

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



Saskia Hesse*, Theo C. M. Bakker, Sebastian A. Baldauf, Timo Thünken

Institute for Evolutionary Biology and Ecology, University of Bonn, Bonn, Germany

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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.

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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

* Correspondence: S. Hesse, Institute for Evolutionary Biology and Ecology, University of Bonn, An der Immenburg 1, 53121 Bonn, Germany.

E-mail address: shesse@evolution.uni-bonn.de (S. Hesse).

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, & Dingemans, 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, Ottenheim, 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

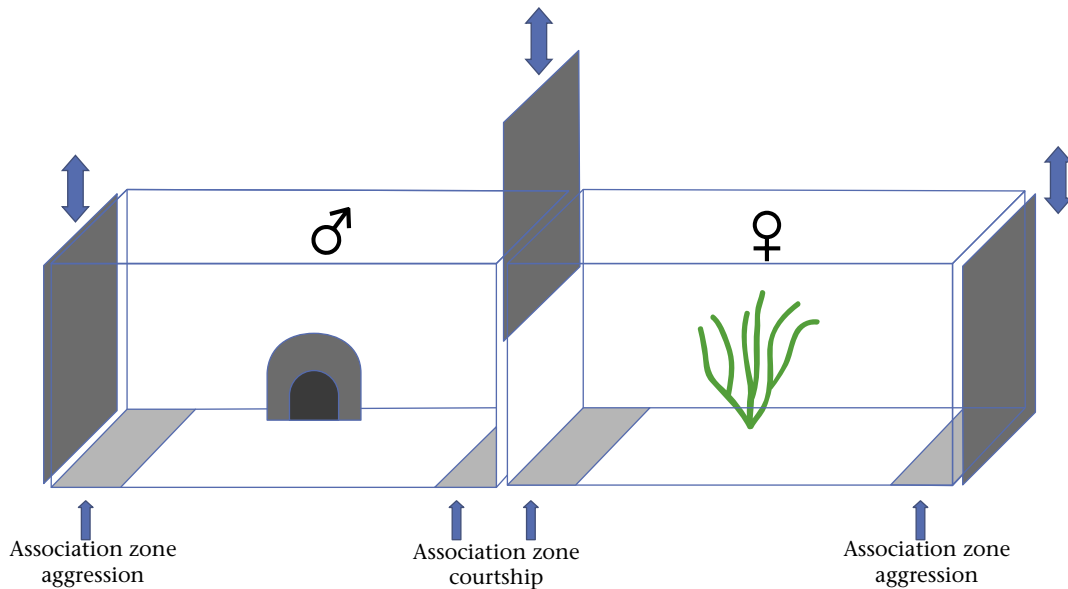


Figure 1. The experimental set-up for courtship (towards an opposite-sex conspecific) and aggression trials (towards mirror image). In tanks of the male test fish, there was a breeding cave and in tanks of the female test fish an artificial plant. Association zones measured 5 cm in front of the side panes. Tanks were separated by removable opaque partitions.

allowed to habituate to the experimental tank for 4 days before the courtship trial began. Aggression trials were conducted the following day. Test fish were fed daily ad libitum with defrosted red mosquito larvae; on experimental days fish were fed after the trials were finished. Tanks were illuminated from above by fluorescent tubes (Osram, Lumilux Daylight 36 W).

To investigate intersexual behaviour, we removed the grey plastic partition to the neighbouring tank, containing an unrelated and unfamiliar test fish of the opposite sex but from the same social environment (i.e. test fish reared in isolation were only paired with test fish reared in isolation and group-reared fish were only paired with group-reared fish). Behaviour was recorded for 20 min after the test fish had entered the association zone (5 cm; marked on the front window) in front of the neighbouring tank. If the test fish did not enter the association zone within 1 h, the plastic partition visually separating the two experimental tanks was put back in place and the trial was registered as invalid.

To measure intrasexual aggressive behaviour, we removed the grey plastic partition on the opposite side uncovering a mirror (20×20 cm). Using a mirror to elicit aggressive behaviour is a well-established method in fish (e.g. Davis, Harris, & Shelby, 1974; Franck et al., 1985; Gonçalves-de-Freitas & Mariguella, 2006; Riebli et al., 2011). Pretests with our study species revealed that both sexes respond well to mirror images (Hesse, Bakker, Sandmann, Jocteur, & Thünken, 2013). Pilot studies with *P. taeniatus* of both sexes ($N_{\text{males}} = 12$, $N_{\text{females}} = 17$) showed that there was no significant difference in the reactions (i.e. lateral display, attacks, spreading of opercula, attacks, s-bends, tail beats) of test fish to mirror images and opponents behind transparent glass (Hesse et al., 2013; see also Balzarini, Taborsky, Wanner, Koch, & Frommen, 2014). Behaviour was recorded for 10 min after the test fish had entered the association zone (5 cm; marked on the front window) in front of the mirror. If the test fish did not enter the association zone within 1 h, the trial was registered as invalid.

Courtship trials were always performed before the aggression trials to make the breeding territory a more valuable resource for males and to introduce females to a mating partner with a valuable resource (breeding territory and cave). Furthermore, this set-up induced aggression in a clearly reproductive context.

Acquisition of Behavioural Data

Recorded films were analysed blindly with regard to the social-rearing environment treatment. We estimated the intensity of intersexual behaviour by quantifying courtship behaviour and the sexual interest in the opposite sex (time spent in the association zone near the opposite sex). Time spent with the opposite sex predicts mating probability in cichlids in general (e.g. Dechaume-Moncharmont et al., 2011) and in *P. taeniatus* in particular (Thünken, 2009; Thünken et al., 2007). The frequency of courtship behaviour was defined by the total occurrence of lateral display (fish aligns laterally with erect fins, both sexes), quivers (both sexes), spreading of opercula (both sexes), tail beats (both sexes) and s-bends (body bends into an s-shape presenting the brightly coloured belly, only females).

The intensity of intrasexual aggression was estimated by quantifying aggressive behaviour and the time spent in the association zone near the opponent. We distinguished between display behaviour (no physical contact) and overt aggression (physical contact). The frequency of display behaviour was defined by the total occurrence of lateral display (fish aligns laterally with erect fins, both sexes), spreading of opercula (both sexes), sand digging (both sexes), tail beats (both sexes) and s-bends (body bends into an s-shape presenting the brightly coloured belly, only females). The frequency of overt aggression was defined by the occurrence of bites directed to the mirror image and attacks (fast move against the mirror image associated with one or more bites usually followed by retreat). Distinguishing between restrained aggression (here termed display behaviour) and overt aggression is common in studies of cichlid fishes (e.g. Riebli et al., 2011).

Data Analysis

Statistics were performed with the R.2.9.1 statistical software package (R Development Core Team, 2009). LMEs (linear mixed-effect models) were performed when original data or residuals of LMEs were normally distributed according to Kolmogorov–Smirnov–Lilliefors tests. If data were not normally distributed, they were log transformed to fit a normal distribution. Reported *P*

values of models refer to the increase in deviance when the respective variable was removed. Tests of statistical significance were based on likelihood ratio tests (LRT) following a χ^2 distribution; models use maximum likelihood parameter estimation. Nonsignificant factors were removed from models. Binomial data were analysed with GLMMs (generalized linear mixed-effect models; no overdispersion was detected). *P* values are two tailed throughout.

All in all, 100 individuals took part in the trials, 60 group-reared fish and 40 fish reared in isolation, originating from 18 different families. The body size of test fish was not significantly different between isolation and group fish (only test fish with at least one valid trial are included; males: LME: LRT: $N_{\text{group}} = 29$ (mean size \pm SD = 5.393 ± 0.511 cm), $N_{\text{isolation}} = 18$ (mean size \pm SD = 5.172 ± 0.536 cm), $\chi^2 = 0.118$, $P = 0.731$; females: LME: LRT: $N_{\text{group}} = 30$ (mean size \pm SD = 3.903 ± 0.257 cm), $N_{\text{isolation}} = 18$ (mean size \pm SD = 3.872 ± 0.282 cm), $\chi^2 = 2.944$, $P = 0.086$) and neither was the relative size difference in pairs during courtship trials (only fish with valid courtship trials are included; males: LME: LRT: $N_{\text{group}} = 18$, $N_{\text{isolation}} = 17$, $\chi^2 = 3.422$, $P = 0.064$; females: LME: LRT: $N_{\text{group}} = 21$, $N_{\text{isolation}} = 17$, $\chi^2 = 3.325$, $P = 0.068$). We statistically controlled for relative size differences in pairs since pairs in courtship trials were not size matched and mating is size assortative in *P. taeniatus*.

Intersexual behaviour

A total of 73 valid trials investigating courtship behaviour were performed. Males ($N_{\text{group}} = 18$, $N_{\text{isolation}} = 17$) and females ($N_{\text{group}} = 21$, $N_{\text{isolation}} = 17$) were analysed separately. We conducted an LME with interest in mate (i.e. time (s) spent in association zone close to the opposite sex) as the dependent variable, social-rearing environment (reared in a group/reared in isolation), body size of focal fish, relative size difference between male and female test fish and their interactions as explanatory variables and family as a random factor. Occurrence of courtship behaviour was analysed using a GLMM with binomial distribution with occurrence of courtship behaviour (yes/no) as the dependent variable, social-rearing environment (reared in a group/reared in isolation), body size of focal fish, relative size difference between male and female test fish and their interactions as explanatory variables and family as a random factor. All interactions between explanatory variables were not significant for male and female test fish ($P > 0.5$).

Intrasexual behaviour

All in all, 66 valid trials investigating intrasexual aggression were conducted. Males ($N_{\text{group}} = 14$, $N_{\text{isolation}} = 14$) and females ($N_{\text{group}} = 23$, $N_{\text{isolation}} = 15$) were analysed separately. The variable time spent in the association zone near the opponent did not meet the requirements of a normal distribution (even after log transformation). Thus, we calculated the mean time test fish spent with the stimulus and split the data set into fish that were above the mean and those that were below. Then, we conducted a GLMM with binomial distribution with more time spent in the association zone than average (yes/no) as the dependent variable, social-rearing environment (reared in a group/reared in isolation), body size of focal fish and their interactions as explanatory variables and family as a random factor. Occurrence of display behaviour was analysed using a GLMM with binomial distribution with occurrence of display behaviour (yes/no) as the dependent variable, time spent in association zone, social-rearing environment (reared in a group/reared in isolation), body size and their interactions as explanatory variables and family as a random factor. Occurrence of overt aggression was analysed using a GLMM with binomial distribution with occurrence of display behaviour (yes/no) as the dependent

variable, time spent in association zone, social-rearing environment (reared in a group/reared in isolation), body size and their interactions as explanatory variables and family as a random factor. All interactions between explanatory variables were not significant for male and female test fish ($P > 0.5$).

Correlations across contexts

All in all, 58 individual fish performed valid trials in both contexts, i.e. in the inter- and intrasexual context. To examine whether behaviour was correlated across contexts we performed an LME with time spent in the association zone in a courtship context as the dependent variable and time spent in the association zone in an aggressive context, social-rearing environment, body size and their interactions as explanatory variables; family was entered as a random factor.

Ethical Note

The experiments comply with the current laws of Germany. Experimental fish were bred between April and October in the laboratory at the Institute of Evolutionary Biology and Ecology in Bonn. The parental fish were F1 offspring from wild-caught *P. taeniatus* from the Moliwe River, Cameroon. No licences were required for the collection or import of fish or for the study. No fish was harmed during the experiment and no direct physical contact was possible between test fish. After the trials, test fish were again visually separated from the social stimulus and no obvious signs of stress were detected after the trials (i.e. fish fed regularly and were active).

RESULTS

Intersexual Behaviour

In males, interest in the female was significantly explained by social-rearing environment and male body size but not the relative size difference between male and female (Table 1); small males spent more time with the stimulus (Table 1). Occurrence of courtship behaviour was significantly influenced by social-rearing environment but not male body size or the relative size difference between male and female (Table 2, see also Table 3 for an overview).

In females, interest in the male was influenced by social-rearing environment but not by female body size or the relative size difference between male and female (Table 1). Occurrence of courtship behaviour was not influenced by social-rearing environment, female body size or the relative size difference between male and female (Table 2, see also Table 3 for an overview).

Table 1
Interest in mates by male and female test fish

Explanatory variable	Males			Females		
	χ^2	df	<i>P</i>	χ^2	df	<i>P</i>
Social environment	9.030	1	0.003	9.309	1	0.002
Size difference	0.484	1	0.487	0.252	1	0.616
Size	3.985	1	0.046	0.127	1	0.721

Results of an LME model analysing interest in potential mating partner (i.e. the time (s) test fish spent in the association zone) in relation to body size, relative size difference between male and female and social-rearing environment (reared in isolation or in family group); family is included as a random factor. Significant effects ($P < 0.05$) are in bold. Males: $N_{\text{group}} = 18$, $N_{\text{isolation}} = 17$; females: $N_{\text{group}} = 21$, $N_{\text{isolation}} = 17$.

Table 2
Occurrence of courtship behaviour in male and female test fish

Explanatory variable	Males			Females		
	χ^2	df	P	χ^2	df	P
Social environment	8.416	1	0.004	0.065	1	0.799
Size difference	0.220	1	0.639	0.682	1	0.409
Size	0.010	1	0.889	1.934	1	0.164

Results of a binomial GLMM analysing the occurrence of courtship behaviour in test fish in relation to body size, relative size difference between male and female and social-rearing environment (reared in isolation or in family group); family is included as a random factor. Significant effects ($P < 0.05$) are in bold. Males: $N_{\text{group}} = 18$, $N_{\text{isolation}} = 17$; females: $N_{\text{group}} = 21$, $N_{\text{isolation}} = 17$.

Table 3
Overview of intersexual behaviour

Intersexual behaviour	Males		Females	
	Isolation fish	Group fish	Isolation fish	Group fish
Occurrence of courtship behaviour (%)	12	39	12	24
Interest in mate (s)	385.3±376.3	695.5±417.5	517.4±395.1	901.9±353.0

Overview of intersexual behaviour in male and female test fish depending on treatment (reared in isolation or in family group). The table shows percentage of test fish that engaged in courtship behaviour (occurrence of courtship behaviour = yes) and interest in mate (mean time (s) ± SD spent with stimulus).

Intrasexual Behaviour

In males, occurrence of overt aggression was influenced by social-rearing environment but not by male body size (Table 4). Occurrence of display behaviour was not influenced by social-rearing environment or by male body size (Table 4, see also Table 5 for an overview).

Social-rearing environment explained whether males spent more time than average next to the opponent (isolation fish: 36%; group fish: 79%), but male body size did not (Table 4).

In females, occurrence of overt aggression was influenced by social-rearing environment and female body size with larger females being more aggressive than smaller ones (Table 4). Also, the occurrence of display behaviour was influenced by the social-rearing environment but not by female body size (Table 4). Similarly, social-rearing environment explained whether females spent more time than average with the opponent (isolation fish: 20%; group fish: 91%) but female body size did not (Table 4, see also Table 5 for an overview).

Correlations Across Contexts

In males, there was no significant interaction between social-rearing environment and time males spent in the association

Table 4
Overview of the occurrence of (intrasexual) aggression in male and female test fish

Explanatory variable	Overt aggression			Display			Time with opponent		
	χ^2	df	P	χ^2	df	P	χ^2	df	P
Social environment (m)	4.274	1	0.039	1.307	1	0.253	5.445	1	0.010
Size (m)	0.515	1	0.425	0.516	1	0.473	0.057	1	0.811
Social environment (f)	9.432	1	0.002	9.400	1	0.002	34.361	1	<0.001
Size (f)	4.196	1	0.041	3.004	1	0.083	<0.001	1	0.970

Results of a binomial GLMM analysing (1) the occurrence of overt aggression (overt aggression; males (m): $N_{\text{group}} = 14$, $N_{\text{isolation}} = 14$; females (f): $N_{\text{group}} = 23$, $N_{\text{isolation}} = 15$), (2) the occurrence of display behaviour (display; males (m): $N_{\text{group}} = 14$, $N_{\text{isolation}} = 14$; females (f): $N_{\text{group}} = 23$, $N_{\text{isolation}} = 15$) in test fish in relation to social-rearing environment (reared in isolation or in family group) and body size and (3) whether test fish spent more than average time in the association zone in an aggressive context (time with opponent; males (m): $N_{\text{group}} = 14$, $N_{\text{isolation}} = 14$; females (f): $N_{\text{group}} = 23$, $N_{\text{isolation}} = 15$) in relation to social-rearing environment (reared in isolation or in family group) and body size; family is included as a random factor. Significant effects ($P < 0.05$) are in bold.

Table 5
Overview of intrasexual behaviour

Intrasexual behaviour	Males		Females	
	Isolation fish	Group fish	Isolation fish	Group fish
Occurrence of display (%)	43	64	16	70
Occurrence of overt aggression (%)	14	50	12	52

Overview of intrasexual behaviour in male and female test fish depending on treatment (reared in isolation or in family group). The table shows percentage of test fish that engaged in display (occurrence of display behaviour = yes) and overtly aggressive behaviour (occurrence of overt aggression = yes).

zone in an aggressive context (LME: LRT: $N_{\text{group}} = 11$, $N_{\text{isolation}} = 14$, $\chi^2 = 0.062$, $P = 0.803$). Therefore, we pooled the data sets of both rearing environments. The time males spent in the association zone in an aggressive context significantly explained time males spent in the association zone in a courtship context (LME: LRT: $N = 25$, $\chi^2 = 8.131$, $P = 0.004$; Fig. 2).

In females, there was a significant interaction between social-rearing environment and time females spent in the association zone in an aggressive context (LME: LRT: $N = 33$, $\chi^2 = 9.247$; $P = 0.002$; Fig. 3); thus we analysed isolation fish and group fish separately. In group fish, the time females spent in the association zone in an aggressive context significantly explained time females spent in the association zone in a courtship context (LME: LRT: $N = 19$, $\chi^2 = 14.588$, $P < 0.001$; Fig. 3) whereas it did not in isolation fish (LME: LRT: $N = 14$, $\chi^2 = 0.078$, $P = 0.770$; Fig. 3).

DISCUSSION

Social-rearing environment significantly influenced inter- as well as intrasexual behaviour and thus major aspects of reproductive behaviour in both sexes of *P. taeniatus*. Fish reared in isolation were less sexually interested in a potential mating partner and behaved less aggressively towards an opponent than their group-reared full siblings.

Intersexual Behaviour

Fish of both sexes reared in isolation spent significantly less time with the opposite sex than group-reared fish. Effects of long-term social isolation on behaviour, apart from aggression and hormone levels, are poorly known (but see Hesse et al., 2015a, 2015b; Hesse & Thünken, 2014; Paxton, 1996). In birds, social environment experienced during ontogeny affected mating preferences in adults (Adkins-Regan & Krakauer, 2000). The complexity of the social environment affected mating success in cowbirds, *Molothrus ater* (White et al., 2010). In fishes, the (early) social environment can affect courtship behaviour (De Gasperin & Macias Garcia, 2014;

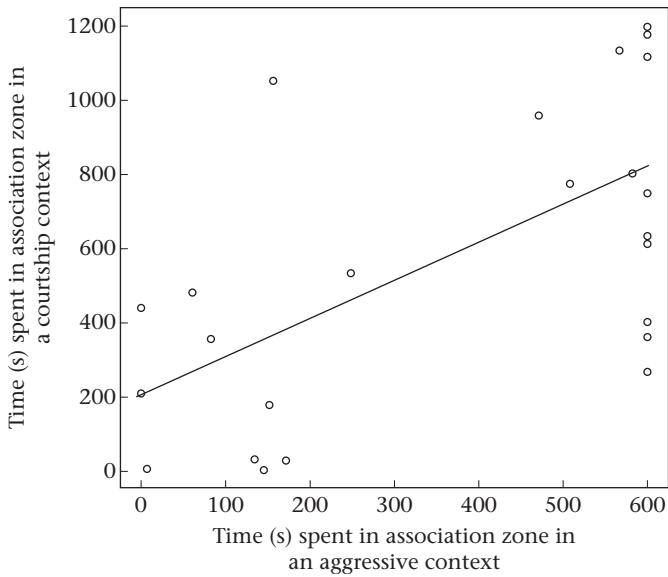


Figure 2. Relationship between intrasexual and intersexual behaviour measured as time (s) males spent in the association zone in a courtship context and time (s) spent in the association zone in an aggressive context. Data of group and isolation fish were pooled. The line is the least square regression line.

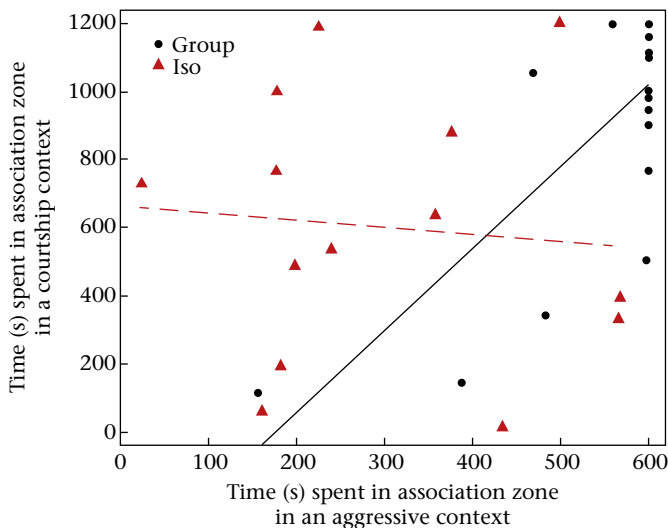


Figure 3. Relationship between intrasexual and intersexual behaviour measured as time (s) females spent in the association zone in a courtship context and time (s) spent in the association zone in an aggressive context separated according to social-rearing environment (group fish: solid line; isolation fish: dashed line). Lines are least square regression lines.

Guevara-Fiore, 2012) and reproductive effort in males (Jordan & Brooks, 2010).

Our results suggest that the intersexual behaviour of isolation fish was severely impaired, may be as a lack of social competence (i.e. the ability of an individual to adjust and optimize its behaviour depending on the social information available (Taborsky & Oliveira, 2012)). Social competence has been shown to be affected by the complexity of the rearing environment (mammals: e.g. Kempes et al., 2008; fishes: e.g. Fischer, Bessert-Nettelbeck, Kotrschal, & Taborsky, 2015; Taborsky et al., 2012). In general, animals reared in a more complex social environment possess enhanced social skills (Arnold & Taborsky, 2010; Branchi, 2009; Gersick et al., 2012). However, other explanations for the lack of interest in mating

partners are also possible. In fishes, preference for and recognition of mating partners as well as courtship patterns may have a learned component (e.g. De Gasperin & Macias Garcia, 2014; Verzijden, Korthof, & ten Caze, 2008; but see Barlow, Francis & Baumgartner et al., 1992). Therefore, lack of interest might at least be partially due to failure to recognize potential mates. Isolation fish were never exposed to conspecifics and imprinting on social stimuli was impossible. Imprinting in fish has received little interest but recent studies indicate that social experience/environment is crucial for various aspects of social behaviour, including mate choice (for a review see Arnold & Taborsky, 2010; Gómez-Laplaza & Gil-Carnicero, 2008; Verzijden et al., 2008).

Furthermore, behaviour of test fish may not be completely independent from the behaviour of the stimulus fish. Since focal fish and stimulus fish were always from the same social environment, there might be a possible influence of the stimulus fish on the behaviour of the focal fish. However, further experiments, preferably with computer animations to keep the stimulus identical for both treatment groups, are necessary to investigate differences in courtship behaviour more profoundly.

Intrasexual Behaviour

Studies on the effects of social isolation on aggressive behaviour have produced conflicting results depending on species, period of isolation, handling procedures and circumstances used to prime aggressive behaviours (for a detailed review see Gómez-Laplaza & Morgan, 2000). Our finding of reduced aggressiveness of fish of both sexes after long-term isolation is consistent with that of comparable studies investigating the effects of short-term isolation on aggressive behaviour. Here, social isolation resulted in a decreased attack readiness in isolated individuals (Davis et al., 1974; Franck et al., 1985; Gonçalves-de-Freitas & Mariguela, 2006; Halperin et al., 1992). Our results suggest that male territory owners reared in isolation less competently protect and maintain their breeding territory. This is also indicated by the reduced association time with a potential competitor and the reduced occurrence of aggression. In contrast, Ichihashi et al. (2004) reported an increased chance of isolated-reared male fighting fish, *Betta splendens*, winning a contest when paired with a socially reared male indicating that fighting ability in fishes might not be impaired by isolation per se. However, a higher win rate could also have been caused by inability of isolation fish to stop fighting after the opponent signalled submission. Females reared in isolation showed reduced association time with and reduced display and aggressive behaviour towards opponents. Since female *P. taeniatus* compete among each other for access to males, competitive behaviour is an important aspect of reproductive success. In another study with juvenile *P. taeniatus*, by contrast, aggression was more severe in isolation fish once it had been triggered (Hesse & Thünken, 2014). Consequently, isolation fish are not less aggressive per se but react improperly in social interactions (i.e. with disproportionate aggression). This might be due to a lack of social competence caused by the absence of a social environment (Taborsky et al., 2012).

Size is often related to dominance in fishes with large individuals being superior to smaller ones and even small size differences may predict the outcome of a fight between opponents (Maan, Groothuis, & Wittenberg, 2001; Maan & Taborsky, 2008; Thünken et al., 2011; but see Bakker, 1986; Barlow, Rogers, & Fraley, 1986). Interestingly, size significantly influenced aggressive behaviour only in females with larger females being more aggressive than smaller ones.

It has been demonstrated that long-term isolation affects hormone levels in fishes. An early study of Hannes and Franck (1983)

showed that long-term isolation in two cichlid species led to reduced levels of androgens. Social stimuli from conspecifics are needed in order to maintain certain levels of steroid hormones, e.g. in male *Haplochromis burtoni* (Hannes & Franck, 1983). Steroids are crucial, for example, in establishing a social hierarchy and maintaining a territory (Cardwell & Liley, 1991; Munro & Pitcher, 1985). Reduced levels of steroids may have contributed to the decreased aggression levels of both sexes in the present study.

Correlations Across Contexts

In males, inter- and intrasexual behaviours were highly correlated. In females, a similar positive correlation across contexts was found in group-reared fish but not in fish reared in isolation. Behavioural correlations across situations at the population level are referred to as behavioural syndromes (Sih, Bell, & Johnson, 2004). They have been studied across various contexts (usually exploration, boldness, aggression, foraging) in fishes (for a review see Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). Courtship has been included less often in studies of behavioural syndromes (but see e.g. Bakker, 1986, 1994; Bakker & Sevenster, 1989; Snekser, Leese, Ganim, & Itzkowitz, 2009). Behavioural syndromes may be influenced by genetic or neural mechanisms (Conrad et al., 2011). It has been shown that neural mechanisms can be affected by social interactions (Hofman & Fernald, 2001; Pollen et al., 2007; Taborsky, Tschirren, Meunier, & Aubin-Horth, 2013) and social isolation affected brain size in fish (Gonda, Herczeg, & Merilä, 2009). Thus, differences in behavioural correlations between isolation and group-reared fish may be expected. It is unclear why social-rearing environment affected the behavioural correlation across contexts only in females.

Conclusions

In summary, our results indicate that long-term social deprivation seriously impairs reproductive behaviour in both sexes of *P. taeniatus*. We demonstrated that courtship behaviour and intrasexual aggression were diminished in fish reared in isolation compared with group-reared fish. Thus, previous interactions with conspecifics seem to contribute the development and formation of reproductive behaviour in particular and to an individual's social competence in general.

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