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Impact of social environment on inter- and intrasexual selection in a cichlid fish with mutual mate choice

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Social-rearing environment has profound effects on behaviour, physiology and development. A complex social environment enhances an individual's social skills and competence in many animal taxa. Consequently, complete social deprivation seriously impairs various aspects of behaviour, development, brain function and hormone levels. Although sexual selection is a major evolutionary force, studies investigating the effects of social environment on the development of reproductive behaviour are scarce. Thus, we aimed to examine how long-term social deprivation influenced sexual behaviour in both sexes of *Pelvicachromis taeniatus*, a biparental cichlid fish with mutual mate choice. In particular, we focused on intersexual behaviour, i.e. courtship and intrasexual aggression of fish reared and maintained either in a group or in isolation. We found significant differences between socially deprived and group-reared fish. Males and females reared in isolation were less likely to perform courtship behaviour and showed less interest towards potential mates than group-reared fish. Intrasexual aggression of isolated fish was reduced as well in both sexes. Furthermore, in males we found positive behavioural correlations between inter- and intrasexual behaviour at the individual level independent from the social-rearing environment. In females, this correlation was only found in group-reared fish, indicating an effect of social environment on behavioural correlations. Consequently, our results suggest that long-term social isolation seriously impairs social competence of *P. taeniatus* in sexual selection.

Sexual selection is a major force of evolution (Darwin, 1871). It shapes behaviour, physiology and morphology and has been intensively investigated since the 1970s (e.g. Andersson, 1994; Salzburger, 2009; West-Eberhard, 1979). Successful reproduction depends on access to mating partners, which is often limited. As a consequence, there is competition between individuals of the same sex (intrasexual selection) as well as between males and females (intersexual selection) for the optimal mating partner especially when mate choice is mutual (Baldauf, Kullmann, Schroth, Thünken, & Bakker, 2009). Competition is often mediated by ritualized social interactions, for example combat or threat display, in intrasexual selection. Functional aspects of reproductive behaviour have received major attention, but the development of sexual behaviour has been studied less well.

Social learning is widespread in all animal taxa (Hoppit & Laland, 2013), including humans (Boyt, Richerson, & Henrich, 2011; Little, Jones, DeBruine, & Caldwell, 2011). It is defined as 'learning that is facilitated by observation of, or interaction with, another individual' (Hoppit & Laland, 2013, page 4). Social experience influences both components of sexual selection (inter- and intrasexual selection; Andersson, 1994). Reproductive success depends, among other things, on an individual's social skills and competence in order to assess the quality of a mate (e.g. through direct mate choice or mate choice copying, Witte & Ryan, 2002) and/or that of a rival (e.g. through direct competition or 'eavesdropping' on a fight, McGregor, 1993; Oliveira, McGregor, & Latruffe, 1998) (for a general review on social competence see Taborsky & Oliveira, 2012). Especially in species with mutual mate choice, assessing a mate's quality and advertising one's own qualities is essential (Baldauf et al., 2009).

The social-rearing environment has profound effects on an individual's social skills (Branchi, 2009; Kempes, Gulickx, van Daalen, Louwerse, & Sterck, 2008; Taborsky, Arnold, Junker, & Tschopp, 2012), behaviour (Adkins-Regan & Krakauer, 2000; Moretz, Martins, & Robison, 2007; Ros-Simo & Valverde, 2012; Toth, Halasz, Mikics, Barsy, & Haller, 2008; Toth, Mikics, Tulogdi, Aliczki & Haller, 2011), development (Matsumoto, Ono, Ouchi, Tsushima, & Murakami, 2012) and brain function (Branchi, 2009; Zhao et al., 2009). The impact of the early social environment has been well

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studied in mammals, most notably in rodents and monkeys (e.g. Kempes et al., 2008; Levy, Melo, Galef, Madden, & Fleming, 2003; for a review see Branchi, 2009), in birds (e.g. Adkins-Regan & Krakauer, 2000; Gersick, Snyder-Mackler, & White, 2012; White, Gersick, Freed-Brown, & Snyder-Mackler, 2010) and in fishes (Ichihashi, Ichikawa, & Matsushima, 2004; Moretz et al., 2007). Complete social deprivation (i.e. social isolation) has severe effects on social performance in group-living animals (rodents: Toth et al., 2008, 2011; fishes: Gómez-Laplaza & Morgan, 2000; Hesse, Anaya-Rochas, Frommen, & Thünken, 2015a; Hesse, Anaya-Rochas, Frommen, & Thünken, 2015b; Hesse & Thünken, 2014) and on hormone levels (Veenema, 2009).

Most studies on fishes have dealt with the effects of short-term isolation. Aggressive behaviour and hormone levels (especially sexual hormones) have received most attention (Franck, Hannes, Lanfermann, & Ribowski, 1985; Gonçalves-de-Freitas & Mariguela, 2006; Halperin & Dunham, 1993; Halperin, Dunham, & Ye, 1992). The impact of long-term isolation in fishes has been less well studied. However, studies have shown an effect on imprinting (filial, sexual and chemical; Gómez-Laplaza & Gil-Carnicero, 2008; Hesse, Bakker, Baldauf, & Thünken, 2012; Olsén & Winberg, 1996), growth and social behaviour (Hesse & Thünken, 2014; Hesse et al., 2015a, 2015b). To what extent long-term isolation affects social skills apart from aggression is mostly unknown in fishes (an exception is kin recognition: Hesse et al., 2012; Olsén & Winberg, 1996; Thünken, Bakker, & Baldauf, 2014). Antipredator behaviour, foraging, migration and mate choice have learned components in fishes (Brown, Davidson, & Laland, 2003). Several studies report that prior experience influences female preferences (Bailey & Zuk, 2008; Hebets, 2003; Qvarnström, Pärt, & Sheldon, 2000; Wong, So, & Cummings, 2011) for example. through mate choice copying (Godin, Herdman, & Dugatkin, 2005), imprinting (Slagsvold, Hansen, Johannessen, & Lifjeld, 2002), context dependence (Royle, Lindström, & Metcalfe, 2008) and learning (Svensson, Eroukhmanoff, Karlsson, Runemark, & Brodin, 2010). Thus, the context of sexual selection is well suited to investigate the effects of long-term isolation.

The present study was designed to elucidate, first, the impact of social environment on sexual behaviour in *Pelvicachromis taeniatus*, a biparental, monogamous cichlid fish with mutual mate choice (Thünken, Bakker, Baldauf, & Kullmann, 2007). Both sexes of this species are competitive against same-sex rivals and choosy in mate choice (Baldauf et al., 2009). Therefore, we investigated both intersexual selection, i.e. courtship behaviour, and intrasexual selection, i.e. aggression, in adult fish that had been reared and maintained in a family group or in isolation from an early age. Second, we aimed to investigate possible behavioural correlations between intrasexual and intersexual behaviour at the individual level. Both contexts are usually examined separately. However, they are expected to be closely connected since individuals might differentially invest in aggression and courtship resulting in trade-offs (Kuijper, Pen, & Weissing, 2012). Alternatively, inter- and intrasexual behaviour can be positively associated as predicted by behavioural syndrome theory (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Schuett, Treganza, & Dall, 2010).

METHODS

Study Species

Pelvicachromis taeniatus is a small cave-breeding cichlid from Western Africa. Our population originates from the Moliwe River in Cameroon (Langen, Schwarzer, Kullmann, Bakker, & Thünken, 2011). The species is sexually dichromatic and dimorphic with males being larger than females (Baldauf et al., 2009). Males occupy and defend a breeding territory and females compete among each other for access to territory owners (Baldauf, Kullmann, Bakker, & Thünken, 2011; Thünken et al., 2011). Mate choice is mutual (Baldauf, Engqvist, Ottenheym, Bakker, & Thünken, 2013; Baldauf, Engqvist, & Weissing, 2014; Thünken et al., 2007; Thünken, Meuthen, Bakker, & Baldauf, 2012). Courtship behaviour usually includes performance of threat display (Barlow, 2002). Both sexes prefer larger mates (Baldauf et al., 2009; Thünken et al., 2012); however, due to sexual conflict over mates, realized mating is usually size assortative. Kin are preferred over nonkin as mating partners (Thünken et al., 2007). These fish form socially (and most likely also genetically, Langen, Thünken, & Bakker, 2013) monogamous pairs and perform biparental brood care. Juvenile life stages are characterized by diverse interactions with conspecifics. They stay in the parents' territory and are guarded by them for several weeks (Thünken, Meuthen, Bakker, & Kullmann, 2010). Thereafter they live in loose shoals until they reach sexual maturity (Lamboj, 2006). Juvenile *P. taeniatus* are able to differentiate between kin and nonkin (Hesse et al., 2012) and they prefer to shoal with kin which seems to be adaptive as individuals grow better in kin shoals than in shoals of mixed relatedness (Thünken, Hesse, Bakker & Baldauf et al., in press). Furthermore, siblings show better shoaling performance and are more cooperative during predator inspection visits than nonsiblings (Hesse & Thünken, 2014; Hesse et al., 2015a, 2015b).

Experimental Fish

All experimental fish were F2 offspring from wild-caught fish and bred under standardized conditions between April and October 2011 at the laboratory of the Institute for Evolutionary Biology and Ecology of the University of Bonn (see Hesse & Thünken, 2014 and Hesse et al., 2015a, 2015b for details). Fish were housed in family groups in tanks (50 × 30 cm and 30 cm high) equipped with a filter (model: 'gully filter' by Dohse, Grafschaft-Gelsdorf, Germany), sand and java moss, *Taxiphyllum barbieri*. The water temperature was kept at 24 ± 1 °C and the experimental fish were held under a light:dark regime of 12:12 h. All tanks were illuminated from above by fluorescent tubes (Osram, Lumilux Daylight 36 W). Additionally, up to six fish of each family were kept in isolation from an early age (14 ± 1 days old) and housed individually (tank size: 30 × 20 cm and 20 cm high) under the same environmental conditions. All tanks were surrounded by opaque plastic sheets to prevent visual contact between inhabitants of different tanks. Experimental fish were fed daily with a mixture of defrosted *Chironomus* larvae and *Artemia*. Fish were between 24 and 28 months old at the time of testing.

Behavioural Experiments

The aim of our study was to examine the effects of social-rearing environment (reared in isolation versus reared in a group) on inter- and intrasexual sexual behaviour. Furthermore, we aimed to investigate whether individual behaviour was correlated between the two contexts in order to examine possible behavioural syndromes. To investigate behaviour in individual test fish, reproductively active, i.e. brightly coloured fish, were transferred to an experimental tank (30 × 20 cm and 20 cm high; water level: 10 cm; water temperature: 24 ± 1 °C) equipped with an airstone (for oxygen supply), gravel and a cave (for males) or a plastic plant (for females) (Fig. 1). The experimental tank was surrounded by grey plastic sheets on three sides; the front was left uncovered to record behaviour of test fish with a camera (webcam from Logitech). The grey plastic sheets on the short sides were removable in order to investigate courtship behaviour and aggression. Test fish were