

Early experience affects learning performance and neophobia in a cooperatively breeding cichlid

Francis Bannier¹ | Sabine Tebbich² | Barbara Taborsky¹ 

¹Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

²Department for Behavioural Biology, University of Vienna, Vienna, Austria

Correspondence

Barbara Taborsky, Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland.
Email: barbara.taborsky@iee.unibe.ch

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Abstract

The ability to respond flexibly to environmental challenges, for instance by learning or by responding appropriately to novel stimuli, may be crucial for survival and reproductive success. Experiences made during early ontogeny can shape the degree of behavioural flexibility maintained by individuals during later life. In natural habitats, animals are exposed to a multitude of social and non-social ecological factors during early ontogeny, but their relative influences on future learning ability and behavioural flexibility are only poorly understood. In the cooperatively breeding cichlid *Neolamprologus pulcher*, we investigated whether early social and predator experiences shape the learning performance, flexibility, and response to novelty of adults. Fish were reared either with or without parents and helpers and with or without perceived predation risk in a full-factorial experiment. We investigated the influence of these treatments on learning performance and flexibility in a spatial acquisition and reversal learning task. To test for response to novelty, we performed a neophobia test. We found that fish reared with predator experience, but without the presence of older group members outperformed fish with other rearing backgrounds in reversal learning and that individuals, which had been reared in a socially more complex environment together with older group members responded less neophobic toward a novel object than individuals reared among siblings only. Comparative evidence from fish and rats suggests that these developmental effects may be driven by the cues of safety perceived in the presence of guarding parents.

KEYWORDS

cichlid, developmental plasticity, early experience, learning, neophobia, reversal task

1 | INTRODUCTION

Phenotypic plasticity, the ability of a genotype to express different phenotypes, can be a powerful mechanism enabling organisms to cope with changing environments. It occurs at all levels of organismic organization including morphology, physiology, neural organization, and behaviour (Fischer, Bessert-Nettelbeck, Kotschal, & Taborsky, 2015; Mery & Burns, 2010; Rosenzweig & Bennett, 1995; Sword, 2002). Behavioural flexibility is a form of plasticity that enables animals to respond rapidly to environmental changes (Mery & Burns, 2010; Taborsky & Oliveira, 2012). The degree of behavioural

flexibility shown by animal can depend on their social organization and ecology. For example, highly social species are expected to express more flexible behaviour than less social species (Bond, Kamil, & Balda, 2007; Easton, 2005). Also variation in biotic and abiotic ecological factors, including food abundance and predation risk, can favour the evolution of greater behavioural flexibility, where more variable environments are expected to favour greater flexibility than stable environments (Day, Coe, Kendal, & Laland, 2003; Jones, 2005; Sol, Griffin, Bartomeus, & Boyce, 2011; Tebbich, Stankewitz, & Teschke, 2012; Tebbich & Teschke, 2014; Tomasello & Call, 1997). Learning is an important form of behavioural flexibility enabling animals to adapt to

local environmental conditions and to cope with short-term environmental fluctuations (Mery & Burns, 2010). Another prominent aspect of behavioural flexibility is the way how animals deal with environmental novelty. Reduced neophobia, for instance, can help individuals to invade novel or anthropogenic habitats, or to use larger parts of an ecological niche (generalists) (Sol, Timmermans, & Lefebvre, 2002).

Early life experiences can persistently impact later life learning ability and neophobia via developmental plasticity. Several studies reported long-term effects of early environmental conditions on behavioural flexibility in the social domain (aka "social competence"; Arnold & Taborsky, 2010; Taborsky, Arnold, Junker, & Tschopp, 2012), learning performance (Braithwaite & Salvanes, 2005; Brust, Krüger, Naguib, & Krause, 2014; Chapman, Ward, & Krause, 2008; Kotschal & Taborsky, 2010; Rosenzweig & Bennett, 1995; Strand et al., 2010; Van Praag, Kempermann, & Gage, 2000), neophobic responses to novel objects (Laviola & Terranova, 1998), and brain structure (Fischer et al., 2015; Leventopoulos et al., 2007; Spinelli et al., 2009). Effects of early life growth conditions on learning performance can persist for many years (Brust et al., 2014). Both social and non-social components of the early environment can influence later-life behavioural flexibility. In general, an increased quantity or quality of early social interactions improves social competence (Bastian, Sponberg, Suomi, & Higley, 2003; Margulis, Nabong, Alaks, Walsh, & Lacy, 2005; Moretz, Martins, & Robinson, 2007; Fischer et al., 2015; reviews in Taborsky & Oliveira, 2012 and Taborsky, 2016a) and, in some cases, also social learning (Chapman et al., 2008). Whether the early social environment also influences *general* cognition has been discussed controversially, however (see Taborsky & Oliveira, 2012). Among non-social factors, spatial enrichment of hatchery environments promoted the learning abilities and behavioural flexibility in Atlantic cod (*Gadus morhua*; Braithwaite & Salvanes, 2005; Kihlslinger & Nevitt, 2006; Strand et al., 2010). Furthermore, a single switch of food ration during ontogeny had long-lasting effects on associative learning in the cichlid fish *Simochromis pleurospilus* (Kotschal & Taborsky, 2010).

Previous experiments investigating early-environment effects on behavioural flexibility in later life manipulated either a single social or non-social ecological parameter (Arnold & Taborsky, 2010; Braithwaite & Salvanes, 2005; Kihlslinger & Nevitt, 2006; Kotschal & Taborsky, 2010; Strand et al., 2010). However, these experiments cannot simulate the degree of environmental complexity that developing organisms are confronted with in the wild (Groothuis & Taborsky, 2015). In natural habitats, animals are exposed to the influence of a multitude of social and non-social ecological factors during all life stages (Mery & Burns, 2010; Pear, 2001). As yet the relative influences of early social vs non-social experiences on cognitive abilities and behavioural flexibility are poorly understood. We may expect additive or even multiplicative effects exerted by the different early experiences on the development of learning and memory, as it has been shown to occur for other behavioural domains (reviewed in Groothuis & Taborsky, 2015; Taborsky, 2017).

To disentangle the effects of social and predation risk experience on learning ability and neophobia, we performed a two-by-two full-factorial rearing experiment in the African cichlid *Neolamprologus*

pulcher. In this cooperatively breeding fish, social group size and composition (Heg, Brouwer, Bachar, & Taborsky, 2005) and predation risk (Brouwer, Heg, & Taborsky, 2005; Groenewoud et al., 2016) are thought to be the two most important ecological drivers of fitness. In the field, successful reproduction requires the presence of brood care helpers, and group survival greatly increases with increasing helper number (Heg et al., 2005; Taborsky, 2016b). For our study, we used *N. pulcher* that had been reared either in the presence or absence of adult group members and/or in the presence or absence of perceived predation risk (Fischer, 2014). We investigated key aspects of behavioural flexibility in these fish by testing their associative learning and reversal learning abilities and their response to novelty. We predicted that individuals from socially more complex rearing treatments (i.e., with adults) will be more flexible than fish reared among siblings only, and therefore will have better learning abilities and reduced neophobia. This prediction is supported by results from laboratory rodents, which consistently show less anxiety-related behaviours after being reared with more or more diverse groups of conspecifics (reviewed in Taborsky, 2016a), and in one study also solved a spatial learning and memory task better (Liu et al. 2000). Furthermore, neophobia has an important role in predator avoidance (e.g., Carter, Goldizen, & Tromp, 2010) and therefore early predator exposure is predicted to enhance neophobia. Predictions for the effect of early predation risk on learning ability are less straightforward. Studies comparing individuals originating from high- vs low-predation populations found that predation risk in the population of origin may either enhance (Huntingford & Wright, 1992) or reduce (Brown & Braithwaite, 2005) the performance in spatial learning tasks. While in these population comparisons genetic differences cannot be excluded, there is evidence that predation risk can affect learning also through developmental plasticity. In three-spined sticklebacks (*Gasterosteus aculeatus*), adult offspring of predator exposed mothers performed poorer in a spatial learning task (Roche, McGhee, & Bell, 2012). Therefore, we predicted that in *N. pulcher* early predator exposure will impair learning performance. This means we expect social and predator experience to affect learning and neophobia additively, where fish reared with adults have a better learning ability and show lower neophobia, and adding predator experience reduces learning performance and enhances neophobia in both social treatments to a similar degree. Finally, we hypothesized *N. pulcher* males, which have a stronger propensity to disperse in the wild (Stiver et al., 2007), to be more flexible than females and thus to perform better in the learning task and be less neophobic.

2 | METHODS

2.1 | Study species

Neolamprologus pulcher is a cooperatively breeding cichlid fish endemic to Lake Tanganyika. Individuals live in social groups composed of a breeder pair and one to 25 helpers, which are organized in a linear size-based hierarchy (Dey, Reddon, O'Connor, & Balshine, 2013; Taborsky, 1984, 1985). *Neolamprologus pulcher* evolved its highly social life-style under the severe selection pressure exerted on this

species by large predatory fish (Brouwer et al., 2005; Groenewoud et al., 2016). Subordinate group members all act as brood care helpers during the juvenile stage. After maturation, they can pursue one of two major life-history trajectories to obtain own reproductive success. They can stay as helpers in their natal group and queue for a position as dominant breeder, or they can disperse to join another group (Stiver et al., 2007). When joining a new group, they can either take over an existing breeding vacancy or they can join a group, in which the queue for the breeding position is shorter than in their natal group. Generally, males disperse more often and farther distances than female do, with the costs of dispersal being predominantly due to predation (Heg, Bachar, Brouwer, & Taborsky, 2004; Stiver et al., 2007).

2.2 | Rearing treatment

The experimental fish used in this study had been reared in four different environment conditions (for details see Fischer, 2014). In brief, experimental clutches were produced and raised by groups consisting of a breeder pair and an unfamiliar, immature helper, which were second- and third-generation offspring of wild caught fish from "Kasakalawe Point" (Groenewoud et al., 2016) at the southern tip of Lake Tanganyika, Zambia, Africa. The experimental offspring were raised by these fish until they had reached the free-swimming stage at day 10 after spawning. At the day of free-swimming, each brood was split randomly into two equally sized groups. Half of the split groups was reared with their parents and helper (+F treatment) and the other half was reared without older family members (-F treatment). Half of these +F and -F groups were additionally exposed to a predator treatment (+P treatment). For the predator treatment, a large *Lepidolamprologus elongatus*, the most dangerous predator of *N. pulcher*, was presented twice a week for 30 min in a neighbouring 50-L compartment of a 200-L tank, and during the presentations olfactory cues obtained from the predator's holding tank water was applied to the experimental fish. The other groups were exposed to an empty 50-L compartment at the same time as control treatment and received tap water as control odour cue (-P treatment). While it might seem preferable to use another fish species or conspecifics of similar size than the predator as control stimulus, in our experiment this was not possible, as in the natural environment virtually all other fish, even herbivores or conspecific, will prey on *N. pulcher* larvae if given the chance. Thus, any other fish would have been perceived as threat to the larvae. Each rearing group was housed in a 100-L compartment of a 200-L tank. The rearing treatments lasted for 63 days. From then on, all fish were kept under identical social conditions (i.e., in sibling groups) and without any predator cues. At day 204 after free swimming, all fish had reached sexual maturity. To prevent reproduction, males and females were separated in 200-L tanks. Full-siblings of the same sex were placed in the same tank; thus, fish of different rearing treatments were merged to rule out potential behavioural differences between rearing treatments due to an accumulated exposure to individuals that had the same early experience. All fish were individually tagged with different colour codes using subcutaneous injection of Visible Implant Elastomer tags (VIE; Northwest Marine Technology).

For the learning and neophobia tests, we used 56 fish from 28 rearing groups (one male and one female from each rearing group; 14 fish per each of the four treatment combinations, +F+P, +F-P, -F+P, -F-P).

2.3 | Experimental set-up

All fish were tested at ages between 2.8 and 3.3 years, that is, more than 2 years after the end of the rearing treatment. We used eight experimental tanks of 200-L (100 × 40 × 40 cm; Figure 1a). The light:dark cycle for all tanks was 13:11 hr L:D with a 10 min dim phase in the morning and evening to mimic natural light conditions at Lake Tanganyika. Water temperature was kept at 27 ± 1°C. In the morning of each experimental day, all eight tanks were separated in the middle by an opaque PVC plate (see "a", Figure 1a), thereby creating 16 test compartments of 100 L each. Each compartment was equipped with a flower-pot half ("b", Figure 1a) placed near the opaque plate to serve as shelter for the tested fish. Furthermore, in each compartment a transparent, vertical Plexiglas divider (length 25 cm; height 40 cm; "c", Figure 1a), was placed along the longitudinal axis of the compartments opposite to the shelter. This divider should evoke a small cost in terms of a delay in reinforcement for those fish that chose the wrong side in the first place because they had to swim around the divider to get to the rewarded side. Delayed reinforcement is a standard tool in operant conditioning procedures (reviewed in Lattal, 2010). On each side of the divider, one Petri dish of 6 cm diameter was placed ("d", Figure 1a). The rims (1.3 cm high) of these Petri dishes were covered by a grey tape to prevent direct sight on the food reward.

2.4 | Training phase

The training phase consisted of 2 days of habituation to the experimental tanks and 2 days of training to feed from the Petri dishes.

2.4.1 | Habituation

Two fish of the same sex were put together in a 200-L tank for 2 days (Saturday, Sunday) before the training started. The opaque wall, which divided the tank in two compartments, was temporarily removed to allow both fish to interact. As *N. pulcher* is a highly social species, habituation to a new environment is faster when fish are not alone (B. Taborsky, pers. obs.). While the opaque divider was absent, each experimental tank was equipped with two brown PET bottles in the middle of the back and the front tank screens mounted near the water surface. These served as additional shelters in case one fish would deny its tank mate the access to the flower pot shelters at the bottom. At the first habituation day, fish were fed commercial flakes (JBL Novo Tanganyika). Food flakes were released at the water surface in the center of the tank to prevent any preferences for specific corners of the tank before the learning trials started. On the second habituation day, the fish received no food, as according to the feeding regime of our aquarium fish have one fasting day per week.

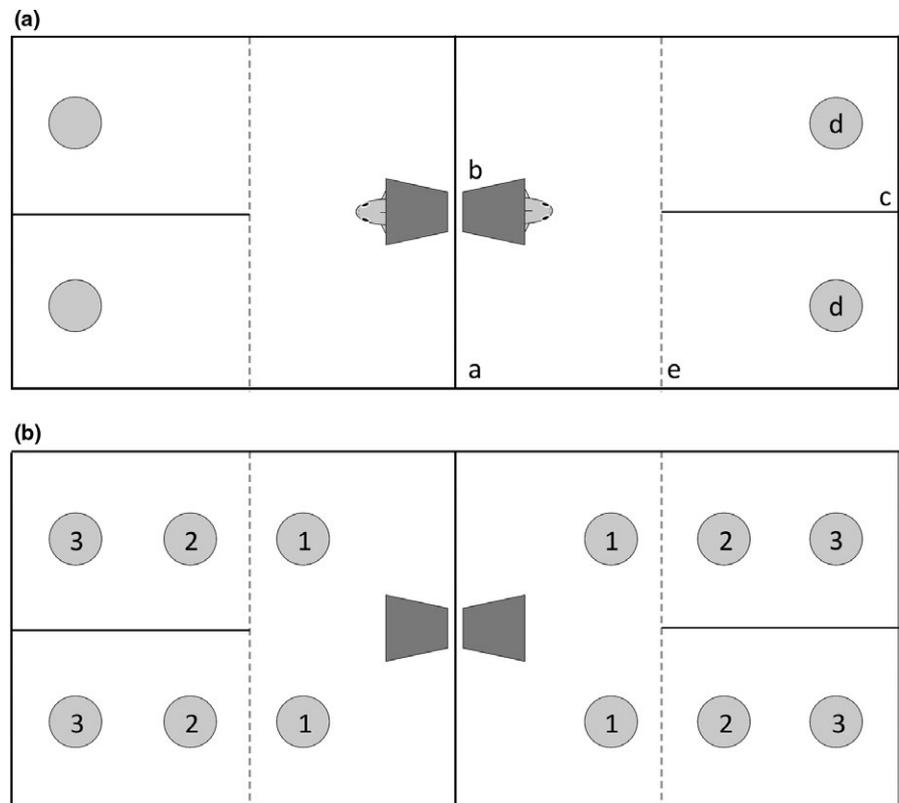


FIGURE 1 (a) Scheme of the experimental set-up used to test for learning performance (200 liter tank seen from above). Letters refer to “a” PVC plate which separated a tank in the middle, “b” flower-pot half, “c” divider, “d” Petri dishes, “e” decision line (dotted line). (b) Scheme of the set-up used to train fish to feed from Petri dishes. Numbers refer to positions of Petri dishes during the training phase. “1” Petri dishes near the shelter, “2” median position of Petri dishes, “3” final position of Petri dishes

2.4.2 | Training

The training served to accustom the test fish to feed from the Petri dishes. In the mornings of the training days, the PET bottle shelters were removed and the opaque divider was put in place to divide the tank into two equal-sized 100-L compartments. Each of the two test individuals was always assigned to the same compartment of a tank until the end of its experimental trials. At the first day of training, the fish was gently guided inside the flower pot shelter with a small piece of transparent Plexiglas, which was also used to temporarily close the entrance of the shelter once the fish had entered it. The shelter represented the standardized starting position for all fish in all trials. For the first stage of training, the two Petri dishes were placed close to the shelter (“positions 1,” see Figure 1b). In each Petri dish, a reward (a thawed piece of commercial krill frozen food) was placed so that the fish could learn that in *both* Petri dishes a reward could be present. Then, the transparent Plexiglas was removed from the entrance of the shelter so that the fish was able to leave the shelter and approach the Petri dishes. During the training and all learning trials, the reward was filled with help of a half-transparent, green plastic tube used as pipette. The tips of these tubes were covered by red sticky tapes so that the fish could not see the reward in the tubes. The second stage of the training followed the procedures of the first step, but the Petri dishes were placed further away from the shelter (“positions 2,” Figure 1b) to train the fish to use both sides of the transparent divider. In the final training stage, the Petri dishes were placed at the positions used also during the learning trials (“positions 3,” Figure 1b). During the first training day, the fish were trained six times, twice at each training position. One training trial

per hour was done for each fish. Directly after applying the krill pieces to the dishes the observer (F.B.) left the room. At the second training day, the Petri dishes were always placed at positions “3.” Again the krill pieces were filled in both dishes and the fish were trained six times, once per hour. At this second day, however, the observer stayed for 5 min in front of the tank after krill application before he left the room to habituate the fish to his presence. All fish learned to feed from the dishes at the positions “3” during the first two training days. At the end of each training day and of each day of the learning test (see below), the opaque divider was removed and bottles placed in the tank again so that the fish could freely interact and socialize during the night.

2.5 | Learning test

2.5.1 | Acquisition phase

The day after the training was terminated fish entered the acquisition phase of the learning test. Each fish did six trials per day. At the beginning of each trial, the test fish was enclosed in the shelter the same way as described for the training phase. Then, the observer placed a reward (a piece of krill) in one of the two Petri dishes, which were positioned at the positions “3” (Figure 1b) to the left and right of the transparent divider. The rewarded side (left or right) was exactly balanced between experimental compartments and within each rearing treatment (half of each treatment group was rewarded on the right and the other half was rewarded on the left side). To provide the reward, the observer inserted two identical green tubes with a red tape at the tip (see section “Training phase”) simultaneously in the tank in

the two Petri dishes. Only the tube inserted in the rewarded dish was loaded with krill, which was gently dropped in the dish after which the two tubes were retracted. This procedure should prevent any association between the tube and the reward distribution. Then, the shelter entrance was opened, and the following parameters were recorded: (i) Latency to leave the shelter with the entire body. (ii) The side chosen by the fish (correct or not); a choice was defined as the test fish having passed the edge of the transparent divider (further termed "decision line," see Figure 1a) with half of its body. If the fish made a wrong choice, we recorded the latency to approach the unrewarded Petri dish. As a measure of flexibility, we analyzed the time needed to change sides after an initial wrong choice. Once the fish chose the rewarded side, either directly or after a wrong choice, we recorded the time between choice and eating the reward. The trial ended when the fish ate the reward or after 5 mins. When a fish reached the learning criterion (see below), it proceeded with the reversal phase. If the fish did not make a choice after three trials, testing ended for this day. If a fish did not eat the reward at three consecutive days, this individual was replaced by another fish of the same sex and rearing group.

2.5.2 | Learning criterion

To define the learning criterion, we combined each set of 12 consecutive trials with a choice being made by the fish to one "block" of trials. As we did six trials per day, a block lasted at least for 2 days. If fish did not make a choice in one or more trials of a block, it took more than 2 days until a block of 12 choices was completed. To reach the learning criterion, the fish had to choose the rewarded side first in 10 out of 12 trials (i.e., 80% of correct choices per block) and in addition it had to have at least five correct choices within the first 6 trials and within the second 6 trials of a block, respectively. If the fish did not reach the learning criterion at the end of a block of 12 trials, the fish entered the next block of 12 trials. This procedure was repeated until the fish either reached the learning criterion or had passed 5 blocks (60 trials) without reaching the criterion. Six fish that did not reach the criterion in the acquisition phase did not take part in the reversal phase.

2.5.3 | Reversal phase

In the reversal phase, the previously non-rewarded side was rewarded. Otherwise, all procedures and recording of behavioural parameters were done as described for the acquisition phase. The reversal phase was ended when a fish first reached the learning criterion or after 5 blocks of 12 choices.

2.6 | Novel object test

For the novel object task, the same experimental tanks were used as for the learning tasks, but the transparent divider and one of the Petri dishes was removed. The remaining Petri dish was placed near the tank wall opposite to the shelter location (same distance from wall as during learning and reversal tasks), but now it was placed in the middle of this tank wall. We created a novel object by covering a plastic vial

of 5.4 cm length with a round opening (diameter 3.0 cm) and a square basis (2.2 x 2.2 cm) entirely with light-green sticky tape. The novel object was placed behind the Petri dish. The novel object task was done after the reversal phase or after the last trial in acquisition phase in case the fish had not reached the learning criterion during the acquisition phase. Before the trial, the fish was confined in its shelter and the Petri dish was supplied with a piece of krill, following the procedures outlined above. We recorded the latency to eat the reward.

2.7 | Control tests

To check that the fish were not able to smell and see the reward before making a choice, two additional trials were carried out, which were preceded by an extinction phase of 2 days.

2.7.1 | Extinction phase

During this phase, we fed the test fish krill from both Petri dishes to extinguish previously existing side preferences developed during the learning and the reversal phases. We put the test fish in a new experimental tank and started the 2-day extinction phase the next morning. We reinstalled the transparent divider and placed two baited Petri dishes left and right of it.

2.7.2 | Test for olfactory cues

The day after the extinction phase, we confined the fish in the shelter and removed both Petri dishes. We placed a reward in one of the dishes and covered it firmly with a clear Petri dish lid to prevent the release of olfactory cues. Then, we placed the closed petri dish with the krill and an open empty Petri dish back into the tank. Next, we inserted a krill piece with the pipette used for the leaning test in the empty dish while at the same time moving a second, empty pipette toward the covered dish. Thus, the use of pipettes was performed exactly in the way as in the acquisition and reversal phases. The sides, where the closed and the open dishes were placed, were determined by a flip of a coin. As during the previous tests, just after filling the open Petri dish we released the fish and we recorded the latency to leave the shelter, the latency to cross the decision line and the side chosen by the fish.

2.7.3 | Test for visual cues

The next day we removed the two Petri dishes after we had confined the fish in the shelter. We filled only one dish with a reward. Then, we covered both dishes with a clear Petri dish lid and placed them back in the tank. The placement of the two dishes (filled or unfilled) was determined by flip of a coin. Then, we moved two empty pipettes toward the two dishes to provide the same cues as during the acquisition and reversal phases and released the fish from the shelter. We recorded the latency to leave the shelter, the latency to cross the decision line, and the side chosen by the fish.

There was no significant difference between the chosen Petri dishes in the olfactory test (binomial test, $N = 24$, $p = .68$) and in the

visual test ($N = 24$, $p = .84$), suggesting that fish did not get olfactory or visual cues of the reward before making a choice.

2.8 | Statistical analyses

The statistical analyses were done with R 3.2.0 (R Core Team 2015), using the packages, “lme4” (Bates, Maechler, Bolker, & Walker, 2015), “nlme” (Pinheiro, Bates, DebRoy, & Sarkar, 2015), “MASS” (Venables & Ripley, 2002), and “survival” (Therneau, 2015). We performed linear mixed models (LMM) and Cox Proportional Hazard models (COXPH). The experimentally controlled factors social rearing treatment, predator rearing treatment, their interaction, and the sex of the fish and were included as fixed effects in all LMM and COXPH models. As the age of the fish varied in a range of 969–1207 days and age can affect learning performance (reviewed in Brushfield, Luu, Callahan, & Gilbert, 2008) and neophobia (Greenberg, 2003) of animals, we also included age as covariate in all initial models. Family of origin was always included as random effect. To simplify the models, we used stepwise backward elimination of non-significant interaction terms and of the covariate that was not experimentally controlled (i.e., age of the fish; Bolker et al., 2009). Significance testing was based on deviance. The change in likelihood was compared to a chi-square distribution (likelihood ratio test, see Crawley, 2007; chi-square values are given in the results tables). Estimates presented in the results tables are based on sum contrasts, where the intercept represents the overall mean of each factor and each estimate shows the difference between the intercept and the factor level of interest. Note that estimates are based on transformed data in case transformations for normality were done. When interaction terms were significant, deviance testing for the main effects contained in the interactions was not possible. To interpret the significant interactions, we performed post-hoc tests.

For the acquisition and the reversal phases, we calculated (i) error rates (number of errors made divided by number of trials to reach the learning criterion) and (ii) number of blocks to reach the learning criterion. To test for effects of the rearing treatments and sex on error rates, we built linear mixed models (LMM). Assumptions of normality of the error term were checked by inspection of the distribution of model residuals using histograms and Quantile–Quantile plots (Zuur, Ieno, & Elphick, 2009). To achieve normality of model residuals, we applied a box-cox transformation of the error rates in the acquisition phase. Error rates in the reversal phase were log-transformed.

Number of blocks to reach the learning criterion: To measure the success of learning in the acquisition and in the reversal phase, we tested whether the treatments or sex of the fish affected the number of blocks (each block consisting of 12 trials) needed to reach the learning criterion. We performed a survival analysis fitting COXPH models (cf. Jahn-Eimermacher, Lasarzik, & Raber, 2011) after having checked the proportional hazard assumptions (Budaev, 1997).

For the analysis of treatment effects on the time to change sides, we linearized the relationship between the dependent variable and trial number by a box-cox transformation of the time to change sides and a square-root transformation of trial number. The transformed variable trial number was included as covariate in the LMM. In addition

to family of origin, we included fish identity as random effect in this model. Normality assumptions were checked by visually inspecting the histogram of residuals and the QQ plot.

We performed a COXPH model to investigate the latency to eat the reward in presence of a novel object after having checked the proportional hazard assumptions. To control for general individual differences in the motivation to take part in food reward trials, we included the latency to leave the shelter during the last learning trial performed before the novel object test as a covariate. We could not use the latency to eat the krill in the last learning trial for this purpose because in these last trials half of the fish made a wrong choice and thus the latency to eat the krill was prolonged by the detour fish had to make to reach the krill. To test whether neophobic tendencies are correlated with learning performance we did Spearman rank correlations for all fish between the latency to eat the reward in the presence of the novel object and (i) number of blocks to reach the learning criterion and (ii) error rate, both in the acquisition and the reversal phases.

3 | RESULTS

3.1 | Learning performance

The error rate in the acquisition phase was not significantly affected by the rearing treatments and sex although fish reared without predator experience tended to have higher error rates (Table 1a, Figure 2a). However, error rates in the reversal phase were influenced by the interaction between social and predator treatment, but not by sex (Table 1b; Figure 2b). Post-hoc tests within the +P and within the –P condition, respectively (see Table 1b), did not reveal significant differences between the social rearing conditions. Error rates significantly decreased with age across all treatments.

Early environments and sex did not affect the times to reach the learning criterion in the acquisition phase (Table 2a, Figure 3a). In the reversal phase, time to reach the criterion was influenced by the interaction between social and predator treatment, but not by sex (Table 2b; Figure 3b). Post-hoc tests within the +P condition revealed that fish reared without older group members (–F+P) reached the criterion faster than fish reared with older group members. Within the –P condition, there was no difference between the social rearing conditions. The criterion in the reversal phase tended to be reached faster with increasing age across all treatments.

3.2 | Time to change sides

With increasing trial number, fish became faster to change sides after a wrong choice (Table 3a). Early environment did not affect the time to change sides (Table 3a), but males changed sides faster than females.

3.3 | Novel object test

Fish reared with older family members (+F) had shorter latencies to eat the krill in the novel object test than fish reared with siblings only (–F) (Table 3b, Figure 4), whereas this latency was not affected

TABLE 1 Results of linear mixed models testing for the effects of rearing treatments and sex on error rates (a) in the acquisition phase ($n = 56$) and (b) in the reversal phase ($n = 50$) of the learning task

Factor	$\beta \pm SE$	Chi ²	<i>p</i>
(a)			
Social	0.002 ± 0.07	0.001	.97
Predator	0.13 ± 0.07	3.52	.06
Sex	0.01 ± 0.07	0.02	.89
(b)			
Social	-0.0009 ± 0.009		
Predator	0.007 ± 0.009		
Sex	-0.009 ± 0.009	1.10	.29
Age	-0.17 ± 0.05	7.77	.005
Social x Predator	0.02 ± 0.009	4.15	.042
Post-hoc comparison "Social" (+F vs. -F condition) within			
+P condition			
Social		2.10	.15
Sex		0.01	.92
Age		3.96	.046
-P condition			
Social		2.41	.12
Sex		1.92	.17
Age		7.09	.0077

Estimates were calculated based on sum contrasts. Significant *p* values are highlighted in bold. Age is left as covariate in final model if $p < .1$.

by early predator experience and sex. The latency to leave the shelter in the last leaning trial performed before the novel object test, a covariate to control for motivation differences to take part in the food reward trial, was positively related to the latency to eat krill in the novel object test (Table 3b). The latency to eat the reward in the novel object test did not correlate with the learning performance in the acquisition phase (days to reach the learning criterion: $\rho = 0.22$, $p = .36$; error rate: $\rho = -0.36$, $p = .09$, $N = 56$), or in the reversal phase (days to reach the learning criterion: $\rho = -0.03$, $p = .91$; error rate: $\rho = 0.10$, $p = .09$, $N = 55$).

4 | DISCUSSION

We had predicted that *N. pulcher* reared in a more complex social rearing environment will be better able to solve an associative learning task and to be more flexible in reversal learning than the individuals reared among siblings only, and that predator experience will reduce the learning performance during acquisition and reversal in both social treatments. In contrast to these predictions, our results provide no evidence that the acquisition of a learning task in adults is influenced by the early rearing treatments applied in this study, but that social and predator experience interactively influenced the reversal learning performance. Visual inspection of Figures 2b and 3b, and post-hoc

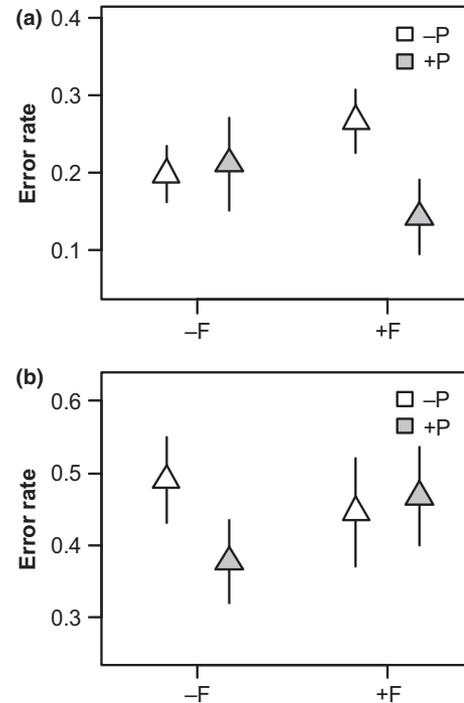


FIGURE 2 The learning error rate in (a) the acquisition phase and (b) in the reversal phase (Mean ± SE are shown). +F and -F refer to the rearing condition with or without older fish present. +P and -P represent rearing conditions with or without predator cues

tests for the time needed to solve the reversal task indicate that fish reared with predator experience but without older group members (-F+P fish) outperformed fish with other rearing backgrounds. The -F+P rearing condition should have been perceived by the juveniles as the most dangerous of all rearing conditions of this study, as during the experience phase juveniles were repeatedly facing danger in the absence of adults to guard and defend them.

Previous studies on the relationship between learning performance and predation report conflicting results depending on the learning context. While predation pressure had an enhancing effect on learning about dangerous feeding patches in three-spined sticklebacks (*G. aculeatus*, Huntingford & Wright, 1989, 1992), it had a negative effect on spatial learning in the poeciliid fish *Brachyrhaphis episcopi* (Brown & Braithwaite, 2005) and sticklebacks (Brydges, Heathcote, & Braithwaite, 2008) and no effect on maze learning in guppies (*Poecilia reticulata*, Burns & Rodd, 2008). Conflicting results may be partly explained by the function of predation as an important stressor, which can affect cognition depending on the intensity and duration of the exposure to the stressful event. Repeated or long-lasting disturbance will result in chronic activation of the stress axis, which may impair flexibility by shifting behavioural activation to inhibition (Wingfield & Romero, 2001). Prolonged exposure to stress can cause irreversible losses of hippocampal neurons and may in part cause the cognitive deficits seen in many aged individuals (e.g., senile dementia; McEwen & Sapolsky, 1995; McEwen, 2000; Fuchs et al., 2001). In contrast, moderate elevations of stress hormones lead to adaptive behavioural and physiological processes, including enhanced attention and memory

TABLE 2 Results of the survival analyses to test for the effects of rearing treatments and sex on the number of blocks to reach the learning criterion (a) in the acquisition phase ($n = 56$) and (b) in the reversal phase ($n = 50$) of the learning task

Factor	$\beta \pm SE$	Chi ²	p
(a) Acquisition phase			
Social	0.05 \pm 0.14	0.11	.75
Predator	-0.12 \pm 0.14	0.67	.41
Sex	-0.005 \pm 0.14	0.001	.97
(b) Reversal phase			
Social	0.22 \pm 0.18	1.59	.21
Predator	-0.09 \pm 0.17	0.25	.62
Sex	-0.08 \pm 0.18	0.22	.64
Age	1.87 \pm 1.12	2.78	.095
Social x Predator	-0.31 \pm 0.19	4.11	.043
Post-hoc comparison "Social" (+F vs. -F condition) within			
+P condition			
Social		4.47	.035
Sex		0.31	.57
Age		0.83	.36
-P condition			
Social		0.32	.57
Sex		2.01	.16
Age		2.23	.14

Estimates were calculated based on sum contrasts. Significant p values are highlighted in bold. Age is left as covariate in final model if $p < .1$.

formation (Sandi & Pinelo-Nava, 2007; Wingfield, 2005). These are both important components of flexibility and the repeated presentations of the predator in combination with the absence of guarding parents (-F+P rearing condition) may have acted as a moderate stressor, enhancing the attention of the experimental fish. Interestingly, we also found that in the reversal phase error rates decreased with age which is difficult to interpret since fish were between 2.8 and 3.3 years old and thus neither juvenile nor senescent. Usually, performance in reversal learning rather decreases with age (reviewed in Brushfield et al., 2008). However, ages were equally distributed among rearing treatments and thus age should not have biased the results on the effect of rearing treatments.

Our results revealed an effect of the social, but not the predator rearing experience on neophobia. The willingness of an individual to take risks when exposed to novelty has been investigated in a wide range of taxa including fish (e.g., Frost, Winrow-Giffen, Ashley, & Sneddon, 2007), amphibians (e.g., Caelson & Langkilde, 2013), reptiles (Carter et al., 2010; Siviter et al., 2017), birds (reviewed in Cockrem, 2007), and mammals (e.g., Carter, Marshall, Heinsohn, & Cowlshaw, 2012) and has important implications for fitness in the context of foraging, reproductive success and predation (e.g., Biro & Stamps, 2008). The ability to survive predator encounters is one of the strongest selective forces (Lima & Dill, 1990; Peacor & Werner, 2004) and it has been

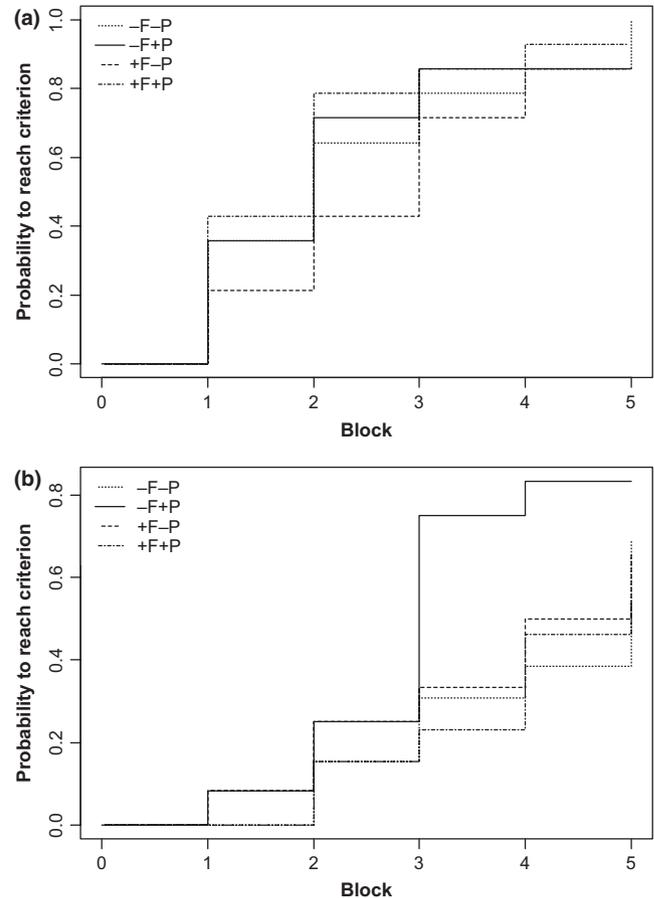


FIGURE 3 Cumulative probability to reach the learning criterion over the five blocks of the acquisition phase (a) and of the reversal phase (b). Different line types represent different rearing conditions

shown that neophobia has an important role in predator avoidance (e.g., Carter et al., 2010). Neophobia is mainly driven by the costs that novelty may hide (Greenberg & Mettke-Hofmann, 2001). For example, a novel object may harbour predators and exploratory behaviour may cause animals to be less vigilant (Lima & Dill, 1990). In contrast to our prediction that the exposure to predators should increase neophobia, the ontogenetic predator treatment did not affect the latency of experimental fish to feed near a novel object. There are two ways how prey can acquire knowledge about predation risk: directly, through personal experience, or indirectly, through observation of conspecifics (Brown, Ferrari, & Chivers, 2011; Griffin, 2004; Mathis, Chivers, & Smith, 1996). In species with brood care, these conspecifics will often be the parents. If young are raised without their parents, they may be able to acquire experiential knowledge about the danger posed by potential predators (Brown et al., 2011). In previous studies, predator stimuli were often paired with olfactory alarm cues. This was not done in our study. However, we have evidence that the predator treatment was indeed effective in both social rearing conditions (+F and -F) despite the absence of alarm cues. Another study conducted with siblings of our experimental fish with the same rearing treatments revealed that fish having received predator cues during the rearing phase showed higher vigilance and were more aggressive toward predators

Factor	$\beta \pm SE.$	Chi-square	<i>p</i> value
(a)			
Social	-0.00046 \pm 0.035	<0.0001	.99
Predator	-0.037 \pm 0.035	1.17	.28
Sex	0.069 \pm 0.035	3.99	.046
Trial number	-0.15 \pm 0.005	756.75	<.0001
(b)			
Social	-0.88 \pm 0.25	11.80	.0006
Predator	-0.31 \pm 0.22	1.97	.16
Sex	-0.37 \pm 0.44	2.80	.094
Latency to leave shelter in last learning trial	-0.89 \pm 0.37	5.61	.018

Significant *p* values are highlighted in bold. Estimates were calculated based on sum contrasts.

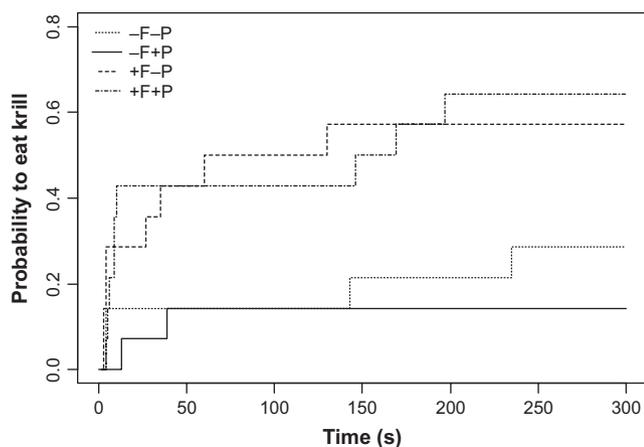


FIGURE 4 Cumulative probability to eat the krill in dependence of time (in seconds) in the novel object test. Lines represent the different rearing treatments

when tested as juveniles (5–8 months of age) and behaved more bold in a predator escape test when tested as adults (12 months of age; Fischer, 2014). Nevertheless, our study revealed that fish reared with older family members (F+) were less neophobic than fish reared with siblings only (-F) (see main effect “Social,” Table 3b). The presence of adults during early ontogeny offers protection against predators. These permanent cues of safety in the presence of guarding parents may have been more reliable cues of environmental risk than the repeated presentation predator cues. Indeed, the main function of parents and helpers in *N. pulcher* is to guard the offspring and protect them from predators, whereas direct interactions between offspring and older group members are virtually absent (Arnold & Taborsky, 2010). Therefore, +F fish, regardless of whether they received predator cues or not, may have experienced their rearing environment as safer than -F fish (see Arnold & Taborsky, 2010 for discussion). Thus, a possible mechanistic explanation for the reduced neophobia of +F fish is that they experienced a safer, less stressful environment during development. Stress levels during the early environment can shape the reactivity of mammalian and avian hypothalamic–pituitary–adrenal

TABLE 3 Results of (a) an LMM to test for effects of rearing treatments and sex on the time to change sides after a wrong choice with individual identity included as additional random factor in the model (see “Methods”) and trial number included as covariate; (b) of a survival analysis to test for effects on the latency to eat a reward in the novel object test

(HPA) stress axis (reviewed in Champagne & Meaney, 2007; Zimmer & Spencer, 2015), which in turn can influence neophobia (reviewed in Champagne & Meaney, 2007; Cockrem, 2007). Previous results in *N. pulcher* support this mechanism (Nyman, Fischer, Aubin-Horth, & Taborsky, 2017; Taborsky, Tschirren, Meunier, & Aubin-Horth, 2013). Fish reared with older family members (+F fish) have a higher expression of the glucocorticoid receptor 1 (GR1) in the telencephalon (Nyman et al., 2017), which is an important receptor of the hypothalamic–pituitary–interrenal (HPI) axis, the poikilotherm homologue of the HPA axis. This receptor is activated by cortisol and is involved in the negative feedback loop that terminates stress responses after experiencing a stressor. The results by Nyman et al. (2017) indicate that the social treatment induces differential programming of the HPI axis, and that +F fish have a lower stress responsiveness than -F fish. Several empirical studies support the idea that physiologic stress reactivity covaries with the “coping style” or “personality” (reviewed in Cockrem, 2007 and Koolhaas, de Boer, Coppens, & Buwalda, 2010). Individuals of a given species differ consistently in their response to environmental challenges. In particular, shy and bold individuals differ in how quickly they are approaching novel stimuli. In our study, we have not tested whether response to novelty is consistent across context, but in the closely related cichlid *Neolamprologus caudopunctatus* experimental evidence shows that the tendency to engage with novelty per se is a consistent trait and part of an exploration syndrome (Martins, Schaedelin, Mann, & Wagner, 2012).

Differences in neophobia can also have fundamental effects on cognitive performance (e.g., Sih & Del Giudice, 2012). Several studies indicate that responses to novelty (measured as the latency to explore novel space or a novel object) and reversal learning are co-varying traits (reviewed in Carere & Locurto, 2011; Groothuis & Carere, 2005; Guillette, Reddon, Hurd, & Sturdy, 2009; Koolhaas et al., 2010). For instance, in great tits (*Parus major*), slow explorers changed a previously established foraging habit more quickly than fast explorers (Drent & Marchetti, 1999; Verbeek, Drent, & Wiepkema, 1994). In chickadees (*Poecile atricapillus*), slow explorers are faster at learning the reversal phase of a discrimination task (Guillette et al. 2011) and more neophobic woodpecker finches (*Cactospiza pallida*) learned the

reverse of reward contingency more quickly (Tebich et al., 2012). Conversely, several other studies did not find a negative correlation between reversal learning and neophobia (e.g., Guillette, Hahn, Hoeschele, Przyluski, & Sturdy, 2015), which is in line with our results. For instance, in great tits, the effects were opposite for males and females (Titulaer, van Oers, & Naguib, 2012). In the reversal stage, fast-exploring males took fewer trials to acquire the task compared to slow-exploring males, whereas in females it was the other way round. Both Guillette et al. (2015) and Titulaer et al. (2012) concluded that the interaction between reversal learning and response to novelty may be complex and may depend on factors such as sex of the individual or difficulty of the learning task.

Sex did not play a role in either task acquisition or reversal learning. A range of studies have shown that male and female cognitive abilities differ and may be under sexual selection (Boogert, Fawcett, & Lefebvre, 2011). For instance, a recent study has shown that differences in learning performance in the bitterling, *Rhodeus ocellatus*, are related to male mating tactics. Sneaker males that have a higher demand in spatial cognition outperform guarder males and females in a maze task. Best performing males had a higher reproductive success (Smith, Philips, & Reichard, 2015). Spatial abilities are the most studied cognitive ability with regard to sex differences and several functional hypotheses have been proposed to explain them (reviewed in Jones, Braithwaite, & Healy, 2003). The dispersal hypothesis proposes that in species with sex-biased dispersal the dispersing sex will show enhanced spatial abilities. However, Jones et al., (2003) point out that this hypothesis is flawed because dispersal is a single movement from home without the necessity to navigate back and therefore does not demand enhanced cognitive abilities. An alternative explanation for the lack of sex difference in our learning essay is that it was too simple to be spatially demanding. However, we found that males were faster in changing sides after a wrong choice. This can be interpreted as a faster response to non-reward and thus could be related to behavioural flexibility a trait that is beneficial when moving to a new environment (Sol et al., 2002, 2011).

5 | CONCLUSION

A range of studies provided evidence of long-lasting effects of environmental enrichment during ontogeny on adult behavioural flexibility mediated via learning. In our study, both cognitive flexibility and response to novelty were influenced by early experience, but in different ways. Improved reversal learning abilities were apparently developed in response to early perceived danger (presence of predators in the absence of guarders). The willingness to take risks in face of a novel situation was enhanced when growing up in a group containing guarding older conspecifics. In combination with results on how the presence of guarders influences the expression of glucocorticoid receptors (Nyman et al., 2017), our finding indicates phenotypic plasticity on the endocrinological level. Our study indicates that in *N. pulcher* the composition of social groups and perceived predation pressure are linked: on the one hand, the safe environment provided by parents

during early life seems to reduce the magnitude of the stress response and, as a consequence, also neophobia. On the other hand, the presence of predators in the absence of guarders may present a mild stressor that enhances learning performance.

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REFERENCES

- Arnold, C., & Taborsky, B. (2010). Social experience in early ontogeny has long lasting effects on social skills in cooperatively breeding cichlids. *Animal Behavior*, 79, 621–630.
- Bastian, M. L., Sponberg, A. C., Suomi, S. J., & Higley, J. D. (2003). Long-term effects of infant rearing condition on the acquisition of dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Developmental Psychobiology*, 42, 44–51.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-8, <URL: <http://CRAN.R-project.org/package=lme4>>
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23, 361–368.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H., & White, J. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127–135.
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial Reversal Learning and the Evolution of Behavioral Flexibility in Three Species of North American Corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, 121, 372–379.
- Boogert, N. J., Fawcett, T. W., & Lefebvre, L. (2011). Mate choice for cognitive traits: A review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, 22, 447–459.
- Braithwaite, V. A., & Salvanes, A. G. V. (2005). Environmental variability in the early rearing environment generates behaviourally flexible cod: Implications for rehabilitating wild populations. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 272, 1107–1113.
- Brouwer, L., Heg, D., & Taborsky, M. (2005). Experimental evidence for helper effects in a cooperatively breeding cichlid. *Behavioral Ecology*, 16, 667–673.
- Brown, C., & Braithwaite, V. A. (2005). Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behavioral Ecology*, 16, 482–487.
- Brown, G. E., Ferrari, M. C. O. & Chivers, D. P. (2011). Learning about danger: Chemical alarm cues and threatsensitive assessment of predation risk by fishes. In C. Brown, K. Laland, J. Krause (Eds.), *Fish cognition and behavior* (2nd ed. pp. 59–80). Oxford: Blackwell.
- Brushfield, A. M., Luu, T., Callahan, B., & Gilbert, P. E. (2008). A comparison of discrimination and reversal learning for olfactory and visual stimuli in aged rats. *Behavioral Neuroscience*, 122, 54–62.
- Brust, V., Krüger, O., Naguib, M., & Krause, T. (2014). Lifelong consequences of early nutritional conditions on learning performance in zebra finches (*Taeniopygia guttata*). *Behavioural Processes*, 103, 320–326.

- Brydges, N. M., Heathcote, R. J., & Braithwaite, V. A. (2008). Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. *Animal Behavior*, *75*, 935–942.
- Budaev, S. V. (1997). The statistical analysis of behavioural latency measures. *ISCP Newsletter*, *14*, 1–4.
- Burns, J. G., & Rodd, H. F. (2008). Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. *Animal Behavior*, *76*, 911–922.
- Caelson, B. E., & Langkilde, T. (2013). Personality traits are expressed in Bullfrog tadpoles during open field trials. *Journal of Herpetology*, *47*, 378–383.
- Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*, 491–498.
- Carter, A. J., Goldizen, A. W., & Tromp, S. A. (2010). Agamas exhibit behavioral syndromes: Bolder males bask and feed more but may suffer higher predation. *Behavioral Ecology*, *21*, 665–661.
- Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlshaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behavior*, *84*, 603–609.
- Champagne, F. A., & Meaney, M. J. (2007). Transgenerational effects of social environment on variations in maternal care and behavioral response to novelty. *Behavioral Neuroscience*, *121*, 1353–1363.
- Chapman, B. B., Ward, A. J. W., & Krause, J. (2008). Schooling and learning: Early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behavior*, *76*, 923–929.
- Cockrem, J. F. (2007). Stress, corticosterone responses and avian personalities. *Journal of Ornithology*, *148*, 169–178.
- Crawley, M. J. (2007). *The R book*. Chichester, England: Wiley.
- Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: A study of intergeneric differences in callitrichid monkeys. *Animal Behavior*, *65*, 559–571.
- Dey, C. J., Reddon, A., O'Connor, C., & Balshine, S. (2013). Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behavior*, *85*, 395–402.
- Drent, P. J., & Marchetti, C. (1999). Individuality, exploration and foraging in hand raised juvenile Great Tits. In N. J. Adams & R. H. Slotow (Eds.), *Proceedings of the 22nd International Ornithological Congress, Durban* (pp. 896–914). Johannesburg: Bird Life South Africa.
- Easton, A. (2005). Behavioural flexibility, social learning, and the frontal cortex. In A. Easton, & N. J. Emery (Eds.), *The cognitive neuroscience of social behaviour* (pp. 59–80). New York: Psychology Press.
- Fischer, S. (2014). *The influences of early and current environment on social and antipredator behaviour in a cooperatively breeding cichlid*. Ph.D. Thesis, University of Bern, Switzerland.
- Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., & Taborsky, B. (2015). Rearing group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, *186*, 123–140.
- Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *274*, 333–339.
- Fuchs, E., Flügge, G., Ohl, F., Lucassen, P., Vollmann-Honsdorf, G., & Michaelis, T. (2001). Psychosocial stress, glucocorticoids, and structural alterations in the tree shrew hippocampus. *Physiology & Behavior*, *73*, 285–291.
- Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). Oxford: Oxford University Press.
- Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. *Current Ornithology*, *16*, 119–178.
- Griffin, A. S. (2004). Social learning about predators: A review and prospectus. *Animal Learning & Behavior*, *32*, 131–140.
- Groenewoud, F., Frommen, J. G., Josi, D., Tanaka, H., Jungwirth, A., & Taborsky, M. (2016). Predation risk drives social complexity in cooperative breeders. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4104–4109.
- Groothuis, T. G. G., & Carere, C. (2005). Avian personalities: Characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, *29*, 137–150.
- Groothuis, T. G. G., & Taborsky, B. (2015). Introducing biological realism into the study of developmental plasticity in behaviour. *Frontiers in Zoology*, *12*, S6.
- Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyślupski, A. M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, *18*, 165–178.
- Guillette, L. M., Reddon, A. R., Hoeschele, M., & Sturdy, C. B. (2011). Sometimes slower is better: Slow-exploring birds are more sensitive to changes in a vocal discrimination task. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *278*, 767–773.
- Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecilia atricapillus*. *Behavioural Processes*, *82*, 265–270.
- Heg, D., Bachar, Z., Brouwer, L., & Taborsky, M. (2004). Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *271*, 2367–2374.
- Heg, D., Brouwer, L., Bachar, Z., & Taborsky, M. (2005). Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, *142*, 1615–1641.
- Huntingford, F. A., & Wright, P. J. (1989). How sticklebacks learn to avoid dangerous feeding patches. *Behavioural Processes*, *19*, 181–189.
- Huntingford, F. A., & Wright, P. J. (1992). Inherited population differences in avoidance-conditioning in 3-spined sticklebacks, *Gasterosteus aculeatus*. *Behaviour*, *122*, 264–273.
- Jahn-Eimermacher, A., Lasarzik, I., & Raber, J. (2011). Statistical analysis of latency outcomes in behavioral experiments. *Behavioral Brain Research*, *221*, 271–275.
- Jones, C. B. (2005). *Behavioral flexibility in primates: Causes and consequences*. New York: Springer-Verlag.
- Jones, C. M., Braithwaite, V. A., & Healy, S. D. (2003). The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, *117*, 403–411.
- Kihlslinger, R. L., & Nevitt, G. A. (2006). Early rearing environment impacts cerebellar growth in juvenile salmon. *Journal of Experimental Biology*, *209*, 504–509.
- Koolhaas, J. M., de Boer, S. F., Coppens, C. M., & Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, *31*, 307–321.
- Kotrschal, A., & Taborsky, B. (2010). Environmental change enhances cognitive abilities in fish. *PLoS Biology*, *8*, e1000351.
- Lattal, K. A. (2010). Delayed reinforcement of operant behaviour. *Journal of the Experimental Analysis of Behavior*, *93*, 129–139.
- Laviola, G., & Terranova, M. L. (1998). The developmental psychobiology of behavioural plasticity in mice: The role of social experiences in the family unit. *Neuroscience and Biobehavioral Reviews*, *23*, 197–213.
- Leventopoulos, M., Rëdi-Bettschen, D., Knuesel, I., Feldon, J., Pryce, C. R., & Opacka-Juffry, J. (2007). Long-term effects of early life deprivation on brain glia in Fischer rats. *Brain Research*, *1142*, 119–126.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.
- Liu, D., Diorio, J., Day, J. C., Francis, D. D., & Meaney, M. J. (2000). Maternal care, hippocampal synaptogenesis and cognitive development in rats. *Nature Neuroscience*, *3*, 799–806.
- Margulis, S. W., Nabong, M., Alaks, G., Walsh, A., & Lacy, R. C. (2005). Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus polionotus*. *Animal Behavior*, *69*, 627–634.

- Martins, C. I. M., Schaedelin, F. C., Mann, M., & Wagner, R. (2012). Exploring novelty: A component trait of behavioural syndromes in a colonial fish. *Behaviour*, *149*, 215–231.
- Mathis, A., Chivers, D. P., & Smith, R. J. F. (1996). Cultural transmission of predator recognition in fishes: Intraspecific and interspecific learning. *Animal Behavior*, *51*, 185–201.
- McEwen, B. S. (2000). Effects of adverse experiences for brain structure and function. *Biological Psychiatry*, *48*, 721–731.
- McEwen, B. S., & Sapolsky, R. M. (1995). Stress and cognitive function. *Current opinion in neurobiology*, *5*, 205–216.
- Mery, F., & Burns, J. G. (2010). Behavioural plasticity: An interaction between evolution and experience. *Evolutionary Ecology*, *24*, 571–583.
- Moretz, J. A., Martins, E. P., & Robinson, B. D. (2007). The effects of early and adult social environment on zebrafish (*Danio rerio*) behaviour. *Environmental Biology of Fishes*, *80*, 91–101.
- Nyman, C., Fischer, S., Aubin-Horth, N., & Taborsky, B. (2017). Effect of the early social environment on behavioural and genomic responses to a social challenge in a cooperatively breeding vertebrate. *Molecular Ecology*, *26*, 3816–3203.
- Peacor, S. D., & Werner, E. E. (2004). Context dependence of nonlethal effects of a predator on prey growth. *Israel Journal of Zoology*, *50*, 139–167.
- Pear, J. J. (2001). *The science of learning* (p. 524). New York: Psychology Press.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2015). *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-120*, <URL: <http://CRAN.R-project.org/package=nlme>>.
- R Core Team. (2015). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria*. URL <http://www.R-project.org/>
- Roche, D. P., McGhee, K. E., & Bell, A. M. (2012). Maternal predator exposure has lifelong consequences for offspring learning in threespined sticklebacks. *Biology Letters*, *8*, 932–935.
- Rosenzweig, M. R., & Bennett, E. L. (1995). Psychobiology of plasticity: Effects of training and experience on brain and behavior. *Behavioral Brain Research*, *78*, 57–65.
- Sandi, C., & Pinelo-Nava, T. M. (2007). Stress and memory: Behavioural effects and neurobiological mechanisms. *Neural Plasticity*, *2007*, 78970.
- Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*, 2762–2772.
- Siviter, H., Deeming, D. C., Rosenberger, J., Burman, O. H., Moszuti, S. A., & Wilkinson, A. (2017). The impact of egg incubation temperature on the personality of oviparous reptiles. *Animal Cognition*, *1*, 109–116.
- Smith, C., Phillips, A., & Reichard, M. (2015). Cognitive ability is heritable and predicts the success of an alternative mating tactic. *Proceedings of the Royal Society B*, *282*, 2015–1046.
- Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS ONE*, *6*, e19535.
- Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, *63*, 495–502.
- Spinelli, S., Chefer, S., Suomi, S. J., Higley, J. D., Barr, C. S., & Stein, E. (2009). Early-life stress induces long-term morphologic changes in primate brain. *Archives of general psychiatry*, *66*, 658–665.
- Stiver, K. A., Desjardins, J. K., Fitzpatrick, J. L., Neff, B., Quinn, J. S., & Balshine, S. (2007). Evidence for size and sex-specific dispersal in a cooperatively breeding cichlid fish. *Molecular Ecology*, *16*, 2974–2984.
- Strand, D. A., Utne-Palm, A. C., Jakobsen, P. J., Braithwaite, V. A., Jensen, K. H., & Salvanes, A. G. V. (2010). Enrichment promotes learning in fish. *Marine Ecology Progress Series*, *412*, 273–282.
- Sword, G. A. (2002). A role for phenotypic plasticity in the evolution of aposematism. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *269*, 1639–1644.
- Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: Their costs and benefits. *Animal Behavior*, *32*, 1236–1252.
- Taborsky, M. (1985). Breeder-helper conflict in a cichlid fish with broodcare helpers—an experimental analysis. *Behaviour*, *95*, 45–75.
- Taborsky, B. (2016a). Opening the black box of developmental experiments: Behavioural mechanisms underlying long-term effects of early social experience. *Ethology*, *122*, 267–283.
- Taborsky, M. (2016b). Ecology and evolution of cooperative breeding in cichlid fish. In W. Koenig, & J. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior*. Cambridge: Cambridge University Press.
- Taborsky, B. (2017). Developmental plasticity: Preparing for life in a complex world. In M. Naguib, J. Podos, L. W. Simmons, L. Barrett, S. Healy & M. Zuk (Eds.), *Advances in the study of behavior*, *49*, 49–99.
- Taborsky, B., Arnold, C., Junker, J., & Tschopp, A. (2012). The early social environment affects social competence in a cooperative breeder. *Animal Behavior*, *83*, 1067–1074.
- Taborsky, B., & Oliveira, R. F. (2012). Social competence: An evolutionary approach. *Trends in Ecology & Evolution*, *27*, 679–688.
- Taborsky, B., Tschirren, L., Meunier, C., & Aubin-Horth, N. (2013). Stable reprogramming of brain transcription profiles by the early social environment in a cooperatively breeding fish. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *280*, 2012–2605.
- Teblich, S., Stankewitz, S., & Teschke, I. (2012). The relationship between foraging, learning abilities and neophobia in two species of Darwin's finches. *Ethology*, *118*, 135–146.
- Teblich, S., & Teschke, I. (2014). Coping with uncertainty: Woodpecker Finches (*Cactospiza pallida*) from an unpredictable habitat are more flexible than birds from a stable habitat. *PLoS ONE*, *9*, e91718.
- Therneau, T. (2015). *A package for survival analysis in S*, v.2.38, <URL: <http://CRAN.R-project.org/package=survival>>.
- Titulaer, M., van Oers, K., & Naguib, M. (2012). Personality affects learning performance in difficult tasks in a sex-dependent way. *Animal Behavior*, *83*, 723–730.
- Tomasello, M., & Call, J. (1997). *Primate Cognition*. Oxford: Oxford University Press.
- Van Praag, H., Kempermann, G., & Gage, F. H. (2000). Neural consequences of environmental enrichment. *Nature Reviews Neuroscience*, *1*, 191–198.
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*, 4th ed.. New York: Springer. ISBN 0-387-95457-0.
- Verbeek, M. E., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behavior*, *48*, 1113–1121.
- Wingfield, J. C. (2005). The concept of allostasis: Coping with a capricious environment. *Journal of Mammalogy*, *86*, 248–254.
- Wingfield, J. C., & Romero, L. M. (2001). Adrenocortical responses to stress and their modulation in free-living vertebrates. In B. S. McEwen (Ed.), *Handbook of Physiology, section 7: The Endocrine System. Coping with the environment: neural and endocrine mechanisms* (pp. 211–236). Oxford: Oxford University Press.
- Zimmer, C., & Spencer, K. A. (2015). Reduced resistance to oxidative stress during reproduction as a cost of early-life stress. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *183*, 9–13.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2009). A protocol for date exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14.

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