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**SI Appendix**

**SI Materials and Methods**

Study species

*Social system. Neolamprologus pulcher* is a cooperatively breeding cichlid endemic to Lake Tanganyika, East Africa. Family units consist of one dominant breeder pair and 1-25 smaller subordinate group members, which act as brood care helpers. Helpers participate in territory defense against predators and space competitors, territory maintenance and direct alloparental brood care of eggs and larvae. This includes fanning (movements of the pectoral fins to supply the eggs with oxygen) and cleaning the eggs from microorganisms (1, 2). Breeder females produce clutches of typically 50-200 eggs, which are attached to the walls of a central breeding shelter (3). Within the following 9-10 days, eggs develop into free swimming juveniles that are independent of direct brood care. Juveniles remain in the natal territory, and above a size of 1.5 to 2 cm standard length (SL; length from the tip of the snout to the posterior end of the vertebral column) they start to act as brood care helpers (4). Helpers mature at a size of around 3.5 cm SL (5) (in the laboratory this corresponds to an age of 10 to 12 months), which is the earliest age at which *N. pulcher* may disperse in nature (6). Many subordinates delay dispersal, however, and stay at the natal territory even long after maturation before either dispersing to another territory elsewhere or inheriting a breeder position at the natal territory (1, 2, 6, 7). They stay at the territory mainly to gain protection from predators (4, 5, 8). Outside the protection of a territory and large group members, survival is virtually impossible for these fish (1, 5). Helpers may be related or unrelated to the breeders (9), and the degree of relatedness decreases with the age of helpers due to frequent exchange rates of breeders by predators (7). If they are related to the breeders, they can accrue indirect benefits in addition to protection. To avoid punishment (10), all subordinates, whether juvenile or adult, contribute to some degree to alloparental care and territory defense in order to remain tolerated at the territory (9, 11-15). The degree of help can vary substantially, however. For instance, in a removal experiment subordinates were temporarily prevented from helping to defend against a dangerous predator. Afterwards, some subordinates appeased dominants by increasing their helping effort, whereas others instead increased the rate of submissive displays (12).

*Influences of early-life experiences on N. pulcher behavior.* Previous research showed that variation of the early social environment strongly influences later social behavior in *N. pulcher*. Individuals reared in socially more complex groups, such as in conjunction with parents and helpers (as opposed to with siblings only) (16, 17) or in larger groups (as opposed to in small groups) (18), displayed more appropriate social responses during experimental, social challenges. This occurred in different social contexts and when fish were pre-assigned different social roles, such as loser/subordinate or winner/dominant. Moreover, fish reared in socially complex environments had shorter contest durations over a resource (16), were tolerated closer to a shelter after losing a contest (17), and were better tolerated when joining a new group as subordinate (17). This suggests that showing appropriate social responses during conflicts had positive fitness consequences, at least in the short term, for instance by reducing energy expenditure and the risk of being injured by conspecifics. Overall, this research suggested that more complex social rearing environments may generally favor the acquisition of better social competence. However, as only one component of the environment (the social component) had been varied in the previous studies, no indication for a life-history specialization was detected.

*Stimulus fish species used during the experiment.* Apart from our focal species, *N. pulcher*, we used two other fish species, which served as stimulus fish in our experiment. The main predator of juvenile and adult *N. pulcher*, the cichlid *Lepidiolamprologus elongatus*, was used as a dangerous stimulus species (19). As a harmless stimulus species we used *Ophthalmotilapia ventralis*, a cichlid feeding on zooplankton or grazing the bio-cover of rocks (20, 21). While *O. ventralis* can prey on fry or very small juvenile cichlids, it poses no threat to *N. pulcher* exceeding a certain size (approx. 1.5 cm standard length) due to its strong gape-size limitation. Both stimulus species occur in sympatry with *N. pulcher* in several populations along the shores of southern Lake Tanganyika (22, 23).

General housing conditions

The experiment was done at the Division of Behavioural Ecology of the Institute of Ecology and Evolution, University of Bern, Switzerland under the license 52/12 from the Veterinary Service of the Canton Bern. Adult breeders and immature helpers were second and third generation offspring of wild caught fish from the ‘Kasakalawe Point’ population at the southern tip of Lake Tanganyika, Zambia, Africa (for exact geographical coordinates see reference 19). The light:dark cycle was set to 13:11 h with 10 min of dimming in the morning and evening to simulate light conditions at Lake Tanganyika. Water temperature was 27 ± 1º C and biochemical parameters were adjusted to values measured at Kasakalawe Point (B. Taborsky unpubl. data). During the rearing of the experimental broods, adult breeders, immature helpers and predators were fed ad libitum six days a week with commercial flake food (5 days) and frozen zooplankton (1 day).

Rearing of experimental broods

*Generating experimental broods.* To create the experimental broods, we established 23 family groups consisting each of a breeder male, a breeder female and an immature helper by haphazardly selecting unfamiliar fish from our institute’s breeding stock. All helpers were smaller than a standard length (SL) of 3.4 cm, which increased the chances of a successful acceptance by the dominant breeder. Breeder males were chosen to be always larger than females to mimic the size differences found in natural pairs (5, 8). Each family group was settled in one of 23 200-L tanks (100 x 40 x 50cm, L x W x H) equipped with a 2 cm layer of sand and eight flowerpot halves serving as shelters and breeding cavities. Two PET-bottles on the water surface provided additional shelters. Two biological filters for oxygen supply were placed 5 cm above the tank floor to prevent fish from using it as a breeding shelter. Out of the 23 helpers, seven had to be removed from the tank during the course of the experiment, because they were exposed to an elevated level of aggression by the breeders. When a pair had produced a clutch, we counted the eggs. Clutches with more than 80 eggs were used for the experiment. Smaller clutches were removed on the day of egg laying.

*Social and ecological rearing treatments.* After the experimental broods had reached the free-swimming stage (defined as ‘Day 0’ of the experiment; free swimming occurs at 10 days after egg laying) the ‘experience phase’ started (Fig. 1). During this phase, juvenile offspring were exposed to different social environments and predator cues. It lasted from Day 0 until experimental Day 63. On Day 0 we caught all offspring and counted them. We divided the 200-L tanks into two equal halves by an opaque division, which was impermeable to water, and then selected haphazardly half of the offspring to be reared with their parents and the helper in one 100-L compartment (50 x 40 x 50cm, L x W x H; +F treatment) and the second half to be reared without older group members (–F treatment, Fig. 1) in a same sized compartment. To concurrently simulate predation risk, we presented single specimens of the predator *L. elongatus* twice weekly in tanks adjacent to half of the rearing tanks (+P treatment, Fig. 1). Presentations lasted for 30 min, during which the predator was visible to the *N. pulcher* groups, while for the rest of the time an opaque barrier prevented the sight on the predator. During the second half of the experience phase (starting from Day 35), 10 ml of ‘predator water’ (water from the home tank of *L. elongatus*) was transferred to the group tanks at the start of each predator presentation to allow also for olfactory perception of the predator. The other half of experimental groups received a perceived low-risk cue. After confirming that young *N. pulcher* perceive cues of all other cichlids as dangerous, which is shown in the next section, we decided to use predator absence (–P) as control treatment for predator presence. –P groups were presented with a same-sized, but empty tank following the same presentation scheme as described above. From Day 35, 10 ml of tap water was added at the start of the presentation. In total, each group received either 17 predator or 17 control presentations. The social and predator rearing treatments were applied in a full-factorial design resulting in groups of juveniles with four different rearing backgrounds. Juveniles reared with older family members and exposed to predators (+F/+P; N=12 rearing groups) or not exposed to predators (+F/–P; N=11), and juveniles reared without older family members and exposed to predators (–F/+P; N=11) or not exposed to predators (–F/–P; N=12).

*Anti-predator responses of N. pulcher young.* For the predator rearing treatment, it was not possible to present a “harmless” heterospecific fish to mimic a low-risk environment, because for *N. pulcher* fry and small juveniles no harmless fish exist. In nature virtually every heterospecific represents a potential predation risk to *N. pulcher* young in their earliest life stage. At the onset of the rearing treatment, fry are only about 0.5 cm in length, and thus are an easy prey for every adult cichlid. In the laboratory, even herbivorous cichlids readily eat fry and small juveniles of other cichlids (B. Taborsky, pers. obs.).

Before deciding on the type of control to be used for predator presence we had investigated the anti-predatory responses of *N. pulcher*. We had performed a separate experimental series, during which we exposed 10-day old *N. pulcher* fry to five olfactory cues, including (i) *Telmatochromis vittatus*, a predator of eggs and fry of *N. pulcher*, (ii) *L. elongatus*, a predator of all life stages of *N. pulcher*, (iii) the herbivore cichlid *O. ventralis*, (iv) conspecific *N. pulcher*, and (v) tap water as control cue. Our experimental results confirm that small *N. pulcher* perceive all heterospecific and even conspecific cichlids as potential predators. Opercula beat rate (OBR) counts were used to quantify the anti-predator responses to the different stimuli. Each trial consisted of two phases, a record of the baseline OBR in home tank water and a record of the response OBR after adding one of the five test cues. We used five siblings of 19 *N. pulcher* broods, where each of the 5 cues was tested with one sibling per brood. The production and storage of cue water and the procedure of baseline and cue exposure follow a protocol published in Stratmann and Taborsky (24) developed for the mouthbrooding Lake Tanganyika cichlid *Simochromis pleurospilus.* *S. pleurospilus* responded to the exposure to predatory cues, by a *reduction* of their OBR (as compared to the home tank water baseline), which represents a freezing response to a perceived threat (25), whereas no reduction occurred when exposed to the herbivore cue or the control cue (tap water). Like the mouthbrooders, *N. pulcher* young did not alter OBR in response to tap water (Paired t-test, N=19, p=0.7), but they significantly reduced OBR in response to cues of all cichlid cues (Paired t-tests, all p<0.01). When comparing the magnitudes of the responses to the tap water control cue and the cichlid cues, *N. pulcher* young had significantly greater responses towards *all* fish cues compared to the response to tap water, regardless whether the fish cues were derived from predatory species (*T. vittatus*, *L. elongatus*), herbivores (*O. ventralis*) or conspecifics (*N. pulcher*) (Linear mixed effect model on the differences between cue OBR and baseline OBR, Table S1, Fig. S1).

**Table S1.**

Comparison of OBR responses of 93 *N. pulcher* fry from 19 broods towards a control (tap water) cue and two predatory cues (*T. vittatus*, *L. elongatus*), a herbivore cue (*O. ventralis*) or a conspecific cue (*N. pulcher*). Brood identity was included as a random effect. To account for individual differences in baseline OBR the dependent variable is the difference between the response OBR shown after application of the five stimulus cues and baseline OBR shown in home tank water. Estimates show the significant reduction of OBR when any fish cue was present compared to the tap water cue (intercept). *P*-values <0.05 are highlighted in bold.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | | **t-value** | | ***P*-value** | |
| Intercept | | -5.443 ± 11.064 | | -0.492 | | 0.624 |
| Egg predator cue | | -59.711 ± 15.696 | | -3.804 | | **<0.001** |
| Predator cue | | -35.791 ± 15.478 | | -2.312 | | **0.024** |
| Herbivore cure | | -53.579 ± 15.696 | | -3.414 | | **0.001** |
| Conspecific cue | | -65.281 ± 15.478 | | -4.218 | | **<0.001** |

This indicates that *N. pulcher* young perceive any fish cue as dangerous during their early juvenile phase. The different results obtained in *N. pulcher* and the mouthbrooder *S. pleurospilus*, which only responded to piscivorous predatory cichlids by freezing (24), are most likely due to differences between the two species in their size-dependent mortality risk as juveniles: *N. pulcher* reach their free-swimming stage at much smaller sizes (0.5 cm) than do mouthbrooder juveniles, which are protected in the maternal buccal cavity until a size of 1.7-1.8 cm, at which size they cannot be easily preyed on anymore by herbivore cichlids.



**Fig. S1**

Opercula beat rate (OBR) changes of *N. pulcher* fry in response to tap water, and olfactory cues of the egg predator *T. vittatus,* the predatory cichlid *L. elongatus*, the herbivore cichlid *O. ventralis*) and the conspecific *N. pulcher*. The differences between cue OBR and baseline OBR are shown, so that negative values indicate a reduction of OBR in response to a stimulus cue. When exposed to tap water (control), young did not change their OBR rate, that is, there was no significant difference from a gray dotted line representing OBR in home tank water. In all other treatments individuals significantly decreased their OBR. Furthermore post-hoc comparisons revealed that all responses to a cichlid cue treatment differed significantly from the control (post-hoc test with Tukey method, all p-values < 0.05) but did not differ among each other (all p-values > 0.05). Data obtained by Tess van den Bergen, Master Thesis, University of Applied Sciences HAS Den Bosch, Netherlands).

*Maintenance after the rearing phase.* On Day 63, at the end of the experience phase, all adult family members were removed from the rearing tanks and reintegrated in our institute’s breeding stock. From then on all juveniles were reared under identical conditions together with same aged siblings and without further predator presentations. On Day 204 all experimental fish had reached sexual maturity and their sexes were determined by inspection of the genital papillae. To prevent reproduction we separated males and females; we placed all same sex full-siblings in the same 200-L tank, thereby merging fish of the two rearing groups produced by the same parents. For identification, fish were permanently marked at Day 204 using subcutaneous injection of Visible Implant Elastomer tags (VIE; Northwest Marine Technology).

*Feeding regime.* Juveniles of the experimental broods received standardized food, starting from experimental Day 0. Until Day 63, all groups of juveniles reared without older family members received 0.087g ± 0.001g (mean ± SD) of commercial fine-grained tropical fish food (TetraMin Baby®). To compensate for the presence of older family members, which also ate part of the ‘Baby‘ food, groups of juveniles reared with older conspecifics were fed 0.152g ± 0.067g (mean ± SD) TetraMin Baby® per group. This food compensation was successful, because body sizes after the experience phase (day 77, mean SL of 5 randomly selected offspring of 42 rearing groups) and specific growth rates across the first 77 days (N=126 growth measurements in three bi-weekly intervals between day 28 and 77;) were homogenous across groups of different treatments (main effects of F treatment, P treatment and their interaction: all *p* > 0.1). After Day 63 when adult family members had been reintegrated into the institute’s breeding stock, all groups of juveniles received 0.087 g ± 0.001 (mean ± SD) Baby food per group. At Day 77 we increased the ration to 0.186 g ± 0.007 (mean ± SD) of Baby food per group to account for increasing size and weight of the fish. From Day 91 onwards, juveniles were able to eat larger food items and all groups now received 0.431 g ± 0.014 (mean ± SD) per group of commercial food with medium sized flakes (TetraMin Junior®). From day 162 until the end of the experiment the diet of all groups was switched to commercial adult fish food flakes (JBL Novo Tanganyika®). We counted the exact number of fish in each group and provided a ration of 0.008 g per fish.

Behavior during experience phase

To analyze how the early experiences influenced the development of social behavior of test fish we did four behavioral recordings during and shortly after the experience phase (on Days 21, 35, 49 and 70). The behavior of 12 +F/+P and –F/–P groups and 9 +F/–P and –F/+P groups was recorded. We observed three randomly chosen fish per group. The random selection of individuals within a tank was done by choosing the xth individual counted alternately from left, right, top or bottom of the tank, with x being determined by a random number table. After two minutes of habituation time, during which the observer (SF or CN) sat motionless in front of the tank, we recorded all social behaviors (3, 16) and the activity of the chosen fish for 5 min. Activity was scored as the number of times an individual crossed a line of a 4x4 grid (=12.5 x 12.5 cm squares) covering the entire front screen of a tank.

Overview over behavioral tests after the experience phase

We performed two tests to evaluate the ability of fish to express adequate social behaviors (social competence). (1) The ‘acceptance by a social group (ACCEPT) test’ (Day 162) was designed to assess the ability to integrate and stably settle in an unfamiliar social group as subordinate. (2) The ‘egg care (EGG) test’ (Day 316) was designed to assess the ability to show alloparental brood care behaviors as subordinate, as this represents an important component of the ‘rent’ subordinate *N. pulcher* pay towards dominants, and thereby reduces aggression levels and risk of eviction by dominants (10, 26). These two social tests were performed in the juvenile and subadult stage, respectively (see Fig. 4).

We did three tests to assess the anti-predator competence of the fish. (1) The ‘vigilance (VIG) test’ (Day 134) was designed to test for the ability to detect a predator. Early predator detection is the prerequisite for a successful predator avoidance (27). (2) At Day 218 we did the ‘predator differentiation (DIFF) test’. It was designed to test for the ability of fish to differentiate between a harmless herbivore and a dangerous predator, as this should reflect the ability to reliably assess local predation risk (28). (3) On Day 407 we performed the ‘escape (ESC) test’, which was designed to assess the ability to flee and hide from a predator attack, as an adequate flight response reliably predicts the success of the escape (27). The three tests were performed in different life stages of *N. pulcher* (juvenile, subadult and adult stage, see Fig. 4), to obtain a long-term estimate of anti-predator abilities.

Finally, in the dispersal choice (DISP) test we let adult fish choose between two divergent key life history strategies *N. pulcher* can adopt as adults. (a) Delaying dispersal and staying in a territory as subordinate for a prolonged time may increase the survival prospects and it may, eventually, allow some subordinates to inherit a breeding position in that territory. (b) Dispersing early is more risky, but if successful it can yield own reproductive success as an independent breeder much earlier compared to strategy (a).

All behavioral observations were done using a laptop and the software Observer 5.0 (Noldus). Immediately after each test the respective test fish received an additional VIE color tag indicating it had been used for this test and was returned to its group. For each test we used different individuals to avoid that behavior was influenced by the experience made in a previous test. After the social tests, all stimulus fish were placed back to their respective home tanks in the breeding stock of the institute. In each test we used two replicate test fish per experimental group, if available, except for the ACCEPT and the DISP tests, where we had only one replicate. In all behavioral tests, the respective observers were blind to the rearing treatment of the test fish when doing direct behavioral recordings or when analyzing video recordings.

Social competence

*Acceptance by a social group* (ACCEPT)*.* On Day 162, we evaluated the ability of test fish to integrate into a social group consisting of unfamiliar members. For this test, we used 11 groups of each rearing treatment, and we tested one fish per group. For each test we combined sets of four different treatment groups to ‘experimental units’, each unit consisting of the +F/+P, –F/–P, +F/–P and –F/+P group that were closest in their ages. All fish of an experimental unit were assigned to the same breeder pair. This was done to account for the large variation among different breeder pairs in their general propensity to accept or to evict new group members, that is, irrespective of the latter’s rearing treatment (17). Of the four treatment groups belonging to a given experimental unit, four test fish (one per group) were selected that were most closely size-matched (average SL=2.67 cm, range=2.46-2.89 cm; mean size difference=0.08 cm, range=0.04-0.20 cm SL). As the test fish were not sexually mature, we could not determine their sex.

The ACCEPT tests were done in two 200-L tanks equipped with a 2 cm layer of sand, two biological water filters, eight flower pots halves at the bottom and two PET-bottles near the water surface serving as shelters. The flowerpot halves were large enough that test fish could use them as hiding places but were unable to monopolize single flowerpot halves and breeder sized fish would accept them as potential breeding shelters. On each experimental day, four test fish were tested from four rearing groups that were closest in age. Each test fish was singly placed into a 200-L tank for habituation to the new environment. The next day the first test fish was confronted with an unfamiliar breeder pair. All breeder pairs used in this test had been taken from the institute's breeding stock. They had been stably paired for over six months and had accepted helpers in their home tanks. Three 15-min behavioral recordings of all submissive and aggressive behaviors of the test fish towards the breeder pair as well as all aggressive behaviors of the breeder pair towards the test fish were done, one recording immediately after transferring a breeder pair to a test tank, and two further recordings 12 h and 24 h later. At the last observation, the acceptance state was determined according to the questionnaire in Table S2 in three categories (1: ‘fully accepted’ and ‘accepted’; 2: ‘fully-tolerated’ and ‘tolerated’; 3: ‘evicted’).

**Table S2:**

Questionnaire to determine the acceptance state in the ACCEPT, the EGG and the DISP choice test. Fish that could not be classified according to this scheme and/or did not behave as subordinates towards the pair or the larger conspecific were classified as ‘undetermined’ and were excluded from experimental trials.

Question 1: Test fish swimming everywhere in the tank and has access to tank bottom?

**YES**: Question 2a: Has the test fish access to the shelter(s)?

**YES**: *fully accepted*

**No**: *accepted*

**NO**: Question 2b: Test fish is hiding in a corner of the tank?

**YES**: *evicted*

**NO**: Question 3: Does test fish show avoidance behavior?

**YES**: *tolerated*

**NO**: *fully tolerated*

For the ACCEPT test, we combined the states ‘fully accepted’ and ‘accepted’, as well as the states ‘fully tolerated’ and ‘tolerated’ into one category each. The more refined distinction of five states shown in Table S2 only became apparent in older test fish and therefore was only applied in the EGG and DISP tests. After the third observation, the breeder pair was transferred to the next test fish of the experimental unit, where three 15 min observations were done following the same schedule as before. The sequence of the exposure of test fish towards the breeder pair was balanced with respect to the four rearing treatments. Thereby we controlled for a possible sequence effect of the presentation of the breeders and for the different habituation times of test fish. All behavioral recordings were done by SF.

*Egg care* (EGG)*.* On Day 316, we evaluated the propensity of test fish to show alloparental brood care behavior. The trials were done in 100-L compartments created by dividing 200-L tanks by opaque PVC-walls. Each experimental compartment was equipped with a 2 cm layer of sand, a biological water filter, and a flowerpot halve at the bottom and a PET-bottle at the surface serving as shelters.

During the EGG trials, the test fish were exposed to a clutch of freshly spawned eggs to observe if they showed direct brood care behavior in form of egg cleaning or fanning. Before the actual trials could be started, each test fish had to become a subordinate group member. A previous study showed that *N. pulcher* will cannibalize eggs if they are not in the role of a subordinate in a social hierarchy (29). Following the procedure of von Siemens (29), we created a stable hierarchy between the test fish and a larger unfamiliar conspecific. In this group of two fish, the test fish always adopted the subordinate role as in *N. pulcher* dominance is strictly determined by size. We ran this test with two replicate test fish per treatment group, one male and one female (except in four trials, for which only same sex fish were available). First we chose two test fish from each experimental rearing group in a size range between 2.5 to 3.5 cm SL (mean= 2.9 cm), as larger individuals do not perform alloparental brood care in natural groups (M. Taborsky pers. comm., see also ref 30). Thereafter, test fish were randomly assigned to one of the experimental compartments. Then a larger conspecific (SL by 1/3 larger than the test fish; mean= 3.84 cm, range= 3.28 - 4.66 cm SL) was placed in a small net cage (17 x 13 x 13cm L x W x H, mesh size 1cm) in the experimental compartment and released after 24 h. All larger conspecifics were derived from the institute’s breeding stock, and they were of the opposite sex than the test fish (except in 9 cases due to a limitation of suitable opposite sex fish). One, 3 and 5 days after the release of the larger fish, the observer scored the acceptance state of the test fish according to the questionnaire presented in Table S2. If the acceptance state of a test fish was scored at least once as ’fully accepted’, ’accepted’ ’fully tolerated’ or ‘tolerated’ the test fish was used for an EGG trial. If the state of a test fish was always classified as ‘evicted’ or ‘undetermined’, the trial was terminated (8 out of 95 trials). Another test fish from the same rearing group replaced the fish, and it was paired with a new conspecific. We tested 87 test fish (45 females and 42 males) from 11 +F/+P, 11 –F/–P, 11 +F/–P and 11 –F/+P groups.

The EGG trials were started 6 to 9 days after introducing the larger conspecific, depending on the availability of eggs from our institute’s breeding stock.After 5 min of habituation, the observer recorded all aggressive and submissive behaviors (3) for 10 min. Afterwards the acceptance state was recorded again according to Table S2. Every 30 s the observer also recorded the distance of the test fish towards the larger conspecific (far, middle, close) and the horizontal location of the test fish within the experimental tank (bottom, water column, near surface). Then we carefully separated the large conspecific from the test fish and confined it in a transparent tube (diameter 15 cm, length 25 cm) standing in the tank in upright position. Exchange of olfactory cues was possible through the top of the transparent tube, which was only sealed by a net. Now a clutch of eggs that had been laid on a plastic film by an unrelated, unfamiliar breeding group of our breeding stock (see also reference 29) was prepared for the trials. Each test fish ready to perform an EGG trial received an equal part of the clutch. To achieve this, we cut the plastic film holding the eggs into equal-sized pieces. We counted the number of eggs each test fish received (mean=28, range=11-74 eggs) so that we could check for egg cannibalism at the end of a trial. The observer mounted the eggs on the inner wall of the shelter and placed the shelter back exactly at its previous position in the experimental compartment. To ensure that all test fish were aware of the presence of eggs, we started the behavioral recordings only after the test fish had stayed in the shelter for at least 5 sec or, at the latest, 10 min after we had inserted the shelter with eggs into the compartment. In a 10 min behavioral recording, we noted all brood care behaviors (the frequency of egg nibbling and the duration of fanning behavior) and the frequency of egg cannibalism (i.e. number of eggs eaten) by the test fish. Fanning occurred too infrequently to be statistical analyzed (only 5 out of 87 individuals showed fanning behavior). At the end of each trial, eggs were removed from the inner wall of the flowerpot halves. All behavioral recordings for the EGG test were done by EO.

Anti-predator competence

*Vigilance* (VIG)*.* On Day 134, we evaluated the ability of test fish to detect a predator. We presented animated pictures of the main predator species, *L. elongatus*, using Microsoft Power Point presentations (for details on production and use of animations in behavioral tests see reference 31). Each trial consisted of the presentation of nine animated pictures of the same predator appearing in front of an olive-green background, but with increasing transparency values at each animation to mimic a patrolling predator at different levels of water turbidity, and thus conspicuousness (c.f 32). This reflects the highly variable visual conditions *N. pulcher* encounter in the field due to a significant seasonal variation of water turbidity (33). In the first animation, the predator picture was hardly visible simulating a predator in very turbid water, whereas in the last animations the predator was clearly visible as it would occur in transparent water conditions. Using animations of predators instead of live specimens allowed us to standardize the movement of the stimulus fish which would have strongly influenced the detectability of the predators. To manipulate the transparency values of subsequent animations we placed an olive-green shape over the predator picture, covering exactly the predator but not its background. In each subsequent animation, we increased the transparency value of the olive-green shape. This means that in the first animation the predator picture was hardly visible simulating a predator in turbid water, whereas the last animations were simulating a predator in clear water. The transparency values of the olive-green shapes at animation 1 through to 9 were respectively, 0.6, 1, 3, 5, 7, 9, 11, 15, 20%. For different test fish, different pictures of altogether six different specimens of *L. elongatus* were used in randomized order. Each of the nine animations was presented for 30 s, during which the predator slowly appeared head first and horizontally from right, then became visible completely on the screen and then left the screen on the opposite side.

We ran 80 trials with 11 +F/+P, 11 –F/+P, and 9 +F/–P, 9 –F/+P rearing groups. From each group, we randomly chose two test fish (mean=2.38 cm, range=1.69-3.02 cm SL). As all test fish were juvenile, we could not determine their sex. We placed them overnight in two unfamiliar 20-L tanks (40 x 25 x 25cm, L x W x H). Each tank was equipped with a 2 cm layer of sand, one flowerpot halve as shelter, which was placed 13 cm from either the right or left side wall of the tank, and an air stone for oxygen supply. On the next day, we placed a flat screen monitor (Compaq 1520, 15'' with a resolution of 1024 × 768), connected to a PC next to the sidewall of the test tank, which was opposite to the side where the shelter was placed. After a habituation time of 10 min the trial started. We first waited for the fish to take up the ‘starting position’ to ensure that they all had the same prerequisites to detect the predator. The test fish had to face away from the monitor, and it had to stay within 13 cm of the tank wall opposite to the monitor. Then the animation was started remotely from a connected keyboard. We recorded at which of the nine successive animations the test fish showed its first response towards the screen (’First response to an animation’ in Fig. 3A). Furthermore, during the time the predator was visible on the screen we recorded nine different aggressive behaviors (spreading of dorsal and pectoral fins; swimming in a head down position; approaching the monitor without touching the tank wall; approaching the monitor with touching the tank wall; opercula gill spreading; presenting the lateral body side with spreading of fins; change of swimming direction when approaching the predator picture with fins raised; following the predator picture with fins raised) and two evasive behaviors (freezing motionless in the water column; switching quickly from normal activity to hiding on the bottom). Two of the 80 test fish had not emerged from the shelter after 30 min when we terminated the trial, decreasing the sample size to 78 trials. The observers (SF and CN) were hiding behind a curtain during the habituation time and the behavioral recordings.

*Predator differentiation* (DIFF)*.* On day 218, we evaluated the ability of test fish to differentiate between a harmless herbivore cichlid (*O. ventralis*) and a dangerous predatory cichlid (*L. elongatus*), using animated pictures (for an example of the experimental presentation see Movie S1). The test was performed using the same sample sizes as in the VIG test with 80 trials in total.

The test involved the presentation of three differently-sized herbivores and three differently-sized predators (large = 12 cm SL; medium = 9 cm SL and small = 5.6 cm SL). Each test fish was exposed to small, medium and large *O. ventralis* and *L. elongatus* shown against a greenish background. Pictures of 9 stones (one stone each of 3.9 x 12.4 cm, 1.3 x 2.7 cm, 1.2 x 3.9 cm, 1.0 x 2 .1 cm and 0.7 x 1.5 cm size; and two stones each of 2.0 x 6.1 cm and 0.9 x 1.9 cm size [height x width]) presented 5 cm above the bottom pasted onto the background near the bottom of the display served as size reference relative to the predator (34, 35). We randomly selected pictures of *L. elongatus* and *O. ventralis* from the six available stimulus individuals and presented them in all three size classes in randomized sequences. The same tank setup as in the VIG test was used, except that the flowerpot halve was placed in the middle of the experimental tank and the opening faced towards the observer. We used animated pictures of predators and herbivores, instead of live specimens, which allowed us to present each stimulus fish individual with three different sizes, thereby controlling for variation in shape and color patterns of the stimulus individuals.

One day before a trial started, we randomly chose two test fish of a given rearing group (one male and one female, if available) with help of a random number table. The standard length and the sex of each test fish were noted (mean SL = 3.15 cm, range SL = 2.4-4.0 cm; 38 males and 41 females). Thereafter the test fish were randomly transferred to one of the two 20-L experimental tanks and allowed to habituate to the new environment overnight.

At each experimental day, we placed the flat-screen monitor also used in the VIG test in balanced order left or right next to the experimental tanks. After a habituation time of 5 min during which only the greenish background was displayed, we waited for the fish to take up the ‘starting position’ for this test defined as the center of the tank close to, but not inside the shelter. Before the start of each of the successive six animations, a test fish had always to take up the starting position. If a test fish did not take up the starting position within 20 min the trial was terminated (1 of 80 trials, in which the fish did not leave its shelter). During the presentation, we recorded the same behaviors as described in the VIG test and, additionally, we recorded attention behaviors as ‘facing towards’ (test fish was facing towards the animations) and following (test fish was following the animated picture without fins raised). The observer (EO) was blind to the order of the presented animations and all behavioral recordings were done from behind a curtain. For data analysis, we expressed the behaviors shown towards the predator relative to the behaviors shown towards the herbivore.

*Escape* (ESC)*.* On day 407, we evaluated the escape ability by eliciting escape responses with help of a marble dropped next to a feeding test fish. Dropping an unfamiliar object (marble) from above represented a novel situation to test fish of all treatments. The test was performed in four 200-L tanks. To allow for a correct analysis of flight paths of fish from 2-D video recordings, the tanks were only filled to a water level of 20 cm to ensure that the flight paths occur predominantly in two dimensions. The tank bottom was covered with a 1 cm layer of white sand, to increase the contrast between the moving fish and the underground for video-recording. The tank was virtually subdivided along its long axis into four vertical zones: a ‘shelter zone’ (15 cm width) containing one flowerpot halve, a feeding zone (50 cm width), a zone where the marble was dropped (10 cm width), and a 25-cm zone which could not be recorded with the webcam from above (Fig. S2) because of a limited maximum recording angle of the camera.



**Fig. S2**

Experimental setup for the escape (ESC) test on day 407. Experimental tanks (200-L) were virtually divided in four zones: (1) the ‘shelter zone’, with the flower pot halve; (2) the ‘feeding zone’, where test fish were accustomed to feed at a standardized position 50 cm away from the flower pot; (3) the ‘marble zone’, where the marble was dropped and (4) the ‘free zone’ where no recordings could be taken, due to the angle of the camera recording from above.

The marble was loosely fitted in a hole drilled in a wooden board that was mounted at a height of approximately 43 cm above the water surface. Beneath the marble a nail was inserted, which was attached to a string. To drop the marble, the observer had to pull the string to remove the nail under the marble. The dropped marble created an obvious splash when it entered the water and sunk rapidly to the ground at a standardized position close to the test fish eliciting an immediate threat response of the fish (see also reference 36). We did 80 trials with 40 males and 40 females taken from 10 +F/+P, 10 –F/–P, 10 +F/–P and 10 –F/+P rearing groups.

We stepwise accustomed fish to the feeding procedure they would encounter during the ESC test. Providing food was necessary to bring the fish to the starting position for this test, as single fish are hesitant to move far away from their shelter in a novel environment. At least one week before trials were done, we started a first training phase. We placed four plastic rings of 3 cm diameter on the bottom of the treatment groups’ home tanks and placed thawed pieces of frozen commercial krill food in the center of the rings. This procedure was done five times and served to accustom fish to take a new food source (krill is highly attractive for *N. pulcher*, but our experimental fish had never received krill before this test) and to feed from the bottom of the tank and the center of the rings. The plastic rings served to prevent the food from diffusing in the tank. One day before the experimental trials started, the test groups were starved for 24 h to raise their feeding motivation. The next day we chose randomly one male and one female test fish from a given treatment group and measured their standard lengths (mean over all trials: SL = 4.16 cm, range SL = 2.99-5.08 cm). Thereafter the two test fish were randomly assigned to two experimental tanks. Test fish could habituate to the new environment for 2 h. Afterwards a second training phase started, where over the course of two days, test fish learned to take krill from the plastic rings in the test tank. At the first day of training, they received krill pieces inside a plastic ring close to the shelter. Once the food had been taken, we moved the baited ring further and further away from the shelter until the end of the next day. This training phase accustomed the test fish to feed at a standardized position, which was 50 cm away from the shelter and hereafter referred to as ‘start position’ (see Fig. S2).

All trials were recorded from the long side of the test tank using a video camera (Sony HandyCam HDR-PJ260 8.9 Mega pixels) and from above using a web cam (Microsoft LifeCam VX-1000) with the Debut Video Capture Software. In addition, a third camera was used (Sony, CCD-IRIS) which transmitted the trials to a monitor (Sony, Trinitron color video monitor) placed behind a curtain next to the observer so that the observer knew when the fish had reached the starting position for dropping the marble. After installing the three cameras at an experimental tank, the observer waited for 5 min to let the fish recover from this disturbance. Then the observer started the three cameras to record the experimental tank and placed one krill piece inside the plastic ring, at the start position. Thereafter the observer hid behind a curtain. To ensure that all test fish had the same prerequisites to respond towards the marble we dropped it only if test fish were feeding in a perpendicular position facing towards the marble. To further control for differences in the angle of the fish’s body axis towards the marble, we later recorded the precise angle from the overhead video recordings and used it as a covariate in the analysis. After the test fish started to feed with the head inside the ring and facing towards the marble the observer dropped the marble. The video recordings were continued for another 15 min after the drop. Fifteen test fish did not feed the offered krill after 30 min, decreasing the sample size from 80 to 65 test fish (30 females and 35 males).

The recordings were analyzed using VLC Media Player, and ImageJ 1.47v (<http://rsb.info.nih.gov/ij>). We analyzed the flight response with respect to five parameters: (1) The latency to respond towards the dropping marble, (2) the distance covered during the initial burst phase of the flight response, which is the distance between the point of first response and the point where the initial burst response was terminated, (3) the distance covered by the total flight path, which consists of the burst phase and the following slower swimming phase until the fish hid in a shelter or stopped swimming. (4) how the flight response was terminated, that is, by entering the shelter or by stopping and staying outside the shelter, and (5) the first behavior shown after the flight response. All experimental procedures and video analyses for the ESC test were done by EO.

Dispersal choice test (DISP)

When the fish had reached an age of 2.5-3.5 years, we tested how they decide between the options either to stay as a helper in a territory or to disperse and pair up with a mate. We only used females, as females are the more philopatric sex in *N. pulcher* (7) and at this advanced age (>1.5 to 2.5 years after sexual maturation) it is very difficult to introduce unfamiliar males as subordinates into a group (B.T. pers. obs.). The trials took two weeks and were performed in 1000-L tanks (260 x 62 x 62cm, L x W x H). Each test female was first made subordinate to an unfamiliar, unrelated breeder pair. During this procedure, which took several days (see below), we did an additional treatment that simulated the presence or absence of current predation risk. We did this to test if fish adjust their decision whether or not to disperse to current risk, and whether this adjustment depends on early predator experience. If a test female was stably accepted by the pair she got the opportunity to disperse and pair up with an unfamiliar, unrelated male mating partner or, alternatively, to stay as helper with the pair.

*Set-up.* Each of the eight 1000-L tanks was separated in five compartments and was equipped with a 2-cm layer of sand, 4 biological water filters, 16 empty flowerpot halves serving as hiding and breeding shelters and plastic bottles close to the water surface as additional hiding possibilities (Fig. S3).



**Fig. S3.** Experimental setup in the dispersal choice (DISP) test. A 1000-L tank of 260 cm length was divided in 5 compartments. The rightmost and leftmost compartments held each a group of five *N. pulcher,* which served as territorial neighbors for the breeder pair and the potential mating partner. Adjacent to the neighbor compartments, there were two compartments in which breeder pairs and potential male mates, respectively, established their territories. The central compartment remained empty. The green fish indicates a test female, here shown as accepted helper in the breeder pair's territory. During the dispersal choice phase of the test, we removed the mesh divider between the pair territory and the empty compartment (as indicated by the black arrow). The divider between the stimulus male and the empty central compartment consisted of a sliding door which was always kept slightly open. In order to disperse a test female had to cross the empty zone and to swim through the sliding door to reach the male territory.

At each side of the test tank, a 30 cm wide compartment was created by inserting a clear Plexiglas divider. In each of these two compartments a group of five *N. pulcher* was settled. The sole purpose of these two groups was to simulate the presence of neighboring groups, as they would occur in a natural *N. pulcher* colony. The presence of these neighboring groups should increase the tendency of breeder pairs to accept the female helper (37), and the tendency of stimulus males to accept a female test fish as mating partner. Adjacent to each of the two neighbor compartments there was a 60 cm compartment. In one of these, the territory of a breeder pair was installed and in the other, the territory of a potential male mating partner for the test fish was built. The breeders’ compartment was equipped with five large (11 cm x 6 cm [L x H]) flowerpot halves suitable for the large breeder pair for hiding and breeding, as well as three medium (10 cm x 6 cm [L x H]) and two small sized (8 cm x 4 cm [L x H]) flowerpot halves. The male’s territory compartment was equipped with four small and two medium sized flowerpot halves, which were suitable for hiding and breeding for the male mating partner, but represented a low-quality habitat for the large breeder pair. This asymmetry of quality should prevent breeder pairs from taking over the male’s territory. The position of breeder territory and male territory in the tanks was balanced between left and right sides. The central compartment of 80 cm width between the two territories was left entirely barren. In order to disperse, a test fish had to cross this empty space between the breeders’ territory and the male’s territory. In nature, crossing barren areas without shelter exposes *N. pulcher* to predation risk, but dispersal requires crossing such open spaces. The aim of the empty compartment was thus to simulate semi-natural dispersal conditions. The breeder territory was separated from the central empty compartment by a removable mesh divider. The male territory was separated from the empty compartment by a clear PVC divider with a sliding door that was always open and allowed free movement between compartments through a slit of 2 cm height and 42 cm width.

*Experimental procedures.* Trials were done with 80 adult female test fish from 11 +F/+P, 11 –F/–P, 11 +F/–P and 10 –F/+P rearing groups; size range: 4.1-5.5 cm; mean 4.62 cm SL; age range: 901-1266 days. Furthermore, we used 28 breeder pairs and 28 potential male mating partners for the female test fish of the DISP test, all taken from our institutes lab stock population (mean size breeder males: 6.45 cm, range 5.4-7.6 cm; breeder females: 5.68 cm, range 4.8-6.8 cm; male mating partners: 5.12 cm, range 4.4-6.1 cm). Breeder females were chosen to be 0.5-1 cm smaller than their male partners to simulate the sexual dimorphism of natural pairs, but were at least 1.0 cm larger than the test female to enhance the chances that the test fish was accepted as subordinate group member. Potential male mating partners were chosen to be 0.5 cm larger than the respective test female. Each breeder pair was always used in combination with the same male partner, and if possible these fish were used four times, once for each rearing treatment, to reduce the variation among different breeder pairs and males in their general propensity to accept or evict new group members or mates (see also ACCEPT test). Of the 80 test females, 33 were ‘fully accepted’ or ‘accepted’ by the breeder pair, 10 +F/+P, 7 –F/–P, 9 +F/–P and 7 –F/+P females (see Table S2 for determination of acceptance state). Only these 33 females were kept for further analysis of the DISP test, as females that were only tolerated or even evicted might have dispersed merely to evade aggression by the pair. The size (-F/-P: mean = 4.6, range = 4.3 – 5.5; -F/+P: mean = 4.5, range = 4.0 – 4.9; +F/-P: mean = 4.7, range = 4.0 – 5.4; +F/+P: mean = 4.5, range = 3.9 – 5.0 [in cm]) and age ranges (-F/-P: mean = 1110.7, range = 1003 – 1281; -F/+P: mean = 1141.7, range = 985 – 1250; +F/-P: mean = 1119.7, range = 901 – 1266; +F/+P: mean = 1136.8, range = 977 – 1281 [in days]) were similar across the four treatments.

Each trial of the DISP tests consisted of five steps:

*Day 1 to 2*. A test female was placed in the breeder’s territory, the breeder pair was temporarily transferred to the empty, central compartment of an experimental tank and a male was placed in the male territory. This compartment was equipped with temporary shelters (flowerpot halves) for the breeder pair. To avoid the male and or the breeder pair to cross the sliding door an additional, opaque PVC divider was inserted temporarily between the male and the central compartment. This phase took two days and allowed all fish to habituate to the experimental tank and setup.

*Day 3 to 4.* The test female was gently placed into a small mesh enclosure (17 x 13 x 13cm L x W x H, mesh size 1cm) that contained one shelter. The enclosure with the test female was placed at the tank bottom in the center of the breeder’s territory, and the breeder pair was transferred from the central compartment to the breeder compartment. There it was allowed to move freely and to establish a territory. This enabled a familiarization of the breeder pair with the unfamiliar test female without risking the test female to be attacked or injured by the breeder pair. The temporary shelters and the opaque PVC dividers were removed from the central compartment allowing the potential male mating partner access both to the male compartment and, by using the open sliding door, to the central compartment.

*Day 4.* In the morning of Day 4 of each trial, between 9:00 and 12:00 h, a first perceived current predation risk treatment was applied. This treatment is described in detail below. Further current risk treatments were done in the mornings of days 6 and 7 of the trials.

*D*ay *5 to 8*. In the morning of Day 5, between 9:00 and 12:00 h, the test female was released from the mesh enclosure and could freely interact with the breeder pair. Between 13:00 and 15:00 h of Day 5 the acceptance state of the test fish was assessed for the first time, using the questionnaire presented in Table S2. This assessment was repeated daily until day 14 of the trials.

*Day 8 to 14.* At 15:00 h of Day 8 we removed the mesh divider between the breeder’s territory and the empty central compartment. Now all fish could move freely to all compartments, except the two neighbor compartments. Between day 8 and 14 we recorded once per day in which compartment the test female stayed. If the female stayed in the male compartment, we also recorded whether the male accepted it as partner using the questionnaire of Table S2. On Day 14 we caught all fish, measured their size and placed them back to their home tanks. During the 14 days all test fish were fed commercial flake food and frozen zooplankton six times per week. The observer (LB) could easily recognize all fish individually by their size (breeder male > breeder female > male mating partner > test fish).

To vary the current perceived predation risk we applied two treatments, one with visual and olfactory predator cues present during the experiment and one with neutral control cues simulating a low risk environment. To simulate a high-risk environment, we presented animated pictures of *L. elongatus* following the method in Fischer*, et al.* (31). In brief, we animated a laterally taken picture of a *L. elongatus* using Microsoft PowerPoint and presented it to the breeder pair and the test female close to the tank bottom. The animated picture moved from right to left or, alternatingly, from left to right, on an olive-green background simulating a patrolling predator close to the territory. After each presentation, we transferred 2 L of stimulus water from another stock tank containing *L. elongatus* in different sizes through a tube so that is was dispensed close to the tank bottom (see reference 38). To simulate a low risk environment and to control for the experimental manipulations we presented the same PowerPoint animation but without a fish picture (i.e. only the background slide) and added 2 L of water taken form the empty compartment of the test tank. The animations were shown 3 times within 10 min. The exact time points when we showed the animations during these 10 min were determined by a random number generator.

Statistical analysis

For statistical analyses, we used R 3.0.2 (39) with the packages ’lme4’ (40), ‘ordinal’ (41), ‘survival’ (42) and ‘afex’ (43). We analyzed generalized linear mixed models (GLMM), linear mixed models (LMM), cumulative link mixed models (CLMM) and cox proportional hazard regression models (COXPH). In each model, the social and predator rearing treatments were fitted as fixed effects and the family-of-origin (i.e. full siblings reared in different treatments) as a random effect (Group ID, Table S3). If multiple observations on the same test fish were done, we included individual identity as a random effect as well (Individual ID, Table S3). Only for the behavioral recordings during the experience phase we averaged the observations from the three full siblings of the same rearing background. In the VIG test, where we used multiple fish with unknown sex from the same rearing groups, we included ‘Tank ID’ as additional random factor to account for their shared housing conditions. In tests where we repeatedly used the same stimulus breeder pairs (in ACCEPT and DISP test) we included the identity of the pair as additional random effect to account for the breeder pair’s behaviors.

Table S3.

Information on the mixed models analyzed during this study, including dependent variables, fixed factors, covariates, random factors, data transformations performed to obtain normally distributed residuals, assumed data distribution and the link functions for GLMM or CLMM models and interaction terms included in the initial, full models. To obtain final models non-significant interactions were step-wise removed. Explanations of dependent variables of the models: ‘Predator’: fish exposed to predators or a control situation during development. ‘Family’ juveniles reared with or without older group members present. ‘Observation day’: refers to the age of test fish when observations were performed. ‘Observation No.’ refer to the three successive observations during the ACCEPT test: directly, 12 h and 24 h after the release of the dominant breeder pair. ‘Size difference’: The size difference between the test fish and the breeding female (ACCEPT) or the larger conspecific (EGG). ‘Treatment’: high or low current predation threat situation in the DISP choice. ‘Group ID’ refers to juveniles having the same parents. ‘Individual ID’: only included if observations on the same individual were done. ‘Pair ID’: the identity of the pair used in the ACCEPT or DISP choice. ‘Test sequence’: the sequence order of the observations in the ACCEPT. ‘Tank ID’: test fish from the same rearing group and the same rearing background

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Dependent variable** | **Factors** | **Covariates** | **Random factor** | **Distribution (Link)** | **Transformation** | **Interactions** |
| Submission (experience phase) | Predator  Family | Observation day | Group ID | Gaussian (Identity) | Sqrt | Predator × Family  Predator × Observation day  Family × Observation day  Family × Predator × Observation day |
| Aggression (experience phase) | Predator  Family | Observation day | Group ID | Gaussian  (Identity) | Log | Predator × Family  Predator × Observation day  Family × Observation day  Family × Predator × Observation day |
| Activity (experience phase) | Predator  Family | Observation day | Group ID | Gaussian  (Identity) | Sqrt | Predator × Family  Predator × Observation day  Family × Observation day  Family × Predator × Observation day |
| Submission towards dominant breeder pair in ACCEPT | Predator  Family | Observation Nr.  Aggression breeder  Size difference | Group ID  Pair ID  Test sequence | Gaussian  (identity) | IHS | Predator × Family  Predator × Observation No.  Family × Observation No.  Predator × Aggression breeder  Family × Aggression breeder  Predator × Family × Observation No.  Predator × Family × Aggression breeder |
| Acceptance in ACCEPT (cumulative link model) | Predator  Family | Size difference | Group ID | Ordinal  (logit) | None | Predator × Social |
| Alloparental brood care in EGG (Yes/No) | Predator  Family  Sex of test fish | Size of test fish | Group ID | Binomial  (Logit) | None | Predator × Social |
| Egg-cannibalism in EGG  (Yes/No) | Predator  Family  Sex of test | Size of test fish | Group ID | Binomial  (Logit) | None | Predator × Social |
| Submission towards larger conspecific in EGG | Predator  Family  Sex of test fish | Size difference  Received aggression | Group ID | Gaussian  (Identity) | Sqrt | Predator × Social  Predator × Received aggression  Social × Received aggression  Predator × Social × Received aggression |
| Received aggression in EGG | Predator  Family  Sex of test fish | Size difference  Distance | Group ID | Gaussian  (Identity) | Log | Predator × Social  Predator × Distance  Social × Distance  Predator × Social × Distance to companion fish |
| Acceptance state in EGG (cumulative link model) | Predator  Family  Sex of test fish | Size difference  Observation day | Group ID | Ordinal  (Logit) | None | Predator × Social  Predator × Day of observation  Social × Day of observation  Predator × Social × Observation day |
| First response to an animation in VIG | Predator  Family | Size of test fish | Group ID  Tank ID | Gaussian  (Identity) | Log | Predator × Family |
| Aggression towards predators in DIFF | Predator  Family  Sex of test fish  Size of stimulus | Size of test fish  Aggression towards herbivore | Group ID  Individual ID | Gaussian  (Identity) | Sqrt | Predator × Family  Predator × Aggression towards herbivore  Family × Aggression towards herbivore  Predator × Family × Aggression towards herbivore |
| Entering shelter in ESC  (Yes/No) | Predator  Family  Sex of test fish | Size of test fish | Group ID | Binomial  (Logit) | None | Predator × Family |
| Fearless behavior after flight in ESC | Predator  Family  Sex of test fish  Shelter enter | Size of test fish | Group ID | Binomial  (Logit) | None | Predator × Family |
| Latency to respond in ESC (survival analysis) | Predator  Family  Sex of test fish | Size of test fish  Feeding position | Group ID | None | None | Predator × Family |
| Initial burst path in ESC | Predator  Family  Sex of test fish | Size of test fish  Initial burst time | Group ID | Gaussian  (Identity) | Log | Predator × Family |
| Total escape path in ESC | Predator  Family  Sex of test fish | Size of test fish  Total escape time | Group ID | Gaussian  (Identity) | Log | Predator × Family |
| Dispersal in DISP | Predator  Family  Current risk | None | Group ID  Pair ID | Binomial  (Logit) | None | Predator x Family |

To simplify the models, we used stepwise backward elimination of non-significant interaction terms (44, 45). We used a logit link in all CLMM models and assumed an equidistant threshold between each level. To validate the assumptions of normality for the LMM models, we inspected the distribution of residuals, predicted vs. fitted value plots and Quantile-Quantile (Q-Q)-plots. Furthermore, we statistically compared each residual distribution to a normal distribution using Shapiro-Wilk and Kolmogorov Smirnov tests. If residual distributions were significantly different from a normal distribution we used log, square root or inverse hyperbolic sine (IHS, see reference 46) transformations. In COXPH models, we validated the proportional hazards assumption for a cox regression model fit. Significance testing was based on deviance when removing respective terms from the model. The change in likelihood was compared to a chi-square distribution (likelihood ratio test, see reference 47). Estimates presented in the 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. Table S3 presents the parameters, link functions and transformations of all models.

If a behavior was very rare and the data were strongly zero-inflated, we used a Friedman rank sum test to analyze this behavior. This applied only to the aggression of test fish towards breeders in the ACCEPT test.

In the ESC test, the first behavioral response after the marble drop was analyzed by a binomial model. The dependent categorical variable had two levels ranked for the extent of anxiousness (‘fearless behavior’, coded as binary variable. 0: stay motionless, 1: swimming freely). As in many fish (see references 48, 49), in *N. pulcher* the more anxious an individual is the less it moves around. To analyze the flight speed of the initial burst phase in the ESC test we analyzed the burst-path distance and included the duration of the burst phase as a covariate in the model. As expected, the burst path distance positively correlated with the duration of the burst phase.

In the EGG test, in addition to egg care and cannibalism, we analyzed also the social relationship between test fish and larger conspecific. To analyze the aggression received by the test fish from the larger conspecific, we combined the distance between the two fish and horizontal position of the test fish into a single covariate, which was fitted as fixed effect in the model. *N. pulcher* that are accepted in the territory by a dominant fish can stay closer to the dominant and can stay closer to the ground. Conversely, non-accepted fish stay far away from dominants and are often forced to stay near the water surface. The amount of social interactions with a dominant, including aggressive interactions, depends on the closeness of a subordinate to the dominant and to the dominant’s territory (tank bottom). Therefore, we calculated a weighted mean of the distance between the two fish. We weighted the time test fish spent close to the larger, dominant conspecific and close to the ground with the highest weight of 9 and assigned the lowest weight of 1 to test fish staying far away from the larger conspecific and spending more time close to the surface. We calculated the weighted mean of the position of the test fish as

where capital letters refer to the horizontal position of the test fish (G = ground, WC = water column, S = surface) and letters in subscript refer to the position of test fish towards the larger conspecific (C = close, M = middle, F = far). To analyze the amount of submission by test fish in the EGG test we included received aggression as a covariate in the model. This is because the amount of submission depends strongly on the amount of received aggression by dominant fish (50).

**SI Results**

**Table S4.**

Behavior of test fish during the experience phase. (A) Submissive behavior (square root transformed, 168 averages of 504 observations, in 21 rearing groups), (B) aggressive behavior (log transformed, 168 averages of 504 observations, in 21 rearing groups) and (C) activity (504 observations, in 21 rearing groups) of juveniles during the experience phase. ‘Predator’: juveniles exposed to predators or to the control condition during rearing. ‘Family’: juveniles reared with or without older group members. ‘Observation day’: age of test fish when observations were performed. Estimates are based on sum contrasts. Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | | **χ2** | | ***P*-value** | |
| 1. **Submissive behavior during and shortly after experience phase** | | | | | | |
| Intercept | | 0.014 ± 0.108 | | - | | - |
| Predator | | 0.001 ± 0.041 | | 2.522 | | 0.112 |
| Family | | -0.092 ± 0.041 | | 9.072 | | **0.003** |
| Observation day | | 0.033 ± 0.002 | | 137.567 | | **<0.001** |
| Predator x Family | | -0.098 ± 0.044 | | 4.401 | | **0.036** |
| 1. **Aggression during and shortly after the experience phase** | | | | | | |
| Intercept | | 0.767 ± 0.110 | | - | | - |
| Predator | | -0.057 ± 0.072 | | 0.624 | | 0.430 |
| Family | | 0.306 ± 0.072 | | 17.164 | | **<0.001** |
| Observation day | | 0.015 ± 0.002 | | 50.778 | | **<0.001** |
| 1. **Activity of test fish** | | | | | | |
| Intercept | | 5.642 ± 0.222 | | - | | - |
| Predator | | 0.072 ± 0.076 | | 0.881 | | 0.348 |
| Family | | -0.002 ± 0.076 | | 0.001 | | 0.977 |
| Observation day | | 0.023 ± 0.004 | | 29.243 | | **<0.001** |

**Table S5.**

Behavior and acceptance state of test fish in the group acceptance (ACCEPT) test. (A) Submissive behavior (IHS transformed) of test fish towards the dominant breeder pair (132 recordings, 22 rearing groups). (B) Likelihood of being accepted during the ACCEPT test. CLMM model with a threshold and spacing of -2.595 ± 4.818 and 1.639 ± 0.665 (estimate ± SE), respectively, and a three-level dependent variable (accepted, tolerated, evicted; 44 observations, 22 rearing groups). ‘Predator’ and ‘Family’: rearing treatments; ‘Size difference’: difference between the test fish and the breeding female. Estimates are based on sum contrasts. Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | **χ2** | ***P*-value** |
| 1. **Submissive behavior** | | | | |
| Intercept | 32.129 ± 7.047 | - | - | |
| Predator | 0.123 ± 0.532 | 2.457 | 0.117 | |
| Family | -0.505 ± 0.533 | 4.708 | **0.030** | |
| Observation No. | -4.490 ± 0.599 | 45.225 | **<0.001** | |
| Aggression breeder | 0.103 ± 0.102 | 0.764 | 0.382 | |
| Predator × Family | -1.619 ± 0.767 | 3.849 | **0.049** | |
| 1. **Acceptance by dominants** | | | | |
| Predator | 0.282 ± 0.408 | 0.478 | 0.489 | |
| Family | -0.395 ± 0.412 | 0.911 | 0.340 | |
| Size difference | -0.588 ± 1.362 | 0.189 | 0.664 | |
| Predator × Family | -1.70 ± 0.800 | 6.313 | **0.012** | |

**Table S6.**

Social behaviors and acceptance of test fish in the egg care (EGG) test. (A) Test fish’s likelihood to show egg cleaning and (B) egg cannibalism (87 observations, 22 rearing groups). (C) The amount of submissive behavior controlled by received aggression (square root transformed, 87 observations, 22 rearing groups) towards and (D) the amount of received aggression (log transformed, 87 observations, 22 rearing groups) by the dominant conspecific; (E) the acceptance state of test fish (86 observations with test fish from 22 rearing groups) before transferring the eggs into the experimental tank. CLMM model with a threshold and spacing of -1.572 ± 42.208 and 2.886 ± 0.324 (estimate ± SE) respectively and a five-level factor (fully accepted, accepted, fully tolerated, tolerated, evicted). Estimates are based on sum contrasts. Note that standard errors of Model E are based on a model excluding the random term given the low between family variance in the acceptance of test fish. ‘Predator’ and ‘Family’: rearing treatments; ‘Size difference’: difference between the larger conspecific and the test fish; ‘Received aggression’: aggression a test fish received from the larger conspecific; ‘Distance to conspecific’: distance between the test fish and the larger conspecific (see Material and Methods). Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | **χ2** | ***P*-value** |
| 1. **Probability of egg cleaning** | | | | |
| Intercept | -2.864 ± 2.820 | - | - | |
| Predator | 0.314 ± 0.333 | 5.860 | **0.015** | |
| Family | -0.412 ± 0.333 | 1.270 | 0.260 | |
| Sex | 0.223 ± 0.272 | 0.681 | 0.410 | |
| Size | 0.480 ± 0.965 | 0.247 | 0.620 | |
| Predator × Family | 0.815 ± 0.335 | 7.600 | **0.006** | |
| 1. **Probability of egg cannibalism** | | | | |
| Intercept | -2.185 ± 2.967 | - | - | |
| Predator | 0.065 ± 0.285 | 0.053 | 0.820 | |
| Family | -0.065 ± 0.285 | 0.051 | 0.821 | |
| Size | 0.211 ± 1.020 | 0.043 | 0.840 | |
| Sex | 0.042 ± 0.287 | 0.021 | 0.884 | |
| 1. **Submissive behavior** | | | | |
| Intercept | 0.982 ± 2.055 | - | - | |
| Predator | -0.267 ± 0.196 | 1.845 | 0.174 | |
| Family | 0.252 ± 0.197 | 1.622 | 0.203 | |
| Received aggression | 0.598 ± 0.170 | 11.445 | **<0.001** | |
| Size difference | 2.643 ± 2.102 | 1.566 | 0.211 | |
| Sex | 0.119 ± 0.197 | 0.363 | 0.547 | |
| 1. **Received aggression** | | | | |
| Intercept | 3.533 ± 0.971 | - | - | |
| Predator | 0.050 ± 0.080 | 0.390 | 0.532 | |
| Family | -0.012 ± 0.083 | 0.022 | 0.882 | |
| Distance to conspecific | -0.925 ± 0.274 | 10.524 | **0.001** | |
| Size difference | -0.697 ± 0.906 | 0.585 | 0.444 | |
| Sex | 0.046 ± 0.083 | -0.47 | 0.64 | |
| 1. **Probability of acceptance** | | | | |
| Predator | 0.061 ± 0.212 | 0.082 | 0.774 | |
| Family | 0.050 ± 0.212 | 0.055 | 0.815 | |
| Size difference | 3.429 ± 2.328 | 2.182 | 0.140 | |
| Sex | 0.350 ± 0.221 | 2.563 | 0.109 | |

**Table S7.**

Comparisons of anti-predator behaviors in the vigilance (VIG) and the predator differentiation (DIFF) test. (A) We tested at which of nine successive predator animations a test fish showed its first response in the VIG test (77 observations, 20 rearing groups). (B) Aggression (square root transformed) towards the picture of a predator relative to the picture of a herbivore (235 observation of 79 test fish, 20 rearing groups). ‘Medium sized stimulus’ and ‘small sized stimulus’: size of the presented stimulus picture. ‘Predator’ and ‘Family’: rearing treatments. Estimates are based on sum contrasts. Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | **χ2** | ***P*-value** |
| **A) Vigilance test** | | | | |
| Intercept | 1.732 ± 0.404 | - | - | |
| Predator | 0.102 ± 0.048 | 4.008 | **0.045** | |
| Family | 0.005 ± 0.048 | 0.013 | 0.910 | |
| Size | -0.133 ± 0.167 | 0.603 | 0.437 | |
| **B) Predator differentiation test** | | | | |
| Intercept | 0.959 ± 0.511 | - | - | |
| Predator | 0.185 ± 0.105 | 2.915 | 0.087 | |
| Family | -0.133 ± 0.104 | 1.615 | 0.204 | |
| Aggression herbivore | 0.582 ± 0.053 | 23.418 | **<0.001** | |
| Medium sized stimulus | -0.061 ± 0.082 | 4.638 | 0.098 | |
| Small sized stimulus | 0.175 ± 0.082 |  |  | |
| Size | -0.146 ± 0.159 | 0.851 | 0.356 | |
| Sex | 0.072 ±0.059 | 1.447 | 0.229 | |
| Predator x Aggression herbivore | -0.139 ± 0.054 | 6.232 | **0.013** | |
| Family x Aggression herbivore | 0.060 ± 0.053 | 1.264 | 0.261 | |

**Table S8:**

Comparisons of escape characteristics during the escape (ESC) test. The probability of test fish (A) to enter the shelter and (B) to show anxious behaviors after the flight response. (C) The latency to react towards the dropping marble. (D) The burst path distance controlled by the duration of the burst phase (log transformed) and (E) the total escape path distance (log transformed). ‘Predator’ and ‘Family’: rearing treatments; ‘Feeding position’: Test fish’s head orientation while the marble was dropped (see Material and Methods). All analyses are based on 65 observations with 20 rearing groups. ‘Shelter entering’: Binomial response variable if test fish entered the shelter after the flight response. Estimates are based on sum contrasts. Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | **χ2** | ***P*-value** |
| 1. **Shelter entering** | | | | |
| Intercept | 1.709 ± 4.104 | - | - | |
| Predator | 0.846 ± 0.349 | 7.593 | **0.006** | |
| Family | -0.240 ± 0.304 | 0.628 | 0.428 | |
| Size | -0.448 ± 0.983 | 0.505 | 0.650 | |
| Sex | 0.055 ± 0.310 | 0.032 | 0.858 | |
| 1. **Fearless behaviors** | | | | |
| Intercept | -6.268 ± 4.852 | - | - | |
| Predator | -0.842 ± 0.387 | 5.882 | **0.015** | |
| Family | -0.293 ± 0.342 | 0.760 | 0.383 | |
| Size | 1.15 ± 1.126 | 1.221 | 0.269 | |
| Sex | 0.108 ± 0.335 | 0.104 | 0.747 | |
| Shelter entering | 1.207 ± 0.459 | 11.043 | **<0.001** | |
| 1. **Latency** | | | | |
| Intercept |  | - | - | |
| Predator | 0.018 ± 0.137 | -0.012 | 1.0 | |
| Family | 0.168 ± 0.136 | -0.135 | 1.0 | |
| Size | 0.002 ± 0.466 | 0.016 | 0.842 | |
| Sex | 0.031 ± 0.134 | 0.287 | 0.596 | |
| Feeding position | 0.007 ± 0.006 | 4.130 | 0.118 | |
| 1. **Burst path distance** | | | | |
| Intercept | 6.080 ± 0.560 | - | - | |
| Predator | -0.026 ± 0.026 | 0.965 | 0.326 | |
| Family | -0.035 ± 0.026 | 1.759 | 0.185 | |
| Size | -0.263 ± 0.342 | 0.588 | 0.443 | |
| Sex | 0 ± 0.027 | 0 | 0.987 | |
| Duration of burst phase | 6.026 ± 0.519 | 72.986 | **<0.001** | |
| 1. **Total escape path distance** | | | | |
| Intercept | 4.067 ±0.388 | - | - | |
| Predator | 0.012 ± 0.019 | 0.359 | 0.549 | |
| Family | 0.013 ± 0.019 | 0.437 | 0.508 | |
| Size | -0.103 ± 0.253 | 0.165 | 0.685 | |
| Sex | 0.018 ± 0.020 | 0.820 | 0.365 | |
| Duration of escape | -0.010 ± 0.041 | 0.058 | 0.810 | |

**Table S9:**

Probability to disperse in the dispersal (DISP) choice test. 33 females of 19 rearing groups, which were accepted as helpers by the breeder pair were tested for their probability to disperse; 16 females dispersed and 17 remained in the breeder pair’s territory. ‘Predator’ and ‘Family’: rearing treatments; ‘Current risk’: high or low current predation risk treatment during the trials. Estimates are based on sum contrasts. Significance testing was done by likelihood tests. *P*-values <0.05 are highlighted in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Factors** | **Estimate ± SE** | **χ2** | ***P*-value** |
| Intercept | 0.074 ± 0.493 | - | - |
| Predator | 0.067 ± 0.431 | 0.024 | 0.876 |
| Family | -0.038 ± 0.428 | 0.008 | 0.929 |
| Current risk | 0.414 ± 0.582 | 0.633 | 0.426 |
| Predator x Family | 0.100 ± 0.578 | 4.866 | **0.027** |

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