

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

Juliette TARIEL^{1*}, Sandrine PLÉNET¹ and Émilien LUQUET¹

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

*Corresponding author: juliettetariel@gmail.com

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I Abstract

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.

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

II 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, referred thereafter to *group diversity in personality*; Schindler et al. 2010; Wolf & Weissing 2012) 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, referred thereafter to *group diversity in immediate plasticity*; Dingemanse et al. 2012; Mitchell & Biro 2017). 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 (Wolf & Weissing 2012; Dingemanse & Wolf 2013). 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; West-Eberhard 2003). Several studies have shown that developmental environment not only influence mean personality of a group of individuals (referred thereafter to *group mean in personality*), but can also influence group diversity in personality (Biro et al. 2010; DiRienzo et al. 2015, 2019; Urszán et al. 2015; Han & Dingemanse 2017; Royauté & Dochtermann 2017; Niemelä et al. 2019). 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 (DiRienzo et al. 2015). Similarly, developmental environment influences mean immediate plasticity of a group of individuals (referred thereafter to *group mean in immediate plasticity*; Giudice 2015) and group diversity in immediate plasticity (Dingemanse et al. 2012; Briffa et al. 2013; Urszán et al. 2018). 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 (Urszán et al. 2018). 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*; Agrawal et al. 1999;

Donelan et al. 2020), it has been shown that parental environment influences mean behaviour (Dias & Ressler 2014; Donelan & Trussell 2018; Tariel et al. 2020b), 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 (Alexander & Covich 1991; DeWitt 1998; Auld & Relyea 2011). We have recently demonstrated transgenerational plasticity on the proportion of *P. acuta* individuals exhibiting an escape behaviour: proportion of offspring out of water was higher in offspring from parents exposed to predator cues than in offspring from unexposed parents (Luquet & Tariel 2016). 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. (2015, 2018) for developmental environment.

III Material & Methods

III.1 Animal collection and experimental design

We collected adult *P. acuta* snails (F0, n = 86) in a population from 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 interbreeding; Henry et al. 2005; see supplementary material for a figure of the experimental design). Next, adult F0 snails were isolated and left to lay eggs for 24h 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 12h/12h. 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 one hour before use (one snail for every 4 L). Snails were kept in groups of 6 siblings for seven 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](#); $n_c = 132$, $n_p = 124$ snails).

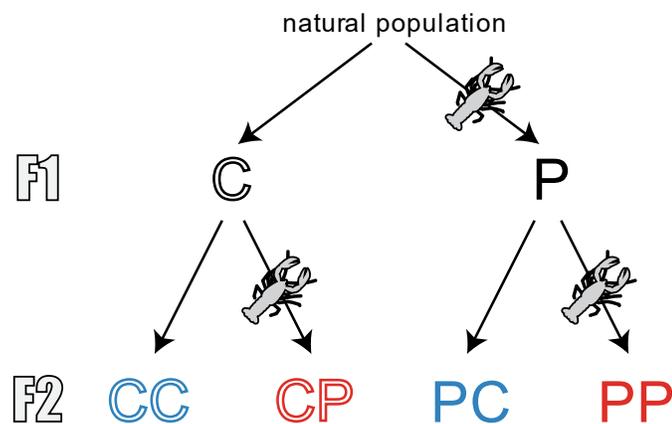


Figure 1. Experimental design. The F1 generation experienced two different developmental environments (control C and predator-cue P environments). The F2 generation was a 2x2 full factorial design with four combinations of parental and developmental environments (CC, CP, PC and PP). For instance, CP illustrated a combination with a control parental environment and a predator-cue developmental environment. 20 snails were scored for each combination of environments.

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 24h. Among these 30 F1 reproducing snails per environment, 26 (control F1 treatment) and 25 (predator-cue F1 treatment) snails laid eggs in 24h. 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; $n_{CC} = 133$, $n_{CP} = 115$, $n_{PC} = 136$, $n_{PP} = 129$ snails). In summary, the F2 generation consisted of four combinations of parental and developmental environments (CC, CP, PC and PP; [Figure 1](#)).

III.2 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 (Alexander & Covich 1991). 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 one minute. Then time to reach the surface was recorded using JWatcher in real time (Blumstein & Daniel 2007) and the experiment stopped after five minutes. 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 one day, with a time between the scores standardized to two hours. Finally, total mass (body and shell) was measured for each snail with an electronic scale at the nearest 0.0001 g.

III.3 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 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 supplementary material. All analyses were done in R 3.4.1 (R Development Core Team 2019).

III.3.a 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 estimated means and contrasts between these estimated means using the package `emmeans` (Lenth 2019).

III.3.b 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 (Dingemanse et al. 2010):

- LM0, a null model with only a residual variance σ_{res}^2 .
- LMM1, a random intercept model with σ_{res}^2 and a variance in intercept σ_i^2 .
- LMM2, a random slope model with σ_{res}^2 , σ_i^2 , a variance in slope σ_s^2 and a correlation between intercept and slope $cor_{is} = cov_{is} / \sqrt{\sigma_i^2 \times \sigma_s^2}$.

These models were fitted with restricted maximum likelihood estimation using the package `lme4` Bates et al. 2015. We tested significance of group diversity in personality (LM0 vs LMM1) and group diversity in immediate plasticity (LMM1 vs LMM2) using likelihood ratio tests (LRT).

Using LMM1, we calculated the repeatability R of the escape behaviour defined as $R =$

$$\frac{\sigma_i^2}{\sqrt{\sigma_i^2 \times \sigma_{res}^2}}$$

III.3.c 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 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_i^2 for each treatment (for a total of four σ_i^2) and a residual variance σ_{res}^2 . We carried out a Bayesian Markov chains Monte-Carlo (MCMC) procedure implemented in the `MCMCglmm` package (Hadfield 2010) 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_i^2 in developmental environment C superior or equal to σ_i^2 for developmental environment P) by the total number of iterations. Details about the LMM3 modelling procedures is given in the supplementary material.

IV Results

IV.1 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 x developmental and immediate x parental environments in [Tableau 1](#); [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 [Tableau 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 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 vs C: contrast = 0.071 [-0.004, 0.143]; developmental environment P vs 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 sec (24%) and 28s (36%) slower, respectively; parental environment P vs C: contrast = -0.086 [-0.156, -0.014]; developmental environment P vs C: contrast = -0.137 [-0.208, -0.061]).

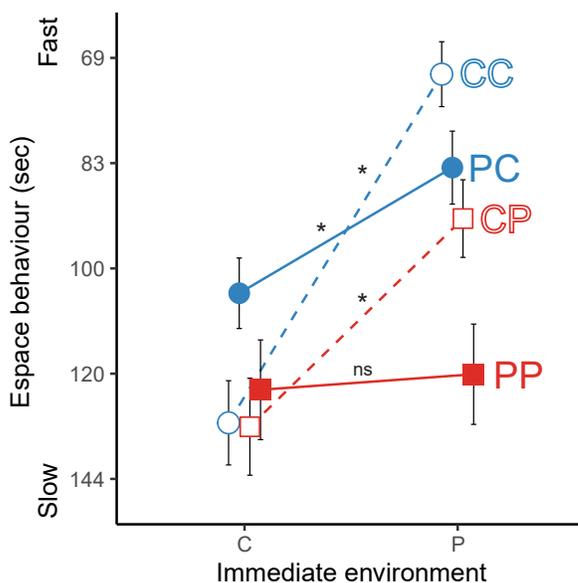


Figure 2. Effects of parental and developmental environments on group mean in personality and immediate plasticity. The y-axis is the log10 of time to crawl-out (our proxy of escape behaviour) with the y-scale back-transformed in seconds. The x-axis is the immediate environment with “C” and “P” for control 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. “*” symbol and “ns” indicate significant and non-significant group mean in immediate plasticity, respectively. Points are mean \pm SE.

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. x Dev.	-0.094	[-0.168, -0.019]	0.011
Im. x Par.	-0.157	[-0.230, -0.080]	<0.001
Dev. x Par.	-0.027	[-0.146, 0.105]	0.670
Im. x Dev. x Par.	0.023	[-0.126, 0.174]	0.779

Tableau 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 supplementary material.

IV.2 Group diversity in personality and immediate plasticity

We found significant group diversity in personality ([Tableau 2](#): comparison LM0 vs 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 ([Tableau 2](#): comparison LMM1 vs LMM2; [Figure 3](#)).

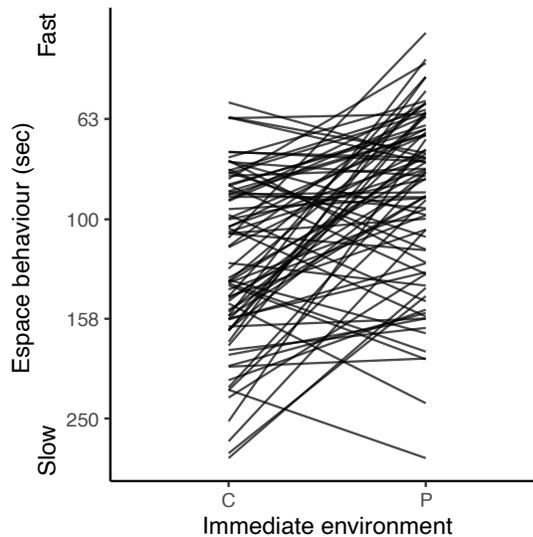


Figure 3. Group diversity in immediate plasticity. Each line represents the immediate plasticity of one individual. The y-axis is the log10 of time to crawl-out (escape behaviour) with the y-scale back-

transformed in seconds. The x-axis is the immediate environment with “C” and “P” for control and predator-cue.

IV.3 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](#); $P = 0.305$).

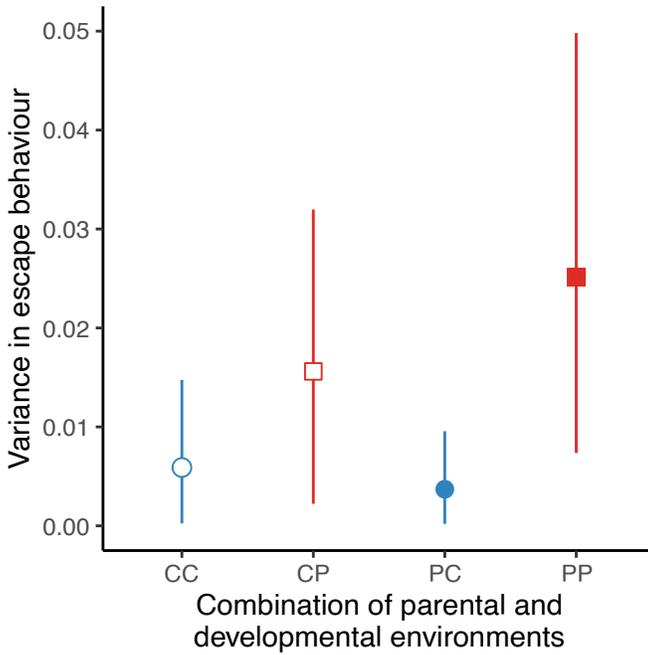


Figure 4. Effects of parental and developmental environments on group diversity in personality. Dots represent estimates of variances in intercept (σ_i^2) with their 95% confidence interval. We extracted these variances from the random part of the linear mixed model LMM3. The random part of the LMM3 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.

Model	σ_{res}^2	σ_i^2	σ_s^2	cor_{Is}	Tested models	χ^2_{df}	P
LM0	0.040	[0.034, 0.047]			0 vs 1	26.281	<0.001
LMM1	0.029	[0.024, 0.034]	0.011	[0.006, 0.018]	1 vs 2	0.562	0.756
LMM2	0.028	[0.022, 0.033]	0.013	[0.006, 0.025]	1 vs 2	0.562	0.756

Tableau 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_{res}^2 , residual variance). LMM1 = random intercept model (σ_i^2 , variance in intercept = group diversity in personality). LMM2 = random slope model (σ_s^2 , variance in slope = group diversity in immediate plasticity; cor_{Is} , correlation between intercept and slope). Bold P-values indicates $P < 0.05$.

V Discussion

We investigated effects of developmental and parental environments on (1) group mean in personality and immediate plasticity, and (2) 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 (Alexander & Covich 1991; DeWitt 1998). 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 (DeWitt et al. 1999). 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.

V.1 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 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.* Storm & Lima 2010; Giesing et al. 2011; Luquet & Turiel 2016). This pattern is traditionally explained as pre-adaptation: if cues present at the parental generation or during development accurately predict 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 (Donelan & Trussell 2018; Urszán et al. 2018), 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.* DeWitt et al. 1999; Chivers et al. 2007; Ahlgren et al. 2015; Dijk et al. 2016), thus saving the costs of having both morphological and behavioural defences. Parental and developmental exposures to predator cues can induce production of morphological defences in many species (*e.g.* Agrawal et al. 1999; Bestion et al. 2014), including *P. acuta* (thicker shell; Luquet & Turiel 2016). However, some studies have rather shown that individuals with high morphological defences also have high anti-predator behaviour (trait co-specialisation; Mikolajewski & Johansson 2004; Marshall & Wund 2017). The compensation or co-specialisation of behavioural and morphological defences may depend on the efficiency of the defences and predator density (Steiner & Pfeiffer 2007). 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 (Christoffersen 1997). Habituation may persist a while after the stimulus has disappeared (long-term habituation; Christoffersen 1997). In the context of predation, long-term habituation has been demonstrated after repeated exposure to harmless predator cues (Deecke et al. 2002; Hemmi & Merkle 2009). This habituation may involve sensory habituation, where olfactory receptors lose their sensitivity to the odour as the odour persists. 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 (Das et al. 2011). 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 (Rodríguez-Prieto et al. 2009; Ferrari et al. 2010). 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 transgenerational transfer of conditioning or sensory imprinting to an odour have already been described in nematodes, rodents and butterflies (Remy 2010; Dias & Ressler 2014; Gowri et al. 2019).

V.2 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; DeWitt et al. 1999) with an estimated repeatability of 0.28, similarly to other types of behaviour on various animals (Bell et al. 2009). 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 (Stamps & Groothuis 2010; Wolf & Weissing 2012). Here, developmental exposure to predator cues increased group diversity in personality, similarly to another study on agile frog tadpoles (Urszán et al. 2015). 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. In contrast to developmental environment, parental environment did not clearly increase group diversity in personality. Parental environment may therefore 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 (Buskirk 2000; Steiner 2007). 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 (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010; Urszán et al. 2018), 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; Yampolsky & Scheiner 1994; Debat & David 2001). Developmental noise has been proposed to explain emergence of group diversity in personality in clonal animals raised in nearly identical environments and without any social contact (Vogt et al. 2008; Bierbach et al. 2017). 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 (Willmore et al. 2007; Lazić et al. 2015). 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 (Wolf & Weissing 2012). 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 environment may nevertheless help population persistence by shaping an appropriate mean behavioural response to the environmental change (see paragraph above on group mean; Donelson et al. 2018).

V.3 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 (Dingemanse et al. 2012; Stamps 2016; Mitchell & Biro 2017), the causes of this diversity are unknown. Some studies have shown that developmental environment modulates group diversity in immediate plasticity (Dingemanse et al. 2012; Briffa et al. 2013; Gribben et al. 2013) 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 Kim 2016. However, caution should be taken in overinterpreting absence of group diversity in immediate plasticity as this diversity is hard to detect and requires large data sets (Martin et al. 2011; van de Pol 2012).

V.4 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.

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VII Data accessibility

The data and R code that support the findings of this study are openly available in the archive Zenodo (<https://zenodo.org/>) at <https://doi.org/10.5281/zenodo.4243834> (Tariel et al. 2020a).

VIII Authors' contributions

J.T. carried out the data analysis, drafted and strongly revised the manuscript; S.L. 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.

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