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The influence of environmental gradients on individual behaviour: Individual plasticity is consistent across risk and temperature gradients

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Summary

1. The expression of individual behaviour as a function of environmental variation (behavioural plasticity) is recognised as a means for animals to modify their phenotypes in response to changing conditions. Plasticity has been studied extensively in recent years, leading to an accumulation of evidence for behavioural plasticity within natural populations.
2. Despite the recent attention given to studying individual variation in behavioural plasticity, there is still a lack of consensus regarding its causes and constraints. One pressing question related to this is whether individual plasticity carries over across temporal and environmental gradients. That is, are some individuals more plastic (responsive) than others in general?
3. Here, we examined the influence of temporal and environmental gradients on individual behavioural responses in a marine gastropod, *Littoraria irrorata*. We measured individual boldness repeatedly over time and in response to tidal cycle (high vs low, an index of risk) and daily temperature fluctuations (known to affect metabolism), in a controlled field experiment.

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4. On average, boldness increased from high to low tide and with increasing temperature but decreased marginally over time. Individuals also differed in their responses to variation in tide and temperature, but not over time. Those that were relatively bold at high tide (when predation risk is greater) were similarly bold at low tide, whereas shy individuals became much more 'bold' at low tide. Most notably, individuals that were more responsive to tide (and thus risk) were also more responsive to temperature changes, indicating that plasticity was correlated across contexts ($r = 0.57$) and that bolder individuals were least plastic overall.
 5. This study provides a rare and possibly first example of consistency of individual behavioural plasticity across contexts, suggesting underlying physiology as a common mechanism, and raises the possibility of correlational selection on plasticity.

Key-words animal personality, behavioural plasticity, boldness, linear mixed model, *Littoraria irrorata*, reaction norm, state-behaviour feedback.

Introduction

Plasticity has long been recognised as a means for animals to modify their phenotypes in response to varying conditions and has been extensively studied, but primarily from a developmental perspective. More recently, the study of plasticity has shifted to examining short-term reversible physiological and behavioural plasticity, from an individual perspective, with a focus on understanding the causes and consequences of individual behavioural variation (see Dingemanse & Wolf 2013; Snell-Rood 2013; Stamps 2016). Individual variation in plasticity

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is important to study because it indicates that the amount of variation that selection can act upon is not constant across environments (Dingemanse *et al.* 2012), and indicates that plasticity may be heritable (e.g. Scheiner 1993; Nussey *et al.* 2005). Furthermore, plasticity can have important ecological implications (Toscano 2017) such as those associated with population expansion (Schou *et al.* 2017), stability and persistence (Dingemanse & Wolf 2013).

Evidence for individual variation in behavioural plasticity is rapidly accumulating, showing that responses to environmental variation often differ significantly among individuals, for a wide range of environmental and ecological gradients (e.g. Briffa, Rundle & Fryer 2008; Westneat *et al.* 2011; Hewes, Delventhal & Chaves-Campos 2017; Mitchell & Biro 2017; Toscano 2017, see also reviews by Dingemanse & Wolf 2013; Stamps 2016). Most recently, two studies have shown that individual differences in plasticity are consistent over time and can be heritable (Araya-Ajoy & Dingemanse 2017; Mitchell & Biro 2017), indicating that individual behavioural plasticity is a consistent individual attribute, at least for the gradient(s) considered.

Despite recent evidence for behavioural plasticity and the attempts to elucidate its mechanisms (Mathot *et al.* 2012; Mitchell & Biro 2017), there is still a lack of an overall understanding of its origins (Snell-Rood 2013) and the factors that constrain it (Stamps 2016). One recent suggestion centres on the assumption that individual plasticity may correlate across environmental gradients (or is domain-general), as a result of common proximate mechanisms (Stamps 2016), such as those related to individual physiology, e.g. metabolic rate (Mitchell & Biro 2017) and metabolic scope (Biro *et al.* 2018). However, despite previous investigations examining covariance among reaction norm (RN) slopes (i.e. correlation of plasticity across gradients), support for this assumption is currently absent (Westneat *et al.* 2011; Biro,

Adriaenssens & Sampson 2014; Mitchell & Biro 2017) and is very rarely studied. Consequently, domain generality of behavioural RNs remains an outstanding question and, if valid, could help reveal the factors underpinning behavioural phenotypic variation (Stamps 2016; Mitchell & Biro 2017).

Recent proposals also suggest that among-individual variation in behaviour, including plasticity, may arise from differences in individual state. In this context, an individuals' state could be related to relatively labile internal characteristics such as energy metabolism and energy reserves (Careau *et al.* 2008; Biro & Stamps 2010; Metcalfe, Van Leeuwen & Killen 2016) as well as to individual information state variables such as social rank (Bergmüller & Taborsky 2010; Colléter & Brown 2011), risk perception (e.g. Dorset, Sakaluk, & Thompson, 2017) and prior experience with external stimuli (Frost *et al.* 2007; Urszán *et al.* 2015, 2018). Individual state can also be influenced by environmental factors such as temperature (Biro, Beckmann & Stamps 2010; Briffa, Bridger & Biro 2013; Nakayama *et al.* 2016; Schou *et al.* 2017), time of day (Dingemanse *et al.* 2002; Biro *et al.* 2014), predator-prey interactions (Urszán *et al.* 2015, 2018; Foster *et al.* 2017) and habitat quality (Belgrad & Griffen 2017; Belgrad, Karan & Griffen 2017). Yet, empirical studies that evaluate the relationships between individual state and individual behavioural differences, particularly relating to plasticity under different contextual gradients, are still lacking (but see Nakayama *et al.* 2016; Mitchell & Biro 2017).

Here, we quantified how boldness (risk-taking propensity) in *Littoraria irrorata* (the saltmarsh periwinkle) was simultaneously influenced by repeated handling over time (trial number), along with two environmental gradients that can affect changes in internal physiological or information state: tidal inundation and daily temperature fluctuations, under semi-natural conditions. Our study aimed to identify (a) whether there is evidence of among-individual variation in plasticity across contextual gradients and over time, and (b) whether plasticity is correlated across these different gradients. *L. irrorata* is a widespread herbivore on

saltmarshes of the Eastern USA and is typically found on or amongst the stems of the habitat-forming cordgrass, *Spartina alterniflora*, across high, mid and low marsh areas (Hamilton 1978; Stiven & Kuenzler 1979). An important prey species for numerous saltmarsh consumers, *L. irrorata* is known to undertake daily vertical migrations on *S. alterniflora* stems (Stiven & Kuenzler 1979; Henry, McBride & Williams 1993), to avoid predation at high tide (West & Williams 1986; Vaughn & Fisher 1988, 1992). Thus, we used tide as an index of predation risk in our study.

We predicted an increase in mean boldness with increased temperatures due to increased metabolism (Clarke & Johnston 1999) and the hypothesised links between metabolism and behaviour (Careau *et al.* 2008; Biro & Stamps 2010; Metcalfe *et al.* 2016). Further, individual variation in metabolic responsiveness to temperature (Careau, Gifford & Biro 2014) should lead to individual variation in behavioural responsiveness to temperature (Biro *et al.* 2010; Briffa *et al.* 2013). With respect to risk, we predicted boldness to increase on average at low tide when risk of predation is low (West & Williams 1986; Vaughn & Fisher 1988, 1992). We also expected individuals to differ in their responses to risk (e.g. Dammhahn & Almeling 2012; Thomson *et al.* 2012; Briffa 2013) due to differences in perception of risk and stress responsiveness (e.g. Carere, Caramaschi & Fawcett 2010; Dorset *et al.* 2017). Finally, we expected individuals to differ in temporal changes in boldness across the many repeated behavioural assays, as these differences may reflect habituation to protocols and/or some other internal or external factor varying over time (e.g. Bell & Peeke 2012; Dingemanse *et al.* 2012; Stamps *et al.* 2012; Briffa *et al.* 2016).

In addition, since unpredictable behaviour under threat of predation is thought to increase the chances of evading capture (Brembs 2011; Jones, Jackson & Ruxton 2011), we also expected that predictability (residual intra-individual variation) of behaviour would increase in response to risk perception at high tide (Maye *et al.* 2007; Briffa 2013).

Materials and methods

Experimental design

Data collection for this study was undertaken at the Virginia Institute of Marine Science (VIMS), Eastern Shore Laboratory, Wachapreague, VA, USA. Experimental materials were obtained from the high salinity marshes behind the U.S. Atlantic barrier island system along the Virginia coastline consisting of expansive monotypic *S. alterniflora*. The region has limited or no barrier island development and limited public access, resulting in low anthropogenic stressors that might confound behavioural responses. A mean high water of 1.28 m and mean low water of 0.05 m results in regular inundation of *S. alterniflora* in the upper intertidal range to an approximate 0.3 m height (NOAA 2018). The experimental set up consisted of two water tables (approx. 248cm x 61cm x 20cm) connected to a flow-through system, drawing seawater from, and returning to the adjacent Wachapreague channel. In each table, two 'replica marsh plots' (0.30m^2) ($N = 4$) were created by filling open top mesh cages (60 x 50 x 5cm) with 5cm deep marsh cores, complete with cordgrass roots and intact stems, taken from the nearby marsh system in Wachapreague, VA (37°36'31.2"N 75°41'09.3"W).

Incoming and outgoing tides were simulated daily, within each flow-through table, by replicating the tidal patterns seen in the surrounding, natural marsh. Daily maximum water level within the marsh plots, at high tide (mean \pm s.d., $11.83 \pm 1.67\text{cm}$), along with incoming tide duration were approximated by recording the rate of incoming water on the natural marsh, referring to a guide measure placed in the natural marsh at the point of core collection, and by adjusting the flow to the water tables accordingly. At low tide, substrate within the marsh plots, like that of the natural marsh, were not submerged.

Biomass-density (biomass $\text{m}^{-2} \pm \text{s.d.}$, $215.3 \pm 2.1\text{g}$) and average stem height (mean \pm s.d., $143 \pm 12.83\text{cm}$) of *S. alterniflora* were consistent in each marsh plot and were comparable to that observed in the surrounding, natural marsh from which the cores and the study subjects were collected (biomass $\text{m}^{-2} \pm \text{s.d.}$, $255.3 \pm 103.1\text{g}$; stem height $\pm \text{s.d.}$, $178 \pm 32.83\text{cm}$).

Collection and husbandry

Adult snails (as defined by Hamilton 1978), $N = 80$; 17-28mm shell length, were collected haphazardly from a patch of high-marsh (approx. 5m^{-2}), at low tide, from nearby *S. alterniflora*-dominated saltmarsh ($37^{\circ}36'31.2''\text{N}$ $75^{\circ}41'09.3''\text{W}$) in July 2016. Individuals were transported to the VIMS Eastern Shore Laboratory where they were placed in seawater for 30 minutes to allow all individuals time to fully hydrate (Iacarella & Helmuth 2011). To minimize variation in the mantle cavity fluid (Henry *et al.* 1993; Iacarella & Helmuth 2011) and before being weighed (total wet weight, g), each specimen was stimulated to retract into its shell and to close the operculum by applying gentle pressure to the exposed foot with a blunt-ended seeker (dissection probe). Excess water was then removed using tissue paper. Shell length (mm) was measured using Vernier callipers and all individuals were weighed (mean $\pm \text{s.d.}$, $2.98 \pm 0.85\text{mm}$). Sex was then determined, for each individual, by visual inspection for the presence or absence of male reproductive organs (46 females and 34 males). In this species, the male sex organ is visible on gently lifting the shell while the foot of the snail is attached to a flat surface.

The snails were number-marked using acrylic paint covered with clear, non-toxic aquarium glue (Stagg & Mendelsohn 2012) and transported to the replica marsh plots. 20 snails were randomly assigned to each of the four experimental plots. Snail densities in each plot (66 snails m^{-2}) were comparable to the densities found in the surrounding marsh areas (mean $\pm \text{s.d.}$,

85 ± 15 snails m⁻²). All individuals were free to feed, ad libitum, on living and dead cordgrass and benthic material within the replica marsh plots.

Individual snails were checked twice daily to ensure they remained within their assigned marsh plot. Any escapes were recorded and wandering snails placed back into the centre of their respective marsh plot. During the experiment, seven individuals were found to be missing and were omitted from the analysis, reducing the overall sample size to $N = 73$ individuals (43 females and 30 males).

Data collection

A bioassay approach was used to determine the effects of tidal gradient extremes (high vs low tide) and daily temperature changes (range: 23°C – 34°C) on individual boldness. Here, individual boldness was determined by the latency to emerge from a hiding response (Seaman & Briffa 2015). Each snail was lifted from its resident marsh plot and held over a white photo tray. Pressure was applied to the foot of the snail with a blunt-ended seeker, causing the foot to be retracted into the shell and for the operculum to be fully closed over the shell aperture. The snail was then placed on the photo tray, with the aperture facing upwards. Response latencies, recorded as the time taken (in seconds) for the operculum to reopen and for the first antennae to become visible to the observer (Seaman & Briffa 2015), ranged from 2 – 183s (mean ± s.d., 30.79 ± 22.70s). All observations were conducted by a single observer (T.C.).

Individual latencies were recorded in a random order, twice daily for twelve consecutive days, August 1-12, 2016; during which time the magnitude of tidal range remained relatively consistent in the natural marsh (mean ± s.d., 1.13 ± 0.22m). All recordings took place between 07:00 – 18:00 and were dictated by the tidal cycle. For the first six days, latencies were recorded first at high tide (am) and then at low tide (pm); for the last six days, this pattern was

reversed so that low tide (am) observations were recorded before high tide (pm) observations. This design, together with tide times changing by one hour each day, ensured no systematic confound between tide, temperature and time of day. Specifically, although temperatures were influenced by incoming water, high tide temperatures were not always higher or lower than low tide temperatures. At high tide, snails could be found both above and below the water line, although the majority climbed just above the water and were found feeding, 'attached' or 'glued' to the cordgrass stems (Iacarella & Helmuth 2011). Others remained below the water line, at the base of stems, or attached to stems at the water line. At low tide, all snails were above the water line, fewer snails could be found climbing and the majority were found moving around and or feeding on the exposed marsh surface substrate.

Substrate surface temperature (mean \pm s.d., $30.2 \pm 3.35^{\circ}\text{C}$) was recorded continuously, in each marsh plot, over the period of the study using waterproofed iBUTTON (DS1920) digital temperature loggers (Maxim integratedTM, CA, USA). With a single temperature logger in each plot, a subset of individual snail temperatures was also taken using a non-contact infrared digital thermometer (MD-H6-UKA, Hyology). Simple, one-way ANOVAs were performed to ensure snail temperatures were consistent at the mean level with water temperature during high tide (ANOVA: $F_{1,50} = 2.449$, $p = 0.124$) and with substrate temperature at low tide (ANOVA: $F_{1,50} = 2.772$, $p = 0.102$). Substrate surface temperature was found to be consistent across all marsh plots and between the plots and the surrounding, natural marsh (ANOVA: $F_{4,115} = 0.0137$, $p = 0.999$).

Statistical analyses

Boldness was modelled as the inverse (1/latency) of re-emergence latencies following a hiding response, using a linear mixed effects model. Boldness data were ln-transformed to ensure normality and then standardised to a mean of zero and variance of one (z-transformed). Linear mixed model analysis was undertaken to examine the influence of tide, temperature and time (trial number) on boldness using a fully saturated model containing intercept, tide (high vs low), temperature, trial number, time of day, mass, plot and sex, as fixed effects.

The mean level model:

$$\ln(1/\text{latency}) = \text{intercept} + \text{tide} + \text{temp} + \text{trial} + \text{time} + \text{sex} + \text{patch} + \text{mass}$$

To test for individual differences in mean level boldness and responsiveness to tide, temperature and trial number, we additionally specified the intercept, tide, temperature and trial number effects as random (see below for more details and supporting information **S1** for model code).

The effect of tide was defined such that high tide = 0 and low tide = 1, and temperature data was left-centred, meaning that the intercept variance represented among-individual variation in boldness at high tide and at 23°C. The random slope effect of tide quantifies among-individual variation in responsiveness (changes in boldness) from high tide to low tide. Individual differences in behaviour patterns across days (e.g. Stamps *et al.* 2012), and individual differences in behavioural responses to temperature (Biro *et al.* 2010), were quantified by the random slope effects of trial number and temperature, respectively. Specifying each of these effects as 'random' fits a parameter describing the population mean and a variance parameter describing variation across individuals for each parameter (see Singer & Willett 2003; West *et al.* 2011).

An ‘unstructured’ variance-covariance matrix was specified, meaning that covariance parameters were fit to describe correlations between individual intercept and slope values

$$R = \frac{(var_{int} + 2 * cov_{is} * X_1 + var_s * X_1^2 + 2 * cov_{is} * X_2 + 2 * cov_{ss} * X_1 * X_2 + var_s * X_2^2)}{(var_{int} + 2 * cov_{is} * X_1 + var_s * X_1^2 + 2 * cov_{is} * X_2 + 2 * cov_{ss} * X_1 * X_2 + var_s * X_2^2 + var_{residual})}$$

(cov_{is}) and between individual slope values (cov_{ss}), in addition to the intercept (var_i) and slope (var_s) variance parameters. We also fitted a separate residual variance parameter ($var_{residual}$) for high and low tide situations to test the prediction that high tide situations represent higher risk and thus, at high tide, individuals might exhibit less predictable behaviour (Briffa 2013). This was achieved by creating a new categorical predictor variable for tide (see supporting information **S1**). Analysis was implemented using SAS Proc Mixed, using ReML. The Kenward-Roger method was used to calculate denominator degrees of freedom for the fixed effects (generating non-integer df values), and a type III sums of squares approach for fixed effects (Littell *et al.* 2006). Covariances were re-expressed as a correlation coefficient, using the standard formula: $r = cov / \sqrt{var * var}$.

The analysis revealed significant and substantial random slope effects and consequently, repeatability should not be calculated in the ‘standard’ way due to the rank order of individuals changing across contexts (with tide and temperature, but not trial number: Biro & Stamps 2015). With repeatability varying between contexts, the model of summing variance, presented by Singer and Willett (2003) was followed. The model included additional terms to accommodate the additional variance and covariances for the two significant random slope (s) effects that were found to be significantly different from zero (see Biro *et al.* 2014). The following equation was subsequently generated to express situation-specific repeatability for a given tide (X_1) and temperature (X_2) context:

(Equation. 1)

Where var_{int} is the random intercept variance, var_s is the random slope variance, cov_{is} is the covariance between slopes and intercepts and $\text{var}_{residual}$ is the residual (within-individual) variance.

Results

Mean level results

On average, snails showed a very weak tendency for reduced boldness across trials (Est = -0.0004, SE = 0.001, $F_{1,1521} = 7.8$, $p < 0.005$), however there was a strong trend for increased boldness with increases in temperature from 23°C to 34°C (Est = 0.15, SE = 0.006, $F_{1,109} = 634$, $p < 0.0001$). There was also a strong tendency for increased boldness at low tide (Est = 0.74, SE = 0.05, $F_{1,72.1} = 218$, $p < 0.0001$) compared to high tide (Est = -0.65). Both time of day ($F_{1,947} = 0.94$, $p = 0.33$) and sex ($F_{1,67} = 0.45$, $p = 0.51$) had no effect on mean level boldness. However, mass did have a modest effect ($F_{1,67} = 5.1$, $p = 0.027$) with smaller snails being, on average, bolder than larger individuals. Finally, marsh plot may have had a small effect ($F_{3,67} = 2.3$, $p = 0.09$). The mean-level effects of tidal inundation, temperature and trial number are represented by the red trend-lines in Fig. 1.

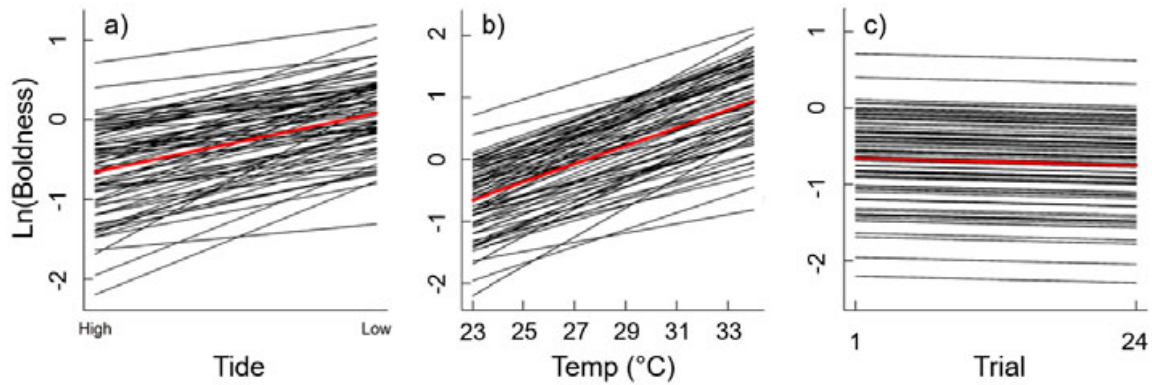


Fig. 1 Individual reaction norms across tides (a) temperatures (b) and trials (c). Black lines represent individual reaction norms and red lines represent the mean-level trend for the population ($N = 73$). Boldness values are expressed in units of standard deviation (see Methods).

Individual-level results

There was substantial individual variation in boldness at high tide (random intercept effect; variance_{high tide} = 0.38, SE = 0.076, $p < 0.0001$), and individuals also differed substantially in responses to changes in tidal cycle, from high to low tide (slope variance = 0.15, SE = 0.030, $p < 0.0001$; see Fig. 1a). Individuals exhibiting higher than average boldness at high tide tended to also exhibit higher boldness at low tide, whereas individuals that were relatively shy at high tide tended to become bolder at low tide (correlation between intercepts and slopes, $r = -0.57$, covariance = -0.136, SE = 0.04, $p = 0.0007$; Fig. 2a). The presence of a significant negative intercept-slope covariance indicates that individual RNs are converging at low tide (i.e. lower variation among individuals at low tide compared to high tide; Fig. 2a).

Individuals also differed in their sensitivity to temperature, with some exhibiting substantially increased boldness with increasing temperatures and others less so (slope variance = 0.0015, SE = 0.00033, $p < 0.0001$; see Fig. 1b). There was some indication that individuals exhibiting higher than average boldness at 23°C were less responsive to increases in temperature, but this effect was small and uncertain (correlation between intercepts and slopes, $r = -0.25$, covariance = -0.0060, SE = 0.0037, $p = 0.107$; Fig. 2b).

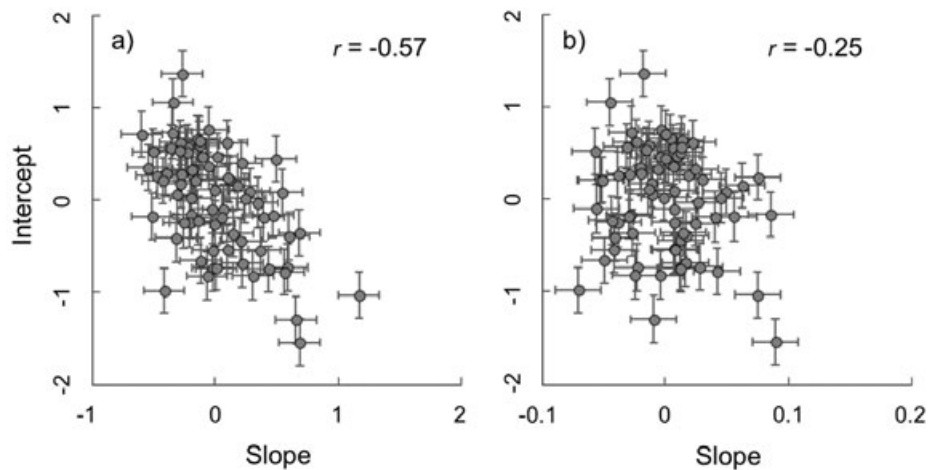


Fig. 2 Estimates of individual intercepts and slopes with regard to tide (a) and to temperature (b). Error bars denote standard error of the predicted values for each individual. Correlation values were estimated from the mixed model, using model variances and covariances.

After accounting for tide and temperature effects, individuals did not differ in their trends of boldness over time, across the many repeated trials. The random effect of trial number, which captures any time-varying factor, including possible habituation, was estimated to be zero - thus, there were no individual differences in temporal RN slopes (Fig. 1c) meaning that individual predicted mean values were maintained relative to one another; this term was thus removed from the model and all estimates of tide and temperature effects (above) are from this reduced model.

Individual plasticity, the responsiveness of individuals to tide and temperature, was correlated across situations such that individuals with stronger positive responses to tide also exhibited stronger positive responses to temperature (covariance between slopes, $r = 0.57$, cov_{ss}

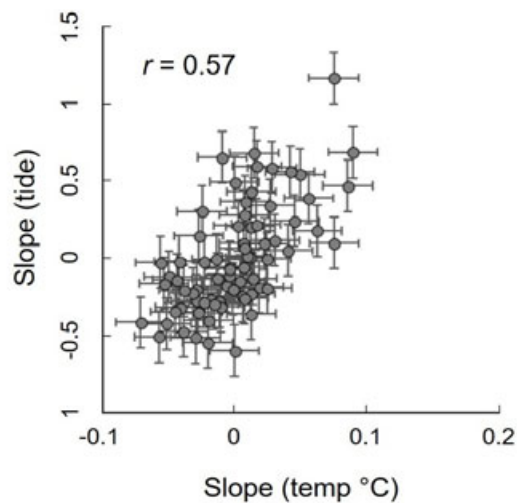


Fig. 3 Individual predicted slopes for reaction norms with respect to tide and to temperature; standard errors of these values is shown. The significant correlation indicates more responsive (plastic) individuals with regard to tidal response were also more responsive to increases in temperature. Correlation value was estimated from the mixed model, using slope variances and the cov_{ss} = 0.0086, SE = 0.0025, $p = 0.0005$; Fig. 3).

The inclusion of a separate residual variance for high and low tide situations provided an improved fit for the data and proved highly significant (Likelihood ratio test: $X_1^2 = 216$, $p < 0.0001$). This separate residual variance provided estimates of unpredictability, another form of plasticity, which was three times higher at high tide (Est = 0.29, SE = 0.015) than at low tide (Est = 0.092, SE = 0.0049). Based on the (co-)variances and residual variance at high tide, repeatability of boldness at high tide and 23°C was $R = 0.57$, and at high tide and 34°C was $R = 0.61$. At low tide and 23°C it was $R = 0.74$, and at low tide and 34°C was $R = 0.85$.

Discussion

Discussions on the causes and consequences of behavioural plasticity often include domain generality as a common assumption, meaning that some individuals are expected to be more plastic, in general, than others (DeWitt, Sih & Wilson 1998; Sih & Del Giudice 2012). However, thus far there is a lack of empirical evidence to support this in labile behavioural traits (Stamps 2016; Mitchell & Biro 2017). Our results revealed that there was indeed a correlation between individual reaction norm (RN) slopes for tide and temperature, such that individuals that increased boldness more in response to increased temperature also increased boldness more in response to low tide conditions. This study therefore seemingly provides the first support for consistent behavioural plasticity across environmental gradients. Our study also revealed that individual predicted mean values of boldness were highly consistent over time in a given tide and temperature context, given the lack of any temporal plasticity (Fig. 1c). Boldness was also highly predictable in a given tide and temperature context, given the rather high situation-specific repeatability (R) estimates (0.57 to 0.87), indicating that individual reaction norms were quite distinct and predictable.

Our findings, that some individuals were more plastic than others in their expression of boldness across tide and temperature gradients, could support the idea that phenotypic behavioural variation is underpinned by one or more common underlying variables (Stamps 2016; Mitchell & Biro 2017), such as those associated with individual metabolism (Van Dijk, Staaks & Hardewig 2002; Careau *et al.* 2008; Biro & Stamps 2010; Biro *et al.* 2018) or individual information states (e.g. risk perception: Rodríguez-Prieto *et al.* 2010; Briffa 2013; Dorset *et al.* 2017). In the context of this study, the propensity for boldness (risk-taking) should be higher under less risky situations (Dammhahn & Almeling 2012; Thomson *et al.* 2012). Indeed, we observed this mean-level effect at low tide, a finding that supports previous work on *L. irrorata* showing that the incoming tide represents a considerably higher risk of predation (Warren 1985;

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West & Williams 1986; Vaughn & Fisher 1988, 1992). The individual differences in responsiveness to tide (=risk) we observed could be linked to differences in metabolism (Killen, Marras & McKenzie 2011; Killen *et al.* 2012; Robison, Chapman & Bidwell 2018), providing a mechanistic 'bridge' for why responsiveness to risk was linked to temperature. Indeed, ectotherm metabolism is directly affected by changes in external temperature (Clarke & Johnston 1999), and we observed the expected mean-level increase in boldness with temperature, in addition to among-individual responses to temperature. This seems to indicate individual variation in sensitivity to metabolic state (Biro *et al.* 2010; Pruitt, Demes & Dittrich-Reed 2011; Careau *et al.* 2014; Mitchell & Biro 2017), which in turn might explain the covarying behavioural patterns observed. If valid, we would expect to observe similar patterns of correlated plasticity in other traits previously linked to risk taking, such as activity and aggression, where behavioural syndromes are present (Sih & Bell 2008). Similar patterns might also be expected for individual growth; where bolder individuals are expected to experience higher growth rates as a result of increased food intake (Stamps 2007; Biro & Stamps 2008; Biro *et al.* 2014).

In our study, individuals that were less responsive to changes in tide-related risk and to temperature also tended to be bolder overall. Evidence for this comes from the strong negative covariance between predicted boldness at high tide compared to low tide. Simply put, bolder individuals had relatively high and flat reaction norms with respect to tide and temperature contexts. This seems to suggest that bold individuals have reduced scope to express variation in behaviour and/or low sensitivity to external and internal cues that influence information gathering relating to risk and affect metabolism, respectively. Thus, supporting the suggestion that bolder (or more pro-active) individuals should be generally less flexible than shy (reactive) individuals (see e.g. Benus, Koolhaas & Van Oortmerssen 1987; Benus *et al.* 1990; Koolhaas *et al.* 1999). Low responsiveness to risk cues and temperature could be due to low-

stress responsiveness (Groothuis & Carere 2005) or potentially due to a reduced aerobic scope that in turn reduces the latitude for behavioural flexibility (Biro *et al.* 2018).

An individual's assessment of risk has previously been found to affect plasticity of a variety of traits including boldness (Briffa 2013) and exploration (Quinn *et al.* 2012) as well as behaviour relating to foraging (Quinn & Cresswell 2005), parental care (Ghalambor 2002) and nest site placement (Peluc *et al.* 2008). Consequently, assessment of risk should be considered an important factor in modifying behaviour in variable environments. Indeed, individual boldness changed significantly across high and low tide situations, which carry different levels of risk. Individual response to risk was also evident where individuals were significantly less predictable in a high risk (high tide) situation. This finding, although contrary to those reported for amphibian, *Rana dalmatina*, tadpoles (Urszán *et al.* 2018), is consistent with similar observations in intertidal invertebrates (Briffa 2013), and with previous suggestions that behaviour should be less predictable under high-risk situations (Maye *et al.* 2007; Brembs 2011). This provides further insight into state-behaviour relationships; where extrinsic information regarding risk (perception of risk), associated with different situations, may well be considered as an important factor affecting individual state.

The highly labile nature of behavioural traits makes studying individual variation in plasticity challenging, from both experimental and statistical (sample size) perspectives. That we were able to detect covariance between individual plasticity on two environmental gradients is likely due to a combination of substantial among individual variation, substantial samples sizes ($N = 73 \text{ IDs} \times 24 \text{ reps} = 1752$) that enhance power and precision of model parameters, and the semi-controlled conditions leading to individual RNs that were quite predictable and distinct from one another. This was reflected by the rather high situation-specific repeatability of boldness across all situations (range: $R = 0.57 - 0.85$). Repeatability was lower at high tide and

23°C and highest at low tide and 34°C, in significant part due to residual (intra-individual) variation being much lower at low tide than high tide.

We notably found no evidence of among-individual variation in temporal patterns of boldness (i.e. no temporal plasticity). Often, studies find evidence for individual changes in behaviour over time indicative of acclimation or habituation to protocols (Bell & Peeke 2012; Dingemanse *et al.* 2012; Stamps *et al.* 2012; Briffa *et al.* 2016). Lack of temporal plasticity indicates that individual predicted mean values were highly consistent over time in a given tide and temperature situation. Thus, in addition to showing that individuals differed in plasticity in response to two environmental gradients, we also provide strong evidence of consistent individual differences in boldness over time, a hallmark of personality.

To summarise, our most novel and interesting observation is that of covariance between individual temperature and tide RN slopes indicating some individuals are more plastic than others in their expression of boldness across tide and temperature gradients. Both tide along with its risk-related information state, and temperature with its internal metabolic state, had significant influences on the behaviour of *L. irrorata* and therefore, this study provides further support for the influence of state variables as possible drivers of individual behaviour. Although this variation in plasticity might represent a strategy for coping with risk, future work should incorporate predation into the experimental design in order to examine the fitness consequences of the variation observed here (Briffa 2013). The findings of this study also support previous suggestions that fluctuating environments may increase the variability of behavioural phenotypes (Luttbeg & Sih 2010), and lead to the question of whether intertidal environments, themselves, select for greater flexibility in behavioural response to risk. In this regard, *L. irrorata* represents a potential model organism for future studies in which to compare labile behavioural traits of individuals exposed to the highly variable saltmarsh environment.

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Author contributions

T.C. designed the experiment, coordinated and carried out data collection; participated in data analysis and led the writing of the manuscript. P.A.B. led on the statistical analysis and supported the drafting of the manuscript. R.S. facilitated field data collection supported manuscript revisions. I.D.M. supported the conception of the study, the experimental design and the drafting of the manuscript. All authors contributed conceptually to study and manuscript drafts and all authors gave final approval for publication.

Data Accessibility

Data and code are available at <http://doi.org/10.5061/dryad.n5b54j0> (Cornwell *et al.* 2018).

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Fig. 1 Individual reaction norms across tides (a) temperatures (b) and trials (c). Black lines represent individual reaction norms and red lines represent the mean-level trend for the population ($n = 73$). Boldness values are expressed in units of standard deviation (see Methods).

Fig. 2 Estimates of individual intercepts and slopes with regard to tide (a) and to temperature (b). Error bars denote standard error of the predicted values for each individual. Correlation values were estimated from the mixed model, using model variances and covariances.

Fig. 3 Individual predicted slopes for reaction norms with respect to tide and to temperature; standard errors of these values is shown. The significant correlation indicates more responsive (plastic) individuals with regard to tidal response were also more responsive to increases in temperature. Correlation value was estimated from the mixed model, using slope variances and the covariance.