

Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship

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Abstract Living in groups is a widespread phenomenon in many animal taxa. The reduction of predation risk is thought to be an important cause for the formation of groups. Consequently, grouping behavior is particularly pronounced during vulnerable life stages, i.e., as juveniles. However, group living does not only provide benefits but also imposes costs on group members, e.g., increased competition for food. Thus, benefits of grouping behavior might not be evident when predation risk is absent. The adaptive significance of living and also developing in a group independent from predation risk has received relatively little attention although this might have important implications on the evolution and maintenance of group living. The first aim of the present study was to examine whether the social environment affects juvenile performance in the cichlid fish *Pelvicachromis taeniatus* and, secondly, whether kinship affects social behavior. Kin selection theory predicts benefits from grouping with kin. Here, we demonstrate that juveniles reared in a group grow on average faster compared to juveniles reared in isolation under standardized laboratory conditions without predation risk. Furthermore, we found significant differences in social behavior between juveniles reared in a group and reared in isolation. Fish reared in isolation were significantly more aggressive and less willing to shoal than group-reared fish. As expected, genetic relatedness influenced social behavior in group-reared fish as well: dyads of juveniles consisting of kin showed increased group cohesiveness compared to non-kin dyads. We discuss the potential benefits of group living in general and living with kin in particular.

Keywords Kin discrimination · Shoaling · Social deprivation · *Pelvicachromis taeniatus* · Group living · Sociality · Inclusive fitness · Cooperation

Introduction

Group living is widespread throughout the animal kingdom, and the examination of the ultimate and proximate causes of group living is a central research topic in behavioral ecology (Krause and Ruxton 2002). Living in a group provides several benefits for an individual, for example, an increased probability to find food (Sullivan 1984; Krause and Ruxton 2002) or/and protection against predation, e.g., through the dilution effect (Hamilton 1971; Milinski 1977; Inman and Krebs 1987). Protection against predation is assumed to be an important cause for the evolution of group living in prey organisms (Foster and Treherne 1981; Magurran 1990; Pitcher et al. 1996; Krause and Ruxton 2002). However, the social environment provided by group mates emerging as a by-product of group living may act itself as an important selective force. For instance, sociality allows the evolution of advanced anti-predator or foraging strategies (Pitcher et al. 1986; Croft et al 2003), which depend on complex social behavior. These strategies require a good amount of cooperation and coordination between interacting individuals in order to perform optimally in a social group. Social skills are assumed to be based on experiential learning, i.e., prior interactions with other individuals such as siblings, parents, or other conspecifics (Brown and Laland 2003; Mateo 2004; Arnold and Taborsky 2010). As a consequence, individuals might be highly adapted to and thus depend on the presence of conspecifics during development.

However, increased competition between individuals within a group for food and access to mates inflicts costs on an individual (Krause and Ruxton 2002). Therefore, living in a

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group might reduce individual fitness in the absence of predation. The impact of group living relative to living solitary in prey organisms independent from predation has received little attention but might be of immense importance because of its potential to counteract the costs and contribute to the benefits of group living. Social isolation in group-living animals can severely affect social behavior and social competence. Studies on mice (*Mus musculus*) and rats (*Rattus norvegicus*) revealed an increase in stress hormone levels (Veenema 2009), atypical aggressive behavior (Toth et al. 2008, 2011), increased anxiety in novel situations (Ros-Simó and Valverde 2012), altered brain development (Zhao et al. 2009), and hyperactivity (Zhao et al. 2009; Ros-Simó and Valverde 2012) caused by social deprivation. However, those studies on mammals, which act as a model for human mental diseases, are not necessarily transferable to other species. Although many non-mammalian taxa also live in groups, effects of social deprivation are not well studied. In fishes, for instance, studies investigating the effects of long-term separation from conspecifics on individual development and social behavior are scarce. However, it appears that imprinting (filial, sexual, and chemical) is affected (e.g., Olsén and Winberg 1996; Gómez-Laplaza and Gil-Carnicero 2008). Most studies on fishes deal with short-term isolation and its influence on aggression (Franck et al. 1985; Halperin et al. 1992; Halperin and Dunham 1993; Gonçalves-de-Freitas and Mariguela 2006), retaining of memories (Baht and Magurran 2006), and hormone levels (especially sexual hormones, e.g., Hannes and Franck 1983) in sexually mature males (but see Newton 1982). Studies on aggression produced conflicting results depending on species, experimental procedure, and period of isolation (for a detailed review, see Gómez-Laplaza and Morgan 2000).

Groups in the wild are usually not just random assemblages but often consist of individuals featuring certain common characteristics (Godin 1997). Kin selection theory predicts that grouping with kin can increase the inclusive fitness of an individual (Hamilton 1964). Accordingly, natural groups are often composed of kin (fish: Pouyaud et al. 1999; Piyapong et al. 2011; mammals: de Ruiter and Geffen 1998; birds: Lee et al. 2010). Kin recognition abilities help individuals adjust their behavior according to the genetic relatedness of encountered individuals. Numerous studies have shown that individuals prefer to group with relatives (reviewed for instance in Krause and Ruxton 2002; Penn and Frommen 2010). However, the consequences of kin-biased behavior are less well studied, and the results are ambiguous. Enhanced cooperation and less aggression between kin were found in some studies (Holmes and Sherman 1982; Olsén et al. 1996; Markman et al. 2009; Edenbrow and Croft 2011) but not in others (e.g., Gerlach et al. 2007; Mehliis et al. 2008; Toth et al. 2009). In addition, familiarity plays an important role in group-living animals. Familiarity may increase foraging rates

(Griffiths et al. 2004), enhance anti-predator responses (Hain and Neff 2009), and reduce aggressive behavior (Gómez-Laplaza 2005). Kinship and familiarity may be linked for instance when siblings grew up together, and as a consequence, familiarity may confound effects of kin-biased behavior. In fishes, for example, association shoaling preferences are influenced not only by kinship but also by familiarity (Ward and Hart 2003). Thus, in order to make well-grounded statements concerning effects of kinship, it is essential to control for familiarity.

This study aims to investigate whether and how the social environment—and within a group whether kinship and familiarity—affect the (social) performance of juveniles in the cichlid fish *Pelvicachromis taeniatus*. *P. taeniatus* is a small, socially monogamous cave-breeding cichlid from Western Africa. Our study population originates from the Moliwe River in Cameroon. *P. taeniatus* is an actively inbreeding cichlid fish, which prefers close relatives as mating partners and forms socially monogamous pairs (Thünken et al. 2007a, b). Parental fish perform biparental brood care. Adult fish, as well as juveniles, recognize relatives via phenotype matching. In juveniles, phenotype matching is based on familial imprinting (Thünken et al. 2007b; Hesse et al. 2012); in adult males, phenotype matching is based on self-reference (Thünken et al. 2014). After a period of extensive brood care that is provided by both parents (Thünken et al. 2010), juveniles live in groups until they reach sexual maturity (Lamboj 2006). Shoaling is an effective strategy to reduce predation in fishes in general and in cichlids in particular (Pitcher et al. 1996). Shoals are often kin-structured (Pouyaud et al. 1999; Piyapong et al. 2011), and preference for familiar kin is present in juveniles of our study species (TT, SH, Theo C. M. Bakker, and Sebastian Baldauf, unpublished data).

In the present study, we first investigated the effect of social rearing environment on growth and behavior of juvenile *P. taeniatus*. Previous studies on fishes focused on behavior and hormone physiology, but the consequences of the observed effects often remained unclear. Therefore, in addition to behavior, we examined growth, a fitness-relevant trait in fishes (Sogard 1997), of juveniles reared either in isolation or in a group. On one hand, group living may increase competition such that isolated-reared fish might have advantages (see Newton 1982); on the other hand, benefits of group living might exceed the costs even in the absence of predation, and optimal juvenile development might depend on the presence of conspecifics in *P. taeniatus*. In our first experiment, we therefore compared the growth of fish either reared in isolation or in group. In a second experiment, we compared aggression and shoaling behavior of isolation-reared and group-reared fish to investigate the influence of social deprivation from an early developmental stage on social behavior. Generally, we expected isolation-reared fish to show significant shortcomings, as juvenile *P. taeniatus* are highly social fish.

Secondly, we examined the effects of kinship and familiarity on social behavior in group-reared fish. Kin selection theory predicts benefits from associating with kin (Hamilton 1964). Furthermore, positive kinship effects might be enforced by familiarity (see Olsén et al. 1996; Gómez-Laplaza 2005). Therefore, we expected fewer aggressive interactions and better shoaling behavior among kin.

Material and methods

Experimental fish

All experimental fish were F_2 offspring from wild-caught fish and bred under standardized conditions between April and October 2011 at the laboratory of the Institute of Evolutionary Biology and Ecology of the University of Bonn. To create different families, 18 breeding pairs of *P. taeniatus* were established, and each was introduced into a breeding tank (length \times width \times height, 45 cm \times 40 cm \times 30 cm), which was equipped with a standard breeding cave, an aquarium heater, a filter (model: “gully filter” by HOBBY), gravel, and java moss (*Taxiphyllum barbieri*, 2.5 g). The water temperature was kept at 25 ± 1 °C, and the experimental subjects were held under a light/dark regime of 12:12 h. They were fed daily with a mixture of defrosted *Chironomus* larvae and *Artemia*. Until spawning occurred, approximately 30 % of the water was changed weekly to increase spawning probability. Breeding caves were checked for eggs daily. If a pair had spawned, the date was noted and eggs were transferred to a small plastic tank (16 cm \times 9 cm \times 10 cm) filled with tap water and equipped with an airstone for oxygen supply; approximately two thirds of the water was changed daily. After 14 ± 1 days, fry were transferred to the different rearing regimes. All free-swimming fry were fed with living *Artemia* nauplii provided in a highly concentrated suspension (10 μ l/fish).

Rearing conditions of experimental fish

Sibling groups were split into two subgroups of 10 to 15 fish in order to create unfamiliar kin. Each sibling group was housed in a tank (30 cm \times 20 cm \times 20 cm) equipped with 300 ml sand, 1 g java moss, and an airstone for oxygen supply. Additionally, three to six fish of each family were reared in isolation in small plastic tanks (16 cm \times 9 cm \times 10 cm) equipped with 100 ml sand, 0.3 g java moss, and an airstone for oxygen supply. All tanks were surrounded by opaque plastic sheets to prevent visual contact between the inhabitants of different tanks. The water temperature was kept at 23 ± 1 °C, and the experimental subjects were held under a light/dark regime of 12:12 h. Twice every week, approximately 60 % of the water was changed. Experimental fish were fed a highly concentrated suspension of living *Artemia* nauplii, and the

amount of food per fish was adjusted to their age: 10 μ l/fish until 26–29 days after spawning, 20 μ l/fish until 60 ± 1 days after spawning, 40 μ l/fish until 90 ± 1 days after spawning, and 60 μ l/fish after 90 ± 1 days after spawning. After 60 days, the total number of fish in each family tank was noted and the amount of food was adjusted in case of any deaths (dead individuals: $N=34$ from initially 497 individuals). Mortality in isolation-reared fish was 6.98 % and in group-reared fish 6.82 %.

Size measurements

To compare growth of group-reared and isolation-reared fish (isolation-reared fish: $N=40$; group-reared fish: $N=423$), total length of each experimental fish was measured with a digital caliper after 90 days (see section “Data analysis” for further details).

Behavioral experiments

The aim was to examine the impact of social environment (reared in isolation compared to reared in a group) and—within group-reared fish—social relationship (comparing familiar kin, unfamiliar kin, and unfamiliar non-kin) on juvenile social behavior (see section “Data analysis” for details of the different treatments). Social behavior was investigated in dyads of fish. The experimental tank (40 cm \times 45 cm \times 40 cm) was covered with grey plastic sheets on the inner surface, and additionally, the experimental tank was surrounded by Styrofoam to minimize outside disturbances. It was illuminated from above by a fluorescent tube (Osram Lumilux L58W). The tank was filled with aged, substrate-treated tap water (23 ± 1 °C) (for more detailed information, see Meuthen et al. 2011); water level was 6 cm. After each behavioral trial, the tank was cleaned and rinsed with hot water and refilled.

To test for effects of social environment on behavior, we haphazardly paired either two group-reared fish or two fish reared in isolation and recorded the behavior of these fish. To test for an effect of social relatedness using the group-reared fish, we haphazardly paired fish that were either two familiar kin, or two unfamiliar kin, or two unfamiliar non-kin. Focal fish were aged between 99 and 183 days. At this age, fish are still too young to be sexed with certainty; therefore, sex could not be taken into account. Test fish were caught from their home tanks, and each was transferred into a small plastic tank (16 cm \times 9 cm \times 10 cm) filled with 200 ml of aged tap water. They were introduced into the experimental tank by gently setting the plastic tank into the experimental tank and turning it over. Test fish were introduced simultaneously on opposite sides.

Behavior of test fish was recorded from above using a webcam (Logitech). When both experimental fish swam and

behaved normally (i.e., fish swimming around and exploring the test tank actively, no erratic movement, e.g., swimming into side walls), their behavior was recorded for 30 min. After each trial, experimental fish were weighed and their standard length (length from the tip of the snout to the base of the tail) was measured.

Acquisition of behavioral data

Behaviors from films were recorded blindly with regard to the identity of test fish (social environment and social relationship). The time when both focal fish started to swim normally was noted, and behaviors were recorded for a period of 30 min. If the fish did not show normal behavior after 60 min or only one test fish did, the pair was removed from the test tank and another one of the same treatment combination was tested.

Aggressive behavior was defined as bites directed to the companion fish and incidence and duration of mouth fighting (interlocking jaws and pushing) and circling (chasing each other in a close circles and biting). It was noted for each trial whether aggression occurred or not. Additionally, the total number of bites was noted for each trial. Mouth fighting and circling rarely occurred (mouth fighting only occurred in 12 and circling in 2 trials, out of a total of 95 trials (both experiments combined)) and were therefore not analyzed separately. Additionally, screenshots were taken every 5 s for the first 10 min (120 frames/film). Distances (measured from the tip of snout to the tip of the snout) between the test fish was measured using ImageJ 1.46e for each frame. The mean distances for the first 10 min were calculated. Distances between fish were measured as a parameter for shoal cohesiveness (Salvanes et al. 2007). Tight shoals are an effective anti-predator strategy (Magurran 1990). Only trials without any aggressive behavior were used to evaluate shoaling distances since occurrence of aggression tended to reduce distances between fish (for isolation-reared fish and group-reared fish: linear mixed effect model (LME), $N=60$, $\chi^2=3.6995$, $p=0.054$) and therefore may confound investigations of shoal cohesiveness and lead to false conclusions.

Data analysis

Statistics were performed with the R. 2.9.1 statistical software package. LMEs were used when original data and—if those were not normally distributed—log transformed data were normally distributed according to Kolmogorov-Smirnov-Lilliefors tests and showed homogeneous variances according to Bartlett tests. 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), which follow a χ^2 distribution. These models use maximum likelihood parameter estimation. Non-

significant factors were removed from the models. Binomial data were analyzed with a generalized mixed effect model (GLMM). p values are two-tailed throughout.

Effects of social isolation on growth and juvenile social behavior

Growth

In total, growth of 40 isolation-reared fish was compared with that of 423 fish reared in 32 full-sibling groups originating from 18 different families. We conducted a LME with body size (at day 90) as dependent variable, social environment (reared in a group/reared in isolation) as explanatory variable, and family and tank nested in family as random factors. Additionally, using a similar LME, we compared the size of the smallest fish in each group with the size of the isolation fish. In 16 out of 32 tanks, one to three fish died due to unknown reasons. Therefore, a food index was calculated and introduced into all models to correct for variation in amount of food available for each individual. Food index was calculated in the following way: number of expected individuals per group/number of actual individuals per group. Value of food indices ranged between 1 (no death) and 1.3 (three fish died). We additionally ran an analysis that excluded all replicates where at least one fish died, and this model returned similar results to those reported in the “Results”.

Social behavior

Forty-three pairs composed of group-reared fish (29 unfamiliar kin pairs and 14 unfamiliar non-kin pairs) were compared concerning social behavior with 17 pairs composed of isolation-reared fish (11 unfamiliar kin pairs and 6 unfamiliar non-kin pairs). We did not include test fish from familiar kin pairs in our analysis since familiarity could confound the results. In order to compare the periods until normal swimming behavior occurred between group-reared fish and isolation-reared fish, we used an LME with latency (time in seconds, log transformed) as dependent variable, social environment (reared in isolation/reared in a group) and kinship (kin/non-kin) as explanatory variables, and family combination as a random factor to account for variation explained by family. Kinship was included to control kinship effects in group-reared fish only since juveniles reared in isolation cannot recognize kin (because kin recognition is based on familial imprinting, Hesse et al. 2012).

To test whether aggression depends on social rearing environment, we used a GLMM with binominal distribution and occurrence of aggression (yes/no) as dependent variable, social environment and size difference between fish as explanatory variables, and family combination as random factor. When aggression occurred, we used a LME to test the impact

of social environment and size difference between test fish (explanatory variables) on number of bites directed to an opponent (dependent variable); family combination was entered as random factor. Again, kinship was added as an explanatory variable to account for kinship effects in group-reared fish.

To investigate the effects of social isolation on shoal cohesiveness, we used an LME with mean distance (log transformed) between test fish as dependent variable. Social environment, kinship, and size difference between test fish were included as explanatory variables and family combination as a random factor in the model.

Effects of kinship and familiarity on juvenile social behavior

The effects of kinship and familiarity on juvenile social behavior were examined in group-reared fish only because kin recognition in juvenile *P. taeniatus* most likely relies on familial imprinting (Hesse et al. 2012), and thus, fish reared without kin probably cannot recognize kin. Thirty-five pairs of familiar kin (fish of the same family taken from the same housing tank), 29 pairs of unfamiliar kin (fish of the same family but taken from different housing tanks), and 14 pairs of unfamiliar non-kin (fish of different families taken from different housing tanks) originating from 18 families were available for the experiment. We assessed whether aggression depended on kinship and familiarity using a GLMM with a binomial distribution. Occurrence of aggression (yes/no) was the dependent variable, and social relationship (familiar kin, unfamiliar kin, and unfamiliar non-kin) and size difference between test fish were used as explanatory variables. Family was included as a random factor in the analysis. Influences of kinship and familiarity on number of bites were analyzed using a LME with number of bites as dependent variable, social relationship (familiar kin, unfamiliar kin, and unfamiliar non-kin) and size difference between test fish as explanatory variables, and family combination as a random factor.

Shoal cohesiveness was analyzed using a LME with mean distance between test fish as dependent variable, size difference between test fish and social relationship (familiar kin, unfamiliar kin, and unfamiliar non-kin) as explanatory variables, and family combination as a random factor. Tukey's HSD test was used for post-hoc multiple comparisons of social relationship groups.

Ethical note

The experiments comply with the current laws of Germany. The parental fish were F_1 offspring from wild-caught *P. taeniatus* from the Moliwe River near Limbe, Cameroon (04°04'N/09°16'E) in June 2007. Wild-caught fish were

transported in fish bags filled with river water to the institute in Germany. All fish survived the flight and were in good condition when arriving at the institute. No licenses were required for the collection or import of fish or for the study. Since experiments were non-invasive and involved behavioral experiments only, no local institutional ethics approval was necessary.

Aggressive contest behavior is highly ritualized in *P. taeniatus*. Display (fish swim aligned to each other with erected fins and start tail-beating; not evaluated in this study) often precedes bites (opponents bite each other mainly in the flank with bites being more like blows causing no injuries). Aggressive interactions rarely involve mouth fights (see “Results”) and hardly ever circling. No extreme responses were observed during the experiments, and the tank was large enough to allow inferior fish to keep their distance from the aggressor. No injuries (skin lesion, damaged fins) occurred, and no test fish died during or after the behavioral experiments.

A period of 30 min was chosen for each experiment to ensure that experimental fish were fully acclimatized to the new environment and showed the whole range of characteristic behavior. Aggression never occurred continuously throughout the period of 30 min but was restricted to brief periods of contest behavior usually followed by shoaling/ exploring together.

After the experiments, fish have been kept in the laboratory and they will take part in several other behavioral experiments focusing on effects of isolation on various behavioral and cognitive aspects.

Results

Effects of social isolation on growth and juvenile social behavior

Growth

Juveniles reared in a group were on average larger than juveniles reared in isolation after 90 days (Fig. 1, Table 1). Variances in body size between social environments (reared in isolation/reared in a group) were not significantly different from each other (Bartlett test of homogeneity of variances, $N_{\text{isolation}}=40$, $N_{\text{group}}=423$, $K\text{-squared}=1.027$, $p=0.311$). When comparing only the smallest individual of each group with isolation-reared fish, isolation-reared fish were on average larger than the smallest individual of each group of group-reared fish (mean size group-reared fish \pm SD, 21.197 \pm 1.609; mean size isolation-reared fish \pm SD, 22.195 \pm 1.595; LME: LRT, $N_{\text{isolation}}=40$, $N_{\text{group}}=31$, $\chi^2=17.285$, $p<0.001$).

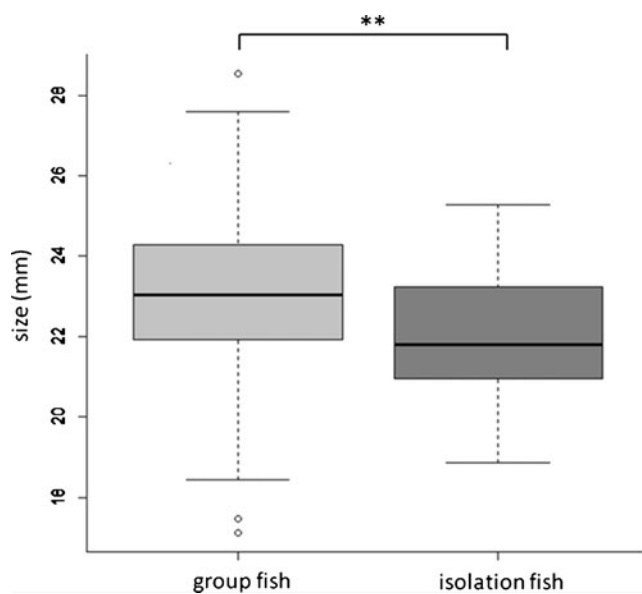


Fig. 1 Body size of 90-day-old fish either reared in isolation ($N=40$) or within a group ($N=423$). Median, first and third quartile, and whiskers are shown. ****** $p<0.01$

Social behavior

Isolation fish started to swim normally significantly sooner than group-reared fish (mean time (s) \pm SD group-reared fish, $1,678.186\pm 1088.028$; mean time (s) \pm SD isolation-reared fish, 744.000 ± 524.347 ; LME: LRT, $N_{\text{isolation}}=17$, $N_{\text{group}}=43$, $\chi^2=18.916$, $p<0.001$). There was no significant difference in the occurrence of aggressive interactions between group-reared fish and fish reared in isolation (GLMM: LRT, $N_{\text{isolation}}=17$, $N_{\text{group}}=43$, $df=1$, $\chi^2=0.275$, $p=0.600$), but size difference influenced occurrence of aggression with fish more similar in size being more likely to be involved in aggressive interactions (GLMM: LRT, $N_{\text{isolation}}=17$, $N_{\text{group}}=43$, $df=1$, $\chi^2=5.741$, $p=0.017$). Fish reared in isolation directed more bites towards their companion fish than group-reared fish (Fig. 2, Table 2). Size difference had no significant effect on number of bites directed to an opponent (Table 2). Both circling events took place between isolation fish.

Fish reared in a group stayed significantly closer to each other than isolation-reared fish (Fig. 3, Table 3). Size

Table 1 Results of a LME analyzing body size of test fish at day 90 in relation to social environment

Step	Simplification	χ^2	p	df
Maximum model	–	–	–	–
1	Social environment	13.987	<i>0.001</i>	1

Family and tank nested in family were included as random factors. A food index was introduced into the model to correct for variation in amount of food available for each individual. Significant effects ($p<0.05$) are in italic font

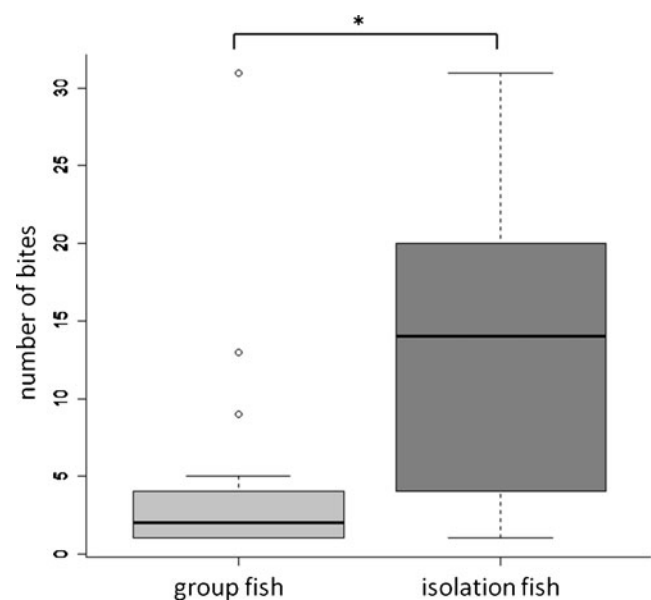


Fig. 2 Number of bites (back-transformed) directed to an opponent in fish reared in isolation ($N=9$) or in a group ($N=15$). Median, first and third quartile, and whiskers are indicated. ***** $p<0.05$

difference between fish did not significantly influence distances between fish (Table 3).

Effects of kinship and familiarity on juvenile social behavior

There was no significant difference in the occurrence of aggressive interactions depending on social relationship (familiar kin, unfamiliar kin, and unfamiliar non-kin) (GLMM: $N_{\text{fam. kin}}=35$, $N_{\text{unfam. kin}}=29$, $N_{\text{unfam. non-kin}}=14$, LRT, $df=2$, $\chi^2=0.606$, $p=0.739$), and size difference had no significant effect on the occurrence of aggressive interactions (GLMM: $N=78$, $df=1$, $\chi^2=2.539$, $p=0.111$). Within group-reared fish, there was no significant difference in number of bites between familiar kin, unfamiliar kin, and unfamiliar non-kin (mean number of bites \pm SD: familiar kin= 6.071 ± 6.799 , unfamiliar kin= 4.636 ± 10.392 , unfamiliar non-kin= 6.250 ± 5.737 ; LME: LRT, $N_{\text{fam. kin}}=14$, $N_{\text{unfam. kin}}=11$, $N_{\text{unfam. non-kin}}=4$, $\chi^2=1.796$, $df=1$, $p=0.407$). Size difference had no significant

Table 2 Results of a LME analyzing number of bites directed to an opponent in relation to social environment

Step	Simplification	χ^2	p	df
Maximum model	–	–	–	–
1	Size difference	0.012	0.914	1
2	Kinship	0.340	0.550	1
3	Social environment	6.509	<i>0.011</i>	1

Kinship and size difference between test fish were included as additional factors and family combination as random factor. Significant effects ($p<0.05$) are in italic font

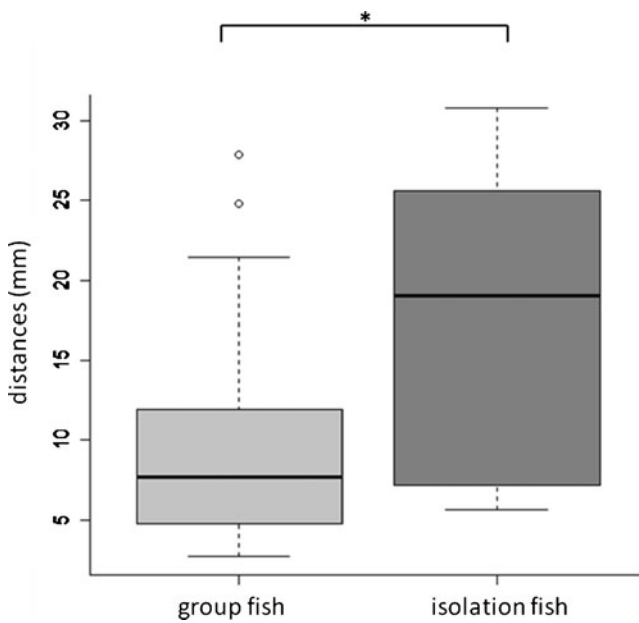


Fig. 3 Shoal cohesiveness measured as distances between the two experimental fish—either reared in a group or in isolation (data were back-transformed; $N_{\text{group-reared}}=28$, $N_{\text{isolation-reared}}=8$). Median, first and third quartile, and whiskers are indicated. * $p<0.05$

effect on number of bites either (LME: LRT, $N=29$, $\chi^2=2.707$, $df=1$, $p=0.100$).

In group-reared fish, social relationship significantly influenced shoaling distances (Fig. 4, Table 4). Kin were closer together than non-kin (Tukey’s HSD test: $N_{\text{fam. kin}}=20$, $N_{\text{unfam. kin}}=18$, $N_{\text{unfam. non-kin}}=10$, familiar kin vs. unfamiliar non-kin: $z=3.769$, $p<0.001$; unfamiliar kin vs. unfamiliar non-kin: $z=-2.827$, $p=0.013$, Fig. 4). Familiarity had no significant effect on distances between kin (Tukey’s HSD test: familiar kin vs. unfamiliar kin: $z=1.060$, $p=0.537$, Fig. 4). Size differences between test fish did not significantly influence distances between test fish either (Table 4).

Discussion

Overall, our study revealed multiple effects of social rearing environment on growth and social behavior in juvenile

Table 3 Results of a LME analyzing distances between test fish in relation to social environment (reared in a group/reared in isolation)

Step	Simplification	χ^2	p	df
Maximum model	–	–	–	–
1	Size difference	0.067	0.796	1
2	Social environment	7.184	<i>0.007</i>	1
3	Kinship	7.023	<i>0.008</i>	1

Kinship and size differences between test fish were included as additional factors and family combination as random factor. Significant effects ($p<0.05$) are in italic font

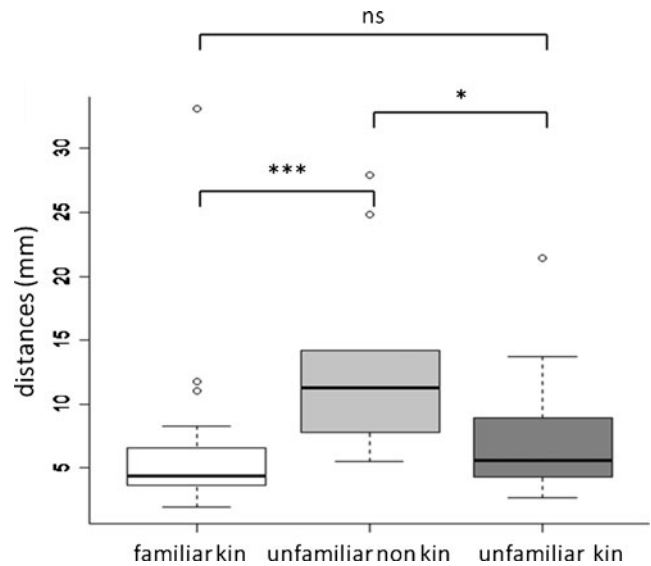


Fig. 4 Shoal cohesiveness measured as distances (back-transformed) between the two test fish (group-reared) differing in social relationship ($N_{\text{familiar kin}}=20$, $N_{\text{unfamiliar kin}}=18$, $N_{\text{unfamiliar non-kin}}=10$). Median, first and third quartile, and whiskers are indicated. *** $p<0.001$, * $p<0.05$; ns indicates $p>0.05$

P. taeniatus. Average growth was impaired by social isolation with isolated fish on average being smaller than group-reared ones. Furthermore, socially deprived fish performed poorly in a social context; they were more aggressive and less likely to shoal. In group-reared fish, kinship affected social interaction between test fish. Kin formed tighter shoals.

Effects of rearing isolation on growth and juvenile social behavior

Growth

Juveniles reared in a group were on average larger than juveniles reared in isolation. Variances in body size between social environments (reared in isolation/reared in a group) were not significantly different, indicating that the social environment effect is not caused by a few large outliers. Body size is a fitness-related trait in many fish species (Sogard 1997). Especially during juvenile life stages, size plays an

Table 4 Results of a LME analyzing distances between test fish in relation to social relationship (familiar kin/unfamiliar kin/unfamiliar non-kin)

Step	Simplification	χ^2	p	df
Maximum model	–	–	–	–
1	Size difference	2.707	0.100	1
2	Relationship	11.714	<i>0.003</i>	1

Size differences between test fish were included as covariate and family combination as random factor. Significant effects ($p<0.05$) are in italic font

important role in survival. Smaller individuals are more vulnerable to predation and are also often preferred as prey by predators (for a review, see Sogard 1997). Sociality enhances growth in juvenile *P. taeniatus* despite possible disadvantages of group living, e.g., competition for food. In guppies (*Poecilia reticulata*), for example, the opposite effect was found. Here, isolated males were larger than group-reared males (Newton 1982), indicating a positive effect of growing up without competition for food resources. However, guppies differ from *P. taeniatus* in their parental care system as well as early social environment. Guppies are live-bearing and provide no parental care for their offspring, and shoaling tendency depends on the origin of the population (high- and low-predation populations, see Paxton 1996). In another species without parental brood care and different lifestyle, the Arctic charr (*Salvelinus alpinus*), isolation did not negatively affect growth as well (Jobling and Baardvik 1994). In Arctic charr, competition for food is high and juveniles live rather solitary (Klemetsen et al. 2003; Jobling and Baardvik 1994). In contrast, most cichlids perform extensive brood care and juveniles form hierarchal structured shoals (Gómez-Laplaza 2006; Gonçalves-de-Freitas et al. 2008). Differential growth in our study species suggests that juveniles are adapted to and benefit from group living in this species.

At the proximate level, social foraging has been shown to increase food intake in various species, especially when members of a group are familiar with each other (birds: Sullivan 1984; invertebrates: Strodl and Schausberger 2012; fish: Griffiths et al. 2004). Social isolation affects food intake rates in fish, which are significantly lower in isolated fish (Jobling and Baardvik 1994; Martins et al. 2006). Martins et al. (2006) showed that the presence of a conspecific stimulated feeding behavior in catfish (*Clarias gariepinus*) and induced higher growth rates of non-isolated individuals compared to isolated individuals. As juveniles in our study were fed with living *Artemia* nauplii (<0.5 mm), no direct observation of food intake rates was possible. Additionally or alternatively, as social living individuals, isolated fish might also have been negatively affected by stress due to social deprivation. Presence of conspecifics has been shown to influence physiology as well as behavior in brook trout (*Salvelinus fontinalis*) (Sloman and Baron 2010). During development, embryos and larvae reared in isolation had lower oxygen consumption rates and higher ammonium excretion rates, indicating a significant influence of isolation rearing on physiological processes. Furthermore, isolation also affects hormone levels in fish, for example, androgen and corticosteroid levels (Hannes and Franck 1983). In rodents, social isolation results in reduced weight gain (Ros-Simó and Valverde 2012). Increased levels of stress hormones have been measured in isolated individuals, too (Veenema 2009).

The smallest group-reared fish were smaller than isolation-reared fish. In shoals, dominant individuals tend to

monopolize food and exclude subordinate individuals from food resources, resulting in faster growth of dominant individuals and retarded growth in subordinates. However, our fish were fed with living *Artemia* nauplii, a food resource that spreads rapidly throughout the whole water body of the tank. This should have made it difficult for dominant fish to monopolize food. Cichlids often live in hierarchically structured groups (Gómez-Laplaza 2006; Gonçalves-de-Freitas et al. 2008). In cooperative breeding species, individuals within a group follow different growth strategies, i.e., individuals adjust growth according to environmental conditions to maximize fitness. Subordinate fish, for instance, may reduce their growth rate in order to avoid conflicts with a larger more dominant individual (Heg et al. 2004). Furthermore, behavioral type and social status have been shown to influence growth in cooperative breeding cichlids (Hofman et al. 1999; Riebli et al. 2011; Heg et al. 2011). Thus far, it is unknown whether such growth strategies are also present in free ranging groups, i.e., shoals of juveniles, and thus to which extent they might explain our findings. Overall, our study indicates that an average juvenile *P. taeniatus* benefits from living in a group but it might also bear costs for certain individuals to live in a group.

Social behavior

Latency to normal swimming behavior was significantly shorter in isolation-reared fish. Social deprivation affects responses to stimuli in fish; this has been demonstrated in brook trout (*S. fontinalis*) (Sloman and Baron 2010). Here, fish reared in isolation showed a delayed response to external stimuli. In contrast, juvenile *P. taeniatus* reared in isolation seemed to react more promptly to new stimuli, i.e., the companion fish and the new environment, than group-reared fish.

Isolation-reared fish showed a similar behavioral repertoire as the group-reared, such as bites, tail beats, and mouth fighting. Thus, different aspects of contest behavior do not need to be learned in this species. Social isolation did not affect the occurrence of aggressive interactions. However, if aggression occurred, it was significantly more pronounced in isolation fish (cf. Fig. 2). Previous studies on effects of short-term social deprivation on aggressive behavior in fish, usually adult males, have found conflicting results. In male swordtails (*Xiphophorus helleri*), social isolation resulted in a decreased attack readiness (Franck et al. 1985). This is consistent with a study performed with Siamese fighting fish (*Betta splendens*) where social isolation caused a decreased readiness to display. But when display behavior was triggered, isolated males showed increased display rates (Halperin et al. 1992). Halperin and Dunham (1993) found an increased aggressiveness in several isolated fish species, too. Conflicting results may be contributed by differences in species biology (e.g., territorial vs. social, breeding status), handling procedure

(e.g., transfer to new environment), and experimental setup (e.g., staged encounters with conspecifics, aggression towards a mirror image, aggression towards a model, “intruder scenario”) (Gómez-Laplaza and Morgan 2000). Social competence has been shown to be affected by rearing conditions in fish (Taborsky and Oliveira 2012). Arnold and Taborsky (2010) showed that juveniles of the cooperative breeding cichlid fish *Neolamprologus pulcher* reared with parents and helpers showed more restrained aggression in an intruder scenario than juveniles reared without parents. Restrained aggression may prevent serious injuries between opponents and reduce the energetic costs of fighting behavior. Socially experienced fish, i.e., fish reared in a more complex social environment, behave therefore more adequately in a given social context. In our case, test fish were introduced into a new, potentially risky environment and encountered an unfamiliar companion fish. This might happen, for example, in nature during a predator attack scattering a shoal. In this situation, restrained aggression should be beneficial. Therefore, the higher number of bites directed to an opponent and the occurrence of escalated fighting (circling) in isolated fish could reflect their social incompetence compared to socially reared fish. Furthermore, we found that size difference influenced the occurrence of aggression between dyads. Fish more similar in size were more likely to involve in aggressive interactions. This is consistent with a study performed on adult males in *P. taeniatus* (Thünken et al. 2011). Here, fish closer in size fought more violently over a scarce resource.

Distances between fish, i.e., shoal cohesiveness, within dyads of group-reared fish were significantly smaller than distances between isolation-reared fish. Tighter shoals offer a more efficient protection against predation, which is regarded as one main reason for the formation of shoals in fish (Magurran 1990). Social environment had an important impact on this behavior in our study species, implying worse anti-predator behavior in isolation-reared fish. Thus, social isolation negatively affected an important behavioral trait in juveniles which are particularly vulnerable to predation.

Effects of kinship and familiarity on juvenile social behavior

Neither kinship nor familiarity had a significant influence on aggression between opponents in group-reared fish. Similar results were found in other fish studies (Gerlach et al. 2007; Mehliis et al. 2008). In contrast, some studies on fishes showed that familiarity as well as kinship reduces aggressive behavior (e.g., Olsén et al. 1996; Gómez-Laplaza 2005; Edenbrow and Croft 2011). The differences between the studies might be explained not only by the different social structure of the examined species but also by the contexts investigated. In our case, the aggression level was generally low in group-reared fish, which may reflect a need for security in a

potentially risky new environment regardless of kinship or familiarity.

Within group-reared fish, distances between familiar kin as well as between unfamiliar kin were significantly smaller than between unfamiliar non-kin, indicating that juvenile *P. taeniatus* are able to identify kin independent of prior familiarity. These results support previous studies on *P. taeniatus* indicating kin recognition by phenotype matching in this species (Thünken et al. 2007b, 2014; Hesse et al. 2012). Familiarity did not reinforce the strength of kin discrimination in juveniles. A similar result was found in adult *P. taeniatus* in a mate choice context (Thünken et al. 2007a) and in a study on kin-shoaling preferences in three-spined sticklebacks (*Gasterosteus aculeatus*) (Frommen et al. 2013). However, a study on shoaling preferences in zebrafish (*Danio rerio*) found opposing results (Gerlach and Lysiak 2006). Here, test fish also preferred to associate with unfamiliar kin compared to non-kin, but familiarity reinforced preference for kin further with familiar kin being preferred to unfamiliar kin. In zebrafish, kin recognition is based on phenotype matching, too (Hinz et al. 2013). The increase of kin preference through familiarity might be due to formation of hierarchies in shoals, and individual recognition facilitates the maintenance of dominance structures in these fish species.

Shoal cohesiveness, measured as distance between fish (e.g., Salvanes et al. 2007), is often analyzed in relation to predation. Under predation risk, fish tend to move closer to each other to increase protection/dilution effect of a shoal (Nordell 1997). Although in our experiments no predation risk was simulated, fish were transferred from their home tanks to a novel environment they had to explore. Exploration of a novel environment may well reveal the presence of a predator. Thus, our results suggest benefits for individuals when interacting with kin under natural conditions because of the increased shoal cohesiveness. A study on the substructure of wild-living guppies (*Poecilia reticulata*) from a high-predation risk population revealed no kin assortment in female dyads (Croft et al. 2012, but see Piyapong et al. 2011). However, our results may further contribute to the understanding of the adaptive significance of kin-shoaling preferences in various fish species (e.g., Arnold 2000; Mehliis et al. 2008; Le Vin et al. 2010).

Conclusion

Social environment had significant influences on growth as well as social behavior in juvenile *P. taeniatus*. Juveniles reared in a group were significantly larger than fish reared in isolation, suggesting a positive effect of sociality. To our knowledge, our study is the first to demonstrate the positive role of social environment on a fitness-relevant trait in fish. Grouping is considered to have evolved as an adaptation to

predation primarily (Magurran 1990), but juvenile *P. taeniatus* seem to be adapted to and depend on group-living also for their development. However, social deprivation did not only influence growth but had a significant impact on social behavior, too. Aggressive behavior was more pronounced in juveniles reared in isolation, and shoal cohesiveness was affected by social environment with group-reared fish being significantly closer together than isolation-reared fish. These observations suggest reduced social competence in fish reared in isolation in a species naturally living in shoals as juveniles. Moreover, in group-reared fish, kinship significantly affected distances between dyads. Cohesiveness between kin was significantly increased compared with unrelated fish. This may reflect shoaling decisions as well as better cooperative exploration behavior between kin, possibly resulting in better protection against predation, and thus increased inclusive fitness.

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