. 79–86) using the R package 'meta' (Schwarzer, 2016). To analyse the effects of the behavioural score or body length on the latency to pair, we used a mixed-effect Cox model with the replicate as a random variable. To assess the effect of the partner's similarity on latency to pair, we computed a similarity index S using the behavioural scores of the two partners: $S = |\text{Score}_{\text{male}} - \text{Score}_{\text{female}}|$. In experiment 2, the preference index P was calculated to assess the preference of the focal individual for a given stimulus (e.g. preference index for the similar stimulus, preference index for the proactive stimulus). It was defined as the proportion of time the focal individual spent in the association area of this stimulus divided by the total amount of time spent in the two association areas. A preference index higher than 50% indicated a preference for this stimulus. This measure has been shown to be a reliable predictor of the observed sexual preference in convict cichlids

(Dechaume-Moncharmont et al., 2011). The preference index was modelled using beta regression (Cribari-Neto & Zeileis, 2010) with the classical transformation $P' = ((n-1)P + 0.5)/n$ in order to comply with the beta regression assumption stating that the data are within the interval]0;1[(Monestier et al., 2016; Smithson & Verkuilen, 2006). To test whether the focal fish expressed a preference for a given stimulus, we calculated the strength of its preference defined as the preference index for the preferred stimulus (regardless of its behavioural type). By definition, this strength of the preference was larger than 50% and could be compared with previously reported values (Dechaume-Moncharmont et al., 2011, 2013). Each preference (preference for the similar partner, preference for the proactive partner, preference for the preferred stimulus) was analysed using the full model including the sex of the chooser, the behavioural score of the chooser and the interaction term between these two variables. We used a negative binomial generalized linear model to analyse the number of visits to the stimuli. The full model also included the sex of the chooser, the behavioural score of the chooser and the interaction term between these two variables. For each model, we identified the covariates with a significant effect by sequentially comparing the nested submodels (i.e. the two models including or not a given covariate) and backward stepwise elimination of nonsignificant variables or interaction term.

Ethical Note

Animal care and all experimental procedures were approved by the French Ministry of Research and Higher Education and the University of Burgundy Ethical Committee (approval number: 2016091911439315_v1#6788). There were no lesions or mortalities associated with the experimental procedures.

RESULTS

Experiment 1: Mutual Mate Choice at the Group Level

After 6 days of free interactions between males and females in the 450-litre tanks, on average eight stable pairs were formed in each replicate (number of pairs out of the maximum number of possible pairs in the replicates: A: 8/12; B: 9/10; C: 8/12; D: 7/10; E: 8/10). We did not observe either homosexual or polygamous behaviours. There was no significant assortative mating for the behavioural score (Fig. 2a; pooled Pearson correlation coefficient: $r = 0.142$, 95% confidence interval, CI [−0.244; 0.489], $P = 0.473$). The latency to pair was not explained by the individuals' behavioural score in either females (mixed-effects Cox model: $\chi^2_1 = 1.715$, $P = 0.190$) or males ($\chi^2_1 = 1.483$, $P = 0.223$). Individuals that were still unpaired at the end of the experiment did not differ in behavioural scores from the paired individuals (females: $\chi^2_1 = 2.859$, $P = 0.091$; males: $\chi^2_1 = 1.862$, $P = 0.172$). The latency to pair was not explained by the similarity between partners ($\chi^2_1 = 0.763$, $P = 0.383$). As a mate choice based on body length was expected (Dechaume-Moncharmont et al., 2013), we also assessed the strength of the assortative mating for body length. It was consistent with previous studies (Alonzo, 2001; Wisenden, 1995) and tended to be larger than for the behavioural score, although nonsignificant (Fig. 2b; pooled $r = 0.341$, 95% CI [−0.037; 0.634], $P = 0.076$). Males that remained single were significantly smaller than paired males ($\chi^2_1 = 12.706$, $P < 0.001$; single males: mean body length = 56 mm, 95% CI [53; 58 mm]; paired males: mean body length = 62 mm, 95% CI [60; 64 mm]), and the latency to pair decreased significantly with the increase in male body length ($\chi^2_1 = 10.399$, $P = 0.001$). The opposite trend was observed in females, although nonsignificant: paired females tended to be smaller than single females ($\chi^2_1 = 3.621$, $P = 0.057$; single females: mean body length = 48 mm, 95% CI [46; 50 mm]; paired females: mean body length = 45 mm, 95% CI [44; 47 mm]). The latency to pair was not significantly explained by female body length ($\chi^2_1 = 2.105$, $P = 0.147$).

Experiment 2: Binary Choice at the Individual Level

Focal individuals did not significantly prefer the similar stimulus. On average, they spent 54.9% (95% CI [48.2; 61.7%]; $t_{36} = 1.406$, $P = 0.168$) of their time on the side of the similar stimulus (Fig. 3a). There was no effect of the focal individual's behavioural score ($F_{1,36} = 0.214$, $P = 0.647$) or sex ($F_{1,36} = 0.461$, $P = 0.502$) nor was there an interaction between these covariates ($F_{1,34} = 0.011$, $P = 0.919$) on the preference index for the similar stimulus (Fig. 3a). We also tested for a directional preference. Focal individuals did not significantly prefer one type of mate (preference index for the proactive stimulus = 47.8%, 95% CI [40.6; 54.5%]; t test: $t_{36} = -0.629$, $P = 0.533$). There was no effect of the focal individual's behavioural score ($F_{1,36} = 1.401$, $P = 0.245$) or sex ($F_{1,36} = 0.078$, $P = 0.782$) nor was there an interaction between these covariates ($F_{1,34} = 0.064$, $P = 0.802$) on the preference index for proactive partner. This absence of preference for behavioural type did not indicate a weak preference because the focal individuals expressed clear preferences: on average, they spent 66.6% (95% CI [62.2; 71.2%]) of their time in front of the preferred stimulus (Fig. 3b). This strength of preference was not explained by the focal individual's behavioural score ($\chi^2_1 = 0.570$, $P = 0.450$) or sex ($\chi^2_1 = 0.617$, $P = 0.432$) or the interaction between these covariates ($\chi^2_1 = 0.310$, $P = 0.577$). Finally, we assessed the influence of the focal individual's behavioural type on its mate-sampling strategy. There was no influence of the focal individual's behavioural score ($\chi^2_1 = 0.094$, $P = 0.759$) or sex ($\chi^2_1 = 2.316$, $P = 0.128$) nor was there an interaction between these covariates ($\chi^2_1 = 2.204$, $P = 0.138$) on the number of visits to the stimuli. Likewise, the time spent in the neutral (no choice) area was not explained by the focal individual's behavioural score ($F_{1,36} = 0.413$, $P = 0.525$) or sex ($F_{1,36} = 0.954$, $P = 0.335$) or the interaction between these covariates ($F_{1,34} = 0.627$, $P = 0.434$).

For both experiments, we also analysed our data with the total number of aggressive behaviours per unit of time instead of the behavioural score derived from the PCA. The two metrics were highly correlated (group level experiment: $r = -0.982$; 95% CI [−0.987; −0.975]; individual level experiment: $r = -0.958$; 95% CI [−0.980; −0.961]) and we obtained similar results (see Appendix Table A3).

DISCUSSION

The two experiments, one at the group level and the other at the individual level, provide evidence that the behavioural type of the partner is not a mate choice criterion in the convict cichlid. Not only were the preferences for a similar partner nonsignificant, but the values of the effect size were also low which indicate that if there is a preference for behavioural type it would be a weak preference.

In the group level experiment, individuals could freely interact and form pairs based on mutual mate choice. Individuals had the opportunity to gauge the behavioural profile of potential mates for a long time and across several contexts including intrasexual competition, nest defence and courtship (Ariyomo & Watt, 2013). However, preference for a behavioural type might have been

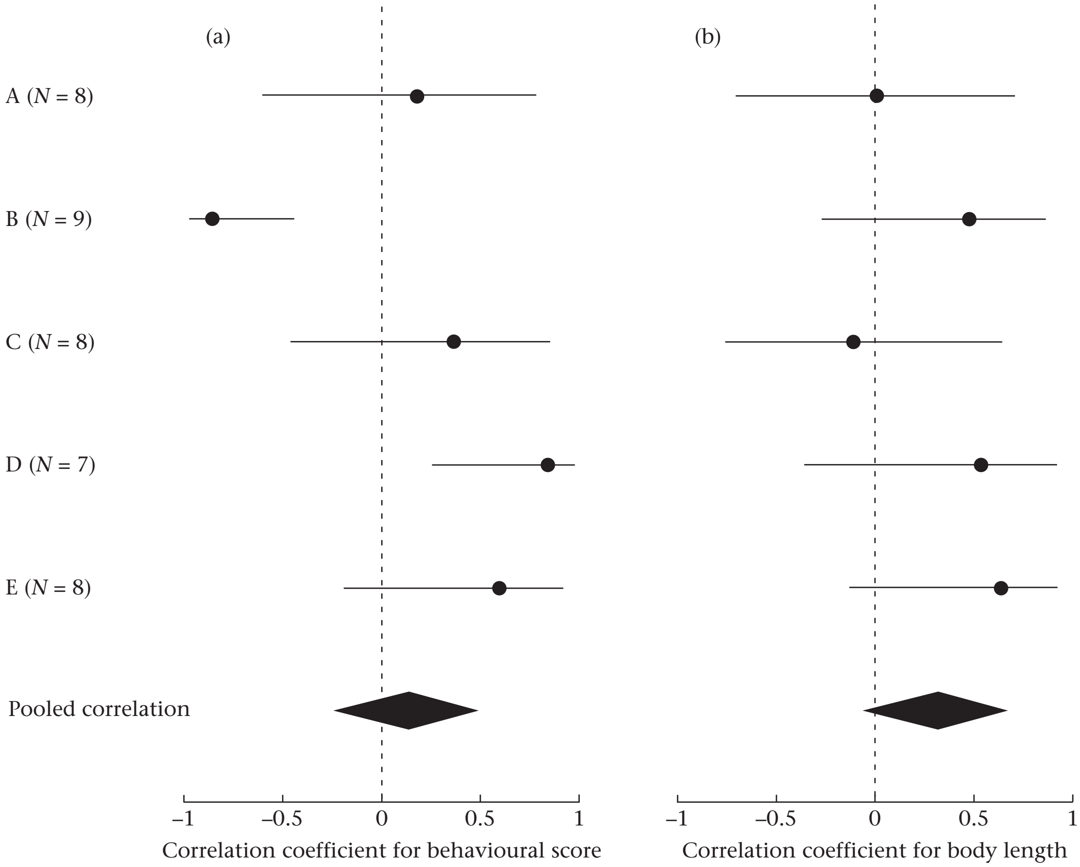

Figure 2. Strength of assortative mating measured as the Pearson correlation coefficient (±95% CI) between (a) the partners' behavioural scores and (b) the partners' body lengths for the five replicates (A, B, C, D and E) of the group level experiment. For each replicate, the number of pairs is given in parentheses. The pooled correlation coefficient (±bootstrapped 95% CI indicated by the range of the diamond) was calculated using Fisher's z-transformation.

underestimated due to confounding factors associated with this set-up mimicking natural conditions (Wagner, 1998). First, the presence of competitors may have reduced the choosiness because the sampling strategy is affected by the trade-off between the benefits associated with finding a high-quality partner and the opportunity costs arising from the sampling (Dechaume-Moncharmont, Brom, & Cézilly, 2016; Etienne, Rousset, Godelle, & Courtiol, 2014). In monogamous species, even an unbiased operational sex ratio is a strong enough competitive situation to inhibit the expression of any mate preference. In such a case, chooser individuals may have no other choice than to pick a partner randomly in order to secure reproduction, whereas they can express a stronger preference in less stringent conditions of competition (Dechaume-Moncharmont et al., 2016). Second, behavioural type may be only one mate choice criterion among multiple others that are more or less relevant to assessing mate quality (Candolin, 2003). The decision could be based on the hierarchical assessment of these cues (Brandstätter, Gigerenzer, & Hertwig, 2006). For instance, body length is known to have an important role in sexual choice for both sexes in convict cichlids (Bloch et al., 2016; Dechaume-Moncharmont et al., 2013; Nuttall & Keenleyside, 1993). The individual may thus prioritize morphological criteria because these cues are quicker and easier to assess accurately than behavioural traits. In contrast to behavioural traits, these cues are not plastic and would not change unpredictably after pairing. In addition, they have been reported to be relevant proxies for skills in terms of nest defence, parental care and even coordination between partners (Gagliardi-Seeley & Itzkowitz, 2006). In the first experiment, individuals differed in both body length and behavioural type. This protocol not only allowed the assessment of assortative mating per behavioural type, but it could also be used for a comparison with assortative mating for body length. The strength of assortative mating for body length was twice the value of that for behavioural type. In addition, there was a sex-specific effect of body length on the pairing status. Unpaired males were smaller on average than paired males, and the pattern was the opposite for females. This is consistent with the ideal size ratio between partners in this species where the ideal male is larger than the female (Bloch et al., 2016; Dechaume-Moncharmont et al., 2013). This ‘male-taller norm’ (Courtiol, Raymond, Godelle, & Ferdy, 2010; Gillis & Avis, 1980; Stulp, Buunk, Pollet, Nettle, & Verhulst, 2013) leads to a pairing pattern where smaller males and larger females remain unpaired at the end of the mate choice process.

If it even exists at all, the preference for behavioural type was weaker than the preference for body length in the group level experiment. In the second experiment, we therefore assessed the preference for behavioural type by controlling for the body length of the stimuli. Such binary choice set-ups are expected to provide a better assessment of individual preference than a more natural

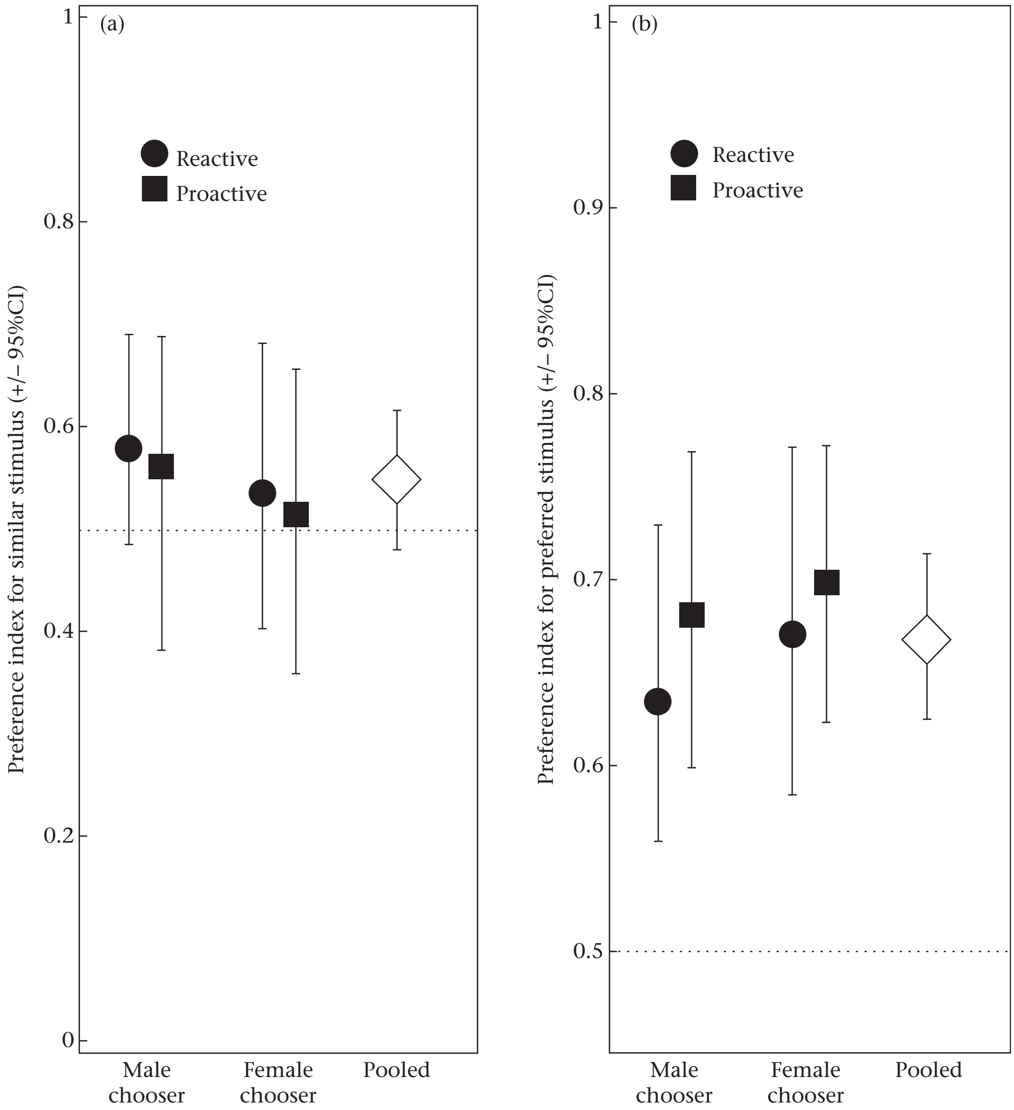

Figure 3. (a) Preference index measured as the proportion of time spent on the side of the similar stimulus as a function of the sex of the focal individual and its behavioural type, and for all focal individuals pooled (white diamond). The horizontal dotted line indicates the absence of preference: a preference index significantly larger than 0.5 corresponds to a preference for the similar stimulus, and a value lower than 0.5 corresponds to a preference for the dissimilar stimulus. (b) Strength of the preference measured as the proportion of time spent on the side of the preferred stimulus (defined as the stimulus in front of which the focal fish spent more than 50% of its time). The higher the value, the stronger is the preference. The error bars correspond to bootstrapped 95% confidence intervals which allow direct significance tests.

set-up based on free interactions between partners at the group level (Wagner, 1998). Instead of recording the choice made under competition conditions, we measured the preference of a single focal fish in controlled conditions in the absence of competitors. This individual could freely compare the two stimuli without being exposed to intrasexual competition. In this case, the behavioural score of the individuals also did not play a significant role in the pairing decision. Focal fish did not show either a relative preference for the similar partner or a directional preference for one specific behavioural type. However, the focal individual did prefer one of the two stimuli, with a preference index consistent with previous experiments in similar set-ups (Dechaume-Moncharmont et al., 2011, 2013). These results can be interpreted as the ability of fish to discriminate between two stimuli based on the assessment of criteria other than size or aggressiveness, such as other morphological or behavioural traits (Schweitzer et al., 2015). It is still possible that the absence of preference for the partner's aggressiveness reported herein resulted from the limited sample size or experimental noise during the behavioural profiling of the fish, but even this case, it indicates that the preference for the behavioural type should be considered as weak in this species.

This experiment also addressed the question of the influence of the chooser's behavioural type on its sampling strategy (David & Cézilly, 2011). Several authors have predicted that proactive individuals paired first due to their cognitive style favouring rapid choice, whereas reactive individuals take longer to make a choice based on a longer assessment of the alternatives (Schuett, Godin, et al., 2011; Sih & Del Giudice, 2012). We therefore expected to observe this difference within a mate choice context. However, contrary to David and Cézilly (2011), we did not find any difference in sampling strategy between reactive and proactive choosers. They did not differ in either sampling strategy or strength of preference. This may be explained by the difference in cognitive complexity between these two studies. In the experiment carried out by David and Cézilly (2011), female zebra finches, *Taeniopygia guttata*, had to choose between four partners, whereas in our study there were only two potential mates and the travelling cost from one stimulus to the other was relatively low. This binary choice may have reduced the complexity of the cognitive task involved in the decision process (Ryan, Akre, & Kirkpatrick, 2007). The sampling task was more complex and the conditions were more ecologically relevant in the first experiment but we did not manage to continuously record the sampling behaviour of all individuals during the complete experimental period. Further work is therefore required to specifically assess the effect of the chooser's personality on its mate-sampling strategy. The effort in assessing potential mates, in terms of both the number of mates sampled and the amount of time spent examining each one, should be investigated in several mate choice tests that vary in complexity to assess the existence of a possible speed—accuracy trade-off linked with the behavioural type of the chooser.

Finally, we conclude that behavioural similarity does not play a crucial role in the sexual choice of individuals in this species. This result differs from previous observations of preference for similar partners in two monogamous birds with biparental care, the zebra finch and great tit, *Parus major* (Carere et al., 2005; Schuett, Godin, et al., 2011). At least one other study has reported preferences consistent with our results. In the guppy, females did not prefer similar males, which was unexpected because, in this species, the behavioural similarity between partners was also positively correlated with reproductive success (Ariyomo & Watt, 2013). Further work is required to address the question of behavioural assortative mating in monogamous species. Given the evolutionary importance of sexual selection, behavioural ecologists should pay attention to this question. If there is no preference for behavioural type, the maintenance of these behavioural types could not result from a mate choice process. The sole observation of a pattern of assortative mating in the field does not imply sexual selection for similar mates. Here, the absence of a strategy for assortative mating before pairing highlights the importance of adjustments between partners after pairing to improve their coordination. Behavioural convergence may be a more efficient way for partners to coordinate parental care than searching for an initially similar mate which can be very costly (Dechaume-Moncharmont et al., 2016). Therefore, the process of mate choice does not appear to be an explanation for the evolution and maintenance of behavioural types in convict cichlids.

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Appendix

Table A1
Repeatability of aggressiveness behaviours

Aggressiveness variables	Repeatability	
	Females	Males
Extended gills	R=0.37 [0.06; 0.66]	R=0.50 [0.26; 0.66]
Frontal displays	ρ=0.40 [0.14; 0.60]	ρ=0.32 [0.05; 0.58]
Lateral displays	R=0.56 [0.34; 0.74]	R=0.49 [0.29; 0.70]
Attempted bites	ρ=0.52 [0.27; 0.72]	ρ=0.58 [0.36; 0.75]
Latency	ρ=0.25 [0.01; 0.46]	ρ=0.10 [−0.20; 0.38]

Repeatability (with 95% confidence intervals given in brackets) for the five variables of aggressiveness over a 1-week interval was assessed for the group of fish used in the second experiment (60 females and 60 males). It was estimated either by the intraclass correlation coefficient R (Nakagawa & Schielzeth, 2010) when possible, or by rank repeatability based on Spearman correlations ρ when the behavioural traits did not meet the assumptions for the parametric estimation of repeatability.

Table A2
Loadings of aggressiveness behaviours on principal component analysis

	First group			Second group		
	PC1	PC2	PC3	PC1	PC2	PC3
Gills	−0.54	0.06	−0.39	−0.62	−0.018	−0.18
Frontal displays	−0.40	−0.58	0.17	0.17	0.74	0.31
Lateral displays	−0.52	0.14	−0.49	−0.36	0.11	0.79
Attempted bites	−0.46	−0.17	0.65	−0.64	−0.05	−0.03
Latency	0.27	0.78	−0.39	0.20	−0.66	0.50
% Variance explained	55.1	21.1	12.7	43.7	26.4	20.1
Eigen value	1.66	1.03	0.80	1.48	1.15	1.00

Loadings of the five variables of aggressiveness on the three principal components for the first group and second group of profiled fish are given. The behavioural score used to characterize the individual behavioural type was derived from the first principal component (PC1).

Table A3
Comparison of results with two metrics of aggressiveness

Group level experiment	Pooled Pearson correlation coefficient		PC score	Frequency of aggressive behaviours
			r=0.142 95% CI [−0.244; 0.489]	r=0.09 95% CI [−0.29; 0.45]
Individual-level experiment	Preference for similar stimulus	BT	$F_{1,\ 36}$=0.214, P=0.647	$F_{1,\ 36}$=0.085, P=0.77
		BT∗sex	$F_{1,\ 34}$=0.011, P=0.919	$F_{1,\ 34}$=0.061, P=0.807
	Preference for proactive	BT	$F_{1,\ 36}$=1.401, P=0.245	$F_{1,\ 36}$=1.163, P=0.288
		BT∗sex	$F_{1,\ 34}$=0.064, P=0.802	$F_{1,\ 34}$<0.001, P=0.990
	Strength of preference	BT	χ^2_1=0.570, P=0.450	χ^2_1=0.654, P=0.418
		BT∗sex	χ^2_1=0.310, P=0.577	χ^2_1=0.317, P=0.573
	Number of visits	BT	χ^2_1=0.094, P=0.759	χ^2_1 =0.236, P=0.627
		BT∗sex	χ^2_1=2.204, P=0.138	χ^2_1=1.585, P=0.208
	Time spent in the neutral area	BT	$F_{1,36}$=0.413, P=0.525	$F_{1,36}$=0.701, P=0.408
		BT∗sex	$F_{1,\ 34}$=0.627, P=0.434	$F_{1,34}$=0.561, P=0.459

Comparison of results with two different metrics of behavioural type of individuals (BT): the PC score is derived from the PCA and the frequency of aggressiveness behaviour is the total aggressiveness behaviour per unit of time. For each experiment, we compared the results with these two metrics.

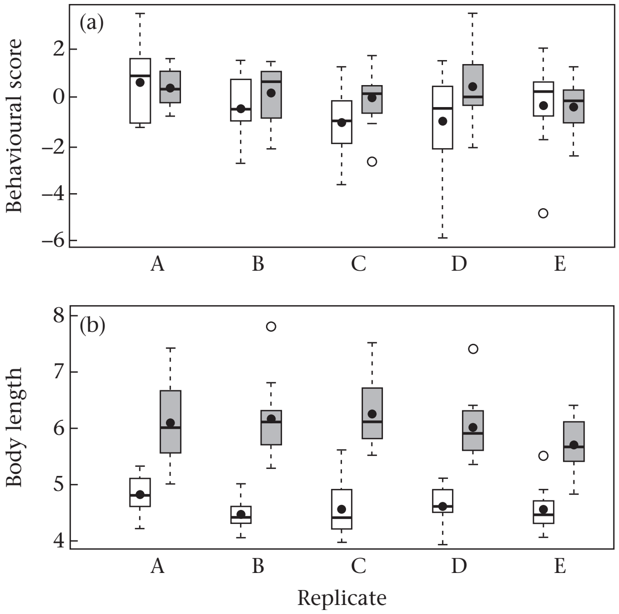

Figure A1. Homogeneity for (a) the behavioural score and (b) body length in females (in white) and males (in grey) over the five replicates (A–E) in experiment 1. The thick line in the middle of each box plot indicates the median and the solid circle indicates the mean. The box indicates the interquartile range (IQR). The dashed vertical line indicates the range of data within 1.5 IQR. Data outside this range of 1.5 IQR (outliers) are shown as open circles.

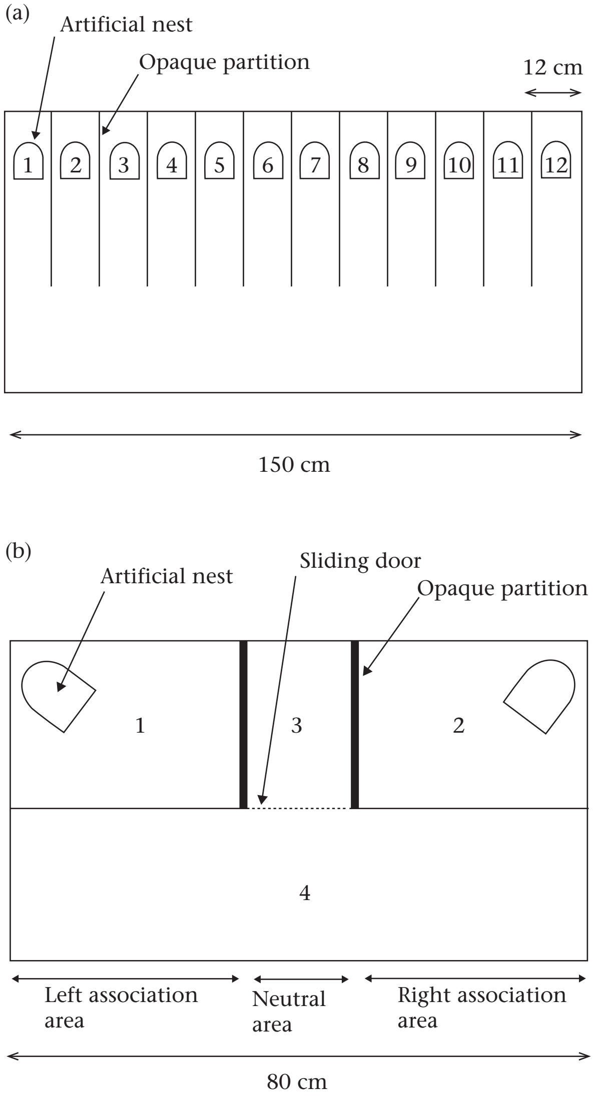

Figure A2. (a) Top view of the apparatus used for the free mate choice set-up. Ten or 12 individuals of each sex were introduced into a 450-litre tank divided into 10 or 12 distinct territories by opaque partitions. Each territory was equipped with an artificial nest and the tanks contained gravel substrate, artificial plants, rocks and air stones. (b) Top view of the apparatus used for the binary choice test. The tank consisted of two compartments for each stimulus (1 and 2), the acclimation zone for the focal fish with an opaque partition on each side to prevent contact with the stimulus before the beginning of the experiment (3), and the large compartment (4) which was virtually delineated in three areas: two association areas in front of the stimuli compartments and a neutral area. Dotted lines indicate the sliding door of the acclimation zone.