PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Tariel J, Plénet S, Luquet E. 2020 How do developmental and parental exposures to predation affect personality and immediate behavioural plasticity in the snail *Physa acuta*? *Proc. R. Soc. B* **287**: 20201761. https://doi.org/10.1098/rspb.2020.1761

Received: 21 July 2020
Accepted: 27 November 2020

Subject Category:
Behaviour

Subject Areas:
behaviour, evolution

Keywords:
transgenerational plasticity, developmental plasticity, animal personality, behavioural reaction norm, antipredator response, *Physa acuta*

Author for correspondence:
Juliette Tariel
e-mail: juliettetariel@gmail.com

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5230613.

THE ROYAL SOCIETY
PUBLISHING

How do developmental and parental exposures to predation affect personality and immediate behavioural plasticity in the snail *Physa acuta*?

Juliette Tariel, Sandrine Plénet and Emilien Luquet

Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France

JT, 0000-0003-1552-4088; EL, 0000-0002-9550-8899

Individuals differ in personality and immediate behavioural plasticity. While developmental environment may explain this group diversity, the effect of parental environment is still unexplored—a surprising observation since parental environment influences mean behaviour. We tested whether developmental and parental environments impacted personality and immediate plasticity. We raised two generations of *Physa acuta* snails in the laboratory with or without developmental exposure to predator cues. Escape behaviour was repeatedly assessed on adult snails with or without predator cues in the immediate environment. On average, snails were slower to escape if they or their parents had been exposed to predator cues during development. Snails were also less plastic in response to immediate predation risk on average if they or their parents had been exposed to predator cues. Group diversity in personality was greater in predator-exposed snails than unexposed snails, while parental environment did not influence it. Group diversity in immediate plasticity was not significant. Our results suggest that only developmental environment plays a key role in the emergence of group diversity in personality, but that parental environment influences mean behavioural responses to the environmental change. Consequently, although different, both developmental and parental cues may have evolutionary implications on behavioural responses.

1. Introduction

Over the last two decades, tremendous interest in individual behaviour has revealed that individuals can consistently differ in their behaviour over time (i.e. personality diversity within a population or within a group of individuals, hereafter called *group diversity in personality* [1,2]) and in their immediate behavioural plasticity (i.e. in the individual responsiveness to changes in the immediate environment that surrounds the individual when the behaviour is expressed, hereafter called *group diversity in immediate plasticity* [3,4]). Both group diversity in personality and immediate plasticity have strong evolutionary implications, such as population stability and persistence in a context of rapid environmental changes [1,5]. It therefore seems important to determine the causes of such a group diversity.

The environment experienced by an individual during its development is known to influence its phenotype, including its behaviour (within-generational plasticity [6]). Several studies have shown that developmental environment not only influence mean personality of a group of individuals (hereafter called *group mean in personality*), but can also influence group diversity in personality [7–13]. For example, field crickets that had been infected with bacteria during their development had similar group mean in boldness than uninfected crickets, but showed less group diversity in boldness [8]. Similarly, developmental environment influences mean immediate plasticity of a group of individuals (hereafter called *group mean in immediate plasticity* [14]) and group diversity in immediate plasticity [3,15,16]. For example, agile frog tadpoles that had been exposed to predator cues during their development had lower group mean in immediate plasticity than unexposed tadpoles (i.e. lower group mean response to immediate predator cues for activity and boldness), but showed greater group diversity in immediate plasticity [16]. Thus, developmental environment appears to shape group diversity in both personality and immediate plasticity.

Following the growing interest over the last two decades that parental environment can profoundly affect offspring phenotype (the so-called transgenerational plasticity [17,18]), it has been shown that parental environment influences mean behaviour [19–21] (but without monitoring consistency of individual behaviour). Like developmental environment, parental environment could influence group mean and group diversity in both personality and immediate plasticity. However, to our knowledge, this has never been explored.

Here, we focused on the context of predator–prey interactions, an ecologically relevant environmental context as predation is a ubiquitous selective pressure strongly impacting prey behaviour. We used the freshwater snail *Physa acuta*, which has been widely studied for its anti-predator behaviour (refuge use and escape by crawling-out of the water [22–24]). We have recently demonstrated transgenerational plasticity on the proportion of *P. acuta* individuals exhibiting an escape behaviour: the proportion of offspring out of water was higher in offspring from parents exposed to predator cues than in offspring from unexposed parents [25]. Consequently, we expected that individual escape behaviour would be influenced by parental exposure to predator cues. We raised two generations of snails with or without predator cues (crayfish and alarm odours) during their development in the laboratory. We then repeatedly assessed escape behaviour (time to crawl-out of the water) of adult snails with or without predator cues in the immediate environment. Using such a full factorial experiment over two generations, we studied for the first time the influence of both developmental and parental environments on group mean and group diversity both in personality and immediate plasticity. Since developmental and parental exposures to predator cues indicate to snails that the environment is risky, we expected that these two exposures would increase group mean in personality and immediate plasticity (i.e. they generate on average an increased anti-predator behavioural response to immediate predator cues). In addition, we expected that developmental and parental exposures would increase group diversity in personality and immediate plasticity, as observed by Urszán *et al.* [10,16] for developmental environment.

2. Material and methods

(a) Animal collection and experimental design

We collected adult *P. acuta* snails (F0, $n = 86$) from a population in a lentic backwater of the Rhône river in Lyon, France (45.80° N, 04.92° E) in February 2017. Snails interbred overnight in a 10 l plastic box filled with dechlorinated tap water (*P. acuta* is a simultaneous hermaphrodite and performs predominantly inter-breeding [26]; see electronic supplementary material for a figure of the experimental design). Next, adult F0 snails were isolated and left to lay eggs for 24 h in 70 ml plastic boxes, to ensure that one box contained the egg capsule of only one F0 snail (i.e. only one F1 maternal family per box, hereafter called ‘family’). We randomly kept 24 boxes (i.e. 24 families). Throughout the experiment, all boxes were kept in the same experimental room with a temperature of 25°C and a photoperiod of 12 h/12 h. Seven days later, snails hatched and were fed ad libitum with bowled and mixed lettuce. Water and food were changed twice a week. Ten days later, each F1 family was separated in two different environments with six siblings remaining together in the control (C) water and six siblings together in the predator-cue (P) water. Predator-cue water was obtained by mixing rearing water of several crayfish (*Orconectes limosus*) reared individually in 4 l dechlorinated tap water and fed twice a week with a smashed *P. acuta* adult. Several smashed *P. acuta* adults were added to the predator-cue water 1 h before use (one snail for every 4 l). Snails were kept in groups of six siblings for 7 days. Then, snails were isolated in the same rearing conditions (control or predator-cue water) for 16 days (F1: $n = 288$ at the beginning of the experiment with 32 dead snails at the end; figure 1; $n_{\mathrm{C}} = 132$, $n_{\mathrm{P}} = 124$ snails).

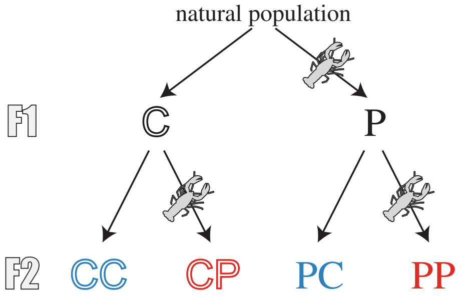

Figure 1. Experimental design. The F1 generation experienced two different developmental environments (control C and predator-cue P environments). The F2 generation was a 2 × 2 full factorial design with four combinations of parental and developmental environments (CC, CP, PC and PP). For instance, CP illustrated a combination with a control parental environment and a predator-cue developmental environment. Twenty snails were scored for each combination of environments. (Online version in colour.)

To get the F2 generation, we randomly combined 15 pairs of F1 snails from the same environment but from different families. We let these snails copulate overnight in control water and then isolated them for 24 h. Among these 30 F1 reproducing snails per environment, 26 (control F1 treatment) and 25 (predator-cue F1 treatment) snails laid eggs in 24 h. These eggs formed the F2 families. We then followed the same protocol as before. F2 snails were kept in isolation longer (46 days instead of 16 days at the F1 generation) to reach a sufficient mass (F2: $n = 612$ at the beginning with 99 dead snails at the end; $n_{\mathrm{CC}} = 133$, $n_{\mathrm{CP}} = 115$, $n_{\mathrm{PC}} = 136$, $n_{\mathrm{PP}} = 129$ snails). In summary, the F2 generation consisted of four combinations of parental and developmental environments (CC, CP, PC and PP) (figure 1).

(b) Behavioural assessments

Escape behaviour of 20 snails per combination of environments was assessed (one snail per family of 20 randomly selected F2 families), for a total of 80 F2 snails scored. Escape behaviour was assessed in both immediate control and predator-cue environments. Escape behaviour was estimated by the time taken by the snail to crawl out of the water, a classic response to benthic predators such as crayfish [22]. Escape behaviour was scored in a rearing box in which 7 mm polystyrene was placed at the bottom delimiting an acclimation chamber (23 mm diameter) in the centre. The snail was placed in the acclimation chamber for 1 min. Then time to reach the surface was recorded using JWatcher in real time [27] and the experiment stopped after 5 min. Time to crawl out was scored four times for each snail, twice in control water and twice in predator-cue water, to estimate individual personality and immediate plasticity for each snail. The four scores were done in 1 day, with time between the scores standardized to 2 h. Finally, total mass (body and shell) was measured for each snail with an electronic scale at the nearest 0.0001 g.

(c) Statistical analysis

Effects of parental and developmental exposures to predator cues on time to crawl out (a proxy for escape behaviour) were studied with linear mixed models (LMMs). Values of time to crawl-out were log10-transformed to achieve normality. In addition, the values were multiplied by – 1 for straightforward interpretation: hence, a small value (short time to crawl out) is associated with high escape behaviour. All LMMs included immediate, developmental and parental environments and all interactions as fixed effects (see model equations in electronic supplementary material). Snail total mass was standardized and added as a fixed covariable to control for size effect. Trial number and interactions with mass were not significant and not included in fixed effects. The random-effect structure depended on the hypothesis tested (see details below). The model equations of all LMMs are given in the electronic supplementary material. All analyses were done in R 3.4.1 [28].

(i) Effects of developmental and parental environments on group mean in personality and immediate plasticity

To test the effects of developmental and parental exposures to predator cues on group mean in personality and immediate plasticity, we analysed the fixed effects of the LMM3 (the random structure of the LMM3 is described below). With the parameter estimates of the LMM3, we calculated the estimated means and contrasts between these estimated means using the package emmeans [29].

(ii) Group diversity in personality and immediate plasticity

To test for the presence of group diversity in personality (variance in intercept) and group diversity in immediate plasticity (variance in slope), we fitted three models differing only in their random structure with the same fixed-effect structure described above [30]:

— LM0, a null model with only a residual variance σ^2_{res}
— LMM1, a random intercept model with σ^2_{res} and a variance in intercept σ^2_i
— LMM2, a random slope model with σ^2_{res}, σ^2_i, a variance in slope σ^2_s and a correlation between intercept and slope $\text{cor}_{is} = \text{cov}_{is}/\sqrt{\sigma^2_i \times \sigma^2_s}$

These models were fitted with restricted maximum likelihood estimation using the package lme4 [31]. We tested the significance of group diversity in personality (LM0 versus LMM1) and group diversity in immediate plasticity (LMM1 versus LMM2) using likelihood ratio tests (LRT). Using LMM1, we calculated the repeatability R of the escape behaviour defined as $R = \sigma^2_i/\sqrt{\sigma^2_i + \sigma^2_{\text{res}}}$.

(iii) Effects of parental and developmental environments on group diversity in personality

Since we found no group diversity in immediate plasticity (see results below), we only tested the effects of developmental and parental environments on group diversity in personality. Based on the fixed-effect structure described above, we fitted the LMM3, a random intercept model with a variance in intercept σ^2_i for each treatment (for a total of four σ^2_i) and a residual variance σ^2_{res}. We carried out a Bayesian Markov chain Monte-Carlo (MCMC) procedure implemented in the MCMCglmm package [32] to obtain the posterior distributions of parameters, their estimates (mean of posterior distribution) and their 95% confidence intervals (CI). To compare variance in intercept between treatments, Bayesian *p*-values were calculated by dividing the number of iterations fulfilling a condition (for instance, σ^2_i in developmental environment C superior or equal to σ^2_i for developmental environment P) by the total number of iterations. Details about the LMM3 modelling procedures is given in the electronic supplementary material.

Table 1. Effects of parental and developmental environments on group mean in personality and immediate plasticity. Parameter estimates (β) of fixed effects are means of parameter posterior distribution with their 95% confidence interval. pMCMC represents Bayesian *p*-value and are bold if pMCMC < 0.05. Random effects of this linear mixed model (LMM3) are represented on figure 4. Model equations are available in the electronic supplementary material.

fixed effects	β	[95% CI]	pMCMC
intercept	−2.023	[−2.054, −1.993]	**<0.001**
mass	0.033	[0.002, 0.061]	**0.030**
immediate (Im.)	0.131	[0.093, 0.168]	**<0.001**
developmental (Dev.)	−0.090	[−0.149, −0.028]	**0.005**
parental (Par.)	−0.008	[−0.067, 0.055]	0.811
Im. × Dev.	−0.094	[−0.168, −0.019]	**0.011**
Im. × Par.	−0.157	[−0.230, −0.080]	**<0.001**
Dev. × Par.	−0.027	[−0.146, 0.105]	0.670
Im. × Dev. × Par.	0.023	[−0.126, 0.174]	0.779

3. Results

(a) Effects of parental and developmental environments on group mean in personality and immediate plasticity

Group mean in personality and immediate plasticity depended on the parental and developmental environments (significant interactions between immediate × developmental and immediate × parental environments in table 1 and figure 2). Parental and developmental exposures to predator cues additively decreased group mean in immediate plasticity (additive because there was no significant effect of the interaction between parental and developmental environments in table 1; figure 2). This group mean in immediate plasticity was significantly different from 0, except for predator-exposed snails from predator-exposed parents (PP snails; see electronic supplementary material for pairwise contrasts; figure 2) meaning that these PP snails were on average not plastic to immediate predator cues. In the control immediate environment, neither parental nor developmental environment influenced group mean in personality (parental environment P versus C: contrast = 0.071 [−0.004, 0.143]; developmental environment P versus C: contrast = −0.043 [−0.115, 0.027]). In the predator-cue immediate environment, both parental and developmental exposures to predator cues influenced group mean in personality. More specifically, they induced on average a slower escape behaviour (20 s (24%) and 28 s (36%) slower, respectively; parental environment P versus C: contrast = −0.086 [−0.156, −0.014]; developmental environment P versus C: contrast = −0.137 [−0.208, −0.061]).

Table 2. Group diversity in personality and in immediate plasticity. Three models differing by their random structure are tested against each other with likelihood ratio tests (tested models), whereas the full fixed-effects structure was constant and is shown in table 1. Variance estimates are given with their 95% confidence interval calculated with parametric bootstrap method on 2000 simulations. *LM0* = null model with no random effect (σ^2_{res}, residual variance). *LMM1* = random intercept model (σ^2_i, variance in intercept = group diversity in personality). *LMM2* = random slope model (σ^2_s, variance in slope = group diversity in immediate plasticity; cor_{is}, correlation between intercept and slope). Bold *p*-values indicates $p < 0.05$.

model	σ^2_{res}	σ^2_i	σ^2_s	cor_{is}	tested models	$\chi^2_{\text{d.f.}}$	*p*-value
LM0	0.040 [0.034, 0.047]						
LMM1	0.029 [0.024, 0.034]	0.011 [0.006, 0.018]			0 versus 1	26.28_1	**<0.001**
LMM2	0.028 [0.022, 0.033]	0.013 [0.006, 0.025]	0.004 [0.000, 0.018]	−0.392 [−1.000, 1.000]	1 versus 2	0.56_2	0.756

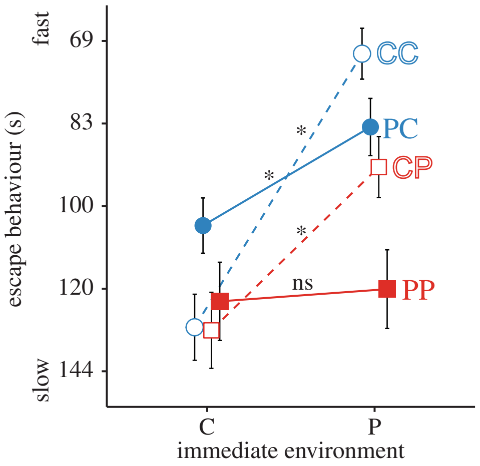

Figure 2. Effects of parental and developmental environments on group mean in personality and immediate plasticity. The *y*-axis is the log10 of time to crawl-out (our proxy of escape behaviour) with the *y*-scale back-transformed in seconds. The *x*-axis is the immediate environment with 'C' and 'P' for control and predator-cue, respectively. Developmental C and P environments are represented with blue circle and red square symbols, respectively. Parental C and P environments are represented with open symbols/dashed lines and closed symbols/solid lines, respectively. Each combination of developmental and parental environments is denoted with two letters, for instance 'CP' meaning parental C environment and developmental P environment. Asterisk and 'ns' indicate significant and non-significant group mean in immediate plasticity, respectively. Points are mean ± s.e. (Online version in colour.)

(b) Group diversity in personality and immediate plasticity

We found significant group diversity in personality (table 2: comparison LM0 versus LMM1). Repeatability of escape behaviour was 0.28 (95% CI: 0.20–0.45). However, we did not highlight significant group diversity in immediate plasticity (table 2: comparison LMM1 versus LMM2; figure 3).

(c) Effects of parental and developmental environments on group diversity in personality

Developmental exposure to predator cues significantly increased group diversity in personality by 4-fold (comparison of blue and red shapes in figure 4; $p = 0.009$). Parental exposure to predator cues increased by 1.3-fold the group diversity in personality but this was not significant (comparison of open and closed shapes in figure 4; $p = 0.305$).

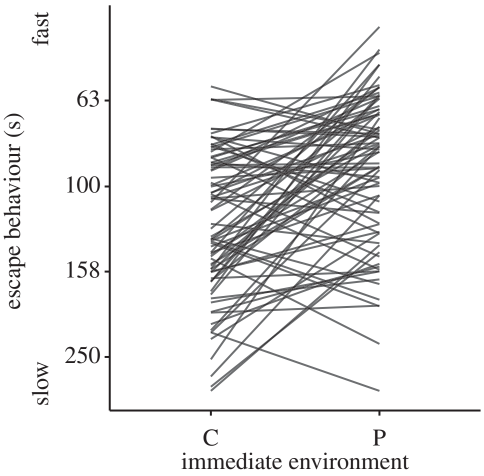

Figure 3. Group diversity in immediate plasticity. Each line represents the immediate plasticity of one individual. The *y*-axis is the log10 of time to crawl out (escape behaviour) with the *y*-scale back-transformed in seconds. The *x*-axis is the immediate environment with 'C' and 'P' for control and predator-cue, respectively.

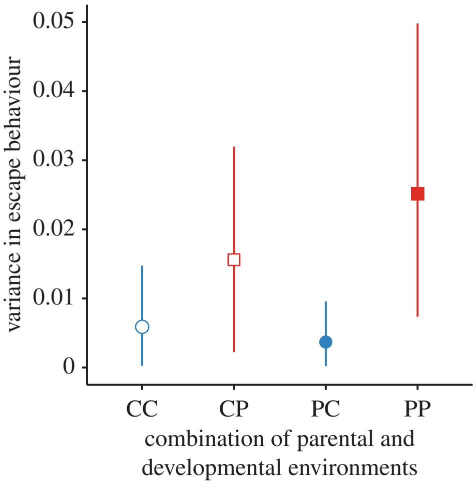

Figure 4. Effects of parental and developmental environments on group diversity in personality. Dots represent estimates of variances in intercept (σ^2_i) with their 95% confidence interval. We extracted these variances from the random part of the linear mixed model LMM3. The random part of the LMM3 is structured with a variance in intercept for each combination of parental and developmental environments ('C' for control and 'P' for predator-cue environments). The fixed part of the LMM3 is shown in table 1. (Online version in colour.)

4. Discussion

We investigated the effects of developmental and parental environments on (i) group mean in personality and immediate plasticity, and (ii) group diversity in personality and immediate plasticity in the freshwater snail *P. acuta*. We raised two generations of snails with or without predator cues (crayfish and alarm odours) during their development in the laboratory and then recorded their escape behaviour (crawling-out of the water) twice with and twice without predator cues in the immediate environment. As expected, snails crawled-out the water on average faster when exposed to predator cues in the immediate environment, the well-known anti-predator immediate plasticity in *Physa* gastropods [22,23]. Parental and developmental exposure to predator cues additively decreased this group mean in immediate plasticity. Moreover, we confirmed group diversity in personality of *P. acuta* with consistent between-individual differences in escape behaviour [33]. Interestingly, developmental exposure to predator cues increased group diversity in personality while the parental environment did not influence it. Finally, our study showed no group diversity in immediate plasticity.

(a) Developmental and parental environments influenced group mean in personality and immediate plasticity

Contrary to our expectations, developmental and parental exposures to predator cues reduced group mean in immediate plasticity. More specifically, snails had on average a reduced anti-predator immediate plasticity if they or their parents were exposed to a risk of predation, to the extent that exposed snails from exposed parents (PP snails) were not plastic to immediate predator cues. Concerning group mean in personality, in the immediate predator-free environment, parental and developmental environments had no effect on group mean in personality (i.e. similar mean escape behaviour among offspring from developmental and parental environments). But in the immediate predator-cue environment, both developmental and parental exposures to predator cues induced on average a slower escape. Cues of the past presence of predators might be conflicting cues in an immediate predator-free environment, whereas they might give relevant information in a predator-cue environment. In the literature on transgenerational plasticity, there is conflicting experimental evidence regarding the direction of the effects of parental and developmental exposures to predator cues on anti-predator behaviour. Parental and developmental exposures increases mean anti-predator behaviour in most cases (e.g. [25,34,35]). This pattern is traditionally explained as pre-adaptation: if cues present at the parental generation or during development accurately predict the presence of predators in the future environment, individuals already exhibiting anti-predator behaviour are pre-adapted to the presence of predators. Conversely, parental and developmental exposures to predator cues can reduce mean anti-predator behaviour [16,20], as in our study. Snails may exhibit low anti-predator behaviour because they are already protected from predators by morphological defences (trait compensation, e.g. [32,37,38]), thus saving the costs of having both morphological and behavioural defences. Parental and developmental exposures to predator cues can induce the production of morphological defences in many species (e.g. [15,35,36]), including *P. acuta* (thicker shell [24]). However, some studies have rather shown that individuals with high morphological defences also have high anti-predator behaviour (trait co-specialization [39,40]). The compensation or co-specialization of behavioural and morphological defences may depend on the efficiency of the defences and predator density [41]. In the other hand, snails may exhibit low anti-predator behaviour because they are strongly habituated to predator cues (crayfish and alarm odours). Habituation is a simple form of learning that occurs when behaviour response to a persistent stimulus is reduced [56]. Habituation may persist a while after the stimulus has disappeared (long-term habituation [42]). In the context of predation, long-term habituation has been demonstrated after repeated exposure to harmless predator cues [43,44]. This habituation may involve sensory habituation, where olfactory receptors lose their sensitivity to the odour as the odour persist. This sensory habituation is thought to allow an animal to focus its cognitive resources on a new or changing odour and better respond to it [45]. This habituation may also involve an active and complex decision from a higher cognitive centre. This would allow the prey to stop regarding a cue as dangerous after a long period of time without being attacked, thus reducing the costs associated with anti-predator behaviour [46,47]. In our case, predator-exposed snails were subjected for 53 days to predator odour and behavioural assessments started a few days after exposure to the predator odour had ceased. Predator-exposed snails may have become habituated to this predator odour and may have reduced their response to a novel exposure of this same predator odour. However, transgenerational transmission of habituation has never been highlighted to our knowledge, even if the transgenerational transfer of conditioning or sensory imprinting to an odour have already been described in nematods, rodents and butterflies [19,36,37].

(b) Developmental environment influenced group diversity in personality, but not parental environment

Our study confirmed *P. acuta* exhibits consistent between-individual differences in escape behaviour (i.e. group diversity in personality) [33] with an estimated repeatability of 0.28, similarly to other types of behaviour on various animals [38]. Group diversity in personality is thought to impact a vast range of ecological and evolutionary dynamics, but our understanding of its proximate causes is still limited [1,39]. Here, developmental exposure to predator cues increased group diversity in personality, similarly to another study on agile frog tadpoles [10]. Thus, developmental exposure to predator cues seems to generate more variable and extreme anti-predator behaviour. For the first time, we have investigated whether parental environment, like developmental environment, can also influence group diversity in personality. By contrast to developmental environment, parental environment did not clearly increase group diversity in personality. Parental environment therefore may impact group mean without impacting group diversity in personality.

Predator cue perception can shift resource and time allocation from traits like foraging, growth and reproduction to the production of anti-predator defences [40,41]. Cue perception at different developmental timing could explain why developmental, but not parental environment, influence group diversity in personality. When predator cues are perceived by parents, offspring are informed very early in their development that they are likely to encounter predators and may then all engage in an anti-predator developmental trajectory (production of behavioural and morphological defences; see paragraph above on group mean). When predator cues are perceived during the development, offspring may be already engaged in diverse developmental trajectories favouring energy allocation in reproduction, growth or anti-predator defences [16,42–44]), generating between-individual differences in anti-predator behaviour.

Alternatively, the developmental exposure to predator cues could increase group diversity in personality through an effect on developmental noise, whereas parental exposure could not influence developmental noise. Random variation in molecular and cellular processes during the development generates phenotypic diversity between individuals, even in the absence of genetic and environmental variation (this process is called developmental noise [45,46]). Developmental noise has been proposed to explain the emergence of group diversity in personality in clonal animals raised in nearly identical environments and without any social contact [47,48]. Level of developmental noise can be modulated by external environments, and stressful developmental environments have already been highlighted to increase developmental noise on morphological traits, generating higher diversity in morphology [49,50]. However, to our knowledge, there are no empirical studies investigating whether parental environment can modulate the level of developmental noise.

Altogether, our results support the idea that developmental environment plays a key role in the emergence of group diversity in personality. Within a population, the increase of group diversity in personality after an environmental change increases the rough material for natural selection and the likelihood that some behavioural phenotypes are adapted to the novel conditions [1]. However, our results suggest that parental environment does not play a role on group diversity in personality, suggesting that parental environment does not impact the evolutionary potential of populations (no influence on behavioural variation). However, there is no other empirical study to our knowledge to compare and generalize this assumption. The effect of parental the environment may nevertheless help population persistence by shaping an appropriate mean behavioural response to the environmental change (see paragraph above on group mean) [51].

(c) Group diversity in immediate plasticity

Despite the recent interest in group diversity in immediate plasticity and its consequences on the ecology and evolution of species [3,4,52], the causes of this diversity are unknown. Some studies have shown that developmental environment modulates group diversity in immediate plasticity [3,15,53] as it is the case for group diversity in personality, but none have investigated whether parental environment can also influence group diversity in immediate plasticity. Here, we found no significant group diversity in immediate plasticity (i.e. individuals were similarly plastic). This lack of diversity suggests a low genetic diversity of immediate plasticity in our population. Past predation history over large generational scales may have selected and canalized all individuals towards a unique and fixed optimal immediate plasticity [54]. However, caution should be taken in overinterpreting the absence of group diversity in immediate plasticity as this diversity is hard to detect and requires large datasets [55,56].

5. Conclusion

Our results show that developmental and parental environments have a strong impact on mean behavioural responses to immediate predation. A labile and reversible trait such as behaviour can therefore be determined by past environments, even over generations. While our study confirmed that developmental environment plays a major role in generating group diversity in personality, it suggests that parental environment played no role. The lack of parental environment effect on group diversity needs, however, to be confirmed in other studies. Altogether, our results suggest that both developmental and parental information may have evolutionary implications through different effects on mean and variation of behavioural responses.

Data accessibility. The data and R code that support the findings of this study are openly available in the Zenodo archive (https://zenodo.org/) at https://doi.org/10.5281/zenodo.4243834 [57].

Authors' contributions. J.T. carried out the data analysis, drafted and strongly revised the manuscript; S.P. designed the study, collected the data and critically revised the manuscript; E.L. designed the study, collected the data and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

Acknowledgements. We thank the three anonymous reviewers for their careful reading of our manuscript and their useful and high-quality comments. We thank Emmanuel Desouhant for the careful and critical reading of our manuscript. We would like to thank the following students for their great support with experiments: Laurent Bensoussan, Justine Boutry, Rachel Arnaud, Marie Bouilloud and Anaïs Seve-Minnaert. We thank Patrice David, Petri Niemelä and Jean-Paul Lena for their advices on statistical analyses. This work was performed within the framework of the EUR H2O'Lyon (ANR-17-EURE-0018) of Université de Lyon (UdL), within the program 'Investissements d'Avenir' operated by the French National Research Agency (ANR).

References

1. Wolf M, Weissing FJ. 2012 Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.* **27**, 452–461. (doi:10.1016/j.tree.2012.05.001)
2. Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS. 2010 Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609–612. (doi:10.1038/nature09060)
3. Dingemanse NJ, Bouwman KM, van de Pol M, van Overveld T, Patrick SC, Matthysen E, Quinn JL. 2012 Variation in personality and behavioural plasticity across four populations of the great tit Parus major: population variation in personality and behavioural plasticity. *J. Anim. Ecol.* **81**, 116–126. (doi:10.1111/j.1365-2656.2011.01877.x)
4. Mitchell DJ, Biro PA. 2017 Is behavioural plasticity consistent across different environmental gradients and through time? *Proc. R. Soc. B* **284**, 20170893. (doi:10.1098/rspb.2017.0893)
5. Dingemanse NJ, Wolf M. 2013 Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim. Behav.* **85**, 1031–1039. (doi:10.1016/j.anbehav.2012.12.032)

6. West-Eberhard MJ. 2003 *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.
7. Biro PA, Beckmann C, Stamps JA. 2010 Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc. R. Soc. B* **277**, 71–77. (doi:10.1098/rspb.2009.1346)
8. DiRienzo N, NiemelÃ PT, Skog A, Vainikka A, Kortet R. 2015 Juvenile pathogen exposure affects the presence of personality in adult field crickets. *Front. Ecol. Evol.* **3**, 36. (doi:10.3389/fevo.2015.00036)
9. DiRienzo N, Johnson JC, Dornhaus A. 2019 Juvenile social experience generates differences in behavioral variation but not averages. *Behav. Ecol.* **30**, 455–464. (doi:10.1093/beheco/ary185)
10. Urszán TJ, Garamszegi LZ, Nagy G, Hettyey A, Török J, Herczeg G. 2015 No personality without experience? A test on *Rana dalmatina* tadpoles. *Ecol. Evol.* **5**, 5847–5856. (doi:10.1002/ece3.1804)
11. Han CS, Dingemanse NJ. 2017 You are what you eat: diet shapes body composition, personality and behavioural stability. *BMC Evol. Biol.* **17**, 8. (doi:10.1186/s12862-016-0852-4)
12. Royauté R, Dochtermann NA. 2017 When the mean no longer matters: developmental diet affects behavioral variation but not population averages in the house cricket (*Acheta domesticus*). *Behav. Ecol.* **28**, 337–345. (doi:10.1093/beheco/arw164)
13. Niemelä PT, Niehoff PP, Gasparini C, Dingemanse NJ, Tuni C. 2019 Crickets become behaviourally more stable when raised under higher temperatures. *Behav. Ecol. Sociobiol.* **73**, 81. (doi:10.1007/s00265-019-2689-5)
14. Giudice MD. 2015 Plasticity as a developing trait: exploring the implications. *Front. Zool.* **12**, S4. (doi:10.1186/1742-9994-12-S1-S4)
15. Briffa M, Bridger D, Biro PA. 2013 How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Anim. Behav.* **86**, 47–54. (doi:10.1016/j.anbehav.2013.04.009)
16. Urszán TJ, Garamszegi LZ, Nagy G, Hettyey A, Török J, Herczeg G. 2018 Experience during development triggers between-individual variation in behavioural plasticity. *J. Anim. Ecol.* **87**, 1264–1273. (doi:10.1111/1365-2656.12847)
17. Agrawal AA, Laforsch C, Tollrian R. 1999 Transgenerational induction of defences in animals and plants. *Nature* **401**, 60–63. (doi:10.1038/43425)
18. Donelan SC, Hellmann JK, Bell AM, Luttbeg B, Sheriff MJ, Sih A. 2020 Transgenerational plasticity in human-altered environments. *Trends Ecol. Evol.* **35**, 115–124. (doi:10.1016/j.tree.2019.09.003)
19. Dias BG, Ressler KJ. 2014 Parental olfactory experience influences behavior and neural structure in subsequent generations. *Nat. Neurosci.* **17**, 89–96. (doi:10.1038/nn.3594)
20. Donelan SC, Trussell GC. 2018 Parental and embryonic experiences with predation risk affect prey offspring behaviour and performance. *Proc. R. Soc. B* **285**, 20180034. (doi:10.1098/rspb.2018.0034)
21. Tariel J, Plénet S, Luquet É. 2020 Transgenerational plasticity of inducible defences: combined effects of grand-parental, parental and current environments. *Ecol. Evol.* **10**, 2367–2376. (doi:10.1002/ece3.6046)
22. Alexander JE, Covich AP. 1991 Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. *Oecologia* **87**, 435–442. (doi:10.1007/BF00634603)
23. DeWitt TJ. 1998 Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *J. Evol. Biol.* **11**, 465–480. (doi:10.1046/j.1420-9101.1998.11040465.x)
24. Auld JR, Relyea RA. 2011 Adaptive plasticity in predator-induced defenses in a common freshwater snail: altered selection and mode of predation due to prey phenotype. *Evol. Ecol.* **25**, 189–202. (doi:10.1007/s10682-010-9394-1)
25. Luquet E, Tariel J. 2016 Offspring reaction norms shaped by parental environment: interaction between within- and trans-generational plasticity of inducible defenses. *BMC Evol. Biol.* **16**, 209. (doi:10.1186/s12862-016-0795-9)
26. Henry P-Y, Bousset L, Sourrouille P, Jarne P. 2005 Partial selfing, ecological disturbance and reproductive assurance in an invasive freshwater snail. *Heredity* **95**, 428–436. (doi:10.1038/sj.hdy.6800731)
27. Blumstein DT, Daniel JC. 2007 *Quantifying behavior the JWatcher way*. Sunderland, UK: Sinauer Associates.
28. R Development Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org.
29. Lenth R. 2019 Emmeans: estimated marginal means, aka least-squares means. See https://CRAN.R-project.org/package=emmeans.
30. Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010 Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* **25**, 81–89. (doi:10.1016/j.tree.2009.07.013)
31. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
32. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Softw.* **33**, 1–22. (doi:10.18637/jss.v033.i02)
33. DeWitt TJ, Sih A, Hucko JA. 1999 Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. *Anim. Behav.* **58**, 397–407. (doi:10.1006/anbe.1999.1158)
34. Storm JJ, Lima SL. 2010 Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *Am. Nat.* **175**, 382–390. (doi:10.1086/650443)
35. Giesing ER, Suski CD, Warner RE, Bell AM. 2011 Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. *Proc. R. Soc. B* **278**, 1753–1759. (doi:10.1098/rspb.2010.1819)
36. Remy J-J. 2010 Stable inheritance of an acquired behavior in *Caenorhabditis elegans*. *Curr. Biol.* **20**, R877–R878. (doi:10.1016/j.cub.2010.08.013)
37. Gowri V, Dion E, Viswanath A, Piel FM, Monteiro A. 2019 Transgenerational inheritance of learned preferences for novel host plant odors in *Bicyclus anynana* butterflies. *Evolution* **73**, 2401–2414. (doi:10.1111/evo.13861)
38. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)
39. Stamps JA, Groothuis TGG. 2010 Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Phil. Trans. R. Soc. B* **365**, 4029–4041. (doi:10.1098/rstb.2010.0218)
40. Steiner UK. 2007 Investment in defense and cost of predator-induced defense along a resource gradient. *Oecologia* **152**, 201–210. (doi:10.1007/s00442-006-0645-3)
41. Buskirk JV. 2000 The costs of an inducible defense in anuran larvae. *Ecology* **81**, 2813–2821. (doi:10.1890/0012-9658(2000)081[2813:TCOAID]2.0.CO;2)
42. Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007 Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**, 581–584. (doi:10.1038/nature05835)
43. Biro PA, Stamps JA. 2008 Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* **23**, 361–368. (doi:10.1016/j.tree.2008.04.003)
44. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010 Personality and the emergence of the pace-of-life syndrome concept at the population level. *Phil. Trans. R. Soc. B* **365**, 4051–4063. (doi:10.1098/rstb.2010.0208)
45. Debat V, David P. 2001 Mapping phenotypes: canalization, plasticity and developmental stability. *Trends Ecol. Evol.* **16**, 555–561. (doi:10.1016/S0169-5347(01)02266-2)
46. Yampolsky LY, Scheiner SM. 1994 Developmental noise, phenotypic plasticity, and allozyme heterozygosity in daphnia. *Evolution* **48**, 1715–1722. (doi:10.2307/2410259)
47. Vogt G, Huber M, Thiemann M, van den Boogaart G, Schmitz OJ, Schubart CD. 2008 Production of different phenotypes from the same genotype in the same environment by developmental variation. *J. Exp. Biol.* **211**, 510–523. (doi:10.1242/jeb.008755)
48. Bierbach D, Laskowski KL, Wolf M. 2017 Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nat. Commun.* **8**, 15361. (doi:10.1038/ncomms15361)
49. Willmore KE, Young NM, Richtsmeier JT. 2007 Phenotypic variability: its components, measurement and underlying developmental processes. *Evol. Biol.* **34**, 99–120. (doi:10.1007/s11692-007-9008-1)
50. Lazić MM, Carretero MA, Crnobrnja-Isailović J, Kaliontzopoulou A. 2015 Effects of environmental disturbance on phenotypic variation: an integrated assessment of canalization, developmental stability,

modularity, and allometry in lizard head shape. *Am. Nat.* **185**, 44–58. (doi:10.1086/679011)

51. Donelson JM, Salinas S, Munday PL, Shama LNS. 2018 Transgenerational plasticity and climate change experiments: where do we go from here? *Glob. Change Biol.* **24**, 13–34. (doi:10.1111/gcb.13903)
52. Stamps JA. 2016 Individual differences in behavioural plasticities: behavioural plasticities. *Biol. Rev.* **91**, 534–567. (doi:10.1111/brv.12186)
53. Gribben PE, O'Connor J, Pedini L, Biro PA. 2013 Personality and plasticity: consistent responses within-, but not across-temperature situations in crabs. *Behaviour* **150**, 799–811. (doi:10.1163/1568539X-00003081)
54. Kim S-Y. 2016 Fixed behavioural plasticity in response to predation risk in the three-spined stickleback. *Anim. Behav.* **112**, 147–152. (doi:10.1016/j.anbehav.2015.12.004)
55. Martin JGA, Nussey DH, Wilson AJ, Réale D. 2011 Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. *Methods Ecol. Evol.* **2**, 362–374. (doi:10.1111/j.2041-210X.2010.00084.x)
56. van de Pol M. 2012 Quantifying individual variation in reaction norms: how study design affects the accuracy, precision and power of random regression models: individual variation in reaction norms. *Methods Ecol. Evol.* **3**, 268–280. (doi:10.1111/j.2041-210X.2011.00160.x)
57. Tariel J, Plénet S, Luquet E. 2020 Data from: How do developmental and parental exposures to predation affect personality and immediate behavioural plasticity in the snail *Physa acuta*? Dryad Digital Repository. (doi:10.5281/zenodo.4243834)