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

Chloé Laubu*, Cécile Schweitzer, Sébastien Motreuil, Philippe Louâpre, François-Xavier Dechaume-Moncharmont

Biogéosciences UMR 6282, CNRS, Université Bourgogne-Franche-Comté, Dijon, France

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.

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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)
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, Gucer, & 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, Leece, & 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 conspecífics (Afonzo, 2001; Gumm & Itzkowitz, 2007; Nicholas Santangelo, 2015; Wisenden, 1994; Wisenden et al., 2016). Parental coordination for defensive behaviours is thus under strong selection (Lampeitch & 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 & Zwyorkin, 2002; Budaev, Zwyorkin, & 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,
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