Original Article

Benefits of kin shoaling in a cichlid fish: familiar and related juveniles show better growth

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Group living is widespread in animals. In nature, groups usually not only differ in phenotypic characteristics but also in the social relationships among group members. Theory predicts that individuals adjusting their shoaling decisions—to join certain groups or not—based on social criteria, such as familiarity or genetic relatedness, can increase their fitness. Although numerous studies report grouping preferences based on social criteria, the benefits actually emerging from such behavioral preferences are less well studied. Here, we examine both shoaling preferences and their consequences in juveniles of *Pelvicachromis taeniatus*, a monogamous cichlid fish from Western Africa with biparental brood care. After juvenile *P. taeniatus* have left their parents, they form loose shoals. Then, juveniles may have the option either to stay in their sibling group or to join a novel shoal. Therefore, in a first experiment, we tested whether juveniles prefer to shoal with their familiar sibling group or a group consisting of unfamiliar unrelated individuals. Second, we examined whether the shoaling decision translates into fitness benefits. We used body size as proxy for fitness and compared the growth in groups consisting exclusively of familiar full-siblings with growth in groups consisting of members of different relatedness and familiarity. Juvenile *P. taeniatus* preferred shoaling with kin over shoaling with non-kin. Growth was significantly higher in kin-only groups than in mixed groups indicating that grouping with familiar kin yields fitness benefits in juvenile *P. taeniatus*. Our results suggest that individual shoaling decisions based on social criteria can be adaptive.

Key words: **familiarity, grouping, kin recognition, kin selection, *Pelvicachromis taeniatus*, social behavior.**

INTRODUCTION

Group living is widespread in animals (Krause and Ruxton 2002). An important reason for group living is the reduction of predation risk, and thus, grouping is reported in a wide range of prey organisms (Foster and Treherne 1981; Magurran 1990; Krause et al. 2000; Kullmann et al. 2008). However, there are also costs associated with living in a group such as increased competition or transfer of parasites (Pulliam and Caraco 1984; Côté and Poulin 1995). Therefore, the decision of an individual to associate with a certain group is usually not random but influenced by several factors such as body size (Ranta et al. 1992; Krause and Godin 1994), hunger level (Krause 1993; Frommen et al. 2007a), group size (Booth 1995; Krause et al. 2000; Thünken, Eigster, et al. 2014), parasite load (Côté and Poulin 1995; Ward et al. 2005), predation level (Brown and Warburton 1997), or coloration (Modarressie et al. 2006). The

relevance of these factors is expected to be dependent from ecological constraints (Pitcher and Parrish 1993).

Furthermore, social factors may influence individual shoaling decisions. Kin selection theory predicts that genetic relatedness between individuals can facilitate cooperation and reduce conflicts between individuals and thus contribute to the evolution of group living (Hamilton 1964; West and Gardner 2010). Social familiarity effects are important as well. For instance, familiarity is a necessary requirement for the establishment of reciprocal interactions and the formation of stable dominance hierarchies (Ward and Hart 2003; Croft et al. 2005). Laboratory and field studies have indeed revealed that groups are often kin structured (e.g., Magurran et al. 1995; Krause et al. 2000; Halverson et al. 2006; Selkoe et al. 2006; Buston et al. 2009; Hatchwell 2010) and that preferences to interact with (familiar) kin can be present (e.g., shoal choice in fishes: Krause et al. 2000; Ward and Hart 2003; Frommen and Bakker 2004; Gerlach and Lysiak 2006; Frommen et al. 2007a, 2007b; Frommen, Mehlis, et al. 2007; but see Croft et al. 2012). However, the actual consequences of grouping based on such social preferences are less well investigated. Although some studies showed

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reduced aggression in kin groups (fishes: Brown GE and Brown JA 1993; Sikkel and Fuller 2010; amphibians: Markman et al. 2009; birds: Toth et al. 2009; mice: Rusu and Krackow 2004; Palanza et al. 2005) or higher cooperation in foraging contexts (subsocial spiders: Ruch et al. 2009; fishes: Griffiths and Armstrong 2002), others found similar aggression levels between related and unrelated individuals (birds: Emlen 1996; fishes: Gerlach et al. 2007; Mehlis et al. 2009). Fitness-related traits such as fecundity (Mappes et al. 1995; Viblanc et al. 2010) or growth rates were positively affected by (familiar) kin grouping in some studies (fishes: Brown GE and Brown JA 1996; Gerlach et al. 2007; amphibians: Hokit and Blaustein 1997; Pakkasmaa and Laurila 2004; spiders: Schneider and Bilde 2008) suggesting that kin bias translates into fitness benefits. In contrast, similar growth in kin and non-kin groups was reported as well (Anderson and Sabado 1999; Smallegange and Tregenza 2008; Ruch et al. 2009), and other studies showed even better growth rates in unrelated groups (amphibians: Hokit and Blaustein 1994; birds: Royle et al. 1999; fishes: Griffiths and Armstrong 2001; plants: Milla et al. 2009). These differences could reflect adaptive variation because the costs and benefits of grouping with kin are expected to strongly depend on the ecological context as well as on the social organization of the respective species (see West et al. 2002).

Furthermore, methodological issues such as experimental settings and contexts may contribute to the observed variation of kin effects (e.g., Kydd and Brown 2009), which might be particularly true for studies trying to simultaneously address both ultimate and proximate questions. For example, the attempt to disentangle familiarity and kinship effects may come at the costs of natural relevance because under natural condition both factors are often highly intertwined and kinship effect might be only present among familiar kin (e.g., Gerlach et al. 2007; Lee-Jenkins and Godin 2013). Therefore, the aim of the present study was to investigate the ultimate consequences and benefits of kin-biased shoaling preferences under conditions resembling those found in nature.

Cichlid fishes are highly suitable to study social behavior because life history of most cichlid species is characterized by a high degree of intraspecific social interactions (Keenleyside 1991; Barlow 2000). Most cichlids spend a considerable part of their life in family groups particularly during juvenile life stages when they benefit from, often intense, parental care. An important reason for juvenile shoaling is the reduction of predation risk (Keenleyside 1991). Although these conditions make cichlids an ideal model system to examine kin-biased behavior, little experimental research has been done on this topic in this taxon (but see Stiver et al. 2008; Jordan et al. 2010; Le Vin et al. 2010; Lee-Jenkins and Godin 2013).

Pelvicachromis taeniatus is a socially monogamous cichlid fish from Western Africa with biparental brood care. *Pelvicachromis taeniatus* prefer close kin as mating partners (Thünken et al. 2007a, 2007b; Thünken et al. 2012; see also Langen et al. 2011). In accordance with the predictions of kin selection theory, we found better cooperation between related breeding pairs relative to unrelated ones, that is, sibling pairs were less aggressive among each other and provided better care (Thünken et al. 2007a) suggesting benefits of inbreeding in our system. Kin recognition is independent of familiarity (Thünken et al. 2007a), that is, *P. taeniatus* are capable of discriminating between unfamiliar kin and non-kin indicating that kin recognition is based on phenotype matching (Blaustein 1983; Lacy and Sherman 1983), which seems to rely on self-reference in adults (Thünken, Bakker, et al. 2014) and familiar imprinting in juveniles (Hesse et al. 2012). As in other fishes (e.g., Quinn and Busack 1985;

Olsen 1989; Gerlach and Lysiak 2006; Mehlis et al. 2008), olfactory cues may play an important role in kin recognition in *P. taeniatus* (Thünken et al. 2009, 2011; Hesse et al. 2012; Thünken, Bakker, et al. 2014).

After juvenile *P. taeniatus* have left their parents, they form loose shoals. Living in shoals provides several advantages for them: they benefit from rather passive dilution or confusion effects against predators as well as from behavioral adaptations, such as active shoaling decisions or predator inspection (Hesse and Thünken 2014; Hesse et al. 2015); also, we found better growth in group-reared fish relative to isolation-reared juveniles (Hesse and Thünken 2014). Siblings formed tighter shoals than nonsiblings (Hesse and Thünken 2014) already indicating potential benefits of kin-biased behavior.

Against this background, in the present study, we aimed to test kin-shoaling preferences and their adaptive significance in juvenile *P. taeniatus* under naturally realistic conditions. After juveniles had left their parents, they may have the option to choose either to remain with their siblings or to join a new group. Therefore, first, juveniles were given the choice between a shoal consisting of familiar kin and a shoal consisting of unfamiliar, unrelated individuals. Second, we aimed to test whether potential shoaling preference translates into fitness benefits by measuring individual growth in groups consisting exclusively of kin and groups of mixed relatedness. Body size is often used as proxy for fitness in evolutionary behavioral ecology (e.g., Hunt and Hodgson 2010). As in other fishes, in *P. taeniatus*, larger individuals should be better protected against gape-limited predators (see Sogard 1997), and they should have advantages in competition (Thünken et al. 2011) and mate choice (Baldauf, Kullmann, Schroth, et al. 2009).

MATERIAL AND METHODS

Model system

Pelvicachromis taeniatus is a small stream dwelling cichlid of Western Africa. Adult males are larger (6–8 cm) than females (4–5 cm). Both sexes are strikingly differently colored. Body coloration and size play important roles in male and female mate choice as well as in intrasexual competition (Baldauf, Kullmann, Schroth, et al. 2009; Baldauf, Kullmann, Thünken, et al. 2009; Baldauf et al. 2010, 2011; Thünken et al. 2011). Reproductively active males occupy territories with appropriate breeding caves and defend them against rivals (Thünken et al. 2009). Females compete among each other for access to males with caves. Both sexes show active courtship and are choosy (Thünken et al. 2007a, 2007b; Baldauf, Kullmann, Schroth, et al. 2009). Females spawn ~20 up to 150 eggs. Subsequently, mainly the female cares for the eggs and larvae within a cave whereas the male protects the territory. After about 1 week, the free-swimming fry leave the cave and are then guarded by both parents for several weeks until independence (Thünken et al. 2010). Our study population originates from the Moliwe River, a small river in Cameroon that is highly inbred (Langen et al. 2011).

Experimental fish

Experimental fish were F1 and F2 outbred offspring of wild-caught *P. taeniatus*. They were bred in the laboratory at the Institute for Evolutionary Biology and Ecology in Bonn under standardized conditions in summer 2008 (August and September) and summer 2009 (May and July). Breeding tanks (length × width × height: 50 cm × 30 cm × 30 cm) contained a standard breeding cave and Java moss. The water temperature was kept at 24 ± 1 °C. Light:dark

regime was 12:12 h. Free-swimming *P. taeniatus* fry were fed daily with living *Artemia* nauplii and later on with a mixture of defrosted *Chironomus* larvae and *Artemia*. Experiments were conducted with juveniles that were kept together with their parents and siblings in the breeding tanks until the start of the experiment. Body size of the experimental fish measured on average 25.62 ± standard deviation [SD] 3.52 mm. At this developmental stage, the sex cannot be determined unambiguously.

Shoaling experiment

Experimental setup

The choice tank (70 cm × 35 cm × 35 cm) was divided in 3 sections. At the far ends of the tank, 2 equally sized compartments (length × width: 12 cm × 35 cm) were arranged in which the stimulus fish groups were located. These compartments were separated from the middle section in which the test fish was located by transparent perforated plexiglass partitions. Thus, visual and olfactory contact between the focal fish and the 2 stimulus shoals was possible. In each trial, the stimulus fish of one compartment were familiar kin of the focal fish, whereas stimulus fish located in the other compartment were composed of unfamiliar non-kin. In front of the 2 stimulus fish compartments, 2 association zones of 5 cm each were marked (which equates approximately 2 times of the body size of the test fish). The water level in the choice tank was 15 cm. Interior sides of the tank were covered with self-sticking coated film to prevent the test fish from interacting with their mirrored self. In the middle section, a perforated plexiglass cylinder (diameter = 11 cm) was placed in which the test fish was put before the start of the experiment. As the cylinder was transparent and perforated visual as well as olfactory contact was possible before the experiment started. The cylinder could be lifted by a pulley to minimize disturbance after habituation. The experiment was recorded with a video camera (CCD Ever Focus model EQ150 Video Camera 1/3″ BW High Resolution Camera with Ever Focus CCTV Lenses) that was fixed to a wooden frame 90 cm above the experimental setup. The choice tank was illuminated from above by a fluorescent tube (Osram lumilux L 58W). Pretests had revealed that juveniles when given the choice between a shoal and an empty compartment preferred to associate with the shoal (Thünken T, unpublished data).

Experimental protocol

Four juvenile stimulus fish from 2 different families each were randomly caught from the breeding tanks. Each sibling group was placed in a small plastic tank (16 cm × 9 cm × 10 cm) filled with 450-mL tap water. After 20 min, the stimulus fish of both families were released in the 2 compartments of the choice tank by pouring out the water with the fish into the compartment. Thus, one compartment contained 4 stimulus fish of one family and both stimulus groups were introduced into their compartments at the same time. Subsequently, a test fish familiar and related to one of the stimulus fish families was placed in the perforated plexiglass cylinder in the middle of the choice tank and permitted 15 min to acclimatize to the new environment. Altogether, 36 focal fish originating from 18 different families were tested. During the acclimatization period, the test fish could see and probably smell the stimulus fish. After 15 min, the video recording was started and the cylinder was lifted using a pulley to release the test fish. The experiment was recorded for 30 min after the test fish entered one of the association zones. If the test fish did not move within the 30 min of the experiment, the experiment was marked as invalid. It was then repeated with another test fish of the same family. After the experiment, the test fish was caught and its total length measured with a digital caliper. Total length was defined as the length from the tip of the fish's snout to the end of its caudal fin. The stimulus fish were again placed for 20 min in 2 holding tanks containing 450-mL tap water. During these 20 min, the choice tank was emptied, rinsed with clear water, and refilled with tap water. Afterwards, the stimulus fish were again placed in their compartments (each shoal on the same side as in the experiment before) and a test fish of the other family was caught. It was also placed in the cylinder and set free after 15 min. As the stimulus fish remained on the same side as in the trial before, the stimulus group consisting of the familiar siblings of the test fish was now on the other side of the tank thus allowing to control for side bias and potential differences in a shoal's phenotypic attractiveness (paired design). After the experiment, the test fish was measured and the stimulus fish were placed in their small tanks once more. The choice tank was again emptied, rinsed with clear water, and filled with tap water. Two more trials were conducted with 2 additional test fish of the 2 families and with the same stimulus shoals following exactly the same experimental protocol. After 2 juveniles of each family had been tested, the stimulus fish were measured with a digital caliper and their standard lengths were noted (variation in the size of the focal fish the stimulus fish as well as size difference between focal and stimulus fish had no significant effect on shoaling preferences, all $P > 0.2$). All test fish were only used once, and stimulus fish were not tested as focal fish.

Behavioral analysis

The videos were analyzed blindly with respect to the origin of the experimental fish. We measured the time each test fish spent in the association zones for 10 min after it has entered a zone (e.g., Le Vin et al. 2010 used the same experimental time). The proportion of time the test fish spent with the related and the unrelated shoal was calculated (in percent relative to the total amount of time it spent in both association zones). In order to control for differences in stimulus shoal attractiveness (e.g., caused by size or behavioral differences), the same stimulus shoals were repeatedly used (see above). Eventually, the same stimulus shoal pair was used in 4 trials with 4 different focal fish (2 from each family).

Growth experiment

Experimental setup

Juveniles were reared either in a group consisting of 14 familiar, related individuals ("kin group" from now on, $N = 10$) or a group consisting of 14 individuals originating from 2 different unfamiliar families ("mixed group" from now on, $N = 10$; each family provided 7 fish). Because of potential growth differences between families (due to genetic differences or environmental differences in previous rearing conditions, e.g., different groups size [ranging from 23 to 50 juveniles or slight differences in age ranging from ~2 to 3 months]), we chose to split the family design: 14 juveniles of a given family were used for the kin group and 7 juveniles of the same family were reared together with 7 individuals from a different family (unfamiliar non-kin) forming the mixed group. The size, that is, the total body length of the juveniles was measured using a digital caliper to the nearest hundredths of a millimeter and groups of size-matched individuals were arranged. Fish of the kin group and mixed groups did not differ significantly in initial size and variation in size (linear mixed effect models ["lme"], all $P > 0.05$). Because we had to assign a certain individual to its family of origin, each tank (17 cm × 19 cm × 32 cm) was divided in 2 equal-sized

compartments each containing the 7 juveniles originating from one family. The compartments were separated by a green mesh (mesh wide: 1 mm) allowing visual, chemical and tactile communication within and between the kin groups. Housing was identical for the kin groups, that is, they were also separated by a mesh into 2 sub-groups. The tanks were equipped with sand and each compartment had an air-stone and ~1 g of Java moss. The tanks were separated from each other by gray plastic sheets to exclude interactions with adjacent groups. Altogether, 10 different families were used. Fish were fed 6 days a week with a mix of frozen *Chironomus* larvae, frozen *Artemia*, and living *Artemia* nauplii ad libitum. Food remains were removed within 1 h after feeding. Once a week, one-third of the water was exchanged. After a period of 30 days, the size of the juveniles was measured again as described above by a person naive to the treatment.

Statistical analysis

Data did not significantly differ from a normal distribution according to Shapiro–Wilk tests. Variances were homogenous according to the Levene tests. Thus, parametric tests were conducted. All calculations were performed with the R. 2.9.1 statistical software package (R Development Core Team 2008).

Shoaling experiment

Altogether 36 individuals originating from 18 different families were tested. In order to control for differences in stimulus shoal attractiveness (e.g., caused by size or behavioral differences), the same stimulus shoal pair was used in 4 trials with 4 different focal fish (2 from each family see above). In order to avoid pseudoreplication, we averaged the relative time the 4 test fish spent with the familiar related and unfamiliar unrelated shoal, respectively, finally resulting in 9 experimental units. Then, preferences for familiar kin versus unfamiliar non-kin were analyzed using a paired *t*-test.

Growth experiment

We calculated the average individual increase in size (from the first to the second measurement) per family in the kin group (the mean individual growth was calculated for both subgroups [7 individuals] and then averaged) and in the corresponding subgroup in the mixed group (7 individuals). Then, we calculated a growth index (increase in the kin group minus increase in the mixed group) and tested whether growth was statistically significantly higher in the kin-only group (positive values) or in the mixed group (negative values) using a binomial test. Additionally, we conducted a lme model examining the impact of the treatment (kin/mixed group) on change in size; family ID was included as random factor.

RESULTS

Shoaling experiment

Test fish spent on average 524 s out of the 600-s total experimental time in both association zones, which equate 87% in association zones and 13% in the neutral zone. They significantly spent more time shoaling with familiar kin than unfamiliar non-kin (paired *t*-test, *t* = 2.806, degrees of freedom [df] = 8, *P* = 0.023, Figure 1).

Growth experiment

Within-family comparisons revealed that in 9 of 10 tested families, the average increase in individual size was higher in the group consisting of familiar kin only than in the corresponding sibling groups,

which were reared together with unfamiliar non-kin (binomial test, *P* = 0.022, Figure 2). Across the experimental period of 30 days, fish on average grew 3.873 ± SD 1.038 mm. Growth in the kin group was better than in the mixed group (4.039 ± SD 1.083 mm vs. 3.542 ± SD 0.863 mm; lme: df = 1, χ^2 = 4.435, *P* = 0.035).

DISCUSSION

In the present study, we showed that juvenile *P. taeniatus* prefer to shoal with familiar siblings over unfamiliar non-kin. Similar grouping preferences have been shown in several other, non-cichlid fishes (e.g., Frommen and Bakker 2004; Gerlach and Lysiak 2006; Frommen et al. 2007a, 2007b; Piyapong et al. 2011); kin structuring was also found in natural cichlid populations (e.g., Pouyaud et al. 1999). However, little is known about the fitness consequences resulting from such kin associations. Our results suggest that juvenile *P. taeniatus* benefit from grouping with their siblings because they grew better in groups consisting exclusively of kin compared with groups also including non-kin. Body size is a fitness-related
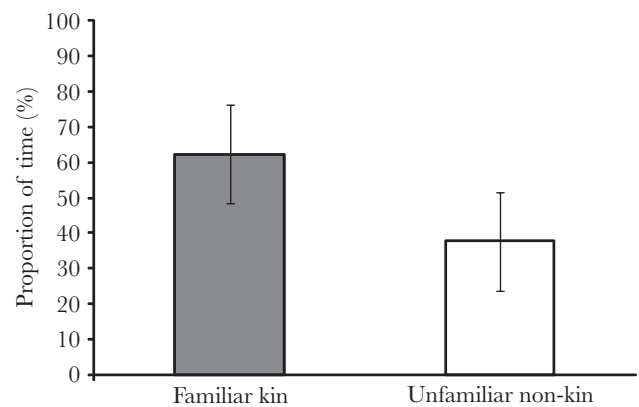
Figure 1
Mean percentage of time (± SD) juveniles spent shoaling with familiar kin and unfamiliar non-kin. Thirty-six fish originating from 18 different families were tested.
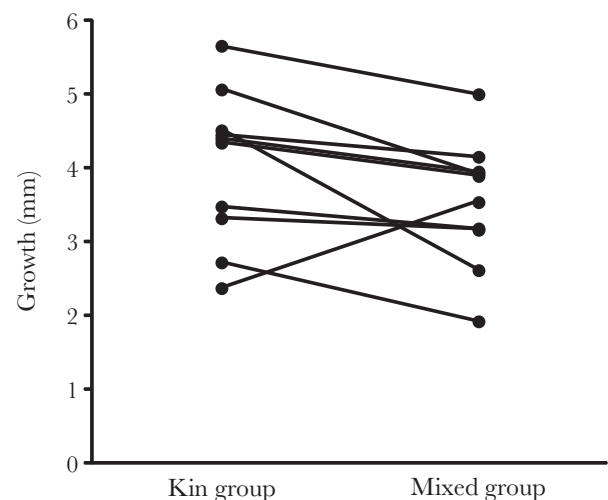
Figure 2
Growth in body size across the 10 tested families during the experimental period of 30 days. Mean values of family subgroups either reared with kin only or reared in a mixed group are shown. Mean values of each family are connected by a line.

trait in many fish species (Sogard 1997). Especially, during juvenile life stages, body size plays an important role for survival under natural conditions. Smaller individuals for example are weaker competitors (Thünken et al. 2011) or more vulnerable to predation (for a review see Sogard 1997). Therefore, our study indicates that behavioral shoaling decisions of juveniles are adaptive. The result adds to that of a recent study showing better growth of juveniles in a group compared with juveniles that grew up in isolation (Hesse and Thünken 2014) suggesting that the social environment in general and its quality or compositions in particular have strong impact on juvenile performance.

We intended to examine juvenile shoaling decisions and the consequences under as natural as possible conditions because the benefits of kin shoaling might potentially result from the addition and/ or the interaction of different effects, for example, from kinship and familiarity effects and therefore efforts to experimentally separate them might crucially affect the results (Frommen et al. 2013). As a consequence, however, we were not able disentangle the importance of both factors that are strongly intertwined because sibling usually grow up together under natural conditions. Interestingly, the 2 other studies in fishes reporting benefits of kin associating found them among familiar siblings (Brown GE and Brown JA 1996; Gerlach et al. 2007). Furthermore, in the convict cichlid *Amatitlania siquia* preferences for kin were only present when they were familiar (Lee-Jenkins and Godin 2013) and juvenile *Pelvicachromis pulcher* preferences for familiar kin were stronger than those for unfamiliar kin (Le Vin et al. 2010) supporting our claims.

Considering previous studies on kin recognition and discrimination in *P. taeniatus* (e.g., Thünken et al. 2007a; Hesse et al. 2012), there are good reasons to assume that kin selection—at least—contributes to better performance of sibling groups. Here, we did not measure behavioral variables, but recent behavioral studies with juvenile *P. taeniatus* indicate better shoal performance and cooperation between (unfamiliar) kin (Hesse and Thünken 2014; Hesse et al. 2016). In the experimental setup of the present study, no interference competition was possible between subgroups. However, higher aggression, for example, including energy-demanding aggressive displays between unrelated subgroups is likely and has been found, for example, in juvenile black perch, *Embiotoca jacksoni* (Sikkel and Fuller 2010). Furthermore, living with non-kin might imply immunological stress because individuals might be adapted to certain microbiota that they share with their familiar relatives. For example, Barribeau et al. (2012) recently showed that in tadpoles of *Xenopus laevis* exposure to water conditioned by major histocompatibility complex–dissimilar conspecifics affected larval development.

Familiarity effects might add to the kinship effects. Several studies showed shoaling preferences for familiars in fishes (e.g., Griffiths and Magurran 1999; Ward and Hart 2003). In guppies, shoaling decision has been suggested to be based on familiarity rather than relatedness (Griffiths and Magurran 1999). Liebgold and Cabe (2008) found that juvenile salamanders showed increased growth when near familiar adults but relatedness had no significant effect. Generally, familiarity is an important prerequisite for the emergence of reciprocal behavior. In our case, juvenile *P. taeniatus* grew up together for several weeks with their parents in a sibling group. During this period, social familiarity may be developed between siblings as well as stable dominance hierarchies. The formation of dominance hierarchies within groups is common in cichlids (Gómez-Laplaza 2006; Gonçalves-de-Freitas et al. 2008). Living in groups with stable social hierarchies may reduce aggression and thus should be beneficial for the individual. In contrast, in newly formed shoals, hierarchies firstly need to be established. This process is associated with mutual assessments as well as stressful and energy-demanding confrontations. Although no direct physical contact was possible between unfamiliar individuals (thereby avoiding potentially serious fights), the mesh dividing the subgroups allowed communication via display behavior and chemical cues both mediating aggression in cichlids (e.g., Barlow 2000; Barata et al. 2007).

In conclusion, our results indicate that the decision of juvenile *P. taeniatus* to shoal with their siblings is adaptive because growth was better in groups consisting exclusively of familiar kin compared with groups of mixed relatedness and familiarity.

FUNDING

REFERENCES

Anderson TW, Sabado BD. 1999. Effects of kinship on growth of a live-bearing reef fish. Mar Biol. 133:115–121.

Baldauf SA, Bakker TCM, Herder F, Kullmann H, Thünken T. 2010. Male mate choice scales female ornament allometry in a cichlid fish. BMC Evol Biol. 10:301.

Baldauf SA, Bakker TCM, Kullmann H, Thünken T. 2011. Female nuptial coloration and its adaptive significance in a mutual mate choice system. Behav Ecol. 22:478–485.

Baldauf SA, Kullmann H, Schroth SH, Thünken T, Bakker TCM. 2009. You can't always get what you want: size assortative mating by mutual mate choice as a resolution of sexual conflict. BMC Evol Biol. 9:129.

Baldauf SA, Kullmann H, Thünken T, Winter S, Bakker TCM. 2009. Computer animation as a tool to study preferences in the cichlid *Pelvicachromis taeniatus*. J Fish Biol. 75:738–746.

Barata EN, Hubbard PC, Almeida OG, Miranda A, Canário AV. 2007. Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). BMC Biol. 5:54.

Barlow GW. 2000. The cichlid fishes. Nature's grand experiment in evolution. Cambridge (MA): Perseus Books.

Barribeau SM, Villinger J, Waldman B. 2012. Ecological immunogenetics of life-history traits in a model amphibian. Biol Lett. 8:405–407.

Blaustein AR. 1983. Kin recognition mechanisms: phenotypic matching or recognition alleles? Am Nat. 121:749–754.

Booth DJ. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. Ecology. 76:91–106.

Brown GE, Brown JA. 1993. Social dynamics in salmonid fishes—do kin make better neighbors? Anim Behav. 45:863–871.

Brown GE, Brown JA. 1996. Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? Behav Ecol. 7:24–29.

Brown C, Warburton K. 1997. Predator recognition and anti-predator responses in the rainbowfish *Melanotaenia eachamensis*. Behav Ecol Sociobiol. 41:61–68.

Buston PM, Fauvelot C, Wong MY, Planes S. 2009. Genetic relatedness in groups of the humbug damselfish *Dascyllus aruanus*: small, similar-sized individuals may be close kin. Mol Ecol. 18:4707–4715.

Côté IM, Poulin R. 1995. Parasitism and group size in social animals: a meta-analysis. Behav Ecol. 6:159–165.

Croft DP, Hamilton PB, Darden SK, Jacoby DM, James R, Bettaney EM, Tyler CR. 2012. The role of relatedness in structuring the social network of a wild guppy population. Oecologia. 170:955–963.

Croft DP, James R, Ward AJ, Botham MS, Mawdsley D, Krause J. 2005. Assortative interactions and social networks in fish. Oecologia. 143:211–219.

Emlen DJ. 1996. Artificial selection on horn length body size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Evolution. 50:1219–1230.

Foster WA, Treherne JE. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature. 293:466–467.

Frommen JG, Bakker TCM. 2004. Adult three-spined sticklebacks prefer to shoal with familiar kin. Behaviour. 141:1401–1410.

Frommen JG, Luz C, Bakker TCM. 2007a. Nutritional state influences shoaling preference for familiars. Zoology. 110:369–376.

Frommen JG, Luz C, Bakker TCM. 2007b. Kin discrimination in sticklebacks is mediated by social learning rather than innate recognition. Ethology. 113:276–282.

Frommen JG, Mehlis M, Brendler C, Bakker TCM. 2007. Shoaling decisions in three-spined sticklebacks (*Gasterosteus aculeatus*)—familiarity kinship and inbreeding. Behav Ecol Sociobiol. 61:533–539.

Frommen JG, Zala SM, Raveh S, Schaedelin FC, Wernisch B, Hettyey A. 2013. Investigating the effect of familiarity on kin recognition of three-spined stickleback (*Gasterosteus aculeatus*). Ethology. 119:531–539.

Gerlach G, Hodgins-Davis A, Macdonald B, Hannah RC. 2007. Benefits of kin association: related and familiar zebrafish larvae (*Danio rerio*) show improved growth. Behav Ecol Sociobiol. 61:1765–1770.

Gerlach G, Lysiak N. 2006. Kin recognition and inbreeding avoidance in zebrafish *Danio rerio* is based on phenotype matching. Anim Behav. 71:371–1377.

Gómez-Laplaza LM. 2006. Shoal choice in juvenile angelfish (*Pterophyllum scalare*): effects of social status and activity. Ethol Ecol Evol. 18:261–273.

Gonçalves-de-Freitas E, Teresa FB, Gomes FS, Giaquinto PC. 2008. Effect of water renewal on dominance hierarchy of the Nile tilapia. Appl Anim Behav Sci. 112:187–195.

Griffiths SW, Armstrong JD. 2001. The benefits of genetic diversity outweigh those of kin association in a territorial animal. Proc Biol Sci. 268:1293–1296.

Griffiths SW, Armstrong JD. 2002. Kin-biased territory overlap and food sharing among Atlantic salmon juveniles. J Anim Ecol. 71:480–486.

Griffiths SW, Magurran AE. 1999. Schooling decisions in guppies (*Poecilia reticulata*) are based on familiarity rather than kin recognition by phenotype matching. Behav Ecol Sociobiol. 45:437–443.

Halverson MA, Skelly DK, Caccone A. 2006. Kin distribution of amphibian larvae in the wild. Mol Ecol. 15:1139–1145.

Hamilton WD. 1964. The genetical evolution of social behaviour. I. J Theor Biol. 7:1–16.

Hatchwell BJ. 2010. Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin directed cooperation. Ethology. 116:203–216.

Hesse S, Anaya-Rojas MJ, Frommen JG, Thünken T. 2015. Effects of social environment on cooperative predator inspection in a cichlid fish. R Soc Open Sci. 2:140–451.

Hesse S, Anaya-Rojas MJ, Frommen JG, Thünken T. 2016. Kinship reinforces cooperative predator inspection in a cichlid fish. J Evol Biol. doi: 10.1111/jeb.12736.

Hesse S, Bakker TCM, Baldauf SA, Thünken T. 2012. Kin recognition by phenotype matching is rather family- than self-referential in juvenile cichlid fish. Anim Behav. 84:451–457.

Hesse S, Thünken T. 2014. Growth and social behavior in a cichlid fish are affected by social rearing environment and kinship. Naturwissenschaften. 101:273–283.

Hokit DG, Blaustein AR. 1994. The effect of kinship on growth and development in tadpoles of *Rana cascada*. Evolution. 48:1383–1388.

Hokit DG, Blaustein AR. 1997. Effects of kinship on interactions between tadpoles of *Rana cascadae*. Ecology. 78:1722–1735.

Hunt J, Hodgson J. 2010. What is fitness, and how do we measure it? In: Westneat D, Fox CW, editors. Evolutionary behavioral ecology. Oxford: Oxford University Press. p. 46–70.

Jordan LA, Wong MYL, Balshine SS. 2010. The effects of familiarity and social hierarchy on group membership decisions in a social fish. Biol Lett. 6:301–303.

Keenleyside MHA. 1991. Cichlid fishes—behaviour ecology and evolution. London: Chapman and Hall.

Krause J. 1993. The influence of hunger on shoal size choice by three-spined sticklebacks *Gasterosteus aculeatus*. J Fish Biol. 43:775–780.

Krause J, Butlin RK, Peuhkuri N, Pritchard VL. 2000. The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. Biol Rev. 75:477–501.

Krause J, Godin JGJ. 1994. Shoal choice in the banded killifish (*Fundulus diaphanus* Teleostei Cyprinodontidae)—effects of predation risk fish size species composition and size of shoals. Ethology. 98:128–136.

Krause J, Ruxton GD. 2002. Living in groups. Oxford: Oxford University Press.

Kullmann H, Thünken T, Baldauf SA, Bakker TCM, Frommen JG. 2008. Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. Biol Lett. 4:458–460.

Kydd E, Brown C. 2009. Loss of shoaling preference for familiar individuals in captive-reared crimson spotted rainbowfish *Melanotaenia duboulayi*. J Fish Biol. 74:2187–2195.

Lacy RC, Sherman PW. 1983. Kin recognition by phenotype matching. Am Nat. 121:489–512.

Langen K, Schwarzer J, Kullmann H, Bakker TCM, Thünken T. 2011. Microsatellite support for active inbreeding in a cichlid fish. PLoS One. 6:246–89.

Liebgold EB, Cabe PR. 2008. Familiarity with adults but not relatedness affects the growth of juvenile red-backed salamanders (*Plethodon cinereus*). Behav Ecol Sociobiol. 63:277–284.

Lee-Jenkins SSY, Godin J-GJ. 2013. Concurrent effects of familiarity and kinship on social affiliations in convict cichlid (*Amatitlania siquia*) young. Behaviour. 150:895–919.

Le Vin AL, Mable BK, Arnold KE. 2010. Kin recognition via phenotype matching in a cooperatively breeding cichlid *Neolamprologus pulcher*. Anim Behav. 79:1109–1114.

Magurran AE. 1990. The adaptive significance of schooling as an anti-predator defence in fish. Ann Zool Fenn. 27:51–66.

Magurran AE, Seghers BH, Shaw PW, Carvallo GR. 1995. The behavioral diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. Adv Stud Behav. 24:155–202.

Mappes T, Ylonen H, Viitala J. 1995. Higher reproductive success among kin groups of bank voles (*Clethrionomys glareolus*). Ecology. 76:1276–1282.

Markman S, Hill N, Todrank J, Heth G, Blaustein L. 2009. Differential aggressiveness between fire salamander (*Salamandra infraimmaculata*) larvae covaries with their genetic similarity. Behav Ecol Sociobiol. 63:1149–1155.

Mehlis M, Bakker TCM, Frommen JG. 2008. Smells like sib spirit: kin recognition in three-spined sticklebacks (*Gasterosteus aculeatus*) is mediated by olfactory cues. Anim Cogn. 11:643–650.

Mehlis M, Bakker TCM, Langen K, Frommen JG. 2009. Cain and Abel reloaded? Kin recognition and male-male aggression in three-spined sticklebacks *Gasterosteus aculeatus* L. J Fish Biol. 75:2154–2162.

Milla R, Forero DM, Escudero A, Iriondo JM. 2009. Growing with siblings: a common ground for cooperation or for fiercer competition among plants? Proc Biol Sci. 276:2531–2540.

Modarressie R, Rick IP, Bakker TCM. 2006. UV matters in shoaling decisions. Proc Biol Sci. 273:849–854.

Olsen KH. 1989. Sibling recognition in juvenile Arctic charr, *Salvelinus alpinus*. J Fish Biol. 34:571–581.

Pakkasmaa S, Laurila A. 2004. Are the effects of kinship modified by environmental conditions in *Rana temporaria* tadpoles? Ann Zool Fenn. 41:413–420.

Palanza P, Della Seta D, Ferrari PF, Parmigiani S. 2005. Female competition in wild house mice depends upon timing of female/male settlement and kinship between females. Anim Behav. 69:1259–1271.

Pitcher TJ, Parrish JK. 1993. Functions of shoaling behaviour in teleosts. In: Pitcher TJ, editor. Behaviour of teleost fishes. London: Chapman and Hall. p. 363–439.

Piyapong C, Butlin RK, Faria JJ, Scruton KJ, Wang J, Krause J. 2011. Kin assortment in juvenile shoals in wild guppy populations. Heredity. 106:749–756.

Pouyaud L, Desmarais E, Chenuil A, Agnese TF, Bonhomme F. 1999. Kin cohesiveness and possible inbreeding in the mouthbrooding tilapia *Sarotherodon melanotheron* (Pisces Cichlidae). Mol Ecol. 8:803–812.

Pulliam HR, Caraco T. 1984. Living in groups: is there an optimal group size? In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach. 2nd ed. Oxford: Blackwell Publishing. p. 122–147.

Quinn TP, Busack CA. 1985. Chemosensory recognition of siblings in juvenile coho Salmon (*Oncorhynchus kisutch*). Anim Behav. 33:51–56.

Ranta E, Lindström K, Peuhkuri N. 1992. Size matters when three-spined sticklebacks go to school. Anim Behav. 43:160–162.

R Development Core Team. 2008. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org

Royle NJ, Hartley IR, Owens IPF, Parker GA. 1999. Sibling competition and the evolution of growth rates in birds. Proc Biol Sci. 266:923–932.

Ruch J, Heinrich L, Bilde T, Schneider JM. 2009. Relatedness facilitates cooperation in the subsocial spider, *Stegodyphus tentoriicola*. BMC Evol Biol. 9:257.

Rusu AS, Krackow S. 2004. Kin-preferential cooperation dominance-dependent reproductive skew and competition for mates in communally nesting female house mice. Behav Ecol Sociobiol. 56:298–305.

Schneider JM, Bilde T. 2008. Benefits of cooperation with genetic kin in a subsocial spider. Proc Natl Acad Sci USA. 105:10843–10846.

Selkoe KA, Gaines SD, Caselle JE, Warner RR. 2006. Current shifts and kin aggregation explain genetic patchiness in fish recruits. Ecology. 87:3082–3094.

Sikkel PC, Fuller CA. 2010. Shoaling preference and evidence for maintenance of sibling groups by juvenile black perch *Embiotoca jacksoni*. J Fish Biol. 76:1671–1681.

Smallegange IM, Tregenza T. 2008. Local competition between foraging relatives: growth and survival of bruchid beetle larvae. J Insect Behav. 21:375–386.

Sogard SM. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci. 60:1129–1157.

Stiver KA, Fitzpatrick J, Desjardins JK, Neff BD, Quinn JS, Balshine S. 2008. The role of genetic relatedness among social mates in a cooperative breeder. Behav Ecol. 19:816–823.

Thünken T, Bakker TCM, Baldauf SA. 2014. "Armpit effect" in an African cichlid fish: self-referent kin recognition in mating decisions of male *Pelvicachromis taeniatus*. Behav Ecol Sociobiol. 68:99–104.

Thünken T, Bakker TCM, Baldauf SA, Kullmann H. 2007a. Active inbreeding in a cichlid fish and its adaptive significance. Curr Biol. 17:225–229.

Thünken T, Bakker TCM, Baldauf SA, Kullmann H. 2007b. Direct familiarity does not alter mating preference for sisters in male *Pelvicachromis taeniatus* (Cichlidae). Ethology. 113:1107–1112.

Thünken T, Baldauf SA, Kullmann H, Schuld J, Hesse S, Bakker TCM. 2011. Size-related inbreeding preference and competitiveness in male *Pelvicachromis taeniatus* (Cichlidae). Behav Ecol. 22:358–362.

Thünken T, Eigster M, Frommen JG. 2014. Context-dependent group size preferences in large shoals of three-spined stickleback. Anim Behav. 90:205–210.

Thünken T, Meuthen D, Bakker TCM, Baldauf SA. 2012. A sex-specific trade-off between mating preferences for genetic compatibility and body size in a cichlid fish with mutual mate choice. Proc Biol Sci. 279:2959–2964.

Thünken T, Meuthen D, Bakker TCM, Kullmann H. 2010. Parental investment in relation to offspring quality in the biparental cichlid fish, *Pelvicachromis taeniatus*. Anim Behav. 80:69–74.

Thünken T, Waltschyk N, Bakker TCM, Kullmann H. 2009. Olfactory self-recognition in a cichlid fish. Anim Cogn. 12:717–724.

Toth Z, Bokony V, Lendvai AZ, Szabo K, Penzes Z, Liker A. 2009. Kinship and aggression: do house sparrows spare their relatives? Behav Ecol Sociobiol. 63:1189–1196.

Viblanc VA, Arnaud CM, Dobson FS, Murie JO. 2010. Kin selection in Columbian ground squirrels (*Urocitellus columbianus*): littermate kin provide individual fitness benefits. Proc Biol Sci. 277:989–994.

Ward AJW, Duff AJ, Krause J, Barber I. 2005. Shoaling behaviour of sticklebacks infected with the microsporidian parasite *Glugea anomala*. Environ Biol Fish. 72:155–160.

Ward AJW, Hart PJB. 2003. The effects of kin and familiarity on interactions between fish. Fish Fish. 4:348–358.

West SA, Gardner A. 2010. Altruism, spite, and greenbeards. Science. 327:1341–1344.

West SA, Pen I, Griffin AS. 2002. Conflict and cooperation—cooperation and competition between relatives. Science. 296:72–75.