RESEARCH ARTICLE

Experience during development triggers between-individual variation in behavioural plasticity

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Abstract

1. Behavioural consistency within and across behaviours (animal personality and behavioural syndrome, respectively) has been vigorously studied in the last decade, leading to the emergence of "animal personality" research. It has been proposed recently that not only mean behaviour (behavioural type), but the environmentally induced behavioural change (behavioural plasticity) might also differ between individuals within populations.

2. While case studies presenting between-individual variation in behavioural plasticity have started to accumulate, the mechanisms behind its emergence are virtually unknown. We have recently demonstrated that ecologically relevant environmental stimuli during ontogeny are necessary for the development of animal personality and behavioural syndromes. However, it is unknown whether between-individual variation in behavioural plasticity is hard-wired or induced.

3. Here, we tested whether experience with predation during development affected predator-induced behavioural plasticity in *Rana dalmatina* tadpoles. We ran a common garden experiment with two ontogenetic predation treatments: tadpoles developed from hatching in either the presence or absence of olfactory predator stimuli. Then, we assayed all tadpoles repeatedly for activity and risk-taking both in the absence and presence of olfactory predator stimuli.

4. We found that (a) between-individual variation in predator-induced behavioural plasticity was present only in the group that developed in the presence of olfactory stimuli from predators and (b) previous experience with predatory stimuli resulted in lower plastic response at the group level. The latter pattern resulted from increased between-individual variation and not from universally lower individual responses. We also found that experience with predation during development increased the predictability (i.e. decreased the within-individual variation unrelated to environmental change) of activity, but not risk-taking. In line with this, tadpoles developing under perceived predatory risk expressed their activity with higher repeatability.

5. We suggest that ecologically relevant environmental stimuli are not only fundamental for the development of animal personality and behavioural syndromes, but also for individual variation in behavioural plasticity. Thus, experience is of central importance for the emergence of individual behavioural variation at many levels.

KEYWORDS
animal personality, behavioural plasticity, predation, *Rana dalmatina*, tadpole

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1 | INTRODUCTION

The statistical and biological significance of consistent between-individual variation in single behaviours (animal personality) or across two or more behaviours (behavioural syndromes) within populations has become widely accepted lately (Dall, Houston, & McNamara, 2004; Gosling, 2001; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). Further, not only mean behaviour (behavioural type) but also environment-induced behavioural change (behavioural plasticity) can vary consistently between individuals (Dingemanse & Wolf, 2013; Stamps, 2016). Understanding the proximate mechanisms behind consistent differences in individual behavioural plasticity is a major goal in current animal personality research (Dingemanse & Wolf, 2013; Stamps, 2016). Such a research agenda put a new emphasis on how environmental information at different levels, for instance genetic, developmental and current, interacts in phenotypic development (Stamps & Frankenhuis, 2016). Similar to the proximate mechanisms that create animal personality (Dingemanse & Wolf, 2013; Kight, David, & Dall, 2013; Sih et al., 2015; Stamps, 2007; Wolf, Van Doorn, Leimar, & Weissing, 2007), consistent between-individual differences in behavioural plasticity may result from the underlying differences in genetics, individual state, environmental effects, past experiences or their combinations (Mathot & Dingemanse, 2015; Mathot, Wright, Kempenaers, & Dingemanse, 2012; Mathot et al., 2011).

Several studies pointed out that animal personality and behavioural syndromes often will not develop without relevant environmental stimuli (Bengston, Pruitt, & Riechert, 2014; DiRienzo & Montiglio, 2016; Sweeney et al., 2013; Urszán, Török, Hettyey, Garamszegi, & Herczeg, 2015; Urszán, Garamszegi, et al., 2015). However, while reports of between-individual variation in behavioural plasticity have started to accumulate (Briffa, Bridger, & Biro, 2013; Dingemanse, Barber, Wright, & Brommer, 2012; Dingemanse, Bouwman, et al., 2012; Porlier et al., 2012; Quinn, Cole, Bates, Pyne, & Cresswell, 2012; Westneat, Hatch, Wetzel, & Ensminger, 2011) and even the consistency of such variation has been supported (Araya-Ajoj & Dingemanse, 2017; Mitchell & Biro, 2017), there is little empirical evidence regarding the contribution of environmental factors to the between-individual differences in behavioural plasticity seen in nature (but see DiRienzo & Montiglio, 2016). In four great tit (*Parus major*) populations, individuals differed in their exploration personality and plasticity, and furthermore, the level of plasticity differed between populations too (Dingemanse, Barber, et al., 2012). Three-spined stickleback (*Gasterosteus aculeatus*) exhibit genetic correlations between mean exploration and plasticity of exploration, however, the sign of the correlation differed between the studied populations (Dingemanse, Bouwman, et al., 2012). Porlier et al. (2012) studied laying date variation between and within four Mediterranean populations of blue tits (*Cyanistes careuleus*) and found population level plasticity induced by temperature, together with significant individual variation in plasticity in two populations. These studies suggest that there is intraspecific variation in the presence/absence of between-individual variation in behavioural plasticity seen in nature, but the significance of environmental conditions for the emergence of between-individual variation in behavioural plasticity has not been proven experimentally yet.

Besides behavioural plasticity, there is another component of within-individual behavioural variation, which is the variation unrelated to environmental change (Biro & Adriaenssens, 2013; Stamps, Briffa, & Biro, 2012). This component was coined "behavioural predictability" (e.g. Briffa, 2013; Briffa et al., 2013). In a theoretical way, this component can be a highly relevant individual trait and estimating the predictability of the given individual can inform us how consistently it expresses its behavioural type in any given environment. However, studies addressing its evolutionary significance have only started to accumulate recently (Bridger, Bonner, & Briffa, 2015; Jennings, Hayden, & Gammel, 2013). Therefore, evaluating the role of ontogenetic experience in the development of behavioural predictability is an important task.

Here, we aimed to test whether ontogenetic experience with an ecologically relevant environmental stimulus was important for the development of between-individual variation in behavioural plasticity induced by the given stimulus. Since we found in our earlier studies in the same model system that consistent between-individual variation in behavioural types (i.e. animal personality and behavioural syndrome) developed only in response to ecologically relevant environmental stimuli (Urszán, Garamszegi, et al., 2015; Urszán, Török, et al., 2015), we hypothesized that between-individual variation in behavioural plasticity would not be expressed without previous experience. To test our hypothesis, we studied agile frog (*Rana dalmatina*) tadpoles in a common garden experiment. We reared tadpoles from hatching in laboratory in either the presence or the absence of olfactory cues from predators (ontogenetic treatment). At the same developmental stage, we assayed their behaviours repeatedly in the presence or the absence of olfactory cues from predators (acute treatment). We expected the ontogenetic treatment to induce alternative developmental pathways affecting antipredator strategies in the long term, while the acute treatment to induce immediate responses permitting the characterization of individual reacting norms. This way, we could test whether (a) plasticity induced by the acute predatory treatment differed between the ontogenetically predator-experienced vs. predator-naive groups (group-level test) and (b) presence/absence of between-individual variation in behavioural plasticity induced by the acute predatory treatment differed between ontogenetically predator-experienced vs. predator-naive groups (individual-level test). In addition, we also tested whether (c) ecologically relevant environmental stimuli had a role in shaping behavioural predictability. Considering the proven effect of such stimuli in emerging individual differences in behavioural type (Urszán, Garamszegi, et al., 2015; Urszán, Török, et al., 2015), we expected predation-experienced individuals to show higher predictability (i.e. lower environment-independent within-individual variation).

2 | MATERIALS AND METHODS

2.1 | Field sampling and the ontogenetic treatment

Rana dalmatina eggs were collected from a pond on the Island of Szentendre near Szigetmonostor (47°40′40.77″N, 19°5′31.47″E). Between March 21 and April 8, 2013, 40 clutches were sampled. Sixty eggs were randomly selected from each clutch and were divided equally between two 1.5 L plastic containers (20.6 × 14.6 × 7.5 cm, length, width, height, respectively) and assigned randomly to the two ontogenetic treatments described below. The containers were filled with 0.8 L of reconstituted soft water (RSW). Rearing temperature was set to 19°C and a 12:12 light-dark photoperiod (light period lasted from 08:00 to 20:00 hr) was provided. Late instar dragonfly (*Anax imperator*) larvae collected from the sampled breeding pond of *R. dalmatina* and a juvenile pike (circa 8 cm long; *Esox lucius*) acquired from a fishery were used as the sources for predator cues. Pike are also present in the sampled breeding pond (T. J. Urszán, pers. obs.). The dragonfly larvae were kept in plastic cups filled with 0.5 L of RSW, while a large container with 8 L of RSW was provided for the pike. The dragonfly larvae were fed every third day in a shifted way, which allowed us to take water from hungry, eating, and satiated larvae each day providing a complex stimulus. As tadpoles available for food were growing continuously, we gave the dragonfly larvae three tadpoles during the first part of the experiment, two in the middle and finally one at the end. The juvenile pike was fed with tadpoles ad libitum. This way, a high overall concentration consisting of a variety of predation cues could be used.

The ontogenetic treatments began when all 30 tadpoles in a given clutch/ontogenetic treatment combination hatched. We haphazardly selected one healthy tadpole from the 30, left it in the rearing container and removed the rest. This way, we had 40 individuals for the "control" and 40 individuals for the "predation" ontogenetic treatments, with individuals coming from the 40 clutches to maximize genetic diversity. As we did not aim to estimate family effects and quantitative genetic parameters, only one individual per family was included in the ontogenetic treatments. Remaining tadpoles were used as food for predators and were kept in large containers filled with RSW. All tadpoles were fed with minced and boiled spinach ad libitum, food being administered 3 hr before the end of the daily light period. Water was changed every 4 days.

In the ontogenetic "predation" treatment, 40 ml of stimulus water was administered twice a day. Stimulus water consisted of 20 ml RSW containing olfactory cues from the predators (taken in a 1:1 ratio from dragonfly larvae and the pike) and 20 ml clear RSW. This project was part of a larger experiment, which contained additional ontogenetic treatment groups, one of which involved adding 20 ml RSW containing olfactory cues from the predators and 20 ml RSW containing olfactory cues from conspecifics (Urszán, Garamszegi, et al., 2015). Therefore, in the predation only treatment (used in the present paper), we needed to add 20 ml clear RSW as a control. In the ontogenetic "control" treatment, tadpoles were reared in clear RSW. 40 ml clear RSW was administered twice a day to the rearing containers of the control tadpoles. Treatment water (containing predator cues or clear) was administered first in the morning between 9:30 and 10:00 hr and second in the evening between 19:30 and 20:00 hr.

2.2 | Behavioural assays and the acute treatment

Individual development was followed daily. When individuals reached developmental stage 32–36 (early stages of toe development, Gosner, 1960), they entered the behavioural plasticity surveys. Behaviour was repeatedly tested both in the presence and absence of predatory cues (acute treatment) for every individual. Within both ontogenetic treatments, individuals were randomly divided into two groups. One group was tested first in its familiar environment (i.e. ontogenetic control treatment tadpoles in clear RSW, ontogenetic predator treatment tadpoles in water containing predatory cues) daily for 3 days and second in the novel environment (i.e. ontogenetic control treatment tadpoles in water containing predatory cues, ontogenetic predator treatment tadpoles in clear RSW) daily for 3 days. The other group was tested first in the novel and then in the familiar environment. This approach enabled us to control for "novelty" to avoid unwanted side-effects of experimental design (Bell, 2013; Urszán, Török, et al., 2015).

For all individuals entering behavioural assays, water was provided on the first day according to the design outlined above. Trials began next day and lasted for 3 days with the first environmental setup and for another three with the second. Between the two sets of trials, water was changed following the design, and the tadpoles were left to rest for a day. We assessed two different behavioural traits: activity and risk-taking. The behaviour of the tadpoles was recorded with webcams using the open source Dorgem software (Fesevur, http://dorgem.sourceforge.net/). Five minutes before each behavioural test, we administered 40 ml clear RSW or stimulus water depending on the acute treatment with a syringe. Activity was assessed between 10:00 and 10:30 hr and then risk-taking between 12:30 and 13:05 hr. Activity was measured first as it is a noninvasive measurement. Activity was estimated by recording tadpoles during the 30 min observation period and subsequently tracking and measuring the distance moved using MATLAB (Hedrick, 2008). Risk-taking was estimated by latency to restart activity (time spent immobile) following a simulated attack. We used a fine paintbrush (#00) to poke the tadpoles at the base of their tail to mimic a predator attack. Tadpoles responded to the stimulus with rapid escape behaviour and subsequent immobility. The duration of this period of immobility was considered as an inverse measure of risk-taking. Individuals that remained immobile for the entire 35 min of the observation period were assigned the maximum score of 2,100 s (11% of observations). A day after the last behavioural trial, each individual was weighed with a digital balance to the nearest 0.001 g.

2.3 | Statistical analysis

A total of 36 and 38 individuals were used from the control and predator ontogenetic treatments, respectively, as some individuals

were lost due to early mortality. Activity and risk-taking were $\log_{10}$ transformed to achieve normal distributions for model residuals. The effect acute treatment was centred (control: −1; predator: 1) for the individual behavioural reaction norm approach (Dingemanse, Kazem, Réale, & Wright, 2010; Mathot & Dingemanse, 2015; Nussey, Wilson, & Brommer, 2007). We ran univariate Linear Mixed Models (LMMs) to address our questions (see below), for which we relied on Markov chain Monte Carlo methods as implemented in the MCMCglmm package developed for R (Hadfield, 2010).

To test for group-level treatment effects on behavioural type and behavioural plasticity, we ran LMMs separately for the two behavioural traits, which had identical predictive parts (fixed and random factor structure). We built models with either activity or risk-taking as the response variable, and with ontogenetic treatment, acute treatment, their interaction, test order (i.e. whether an individual was first tested in the familiar or novel environment), trial day (each tadpole was recorded six times during 6 days) and body weight as fixed effects. The definition of the fixed part of the models was motivated by our predictions in relation to the general treatment effects on behavioural type and plasticity. In accordance, ontogenetic treatment effect would mean that developmental environment had an effect on the mean behaviour of individuals, acute treatment effect would mean that individuals reacted to the presence of predation (i.e. there is plasticity at the treatment group level), and the ontogenetic treatment × acute treatment interaction would mean that the developmental environment had a group-level effect on plasticity.

One of the main questions of our study was whether the presence/absence of individual variation in behavioural plasticity induced by the acute treatment differed between the ontogenetic treatments. To test for individual-level treatment effects, we defined the random part of the model in a way that allowed differentiating individual-specific responses between treatment groups. In accordance, we defined individual (intercept) and individual × acute treatment interaction (random slopes) separately for the control and predatory ontogenetic treatment groups. Detecting considerable variance in random slopes would indicate that individuals depict different behavioural reaction norms (i.e. they differ in their behavioural plasticity). Furthermore, if variance in random slopes differs between the ontogenetic experimental groups, it would signify that predatory and control treatments during ontogeny induce different levels of variations in plasticity among individuals. In our models, we worked with heterogeneous residuals, as these were also estimated separately for the two ontogenetic treatment groups. Estimating different within-individual variances for the predatory and control groups permitted us to make inferences about behavioural predictability (i.e. Briffa et al., 2013).

We defined priors necessary for the Bayesian modelling with inverse-Wishart distribution for the variance structure using parameter settings for noninformative priors (expected variance, $V = 1$; degree of belief, $\nu = 0.002$). The models were run for 130,000 iterations, with 30,000 samples being discarded at the beginning (burning) that were sampled at a thinning interval of 100. The trace and distribution of all variables were checked visually, as well as

autocorrelation between iterations. Each model was run at least four times to check for the consistency of the results (including parameter estimates and Deviance Information Criterion, DIC). Similar to that, we also verified if longer runs, different prior settings (i.e. flat and improper priors) provided qualitatively indistinguishable model outputs. Our model diagnostics also included the investigation of mixing and convergence that were tested by Gelman-Rubin statistics (Gelman & Rubin, 1992).

After these diagnostics procedures, we obtained statistical support for fixed and random effects from the fitted models as follows. We considered that the estimated parameters of fixed effects (both main and interaction terms) are significantly different from zero if their associated 95% credible intervals (95% CI) derived from the underlying posterior distribution did not overlap with zero. The importance of variance components cannot be evaluated by this manner, because variance components are bound to be positive, and because their credible intervals may be sensitive to the prior choice. Therefore, we obtained statistical support for variances by comparing the DIC between the fitted models and models in which the focal variance component was forced to be zero. Lower DIC value offers relatively better fit to the data, thus we considered that a given variance component is significantly different from zero, if the fitted model including it had considerably (deltaDIC > 10) smaller value than the respective null model in which the given component was set to be zero.

Based on the random structure of the above LMMs, we calculated conditional repeatability (e.g. Biro & Stamps, 2015; Nakagawa & Schielzeth, 2010) for the two ontogenetic treatments separately and for the two treatment groups combined. Conditional repeatabilities require a specific state for the predictor, for which we chose the reference point of acute treatment = 0, which reflects the intermediate value of the control/predator axis. To estimate repeatabilities for all treatment combinations (ontogenetic control × acute control; ontogenetic control × acute predator; ontogenetic predator × acute control; ontogenetic predator × acute predator), we ran separate LMMs with test order, trial day and body weight as fixed effects and individual (intercept) as random effect on the corresponding subsets of data and calculated consistency repeatability (e.g. Biro & Stamps, 2015; Nakagawa & Schielzeth, 2010). We provide the repeatabilities for the different hierarchical levels in Table 2.

3 | RESULTS

The Bayesian LMMs testing for group-level patterns revealed qualitatively similar patterns for activity and risk-taking (Table 1). On both behaviours, we detected considerable acute treatment effects showing that in the presence of olfactory predatory cues, tadpoles systematically decreased their activity and risk-taking (Figure 1, Table 1). The ontogenetic treatment × acute treatment interaction revealed that tadpoles from the ontogenetic predation treatment had weaker mean plastic response to the acute

TABLE 1 Results from linear mixed models (LMM) estimating fixed and random effects explaining variation in activity and risk-taking and their plasticity based on different combinations of predatory treatments in *Rana dalmatina* tadpoles. Estimates were derived separately for the two behavioural traits from univariate response models, in which both random intercepts and slopes were considered for individuals and these were grouped along the ontogenetic treatments. The models assumed heterogeneous residuals, thus within-individual variances were estimated separately for the two ontogenetic treatment groups

Model	Activity	Risk-taking
Fixed effects	β (95% CI)	β (95% CI)
Intercept	2.022 (0.928, 2.899)***	2.654 (2.293, 3.029)***
OT	0.315 (−0.044, 0.670)	−0.102 (−0.244, 0.034)
AT	−0.860 (−1.029, −0.703)***	0.422 (0.353, 0.478)***
OT × AT	0.569 (0.352, 0.782)***	−0.246 (−0.352, −0.139)***
ORDER	0.209 (−0.089, 0.537)	−0.118 (−0.232, −0.001)*
TRIAL	0.054 (−0.008, 0.114)	−0.029 (−0.058, −0.005)*
WEIGHT	0.000 (−0.001, 0.002)	−0.001 (−0.001, 0.001)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
OT_{cont} (between-individual)		
$V_{intercepts}$	0.214 (0.001, 0.423)	0.035 (0.004, 0.071)
V_{slopes}	0.037 (0.000, 0.124)	0.007 (0.000, 0.021)
OT_{pred} (between-individual)		
$V_{intercepts}$	0.421 (0.205, 0.681)	0.038 (0.007, 0.077)
V_{slopes}	0.140 (0.039, 0.283)	0.038 (0.010, 0.075)
Residual (within-individual)		
OT_{cont}	1.240 (0.944, 1.526)	0.189 (0.147, 0.233)
OT_{pred}	0.574 (0.443, 0.721)	0.187 (0.146, 0.232)

Notes. OT: ontogenetic predatory treatment (OT_{cont}: control group, OT_{pred}: predatory group); AT: acute predatory treatment; ORDER: order of familiar vs. novel environments during behavioural testing; TRIAL: the day of trial; WEIGHT: body mass measured after the last behavioural test; V: variance. Means of the posterior distribution of parameter estimates and their 95% credible intervals are provided (***pMCMC < 0.001, *pMCMC < 0.05).

predation treatment (flatter group-level behavioural reaction norms), than tadpoles from the ontogenetic control treatment (Figure 1, Table 1). On the other hand, the low parameter estimate for the ontogenetic treatment as main effect suggests that mean behaviour (intercept) remains similar in the two experimental groups (Figure 1, Table 1). Body weight had no effect on the behavioural variables, while weak order and trial day effects suggest habituation for risk-taking (Table 1).

The inspection of the random part of the model suggested that predation-induced behavioural plasticity varied little, if any, between individuals in the ontogenetic control treatment (Figure 1a,c). The between-individual variances in reaction norm slopes were 0.037 and 0.007, for activity and risk-taking, respectively (Table 1). Models that forced this variation to be zero (i.e. not allowing differences in reaction norm slopes among individuals) resulted in similar data fit (activity, DIC = 1257.9 vs. DIC = 1258.6; risk-taking: DIC = 588.2 vs. DIC = 588.3). However, *R. dalmatina* tadpoles reared in the presence of olfactory cues from their predators expressed remarkable between-individual variation in predation-induced behavioural plasticity (Figure 1b,d), as shown by the 3- to 6-fold larger between-individual variance in reaction norm slopes detected in this treatment group (Table 1). Models that forced no differences in reaction norm slopes among individuals provided worse fit to the data (activity, DIC = 1257.9 vs. DIC = 1289.604; risk-taking: DIC = 588.2 vs. DIC = 613.6), further supporting the presence of among-individual variation in behavioural plasticity. Repeatability estimates testing for

the presence of animal personality are given for the different treatments in Table 2.

The residual variance reflecting the component of the within-individual variation that was not accounted for by the fixed and random effects (i.e. behavioural predictability) was lower in the ontogenetic predation than in the ontogenetic control treatment for activity (indicating higher predictability of activity under predation), but not for risk-taking (Table 1). This was also evident from the model fit statistics of models that assumed homogeneous residual structure (activity, DIC = 1257.9 vs. DIC = 1290.8; risk-taking: DIC = 588.2 vs. DIC = 587.1). Therefore, it seems that not only behavioural plasticity, but also behavioural predictability was affected by the ontogenetic treatment. This is fully in line with the patterns found in repeatabilities (Table 2): individuals developing under perceived predation risk showed higher activity repeatabilities, meaning "stronger" activity personality.

4 | DISCUSSION

It has been emphasized that ontogenetic experience is an important factor shaping personality in later life (Butler, Toomey, McGraw, & Rowe, 2012; Dingemanse et al., 2009; Rödel & Monclús, 2011). However, results reveal no general pattern in how the environment—individual state—behavioural consistency link works, because behavioural consistency can both increase or decrease following
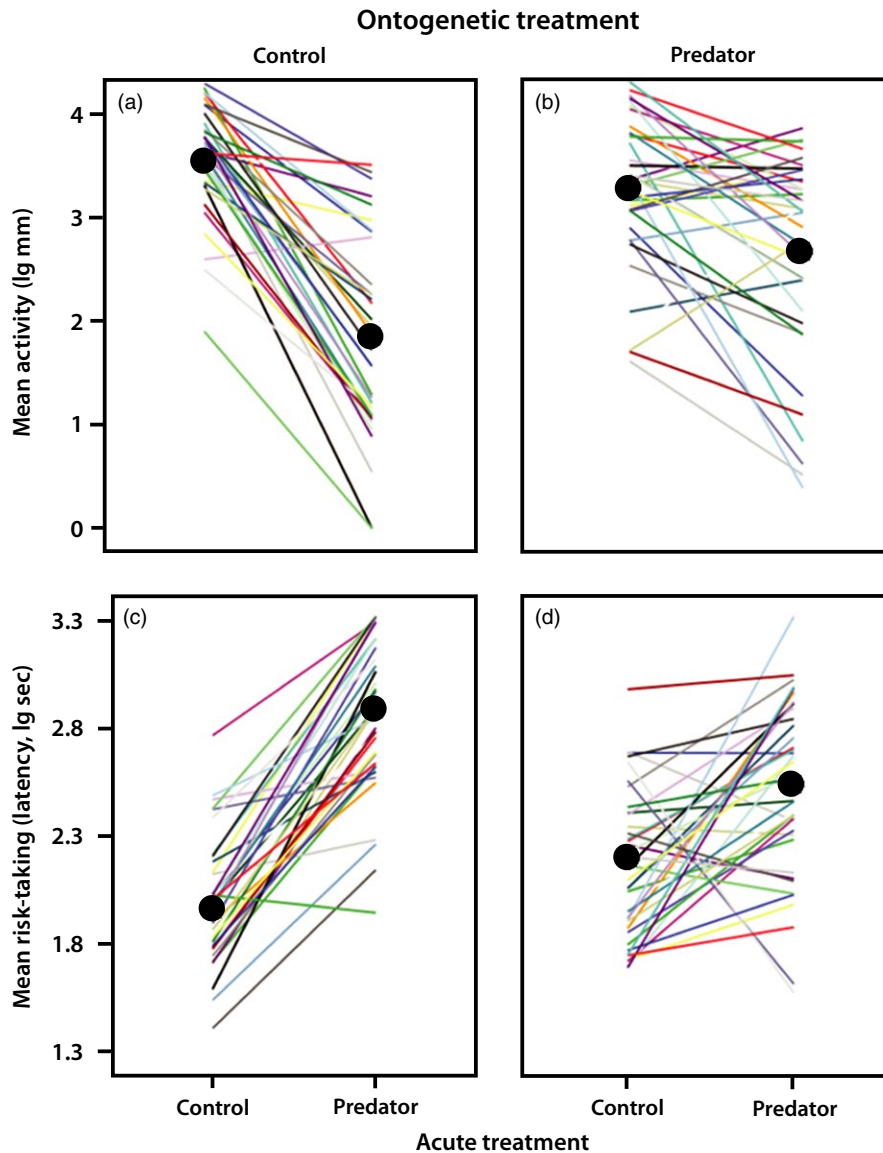
FIGURE 1 Predation-induced individual behavioural reaction norms in *Rana dalmatina* tadpoles reared in the presence/absence of predatory stimuli. (a) Activity in the ontogenetic control treatment (between-individual variation in slope is not supported), (b) activity in the ontogenetic predation treatment (between-individual variation in slope is supported), (c) risk-taking in the ontogenetic control treatment (between-individual variation in slope is not supported) and (d) risk-taking in the ontogenetic predation treatment (between-individual variation in slope is supported). Note that risk-taking is a latency variable (high values represent low risk-taking). Ontogenetic treatment denotes the presence/absence of perceived predation risk during ontogeny from hatching to entering the behavioural assays. Acute treatment denotes the presence/absence of perceived predation risk during behavioural assays. Filled circles represent the means for the given treatment combination [Colour figure can be viewed at wileyonlinelibrary.com]

environmental changes affecting individual state (David, Auclair, Giraldeau, & Cézilly, 2012; DiRienzo & Montiglio, 2016; DiRienzo, Niemelä, Hedrick, & Kortet, 2016; DiRienzo, Niemelä, Skog, Vainikka, & Kortet, 2015; Dosmann, Brooks, & Mateo, 2014; Kekäläinen, Lai, Vainikka, Sirkka, & Kortet, 2014). At any rate, empirical studies supported the idea that ontogenetic experience is a necessary trigger for the development of animal personality and behavioural syndromes (Bell & Sih, 2007; Bengston et al., 2014; Sweeney et al., 2013; Urszán, Garamszegi, et al., 2015; Urszán, Török, et al., 2015). The same is expected for the emergence of between-individual variation in behavioural plasticity (Dingemanse & Wolf, 2013; DiRienzo & Montiglio, 2016; Mery & Burns, 2010), and our study strongly supported this expectation in both activity and risk-taking. We found the expected predation-induced plastic response on group level (Skelly & Werner, 1990; Teplitsky & Laurila, 2007): irrespective of ontogenetic experience, mean activity and risk-taking decreased under perceived predation risk. However, ontogenetic experience with predation had a marked effect on the individual-level variation

in predation-induced behavioural plasticity. Individuals without previous experience with predation expressed their plastic response uniformly. This suggests that there is an invariably strong innate response towards predator odour in our study population, so that tadpoles can immediately respond to predators that appear during their late ontogeny. On the other hand, individuals developing in the permanent presence of predator odour showed marked between-individual variation in behavioural plasticity. Considering that predation stimulus was kept constant, this means that ontogenetic experience with predation brought out the innate variation in individual behavioural reaction norms.

Araya-Ajoj and Dingemanse (2017) reported modest heritability ($h^2 = 0.27$) for individual behavioural reaction norms for aggression in the great tit, and if it was applicable to our species, there is a scope for behavioural plasticity to evolve as a genetically based trait. As adaptive evolution is a result of selection acting on heritable between-individual phenotypic variation, it is of prime interest whether genetic differences translate into phenotypic variation

TABLE 2 Repeatability estimates at different levels. Values of R and 95% credibility intervals are shown

Group	Activity	Risk-taking
Full[a]	0.25 (0.14–0.37)	0.16 (0.08–0.27)
Control OT[a]	0.14 (0.001–0.27)	0.16 (0.03–0.30)
Predator OT[a]	0.41 (0.26–0.57)	0.17 (0.04–0.31)
Control OT – control AT[b]	0.10 (<0.01–0.28)	0.11 (<0.01–0.30)
Control OT – predator AT[b]	0.17 (<0.01–0.39)	0.17 (<0.01–0.37)
Predator OT – control AT[b]	0.50 (0.32–0.69)	0.32 (0.09–0.52)
Predator OT – predator AT[b]	0.43 (0.23–0.63)	0.27 (0.04–0.49)

Notes. OT, ontogenetic treatment; AT, acute treatment. For more details about the calculations, see Materials and methods.
[a]conditional repeatability; [b]consistency repeatability.

differently in different environments or, as seen in our study, do not translate to phenotypic differences at all without being triggered by environmental stimuli. Our studies on *R. dalmatina* tadpoles (Urszán, Garamszegi, et al., 2015; Urszán, Török, et al., 2015; present study) similarly to others (e.g. Bengston et al., 2014; Sweeney et al., 2013) emphasize the key role of environmental triggers for the development of individual behavioural variation, being in the form of animal personality, behavioural syndrome or behavioural plasticity. Further, environment can have a profound effect on adult behavioural consistency as well. Dingemanse, Both, Drent, and Tinbergen (2004) showed that selection acting on great tit behavioural types might vary among years not only in strength, but also in direction in the wild. Garamszegi et al. (2015) studying a wild population of collared flycatchers (*Ficedula albicollis*) demonstrated that strength and direction of behavioural correlations could change among years. In manipulative experiments, Horváth, Martín, López, Garamszegi, and Herczeg (2017) and Horváth, Mészáros, et al. (2017) showed that even short-term manipulation of ecologically relevant environmental factors can "switch" animal personality and behavioural syndromes on and off in adult Carpetan rock lizards (*Iberolacerta cyreni*) or European green lizards (*Lacerta viridis*). Therefore, even if we assume that both behavioural type and behavioural plasticity are heritable in any given system, to understand their evolution, we must consider the prevailing environmental conditions, preferably along several generations and/or years to account for the likely changes in both the selection pressures and the expressed between-individual phenotypic variation. We must note that our study was not designed for drawing quantitative genetic conclusions and thus "innate" differences seen in our standardized common garden study cannot unequivocally be attributed to genetic differences, because maternal, early environmental, epigenetic or transgenerational environmental effects cannot be excluded.

Before interpreting the observed group-level plasticity, we must point out the pitfalls in interpreting group-level reaction norms without looking at individual reaction norms that becomes obvious when

looking at Figure 1. One group can have lower mean slope than another can in two ways: (a) most individuals in the group express lower plasticity, or (b) they express higher variation in plasticity including individuals with no response and even with responses in the opposite direction. The above two cases are biologically different. Based on the ontogenetic treatment level mean reaction norms in our case, one could conclude that predation-experienced tadpoles showed a weaker response to predation, perhaps "lost interest," became desensitized due to the permanent stress, fine-tuned their behaviour, etc. However, looking at the individual reaction norms gives a different picture. The observed group-level decrease in predator-induced plasticity in the predator-experienced group originates from the fact that while almost all predator-naïve individuals strongly decreased activity and risk-taking under perceived predation risk, a considerable amount of predator-experienced tadpoles behaved in a counterintuitive way by either not reacting or actually increasing activity and/or risk-taking. The general notion is that populations adapted to high predation risk express lower behavioural activity coupled with higher predation-induced plasticity than populations in low-risk habitats (e.g. Hettyey et al., 2016; Kiesecker & Blaustein, 1997; Magurran, 1990). However, there are exceptions too. Brown, Jones, and Braithwaite (2005) and Brown, Burgess, and Braithwaite (2007) found that the tropical poeciliid, *Brachyraphis episcopi*, is considerably bolder when adapted to high predation pressure. The authors suggested that under high predation, individuals should evolve higher boldness to be able to carry on with everyday activities. Similar to that, mixed results can be found in group-level plasticity studies: Shah, Ryan, Bevilacqua, and Schlaepfer (2010) found that predator-experienced individuals maintained higher activity under perceived predation risk than their predator-naive conspecifics, while Fraker (2009) reported that predator-experienced individuals react longer to predator stimuli than predator-naive individuals. If such opposite strategies exist on the interspecific level, similar variation is also possible within population. Hence, we suggest that when naïve tadpoles first meet a predatory threat, they just react by drastically decreasing behavioural activity. However, when they develop under permanent perceived predatory threat, highly variable, even opposite, individual strategies emerge. We can only speculate about the biological mechanism behind that variation, but, for instance, it might be related to individual variation in investments to other antipredator traits than behaviour. It is known that effectively induced antipredator responses in other traits, such as morphology, may lower the necessity of strong behavioural response (Dijk, Laurila, Orizaola, & Johansson, 2016; Van Buskirk & McCollum, 2000). It is clear that the generality of our results is unknown, and further studies in various taxa are needed to see whether such hidden strategy variation generally exists or it is a unique pattern in our species/population.

Patterns in the presence/absence/strength of animal personality are partly in line with the results on the presence/absence of between-individual variation in behavioural plasticity and our previous results (Urszán, Garamszegi, et al., 2015). Tadpoles that developed with predator cues showed three times higher repeatability in activity

than predator-naïve tadpoles, further strengthening the notation that ecologically relevant environmental cues are important for the development of personality. However, this effect was not detected for risk-taking. Between-individual variation is not only affected by the distance between individual means, but also strongly depends on the variation around the means (i.e. behavioural predictability). We found more than two times higher predictability of activity in predator-experienced tadpoles than in their predator-naïve conspecifics. Behavioural predictability was only recently accepted as a relevant individual trait (Biro & Adriaenssens, 2013; Stamps et al., 2012) with only a handful of studies testing its ecological and evolutionary relevance. For instance, opposite to our results, Briffa (2013) found that hermit crabs (*Paghurus bernhardus*) became less predictable under predation threat. In the same species, temperature had a negative effect on predictability (Briffa et al., 2013) and metabolic rate showed a negative correlation with predictability (Velasque & Briffa, 2016). In the fallow deer (*Dama dama*), males with intermediate predictability had higher fitness than individuals with either low or high predictability (Jennings et al., 2013). Here, we showed that developmental environment had a direct effect on behavioural predictability, adding more weight to the argument that predictability should be involved in rigorous evolutionary testing in future personality studies. These results support the idea that innate behavioural strategies including behavioural type, behavioural plasticity and behavioural predictability can remain "dormant" and become expressed only after (prolonged) exposure to ecologically relevant environmental stimuli. However, more research is needed to establish the general importance of environmental triggers. For instance, Bierbach, Laskowski, and Wolf (2017) found consistent between-individual behavioural variation in clonal Amazon mollies (*Poecilia formosa*) reared in isolation under standardized settings and concluded that "individuality might be an inevitable and potentially unpredictable outcome of development."

Taken together, we demonstrated that between-individual variation in predator-induced behavioural plasticity develops only among individuals that had previous experience with predation. In other words, the expression of individually variable behavioural reaction norms in *R. dalmatina* tadpoles is triggered by environmental stimuli, suggesting that a genotype × environment interaction might be responsible for the phenomenon. This is very similar to what we have reported about the development of animal personality and behavioural syndromes earlier in the same species (Urszán, Garamszegi, et al., 2015), suggesting that genotype × environment interactions might be of key importance in the development of behavioural consistency at many levels. Further, assuming some genetic basis for the between-individual variation in behavioural plasticity induced by ecologically relevant environmental stimuli, we conclude that this trait warrants rigorous quantitative genetic study to establish its true evolutionary potential.

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AUTHORS' CONTRIBUTIONS

T.J.U., A.H., J.T. and G.H. conceived the ideas and designed methodology; T.J.U. and G.N. collected the data; T.J.U., G.H. and L.Z.G. analysed the data; T.J.U., L.Z.G. and G.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.240n5f6 (Urszán et al., 2018).

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