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Juvenile exposure to predator cues induces a larger egg size in fish

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When females anticipate a hazardous environment for their offspring, they can increase offspring survival by producing larger young. Early environmental experience determines egg size in different animal taxa. We predicted that a higher perceived predation risk by juveniles would cause an increase in the sizes of eggs that they produce as adults. To test this, we exposed juveniles of the mouthbrooding cichlid *Eretmodus cyanostictus* in a split-brood experiment either to cues of a natural predator or to a control situation. After maturation, females that had been confronted with predators produced heavier eggs, whereas clutch size itself was not affected by the treatment. This effect cannot be explained by a differential female body size because the predator treatment did not influence growth trajectories. The observed increase of egg mass is likely to be adaptive, as heavier eggs gave rise to larger young and in fish, juvenile predation risk drops sharply with increasing body size. This study provides the first evidence that predator cues perceived by females early in life positively affect egg mass, suggesting that these cues allow her to predict the predation risk for her offspring.

Keywords: predation; phenotypic plasticity; maternal effects; early environment; egg size; fish

1. INTRODUCTION

Predation is undoubtedly a major selective force resulting in a wide range of anti-predator adaptations [1–4]. Often traits involved in predator defence are plastic and can thus be adjusted to perceived predation risk during the ontogeny of organisms [5–9]. Phenotypic plasticity of these traits ensures that an organism pays the costs to build up defences only when they are expected to be balanced by the fitness gains through enhanced survival [10].

In many insects and birds, mothers lay smaller eggs when these eggs are more likely to experience mortality owing to predation, either to save energy that can be redirected to other functions or to enable them to produce more young and thus to spread the risk [11–13]. This strategy is a 'selfish maternal effect' [14], as a smaller egg often strongly diminishes offspring fitness [15,16]. In contrast, there is a range of predator-induced maternal effects that favour offspring survival [8,17–19]. Gosline & Rodd [20] predicted that the presence of a predator that feeds selectively on small juveniles would induce an increase in offspring size, but their results tended towards the opposite direction. So far, a maternally induced enlarged offspring size in response to predator cues has only been observed for sticklebacks [19] and a viviparous lizard [21]. Viviparity may allow embryos to sense environmental cues and to demand selfishly additional resources from mothers, however. Thus, the evidence that mothers actively respond to an anticipated high predation risk of their young by increasing offspring size is scarce. Moreover, it has never been investigated whether an offspring size adaptation can result from developmental plasticity in response to early predator experience.

We expected that offspring predator cues experienced early in life induce female mouthbrooding cichlids to produce heavier eggs. This expectation is straightforward from the perspective of offspring: in fish, the major predators are gape-size limited, so larger juveniles may outgrow these predators faster [22]. Moreover, larger juveniles have a higher burst swim speed [23,24], which should raise their survival chances in predator encounters. Likewise, females are expected to benefit from an increased investment per egg and thus higher survival chances of individual offspring, as mouthbrooders produce large but relatively few eggs per life, which makes each offspring highly valuable.

We hand-raised individuals of *Eretmodus cyanostictus* from eggs of known sizes and we divided clutches over two predator treatments. Subsequently, we exposed the siblings repeatedly either to an empty tank or to an offspring predator during the juvenile period. We focused on the juvenile period because evidence is accumulating that early experience contributes significantly to egg size plasticity in animals [25–32].

As predicted, *E. cyanostictus* females exposed to predators as juveniles produced heavier eggs than predator-naive females. Our study is the first to expose individuals from known egg sizes in a split-brood set-up to environments that vary with regard to predator cues. This experimental design allows us to demonstrate that predator cues are important determinants of egg mass, while family origin is not. Additionally, we demonstrate for the first time that females are able to adjust egg mass to predator

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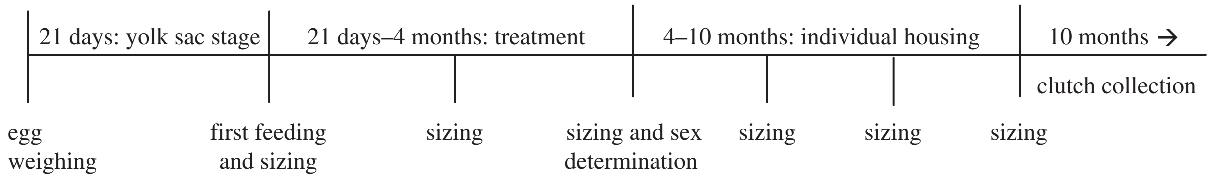

Figure 1. Timeline of the experimental procedure and data collection.

cues experienced in a different life-history stage long before the first clutch is produced.

2. METHODS

(a) *Study species*

Eretmodus cyanostictus is a biparental mouthbrooding cichlid endemic to Lake Tanganyika. Pairs co-defend all-purpose territories in the shallow, rocky parts of the lake [33]. The female broods the eggs for about 7–8 days before she transfers them to her mate. The male subsequently broods the young for 13–16 days [34,35]. After this period, the young are independent.

(b) *Animal husbandry*

In all tanks, water temperatures were kept between 26°C and 28°C, and the light regime was set to a 13 L : 11 D cycle. Unless otherwise mentioned, fish were fed twice a day with Tetramin flakes and once a week with a mixture of small crustaceans. All tanks were equipped with a layer of river sand, biological filters and flower pot halves as shelters.

(c) *Breeding of the parental generation*

The parental generation of our experimental fish was kept in three 200 l and three 400 l tanks in mixed sex groups of 6–12 individuals. The monogamous pairs of *E. cyanostictus* co-defend small territories within the tanks, and thus mates can be easily recognized. We checked daily for brooding females. As soon as possible after spawning (within 1–24 h), we captured the female and her mate, and we removed the eggs from a female's mouth by gently pushing her jaws apart. We then measured the standard lengths (to the nearest 0.1 mm) and mass (to the nearest 0.01 g) of the females, individually marked both pair members by fin-clipping, and returned them to their home tank. Each egg of a clutch was weighed individually (to the nearest 0.1 mg) after being shortly placed on a slightly moistened cotton pad to remove excess water (figure 1).

(d) *Hand-raising of the offspring generation*

After measuring, we hatched the clutches separately in a self-constructed egg tumbler [24]. The eggs hatched after an average of 4–5 days. Five days after hatching, each individual surviving hatchling from a clutch (family) was transferred to its own net cage to finish yolk absorption. The net cages (dimensions 16.5 × 12 × 13.5 cm) were fixed near the water surface of 25 l tanks. At day 21 after spawning, we measured the standard lengths (to the nearest 0.1 mm) of each individual juvenile and began to feed them. Throughout the paper, we will refer to the first day of external feeding of juveniles (day 21 after spawning) as day 0 of the experiment (figure 1). In total, we succeeded in hand-raising 10 clutches to the juvenile stage. We collected clutches during a period of two months. The clutches were each produced by different pairs and consisted of 10–38 eggs. All juveniles of two of the clutches died within one month for unknown reasons after first feeding. Thus, we tested for an effect of egg size on hatchling size in 10 clutches, but the predator exposure experiment was performed only on eight clutches.

(e) *Predator exposure*

After the individual hand-raising of the juveniles, the fish were reunited with their siblings. From experimental day 0 onwards, half of each family was housed in a tank next to a tank holding a natural predator (*Ctenochromis horei*, 9.5–10 cm standard length), whereas the other half was kept next to an empty tank (control treatment). Each tank contained four to five juveniles (in total 74 fish). The set-up consisted of eight blocks of three 25 l tanks with either a predator or a control tank at the centre, so that the central tank was shared by two family groups on either side. All central tanks contained sand, a biological filter and half a flower pot as shelter, and thus only differed by the presence/absence of a predator. During the following four months, we exposed the family groups to the central tanks for 30 min for 5 days a week (figure 1). To reduce the risk of habituation to the experimental stimuli, the exposures were done randomly either in the morning or in the afternoon. We controlled the exposure of juveniles to the central tank by mobile opaque plastic partitions such that the families could never see each other, i.e. exposures were never done at the same time. Moreover, they were never done during feeding of either the predator or experimental fish. Immediately before exposure, 4 ml of water was transferred from the central tank to the juvenile tank to provide an olfactory predator cue together with the visual stimulus. Six days a week the juveniles and the predator were fed ad libitum with Tetramin flakes. After two months, the standard lengths and mass of the fish were taken (figure 1).

After four to five months, the exposure treatment was terminated. At this age, the sex of the fish could be determined by inspection of the genital papilla. Four fish of unknown sex died during the exposure treatment, leaving us with a total of 70 fish (36 males and 34 females). Nineteen females were exposed to the predator, and 15 were exposed to the empty tank. All but one family had females in both treatment groups; from the 10 siblings of one clutch, eight were males and only two were females, and both in the predator treatment. After measuring, both males and females were transferred individually to 25 l tanks (figure 1). During individual housing, the fish were measured approximately every eight weeks.

(f) *Breeding of the offspring generation*

After reaching an age of at least 10 months, females of the offspring generation were housed together with unrelated males from the same and the other treatment in 400 l tanks to promote spawning (figure 1). Both males and females were fin-clipped for individual recognition. We randomized the families and treatments over the breeding tanks. Breeding groups consisted of four to eight fish, usually the same number of females as males. Not all females were able to

Table 1. Distribution of clutches among families and treatments.

family	predator	predator naive
a	2	2
b	2	2
c	2	2
d	2	2
e	1	1
f	1	0
g	1	0
h	0	1

spawn at the same age because we were constrained by the number of 400 l tanks available for breeding. After a female had spawned, her standard length and mass were measured, she and her presumed mate were transferred from the breeding tank to our laboratory stock, and a new male and female were removed from their individual tanks and were added to the breeding tank. The eggs were weighed using the same procedure as described above. We obtained 21 clutches, 10 of the control treatment and 11 of the predator treatment (table 1). Four females did not spawn and nine females died during individual housing and breeding. Wherever possible, we obtained at least two clutches from the same family, one of the predator and one of the control treatment. We succeeded in most cases, but in three families only one female spawned (table 1).

(g) *Data analysis*

All analyses were done with R v. 2.9.2 [36]. All tests are two-tailed with a significance level set to $\alpha = 0.05$. All data were normally distributed (Shapiro–Wilk normality test, all $p > 0.10$). To test whether variance in egg mass within a clutch is smaller than the variance among clutches produced by different females, we used a model II ANOVA with clutch as an explanatory factor. Subsequently, we calculated the variance component to estimate the per cent of variation in egg size among clutches [37].

As an approximation of maternal nutritional state at oviposition, we calculated body condition as mass (g)/standard length $(\text{cm})^3 \times 100$.

To test for an effect of egg mass on hatchling length, we used a linear mixed-effect (LME) model, with clutch of origin included as random factor to control for repeated measurements taken from individuals with the same genetic background [38]. For analysing fish growth during the exposure treatment, we used mean standard length of all individuals in a tank as response variable. Because we measured the tanks repeatedly, we used an LME model with tank nested within family in the random effect term. To linearize the growth trajectory, we analysed the natural logarithm of standard length and included the square of the age of the fish as a covariate in the model. We included the mean egg mass of the clutch of origin in the model because previous work on another mouthbrooding cichlid showed that egg size affects juvenile growth [39]. For model selection, we used step-down protocols [40]. Random intercept models were compared with random intercept and slope models using restricted maximum likelihood (REML). To avoid overparametrization, the initial model contained only the main effects and those interactions for which we had a biologically founded expectation. The full model for growth during the exposure was: treatment + age + age^2 + egg mass + (age × treatment) + (age × egg mass) + random effect (family/tank). We backward-eliminated the non-significant terms ($p > 0.05$) using maximum likelihood (ML) to check for significance. The optimal model was in the end fitted with REML. In the result section, we present the t- and p-values of all significant terms. Additionally, we give the results of the likelihood ratio tests of the non-significant terms that were removed from the model (L- and p-values). When analysing fish growth during individual housing, we used the same approach as described above, but this time individual nested within family was the random effect term. The full model was: treatment + egg + age + age^2 + sex + (age × treatment) + (age × sex) + (age × egg mass) + (sex × treatment) + (age × treatment × sex) + random effect (family/individual).

The clutches of the females from the predator-exposed and control groups were compared using mean egg mass as the response variable. Exposure treatment (predator versus control) was fitted as a factor in an LME model with family as random intercept term. Clutch size and female standard length were added as continuous covariates. We did not include interactions because we had not enough degrees of freedom to do so. One clutch in the control treatment was considered an outlier using the criterion of Cook's distance statistic (D_i of outlier = 1.00, D_i of other observations between 0.0002 and 0.59), indicating that this observation had a disproportionally large influence on the parameter estimates. Because the female that had spawned this clutch was kept much longer in isolation compared with the other fish, which may have affected her reproductive performance (A. Kotrschal & B. Taborsky, 2009, personal observation), the outlier was excluded from further analysis.

3. RESULTS

(a) *Reproductive traits of the parental generation*

Egg mass was more variable between clutches than within clutches ($F_{9,188} = 66.42$, $p < 0.001$). The variance component indicated that 45.6 per cent of the observed variance in egg mass was due to variance among clutches. There was no relationship between maternal length and mean egg mass of her clutch (Spearman rank correlation: $n = 10$, $r_\text{s} = 0.01$, $p = 0.99$); however, fecundity increased with maternal length (Spearman rank correlation: $n = 10$, $r_\text{s} = 0.69$, $p = 0.02$; electronic supplementary material, figure S1) and tended to increase with maternal condition (Spearman rank correlation: $n = 10$, $r_\text{s} = 0.58$, $p = 0.09$; electronic supplementary material, figure S1). After controlling for maternal length, there was no correlation between egg mass and number (partial correlation: $n = 10$, $r_\text{s} = -0.43$, $p = 0.20$).

(b) *Effect of egg mass on juvenile length*

At day 21 after spawning, the standard length of an individual hatchling was positively related to egg mass (LME: $n = 90$, $t = 6.25$, $p < 0.001$; figure 2).

(c) *Growth during predator treatment*

When modelling growth of the offspring generation, the mean egg mass of the clutch of origin positively affected the mean initial standard length of the juveniles in the tanks (that is, at day 21 after spawning; LME: $n = 48$; egg mass: $t = 3.52$, $p = 0.01$), in accordance with the

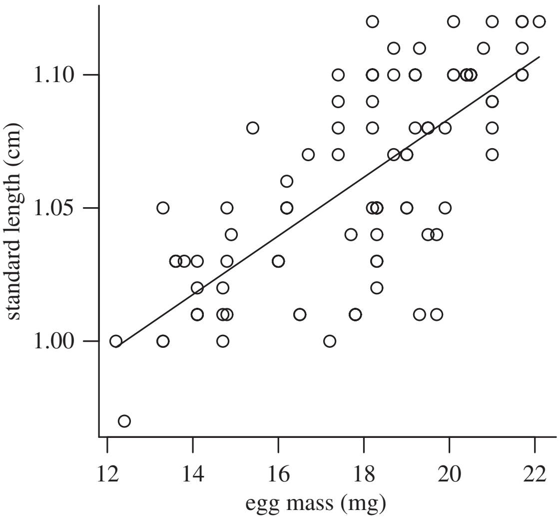

Figure 2. Effect of egg mass on standard length of *E. cyanostictus* juveniles at day 21 after spawning (i.e. before the fish had been subjected to the predator treatment). Each dot represents a single individual. The line of best-fit is shown, which was drawn based on the parameter estimates obtained from the LME model.

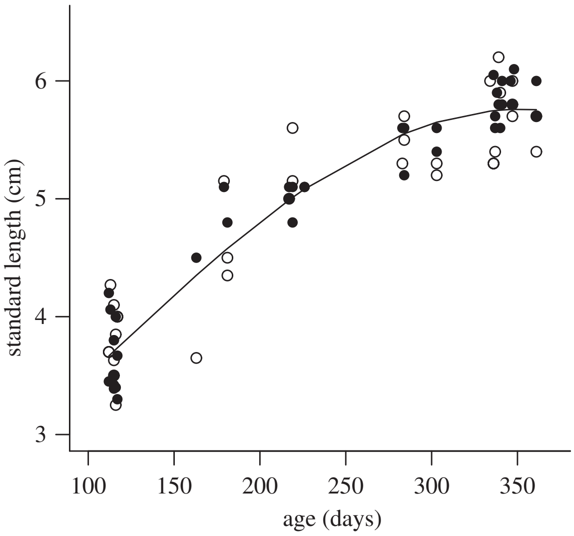

Figure 3. Growth trajectories of the fish when they were housed individually. Only the females are shown. The filled dots are the females that were exposed to predator cues, and the open dots are the control females. The line of best-fit was drawn based on the parameter estimates obtained from the LME model.

results of individual hatchlings described above. There was no initial difference in the lengths between fish allocated to either the predator or to the control treatment (treatment: $L = 0.02$, $p = 0.89$). During the exposure treatment, the fish naturally increased in length (age: $t = 27.26$, $p < 0.001$). As commonly observed in fish, growth rates decreased with time (age^2: $t = -31.31$, $p < 0.001$). Juveniles hatched from clutches with a larger mean egg mass grew slower (egg mass × age: $t = -6.28$, $p < 0.001$). Predator exposure did not affect growth (treatment × age: $L = 0.05$, $p = 0.82$).

(d) *Growth during individual housing*

At the onset of the period of individual housing (figure 1), males were larger than females (sex: $t = -5.43$, $p < 0.001$), and this difference persisted through time (LME: $n = 130$; age × sex: $L = 0.05$, $p = 0.82$). While the fish continued to grow during this period (age: $t = 13.38$, $p < 0.001$), growth rates again decreased with increasing age (age^2: $t = -8.79$, $p < 0.001$; figure 3). Egg mass no longer affected fish length or growth (egg mass: $L = 0.21$, $p = 0.65$; egg mass × age: $L = 0.004$, $p = 0.95$). The predator exposure treatment did not influence the initial length or growth rates during individual housing in either sex (treatment: $L = 2.36$, $p = 0.12$; treatment × sex: $L = 0.61$, $p = 0.43$; treatment × age: $L = 0.04$, $p = 0.85$; treatment × age × sex: $L = 1.24$, $p = 0.27$).

(e) *Reproductive traits of the offspring generation*

Females that had been exposed to predator cues as juveniles spawned heavier eggs than females from the control treatment when accounting for the effect of clutch size (figures 4 and 5; LME: $n = 20$; treatment: $t = 2.57$, $p = 0.03$; clutch size: $t = -4.59$, $p = 0.001$). Mean egg mass tended to increase with maternal length ($t = 1.95$, $p = 0.08$). We retained maternal length in the final model because the ML statistic indicated a significant effect of this factor on egg mass (cf. model selection criteria described in §2; $L = 4.28$, $p = 0.04$). Again, egg mass differed more between different clutches than within the same clutch ($F_{19,231} = 55.66$, $p < 0.001$). The variance component indicated that 43.5 per cent of the observed variance in egg mass was due to variance among clutches. In addition, we tested whether the homogeneity of egg mass within a clutch is influenced by predator exposure; however, there was no difference in the coefficient of variation between treatments (LME: $n = 20$, $L = 2.69$, $p = 0.10$).

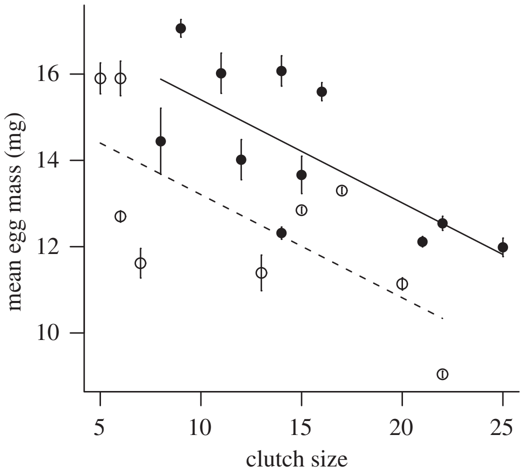

Figure 4. The mean egg mass of a clutch plotted against the number of eggs. The filled dots represent clutches of the females that were exposed to predator cues, and the open dots are clutches from the control females. The error bars are the standard errors of the mean. The continuous line is the best-fit line for the predator treatment, and the dashed line the one for the control treatment.

To test for an inherited component of egg mass, we removed the random factor ‘family’ from the model and instead included the mean egg mass of mothers (‘parental generation’) as an explanatory covariate. We did not include female length in this model because we lacked

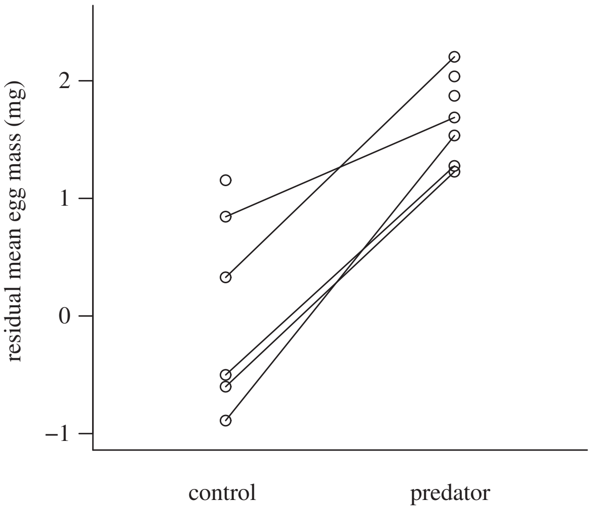

Figure 5. Reaction norms (family means) for residual mean egg mass in response to predator treatment for five families of which at least one clutch in each treatment was available. The residual mean egg masses were plotted because we had to control for clutch size and maternal length (see §3). The unconnected dots represent the residual mean egg mass of the families from which we only obtained one clutch.

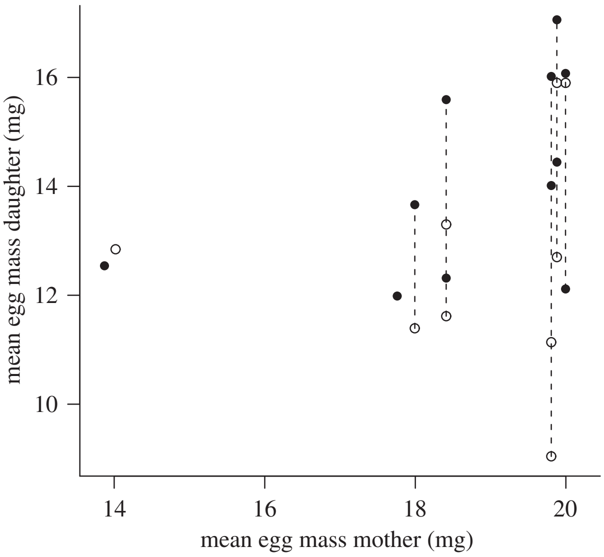

Figure 6. The mean egg mass of the maternal clutch plotted against the mean egg mass of daughters. The filled dots represent daughters that were exposed to predator cues. The vertical lines connect the daughters belonging to the same family.

sufficient degrees of freedom to estimate this effect. Again, predator exposure increased mean egg mass ($F_{3,16} = 7.17$, $R^2 = 0.57$, $p = 0.006$), while mean egg mass decreased with clutch size ($p = 0.002$). There was, however, no relationship between egg mass of mother and daughters ($p = 0.98$; figure 6).

Fecundity was not affected by predator exposure (LME: $n = 20$, $L = 0.17$, $p = 0.68$) and, in contrast to the parental females, it also did not depend on maternal length ($L = 0.04$, $p = 0.85$; electronic supplementary material, figure S1), but fecundity was higher in females with a higher condition ($t = 3.01$, $p = 0.01$; electronic supplementary material, figure S1).

Females in the predator treatment had significantly heavier clutches than control females (LME: $n = 20$, $t = 2.41$, $p = 0.03$), while condition and standard length had no effect on clutch mass ($L = 1.99$, $p = 0.16$ and $L = 0.37$, $p = 0.54$, respectively). There was no significant difference in condition between the females of the two treatments (predator-exposed: 3 ± 0.06 s.e.; control: 2.9 ± 0.08 s.e.; LME: $n = 20$, $t = 1.15$, $p = 0.28$).

4. DISCUSSION

Here, we showed that females of *E. cyanostictus* produce heavier eggs when they have been exposed to visual and chemical predator cues as juveniles. We propose that the observed increase in egg mass and in total investment in response to juvenile predator cues is an adaptive maternal effect [41]. In *E. cyanostictus*, heavier eggs give rise to larger offspring, and in fish, larger offspring will need less time to grow out of the reach of gape-size limited predators [22] and/or can afford to expose themselves less to predation risk by reducing their foraging activity [24]. Thus, our results suggest that based on early experience, females expected offspring predation risk to be high and compensated for the reduced offspring survival chances by increasing their egg size.

Only a small number of studies have previously observed an increase in individual offspring size in response to predator cues [7,19,21,42]. Wild-radish plants (*Raphanus raphanistrum*) increase seed mass when attacked by caterpillars (*Pieris rapae*); however, this response might not be adaptive for the offspring [7]. Tollrian [42] observed larger newborns produced by *Daphnia pulex* exposed to chemical cues from a negative size-selective predator. However, because the presence of negative size-selective predators also induced enhanced growth and a larger size at maturation in *Daphnia*, it was unclear if the production of larger offspring was an adaptive response or resulted from a positive correlation between parent and offspring size. In contrast, we detected neither negative nor positive effects of predator presence on growth in *E. cyanostictus*, and the enlarged egg mass we observed was independent of female size.

Giesing *et al.* [19] observed that when they repeatedly chased adult sticklebacks with a predator model during egg formation, females produced larger eggs with a higher cortisol content. Remarkably, in our study, predator exposure during the juvenile period affected a life-history trait that is expressed much later in life. This suggests that mechanisms other than immediate physiological responses, such as stress reactions, might be responsible for this effect. Our results add to the growing evidence of developmental plasticity of offspring size in fishes [25,43–46]. In *E. cyanostictus*, adults and juveniles co-occur in the shallow littoral zone of Lake Tanganyika, with the highest densities between 0.5 and 4 m of depth [47]. Because this environment is fairly stable over time, both the predator presence experienced by females during their own juvenile phase and the presence of potential offspring predators during the actual production of eggs may convey information to females about the environmental risk for their offspring. It is well possible that in addition to the reported early environment effect, *E. cyanostictus* females can fine-tune egg size to ambient predation risk [19,48], which was kept constant in our experiment. So far, delayed effects of early female environment on egg size have been reported only for resource quality [25,29,32]. Besides egg size, early nutrition also affected growth, body size and other reproductive traits [25,32,49,50]. Here, we show for the first time that early environment effects pertain to predation risk. This effect was not confounded by changes in other important life-history traits, such as growth, body size and clutch size.

Heritability of egg mass in *E. cyanostictus* as estimated by the mother–daughter correlation for this trait appears to be low, whereas our results suggest that investment in an individual egg is strongly influenced by environmental cues. In fish, egg size often increases with female size [51], and accordingly we observed that egg mass tended to increase with maternal length in the daughter generation. In contrast, we did not observe a relationship between female length and egg mass in the maternal generation. Possibly, unknown environmental influences in the breeding tanks might have increased the variance in egg mass among these females and thus have masked a relationship between female size and egg mass.

Eretmodus cyanostictus females of both treatments traded egg mass against egg number (cf. figure 4) as predicted by the model of Smith & Fretwell [52], but remarkably the egg size/number ratio was shifted upwards in females that had been exposed to predator cues. Concurrently, predator-exposed females spawned heavier clutches. This is a surprising result, as for predator-induced plasticity to evolve, the trait of interest must have a cost in the absence of predators [10]. Apparently, the cost of a predator-induced increase in egg size is not compensated by a reduced number of eggs. Possibly, early predator exposure induced a higher total investment per clutch that allowed females to increase egg mass while not jeopardizing fecundity. Fecundity itself, which increased with female body condition, appears rather to be related to resource availability. One should predict that predator-exposed females trade a larger egg mass and a corresponding higher energetic investment per clutch against lower lifetime fecundity, e.g. by producing fewer clutches per life.

Whether a species decreases or increases initial offspring size in response to perceived predation risk should crucially depend on the value of each newborn to the parents, which depends on the survival probability of individual young and how easily they can be replaced if lost. Fontaine & Martin [12] observed a decrease in egg size and clutch mass in eight passerine species under increased nest predation risk. Similarly, in five species of acanthosomatid bugs, females laid smaller eggs at the peripheral, which represents a more vulnerable section of the clutch [11]. In these species, losses to predators occur during the brood care period. Parents cannot effectively defend their offspring against predators, and the chances that young reach independence under high predation risk are low. When risk is high, parents may reduce the energetic investment per young because it would be wasted in risky circumstances. Instead, they allocate the saved energy to future offspring [53,54]. In contrast, in mouthbrooders the buccal cavity is a safe haven for young [55], as a clutch can only be predated during brooding if the female is killed as well. Mouthbrooding, however, is a costly form of parental care because it impairs the breathing and foraging of the parents [56,57], and the value of young to parents increases with the amount of care given [58]. As a possible consequence of the mouth being a safe brooding site, mouthbrooding cichlids produce among the largest eggs relative to body size in teleosts and have a comparatively slow reproductive rate. This makes each single offspring highly valuable, which is why these fish should enlarge their investment per offspring in response to predator cues to increase the survival chance of young after independence.

In conclusion, the maternal perception of changes in predator regime can have positive or negative consequences for offspring. Differences in reproductive biology between species such as the relative value of a single egg for the reproductive success of an individual are likely to be responsible for these opposing results. We showed that predator cues can affect egg size, even if the cues have been perceived early in life, long before the first eggs are spawned. In contrast to previous work on early food manipulations, our results suggest the existence of a proximate mechanism translating early sensory exposure to an environmental trigger into changes of egg size, which is not accompanied by a major reorganization of life-history trajectories.

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