

Presence of parents during early rearing affects offspring responses towards predators

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Social learning about predation threat during early ontogeny can be beneficial in developing appropriate antipredator behaviours. While such learning can be achieved through direct interactions between offspring and parents, it is unknown whether young animals can also learn appropriate responses towards different heterospecifics posing different levels of threat through inadvertent information obtained from witnessing parental interactions with these heterospecifics. In this study, we split sibling groups of the cooperatively breeding cichlid *Neolamprologus pulcher* and raised them with or without parents. Both rearing groups repeatedly received visual and olfactory cues from four types of fish (predators, egg predators, herbivores and conspecifics) during a 4-week experience phase. After a 'neutral phase' of 4 months under identical conditions and without further fish stimuli, individuals from both rearing conditions were tested for their response towards the same four stimulus species. Unlike those reared with parents, the fish reared without parents spent significantly more time in safety and were more vigilant towards the predator, whereas responses to the other three species did not differ. As during the experience phase parental responses towards the stimulus fish were unexpectedly low and indiscriminate, our results suggest that young *N. pulcher* reverse their innate fear of predators when observing parents being unresponsive to a threat ('observational conditioning'). We suggest that learned reduction of fear can be a potent mechanism to prevent responding to false alarms and mitigate potentially harmful effects of chronically elevated predation stress.

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Predation is one of the most influential environmental factors affecting individual life history and fitness (Stearns, 2000; Tollrian, 1995; Walsh & Reznick, 2008) as well as social and population structures (Groenewoud et al., 2016; Heg, Bacher, Brouwer & Taborsky, 2004; Holling, 1965; Preisser & Bolnick, 2008). Besides the direct risk of mortality or injury, prey can suffer from other indirect costs in terms of reduced fecundity, altered foraging and nonconsumptive increase in mortality (see meta-analysis by Preisser & Bolnick, 2008, for references). Many prey species, therefore, have evolved behavioural adaptations such as lateralization (Brown & Braithwaite, 2005), reduced activity (Lawler, 1989; Wooster & Sih, 1995), or mobbing (Bartecki & Heymann, 1987; Gursky, 2005; Heymann, 1990; Srivastava, 1991; Kobayashi, 1994, 1996; Loughry, 1988; Owings & Coss, 1977; Shields, 1984; Tamura, 1989). However, despite their advantages in the presence of a predator, these behaviours can be costly (Hua, Sieving, Fletcher, &

Wright, 2014; Mukherjee, Heithaus, Trexler, Ray-Mukherjee, & Vaudo, 2014; Persons, Walker, & Rypstra, 2002; Skelly, 1992; Baker & Ball 1995), for example by reducing foraging time and thereby limiting food intake (e.g. Orrock, Danielson & Brinkerhoff, 2004; Segers & Taborsky, 2011; Guo, 2017; Donelan & Trussell, 2018).

Many of these behaviours are inducible during development by the presence of reliable predator cues (Chapman, Morrell, Benton, & Krause, 2008; Dalesman, Rundle, & Cotton, 2007, 2009). Developmental plasticity is thus a powerful mechanism to avoid some of these costs. If the future environment of a young animal is predicted to be safe, it can save energy by abstaining from mounting costly antipredator defences. Conversely, if environmental cues predict predator presence, developing appropriate defences can improve survival (Storm & Lima, 2010). As the development of effective morphological or behavioural antipredator defences takes time, this should start as early as possible in life, as soon as cues of risk or safety are available.

Because young animals are particularly vulnerable to predation, direct and repeated sampling of environmental risk is very dangerous. Relying instead on socially available information about risk can be a much safer option. In species with brood care, parents

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are the most easily available and often the only source of social information. Further, it is also in the interest of parents to increase offspring survival. They may actively defend offspring against predators, which may also serve as an indicator of risk for offspring, or they may convey information about risk, either by specific, evolved signals or by altered brood care behaviour (e.g. changed feeding rates). Many species of birds and mammals announce the presence of a predator to the offspring (Caro, 2005; Magrath, Haff, Horn, & Leonard, 2010; Suzuki, 2011) and, as shown in superb fairywrens, *Malurus cyaneus*, even about the kind of risk present in the vicinity (Colombelli-Negrel, Robertson, Sulloway, & Kleindorfer, 2010). This allows offspring to fine-tune their antipredator behaviour. For instance, it is well documented among mammals that the presence of adults, particularly mothers, during development increases the alarm-calling accuracy of juveniles (see review in Thornton & Clutton-Brock, 2011). Even in species where parents do not interact directly with offspring or where parents allow independent juveniles to remain in the natal territory, the offspring can still learn from observing the parents or other adult group members. In Siberian jays, *Perisoreus infaustus*, juveniles that witness adult conspecifics mobbing a predator show more appropriate responses towards predators later on as reflected in their higher survival rates (Suzuki & Griesser, 2017). Similarly, in convict cichlids, *Amatitlania siquia*, in which both parents defend the brood for up to 6 weeks, young fry raised together with parents that were trained to recognize a novel predator show antipredator responses towards this novel species without any prior training (Al-Shaer, Paciorek, Carroll & Itzkowitz, 2016). Although a few such examples exist, no studies have investigated whether indirect information from parents can induce offspring to modulate a general, innate fear towards members of all other species into fine-tuned responses adjusted to the actual threat posed by each of these species.

We studied this question in the highly social, cooperatively breeding cichlid *Neolamprologus pulcher* from Lake Tanganyika. In this species, offspring produced by a dominant breeding pair are defended both by the breeders and by related or unrelated helpers (Taborsky & Limberger, 1981). It is prey to many other fish species and the high predation pressure is a key driver of sociality in this species (Taborsky & Limberger, 1981; Groenewoud et al., 2016). It has been shown that whether parents are present or absent during rearing strongly influences the social behaviour of young *N. pulcher* both during rearing and in later life (Arnold & Taborsky, 2010; Fischer, Bohn, Oberhammer, Nyman, & Taborsky, 2017; Taborsky, Arnold, Junker, & Tschopp, 2012). Whether this is due to social learning and, if so, whether such effects can also be seen in predator evasion behaviour remains unexplored. Parental presence may be important for the development of appropriate offspring antipredator behaviour by way of two, nonexclusive mechanisms. The offspring could be gaining a sense of overall safety in the presence of guarding parents and developing 'normal' antipredator behaviours while those reared without parents may be developing abnormal, exaggerated behaviours due to chronically elevated predation stress. Alternatively, the fry may gather information about actual risk of predation through the parents' defence behaviour, thereby developing appropriate defensive behaviours.

Here we exposed young *N. pulcher* to video presentations of conspecifics and three heterospecifics. These four species pose different levels of predation risk for small young. Experimental young were kept either with their parents, which may provide information to young offspring about the four stimulus species, or without parents and thus without the possibility to learn from parental behaviour. We expected that later in life experimental offspring reared with parents would have better species discrimination and therefore would respond by appropriate predator

avoidance behaviour to predators (but not to other species) compared to offspring reared without parents. We further predicted that, in the absence of guarding parents during rearing, offspring will show higher overall fearfulness, that is, regardless of the type of stimulus the fish face, as compared to offspring reared with parents.

METHODS

Study Species and Housing Conditions

Neolamprologus pulcher is a cichlid species endemic to Lake Tanganyika, Zambia. It lives in social groups composed of a dominant breeding pair and 1–25 subordinate helpers, which may or may not be related to the breeding pair (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Taborsky & Limberger, 1981). The helpers contribute to territory maintenance, defence and tending the dominants' brood. Predation by other lamprologus cichlids such as *Lepidolamprologus* spp., *Lamprologus* spp. and *Altolamprologus* spp. and by masticembelid eels influence the group structure by limiting dispersal and providing benefits of collective defence (Groenewoud et al., 2016; Heg, Bachar, Brouwer, & Taborsky, 2004). Juvenile *N. pulcher* remain and help in the natal territory and delay dispersal often until long after reaching adulthood (Stiver, Dierkes, Taborsky, & Balshine, 2004).

The breeding pairs that would produce the experimental offspring were derived from the laboratory stock at the Ethological Station Hasli, Institute of Ecology and Evolution, University of Bern, Switzerland. Each pair was housed separately in a 60-litre 'home tank', supplied with two clay pot halves as shelters, a 2 cm layer of sand and a biological filter. The light:dark cycle was set to 13:11 h and the water temperature was maintained at 27 ± 1 °C to emulate the natural conditions at Lake Tanganyika. The fish were fed 5 days a week with commercial flake food and 1 day with frozen zooplankton.

Experimental Broods and Experience Phase

Once the pairs had spawned the experimental broods ($N = 10$), fry were raised with their parents until 3 weeks after the free-swimming stage (30 days postfertilization). At 3 weeks, when the fry were large enough to be safely handled, each brood was captured, randomly split in half and immediately moved to new 60-litre tanks, which were also supplied with two clay pot shelters. Half of each brood was reunited with their parents for the experience phase (henceforth referred to as +F fish) while the remaining half was kept with their siblings only (henceforth referred to as -F), resulting in a paired design. All groups were kept without any visual contact with any fish outside their tanks throughout the experiment. During the following 4 weeks ('experience phase') all experimental groups received visual and olfactory cues from four stimulus species: (1) *Lepidolamprologus elongatus*, one of the most common and dangerous predators of juvenile and adult *N. pulcher* (Balshine et al., 2001; Heg et al., 2004; henceforth 'predator'); (2) *Telmatochromis vittatus* which feeds on eggs and larvae (henceforth 'egg predator'); (3) *Ophthalmotilapia ventralis*, a herbivore which may sometimes eat very small fry (henceforth 'herbivore'); and (4) adult conspecifics, which are space competitors for adult *N. pulcher* but would also cannibalize small fry if they successfully entered a foreign territory. Each stimulus presentation included a 5 min video of a single stimulus fish while 10 ml of water from the holding tank of the respective species (see Fischer et al., 2017) was dispensed into the experimental tank at the start of each video presentation. The videos showed the respective stimulus fish swimming around

calmly in a 20-litre tank that was only equipped with a 2 cm layer of sand. Each presentation was preceded by a 2 min visual showing the same, but empty, 20-litre tank to habituate the test fish to the view of this tank before the stimulus appeared in the picture. For every stimulus species, five video clips of five different individuals were filmed ($N=25$ videos per stimulus species). All species were presented at life size but we ensured that their size ranges overlapped. Thus, the larger conspecific and egg predator individuals (ca. 6 cm) were similar in size to the smaller predators. The overall size range of stimuli was between 5.5 cm (smallest conspecific) and 9.5 cm (largest predator) as appearing on screen. During testing, all stimuli were on the same size scale, which were still larger than juvenile *N. pulcher*. Of the 25 videos, one was chosen at random for each presentation trial of a species to avoid pseudoreplication and habituation to a particular video clip or specimen. The videos were presented to the fish on a 25 cm tablet screen (HP Elitepad). All four stimuli were presented to the experimental groups on the same day, in a randomized sequence, 2 h apart. Preliminary observations showed that the fish resume normal behaviour and activity within half an hour of receiving olfactory cues and, hence, it was assumed that in 2 h the cues were sufficiently dissipated not to affect the behaviour of the fish. The stimuli were presented thrice a week with a gap of 1 or 2 days in between. At the end of this 4-week experience phase, all replicate treatment groups (+F and -F) were moved to separate housing tanks of 30 litres, where they were kept under identical conditions in sibling-only groups with no parents and no stimulus presentations ('neutral phase') until behavioural testing (see below). At the beginning of the experiment, the number of fry per group varied between 13 and 20, with the same number of fry being present in the two full-sibling groups of +F and -F siblings (paired design). Across families, however, the group sizes were not adjusted as the variation in clutch sizes was rather small.

A separate set of eight breeding pairs with their 3-week-old fry and eight groups of 3-week-old fry without parents were given a single exposure of the four different stimulus species, which was video-recorded for 5 min in the exact same setting as described above. This data set served to determine the response of the breeders towards each of the stimulus species and to measure the initial fearfulness of fry at the age of 3 weeks when kept with or without parents. At this age, fry sink to the bottom on sensing danger and blend perfectly with the sandy tank bottom, so that they cannot be seen in the video recordings. Hence, the percentage of fry visible swimming above ground at the beginning (10 s) and at the end (300 s) of the stimulus presentation was used to measure the level of fear, with lower percentages indicating more fear. The 100% reference value was the number of fry visible at 1 min after the presentation of an empty tank had started (i.e. 1 min before the stimulus fish appeared on the screen; see details on the structure of video clips above). The time the breeders spent watching the stimulus fish (time spent orienting towards the screen) was recorded and aggressive displays (described 'Behavioural testing' below) were counted as a measure of defence. Overt attacks towards the screen were rare (in three of 32 observations) and were therefore not analysed. The effects of the breeder's sex on each behaviour were also analysed as the response of either breeder may be distinct, and the fry may be more receptive to one of them than the other.

Behavioural Testing

At 5 months old, two individuals from each of the 20 rearing groups were tested for their responses towards the four stimulus species. Two fish died during testing resulting in a sample size of 38 focal individuals (19 in the +F treatment and 19 in the -F

treatment). Each focal fish was tested individually and was tested once with each stimulus. It was moved to a 20-litre tank and allowed to acclimatize overnight. The test tanks were supplied with sand and a clay pot shelter. Stimuli were presented to the focal fish in a similar manner as in the experience phase, that is, a 2 min video of an empty tank followed by a 5 min video presentation accompanied by 10 ml of water from the holding tank of the respective stimulus species. All behavioural observations were video-recorded, and the behaviours were later coded with the Solomon Coder software (developed by András Petér, University of Budapest, Budapest, Hungary), with the observer being blind to the treatment. During each 5 min recording, the frequency of aggression was recorded as a measure of defence behaviour. Only two of 37 fish showed overt attacks. Therefore, only restrained aggressive displays were considered for the analysis. For this analysis we summed the number of all threat displays (fin spread with or without head-down display, opercula spread, fast approach towards the screen; for a detailed ethogram of these behaviours see [Reyes-Contreras, Glauser, Rennison, & Taborsky, 2019](#)). The amount of time spent attentive to the screen was taken as a measure of vigilance. A fish was regarded as attentive if it faced the screen for > 3 s. The time spent in the furthest third of the tank away from the screen was also recorded as a measure of risk avoidance or fearfulness. Lastly, the time spent inside the shelter was measured. Since the behaviour inside the shelter could not be observed, all recorded behaviours were analysed as rates per time spent outside the shelter (see Data analysis below).

Data Analysis

In 44 of 152 stimulus presentations during the test phase focal individuals stayed in the shelter for the entire duration of a recording. These observations were removed from further analysis. One +F focal stayed in the shelter during all presentations, leaving a final sample size of 19 -F and 18 +F individuals.

Attention and time spent in the zone furthest from the video presentation ('time in safety') were calculated as proportions of time outside the shelter.

For statistical analysis, we fitted linear mixed models (LMMs) for the proportions of visible fry, attention time of breeders and attention time and time in safety of 5-month-old focal fish. Generalized linear mixed models (GLMMs) with negative binomial distribution were analysed for aggression counts of breeders and focal fish. The model for focal aggression used the time fish spent outside the shelter as offset. All models were run with the package 'lme4' ([Bates, Machler, Bolker, & Walker, 2015](#)) of the software R version 3.4.2 (R Core Team, 2017). Stimulus species (four levels) and social rearing condition (two levels) and their interaction were included as fixed effects in the models and family identity and individual identity were included as random factors. For fry visibility, the time point of observation was included as an additional fixed effect. Similarly, stimulus species, sex and their interaction were included as fixed effects and family identity as a random effect in models for analysing breeders' behaviour. Normality assumptions for the error terms were tested by Shapiro-Wilk normality tests and by visually examining quantile-quantile (Q-Q) plots as well as histograms of residuals and plots of residuals against fitted values. If the assumptions for normality were violated, we performed log or Box-Cox transformations. If the interaction terms were not significant, we simplified the models by running them without the interaction. The criterion for dropping a nonsignificant interaction term was that the Akaike information criterion (AIC) of the model without the interaction had to be smaller by a value of at least 2 than the AIC of the model with the interaction. Body size of the focal individual was initially included as a fixed effect but had no

significant influence on any of the dependent variables and hence was removed from the final models. Post hoc analyses were conducted for pairwise comparison between rearing treatments for each stimulus species in the package ‘emmeans’ using the Bonferroni method for adjusting *P* values (Lenth, 2018). If no interaction term was involved in the final model, single-step pairwise comparisons with *P* values corrected by Tukey’s HSD method were performed in the package ‘multcomp’ (Hothorn, Bretz, & Westfall, 2008). All post hoc comparisons shown in the tables provide *P* values after correction for multiple testing by standard Bonferroni correction.

Ethical Note

This study was done at the Hasli Ethological Station, University of Bern, Switzerland under licence 74/15 of the Veterinary Office of the Kanton Bern. Although the experiment did not involve direct contact between the focal fish and any of the stimulus fish, which were only presented as videos, ample shelter was available during testing. Two fish died overnight for unknown reasons and were only found the next morning. The water quality of all tanks was tested beforehand and was not likely to have caused the deaths. Further, the fish were alone in the tanks and could not have been attacked by other fish. Therefore, neither of the deaths could have been predicted or prevented. For the presentation of the four stimulus fish we used video presentations rather than live stimuli to decrease the number of animals used in our experiment, in accordance with the ethical framework of the ‘3Rs’ (Replacement, Reduction, Refinement; Russell & Burch, 1959).

RESULTS

Parental Response

The aggressive displays by parents in the presence of 3-week-old fry were not affected by the sex of the parent or by the stimulus species (Table 1, Fig. 1a). The time breeders were attentive to the screen was not influenced by an interaction between parental sex and stimulus species (LMM: $\chi^2=3.91$, $N=63$, $P=0.27$) but after this term was removed, a significant main effect of stimulus species was revealed (Table 1). Post hoc analysis using single-step pairwise comparisons further revealed that the difference was caused by

Table 1
GLMM results for aggressive displays and LMM results for amount of time attentive towards stimulus presentation by parents

Factor	<i>df</i>	χ^2	<i>P</i>	
Aggressive displays				
Stimulus species	3	3.980	0.263	
Sex	1	0.028	0.866	
Attention to screen				
Stimulus species	3	11.132	0.011	
Sex	1	1.615	0.203	
Comparison				
	Estimate	SE	<i>Z</i>	<i>P</i>
Conspecific–herbivore	-0.741	0.034	-2.176	0.130
Conspecific–egg predator	-0.092	0.034	-2.717	0.033
Conspecific–predator	-0.007	0.034	-0.206	0.996
Herbivore–egg predator	-0.018	0.033	-0.551	0.946
Herbivore–predator	0.067	0.033	2.006	0.185
Egg predator–predator	0.085	0.033	2.558	0.051

Results for responses towards stimulus presentations by either parent ($N=63$ observations of eight males and eight females) are shown, followed by results for post hoc comparisons between stimulus species for the time spent attentive to the screen showing the stimulus. Significant *P* values are highlighted in bold.

higher attention towards a conspecific presentation than to an egg predator presentation (Table 1, Fig. 1b).

Response of 3-Week-old Fry

As the raw distribution violated normality assumptions, a power transformation was applied using the Box–Cox method (Box & Cox, 1964) to obtain normally distributed residuals. In the transformed model, there was no significant interactive effect of parental presence, stimulus species and the time point of observation on the percentage of visible fry (LMM: $F=1.00$, $N=128$, $P=0.39$). After this three-way interaction was removed, there were no significant two-way interactions (results not shown). However, there was a significant main effect of treatment: more fry were visible across all stimulus presentations and time points, if their parents were present in the tank (Table 2). Pairwise post hoc comparisons within each time point revealed no differences between stimuli (Table 2). Moreover, more fry tended to be swimming up towards the end of the presentation (300 s after the start of recording) than at the beginning (Table 2, Fig. 2); there was a strong correlation between fry visibility at the two time points (Spearman correlation: $r_s=0.7$, $P<0.0001$).

Aggression

During behavioural testing at 5 months, restrained aggression by focal fish towards the stimulus videos was interactively influenced by stimulus species and treatment. Post hoc analyses within each stimulus species revealed that this difference was probably caused by a differential response towards the herbivore, with –F fish being more aggressive than +F fish (Table 3). The aggression towards the other three species was not affected by the presence or absence of parents during rearing (Table 3, Fig. 3a).

Attention

Time spent being attentive to the stimulus presentations was influenced interactively by stimulus species and rearing treatment (Table 4). Post hoc within-stimulus comparisons showed that attention time towards the predator differed significantly between the rearing treatments. The –F fish spent on average over 60% of their time being attentive to the screen, whereas +F fish were attentive to the predator on average only about 40% of the time (Table 4). Attention towards the other stimulus fish did not differ between rearing treatments (Table 4, Fig. 3b).

Time in Safety

We assumed that a fish indifferent towards the stimulus would spend similar amounts of time in all sectors of the tank, whereas a fish actively engaging in defence against the stimuli would prefer staying close to the presentation and, conversely, a risk-averse fish would prefer staying away from the presentation, close to the shelter. There was a strong trend for time in safety to be influenced by stimulus species but there was no effect of rearing treatment (Table 5). The post hoc analyses revealed a significant contrast between +F and –F fish in the predator treatment (Table 5). The –F fish spent almost the entire duration of observation within this ‘safe zone’ when facing a predator, while the +F fish spent only a little over half the time in doing so. The response towards the other three stimulus species was not influenced by the rearing treatment (Table 5, Fig. 3c).

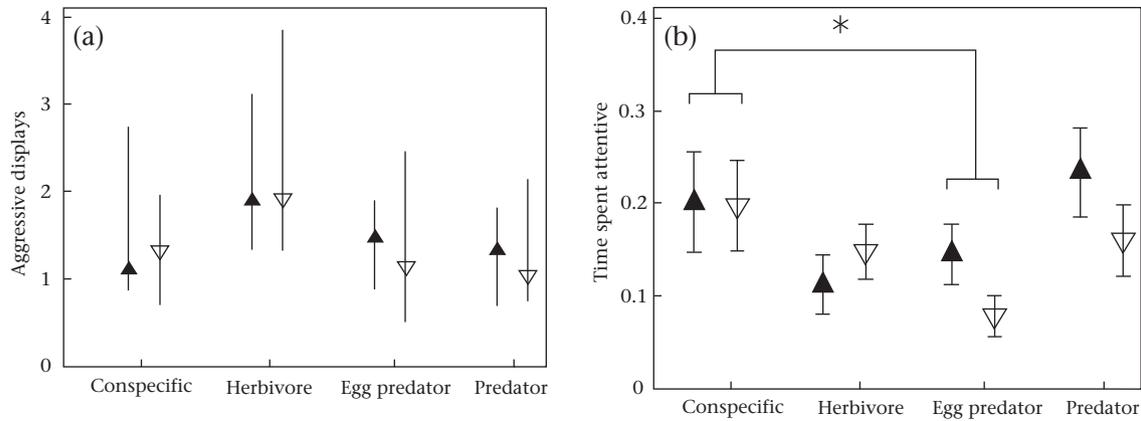


Figure 1. Behaviour of breeding females (black triangles) and males (white inverted triangles) during 5 min video presentations of the four stimulus species. (a) The number of aggressive displays (median and interquartile range). (b) The proportion of time spent being attentive to the video screen (mean±SE). **P* < 0.05.

Table 2
LMM results of the effect of parental presence, stimulus species and time point of observation on the proportion of visible fry

Factor	df	F	P
Treatment	1	12.93	0.002
Stimulus	3	0.48	0.693
Time point	1	2.83	0.095

A Box–Cox-transformed LMM was fitted for the proportion of fry visible 1 min prior to stimulus presentation that were visible after the presentation. Treatment: fry reared with or without parents (*N* = 128 observations of eight groups with and eight without parents). Significant *P* value is highlighted in bold.

DISCUSSION

Here we investigated the effects of early life social experience on the responses towards heterospecific and conspecific stimuli in the later juvenile stage of the social cichlid *N. pulcher*. We expected to find higher species discrimination and better predator recognition in *N. pulcher* raised with their parents, as is often seen in alarm-calling species (Mateo & Holmes, 1997; Thornton & Clutton-Brock, 2011). In contrast to these predictions, we found that only offspring raised without adults behaved more fearfully towards predator presentations, whereas the responses by offspring raised with parents did not differ between stimuli. A previous

experimental study showed that after birth young *N. pulcher* have an innate fear of olfactory cues of conspecifics and of all heterospecifics presented in this study (Fischer et al., 2017). This suggests that our –F focal fish had retained this innate response towards the predator but lost the response towards the other stimuli.

At 10 days old, that is, at a slightly earlier age than when we exposed our experimental fish to the presentations for the first time, naïve laboratory-reared *N. pulcher* significantly reduce their opercular beat rates (as a form of ‘freezing response’) upon receiving olfactory cues from the four stimulus species used in our study, whereas they maintain a normal beat rate when exposed to tap water (Fischer et al., 2017). This is indicative of a generalized fearful response present in 10-day-old *N. pulcher*. At 21 days old, when our study began, the fry still had an indiscriminate response towards the stimulus species; however, the overall level of fear was greatly reduced if parents were present in the immediate proximity. At 5 months of age, though, this difference in generalized fear had vanished with both rearing groups showing a similar response towards the rather harmless heterospecifics or towards conspecifics. Hence, the fearful response towards the predator shown only by offspring reared without parents cannot simply be attributed to –F fish being generally more fearful.

To understand these results, we have to consider the responses of parents towards the different types of stimulus species. Based on

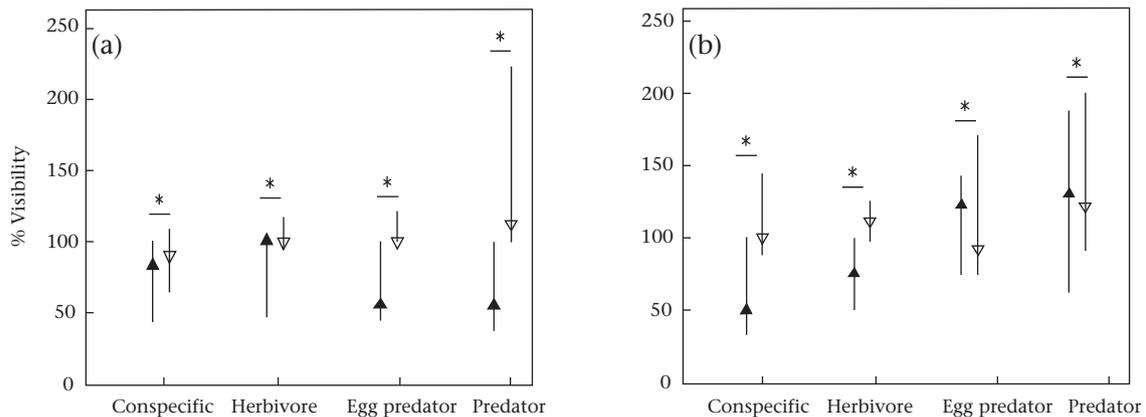


Figure 2. Percentage of fry that were seen swimming above ground during the video presentations of the four stimulus species (a) 10 s and (b) 300 s after the first appearance of a stimulus in the two rearing treatments: without parents (black triangles) and with parents (white inverted triangles). The data are presented as medians and interquartile range as the distribution of raw data was not normal (see model results). We assumed that all the fry were swimming up before the presentation began and sank down during it as a fear response. Therefore, the percentage was calculated assuming this initial number was 100%. However, this was not always true and so, if fewer fry were seen before than during the presentation, the percentage of visible fry is greater than 100. **P* < 0.05.

Table 3
GLMM results of the effect of rearing treatment and stimulus species on the number of aggressive displays by focal fish

Factor	df	χ^2	P	
Stimulus	3	3.84	0.278	
Treatment	1	0.19	0.662	
Stimulus*Treatment	3	12.87	0.004	
Within-stimulus species comparisons of treatments				
	Estimate	SE	Z	P
Conspecific	-0.334	0.406	-0.823	0.410
Herbivore	-1.706	0.442	-2.436	0.014
Egg predator	0.493	0.437	-1.128	0.259
Predator	0.313	0.422	-0.742	0.458

Treatment: fry reared with or without parents ($N = 108$ observations of 18 individuals with and 19 without parents). The time inside the shelter is used as offset in the model. The post hoc results are pairwise comparisons between the rearing treatments compared within each stimulus species. Significant P values are highlighted in bold.

previous work, we had expected parents to be most aggressive towards the herbivore, followed by the conspecific (Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013; Fischer et al., 2014). We found, however, that attack rates by parents towards all stimulus species were very low (Fig. 1a). Moreover, parents devoted more attention to the conspecific presentation than to the potentially more harmful predator (Fig. 1b). Importantly, however, offspring reared without parents lacked the experience of these rather weak and undifferentiated parental responses. We therefore propose that the specific fear response of $-F$ fish towards the predator *L. elongatus* indicates an innate recognition of the visual cues of dangerous predators. The $-F$ fish may have maintained their initial fearfulness (cf. Fischer et al., 2017) towards the predator only, but lost it towards the rather harmless species. On the other hand, offspring reared with parents may have responded weakly and indifferently towards all stimulus species, as their parents did. Thus, it seems that the offspring's innate fearfulness of dangerous predators was eliminated by the weak responses of parents. A potential mechanism underlying this effect could be that the offspring expect a certain response from parents in a situation perceived as threatening and if this expectation is violated the offspring use the parental response to adjust their perception of risk.

Given previous experimental work using animated PowerPoint photos of stimulus fish (Fischer et al., 2014), the indiscriminate and low attack rates of parents towards the stimulus displays were surprising. A possible reason for the similarity of responses may be that all stimulus species pose some risk to very small offspring eliciting a general defence response in parents. However, live displays in previous studies elicited much stronger responses (Heg & Taborsky, 2010; Zöttl et al., 2013). In contrast, in our study breeders rather engaged in vigilance and restrained displays of aggression. In these previous studies, stimulus fish were presented in transparent containers in the middle of the breeders' territories. In contrast, we presented the visual stimuli outside the aquarium, that is, at the periphery of the territory. The breeders may have perceived this as a comparatively nonthreatening situation where no or only little defence was required. Additionally, all previous studies were done in the absence of fry. The presence of vulnerable fry in our study may have reduced the activity of the parents in order to avoid attracting attention from predators.

Previous work showed that observational conditioning is an extremely powerful mechanism for animals to learn about danger from conspecifics. For instance, offspring can learn from parents how to respond more appropriately to predators (Suzuki & Griesser, 2017) or about novel predators (Al-Shaer et al., 2016)

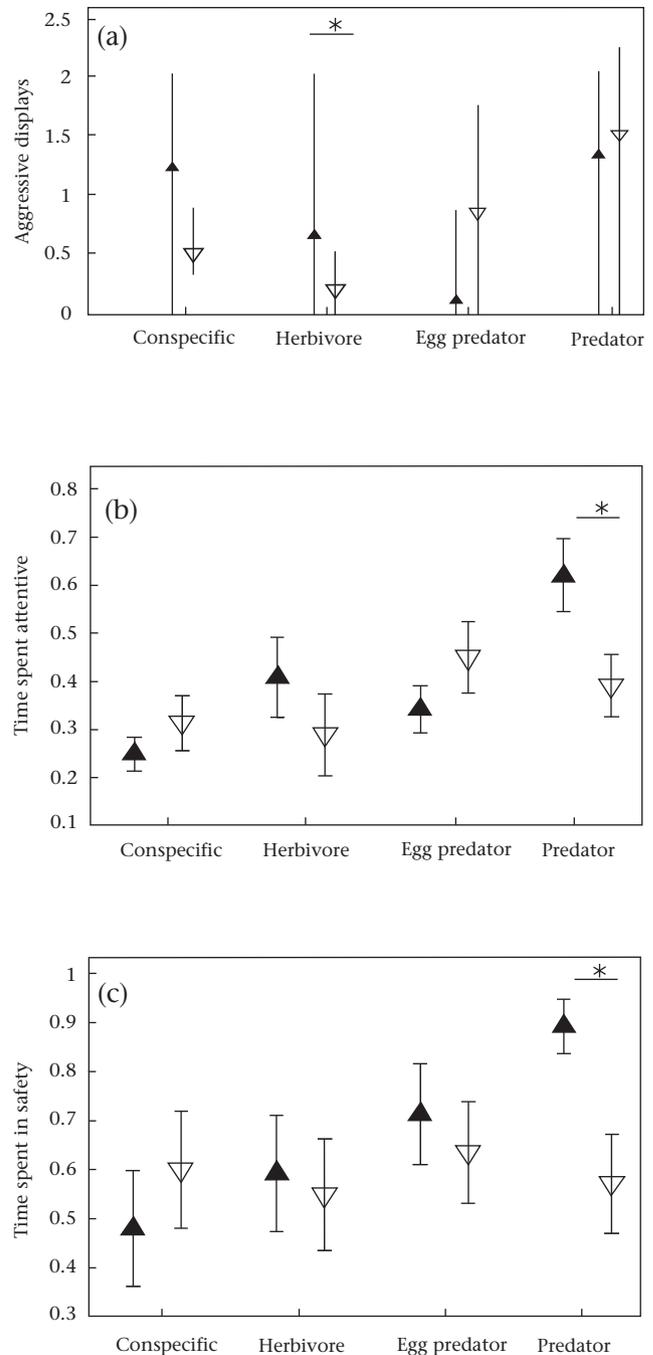


Figure 3. Response of focal fish to the 5 min stimulus presentations. (a) The number of aggressive displays (median and interquartile range). (b) The proportion of time spent being attentive to the video screen (mean \pm SE). (c) The proportion of time spent in the furthest zone from the stimulus presentation, i.e. the 'safe zone' (mean \pm SE). Rearing treatments: without parents (black triangles) and with parents (white inverted triangles). * $P < 0.05$.

simply by witnessing the parental responses to predatory stimuli. Similarly, captive-born rhesus macaques, *Macaca mulatta*, learned to fear snakes but only after witnessing their wild-born parents' fearful response (Mineka, Davidson, Cook, & Keir, 1984). A classic experiment by Curio, Ernst, and Vieth (1978) demonstrated that adult blackbirds, *Turdus merula*, can even be conditioned to show antipredator behaviour towards a harmless honeyeater, *Philemon corniculatus*, when during a conditioning phase they had received the honeyeater stimulus together with conspecifics mobbing a real

Table 4

LMM results of the effect of rearing treatment and stimulus species on time spent being attentive to the screen

Factor	df	F	P	
Stimulus species	3	3.804	0.013	
Treatment	1	0.441	0.513	
Stimulus*Treatment	3	2.866	0.042	
Within-stimulus species comparisons of treatments				
	Estimate	SE	t	P
Conspecific	0.064	0.098	0.652	0.516
Herbivore	-0.117	0.098	-1.194	0.235
Egg predator	0.117	0.091	1.288	0.200
Predator	-0.226	0.098	-2.301	0.023

Treatment: fry reared with or without parents ($N=108$ observations of 18 individuals with and 19 without parents). The post hoc results are pairwise comparisons between the rearing treatments compared within each stimulus species. Significant P values are highlighted in bold.

Table 5

LMM results of the effect of rearing treatment and stimulus species on time spent in safe zone

Factor	df	F	P	
Stimulus species	3	2.671	0.053	
Treatment	1	1.990	0.171	
Within-stimulus species comparison of treatments				
	Estimate	SE	t	P
Conspecific	0.116	0.135	0.862	0.391
Herbivore	0.003	0.134	0.024	0.980
Egg predator	-0.125	0.125	-1.006	0.317
Predator	-0.295	0.134	-2.215	0.029

Treatment: fry reared with or without parents ($N=108$ observations of 18 individuals with and 19 without parents). The post hoc results are pairwise comparisons between the rearing treatments compared within each stimulus species. Significant P values are highlighted in bold.

predator that could not be seen by the focal blackbird. Our results suggest, however, that observational conditioning by parents can also have the opposite effect and can lead to learned habituation to a predator. In a similar experiment on horses, *Equus caballus*, foals were seen losing fear of new, potentially scary objects if their mothers were habituated to these objects (Christensen, 2016). Moreover, while humans are perceived as predators by most species (Rebolo-Ifran, 2015; Carrete & Tella, 2017), repeated exposure frequently leads to habituation (Cook, Weaver, Hutton, & McGraw, 2017; Martin & Reale, 2008). The loss of fear towards humans is often facilitated through various mechanisms of social information transfer (Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014; Schell, Young, Lonsdorf, Santymirr & Mateo, 2018). The important difference between these and our results is that we could demonstrate that such habituation through conditional learning can be specific to certain dangerous species rather than just habituation to threat in general. Moreover, we showed that it can also lead to habituation to a nonpredatory, potential competitor, as focal fish reared without parents attacked the herbivore species more often, whereas fish reared with parents were indifferent to this species.

For a species living under constant predation risk, as important as it is to recognize and respond appropriately to threat, it is equally important to avoid responding to false alarms. As responding to a threat entails its own cost in the form of reduced opportunities for foraging, territory defence or both, differential sensitivity to immediate levels of threat can potentially mitigate this cost. The risk allocation hypothesis (Lima & Bednekoff, 1999) suggests that a consistent and high predation risk would lead to reduced responsiveness towards predator cues allowing for increased foraging

time. Empirical studies show that living under constant high risk does indeed reduce responses to predator cues in intertidal marine snails, *Littorina* spp. (Hamilton & Heithaus, 2001), elk, *Cervus canadensis* (Creel, Winnie, Christianson & Liley, 2008), rainbow trout, *Oncorhynchus mykiss* (Mirza, Mathis, & Chivers, 2006) and damselfly larvae, *Ischnura elegans* (Slos & Stoks, 2006). Avoidance of costly, inappropriate responses to predators can be facilitated by using social information provided by informed conspecifics. For instance, in pied babblers, *Turdoides bicolor*, it has been shown that foragers reduce their response to alarm calls if the surveillance calls given by sentinels indicate low risk, thereby avoiding an undue loss of foraging time (Bell, Radford, Rose, Wade, & Ridley, 2009). This may be beneficial if a negative feedback from the most informed member of the group, such as a defending parent, can reduce offspring sensitivity to low threat (Hamel & Crocrot, 2012).

Conclusion

Here we have shown that *N. pulcher* raised with parents did not respond more towards predators than towards other fish. The lack of a differential response by offspring seems to reflect the undifferentiated parental response. While most previous work has focused on how offspring learn about danger from parents, here we have shown a corresponding effect, that is, offspring learning about the absence of danger. This effect may be beneficial under constant high predation pressure where reducing sensitivity to false alarms can help compensate for the costs otherwise incurred by repeated antipredator behaviours.

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