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**Integration of physiology, behaviour and life-history traits:
personality and pace-of-life in a marine gastropod.**

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ABSTRACT

Attempts to unravel the proximate and ultimate causes of individual behavioural and life history variation have often pointed to predicted correlations between behavioural, physiological and life-history traits, forming pace-of-life syndromes (POLS). The POLS hypothesis predicts that high levels of production (growth, fecundity) require high levels of foraging effort and risk-taking, supported by high metabolism. Despite tremendous interest in this topic, the POLS hypothesis still has limited empirical support, which has led to calls for more stringent empirical tests of the hypothesis and its assumptions. To that end, we examined the associations between risk-taking behaviour (boldness), resting metabolic rate (RMR) and somatic growth rate in a marine gastropod, *Littoraria irrorata*, under controlled laboratory conditions using a longitudinal repeated measures design. After accounting for the effects of sex, size, and time (trial number), a multivariate mixed model revealed that bolder individuals had higher RMR, and grew faster, whereas RMR and growth were not strongly correlated. Further, if individuals were bolder than their average on a given day, then their RMR was also higher. Our study represents rare and compelling support for the POLS hypothesis, simultaneously studying its three key components (behaviour, energetics and life history), the success of which we attribute to careful control, concurrent sampling of each trait, and rigorous analysis of the among- and within-individual patterns of variation and covariance.

Key-words animal personality, boldness, growth rate, *Littoraria irrorata*, metabolic rate, multivariate mixed effects model, pace-of-life.

INTRODUCTION

Recent attempts to explain the evolution of life history and behavioural diversification have highlighted the importance of links between behaviour, physiology and life-history characteristics, which are predicted to form pace-of-life syndromes (POLS; Ricklefs & Wikelski 2002). The POLS hypothesis highlights that individuals within single populations align along a gradient of slow to fast life history (LH) — in particular, it emphasises physiological constraints as being key to constraining life-history variation along this continuum, and points to the integration and co-evolution of behavioural, physiological and life-history characteristics (Ricklefs & Wikelski, 2002).

Keen interest by behavioural ecologists to understand the development and maintenance of consistent behavioural phenotypes (*aka* animal personalities) subsequently led to similar hypotheses being proposed, and refined. For example, Stamps (2007) suggested that trade-offs between growth and mortality could explain the existence of personality trait variation for behaviours related to resource acquisition, such as activity, boldness or territoriality. Later theoretical developments included how resting metabolic rate (RMR) and LH productivity (growth and reproduction) could act as proximate constraints on behaviour to explain animal personality, where behavioural variation is maintained as a result of trade-offs between productivity and mortality, or present and future reproduction (Biro & Stamps, 2008, 2010; Careau, Thomas, Humphries, & Réale, 2008; Wolf & Weissing, 2010). Further theoretical development then brought together an even greater suite of physiological, behavioural and life-history traits (Réale et al., 2010).

In essence, these POLS hypotheses predict that individuals with faster LH should also have higher metabolic rates, fast growth, more active and bolder behaviour, and lower stress responsiveness. While early literature reviews provided substantial evidence for positive correlations between metabolism and behaviours that provide and/or consume significant

energy (Biro & Stamps, 2010; Careau et al., 2008), and between behaviours that provide energy for production of new biomass (Biro & Stamps, 2008), subsequent studies generally have not (Dammhahn, Dingemanse, Niemelä, & Réale, 2018). Indeed, a recent meta-analysis found little to no evidence for positive correlations among these traits as predicted by the POLS hypothesis (Royauté, Berdal, Garrison, & Dochtermann, 2018). However, it did find significant but weak correlations between behaviour and hormones ($r = 0.18$) and between behaviour and growth rate ($r = 0.23$); the work concluded that a reason for weak or no correlations may have resulted from methodological challenges associated with studying and analysing individual behaviour (Royauté *et al.* 2018; see also Niemelä & Dingemanse 2018).

A challenge when studying this topic is the fact that behaviour and physiological traits are highly labile, meaning they are sensitive to study protocols and methods, and to environmental variation (Beckmann & Biro, 2013; Biro, Adriaenssens, & Sampson, 2014; Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013). This is why it is important to study this topic in controlled experiments, using many individuals and repeated measures, where physiology, behaviour and life history are concurrently sampled (Biro et al., 2014; Biro & Stamps, 2008, 2010; Careau et al., 2008). Unfortunately, about a third of recently reviewed POLS studies had no repeated measures for the labile traits considered (Royauté et al., 2018), which tends to downwardly bias any correlation that may be present (Adolph & Hardin, 2007). Conversely, there is also the possibility of upward bias where studies use best linear unbiased predictions (BLUPS) from separate univariate mixed-models to estimate correlations between traits. An approach that fails to account for the error around individual-level predictions — potentially leading to anticonservative hypothesis tests and small confidence intervals (Housley & Wilson, 2017). In addition, another recent meta-analysis also found little support for correlations between behaviours and metabolism or hormones, and painted an even bleaker picture of the quality of data and analyses used in most studies (Niemelä & Dingemanse,

2018). This has led to calls for more stringent empirical research testing the predictions made by the POLS hypothesis (Biro et al., 2014; Dammhahn et al., 2018).

Of particular interest within the POLS hypothesis is the expected association between behavioural traits and metabolic rate (Biro & Stamps, 2010; Careau et al., 2008; Metcalfe, Van Leeuwen, & Killen, 2016; Réale et al., 2010). Proximate explanations for this relationship centre on relatively expensive metabolic ‘machinery’ being necessary to support a comparatively active, fast paced, productive and risky life style (Biro & Stamps, 2010; Careau et al., 2008). Therefore, rapid growth, high fecundity and/or frequent reproduction should require high levels of foraging activity and boldness all else being equal, and high RMR is also expected as it likely reflects the underlying machinery needed to support this (Auer, Salin, Anderson, & Metcalfe, 2016; Biro & Stamps, 2010; Careau & Garland, 2012; Killen, Marras, & McKenzie, 2011; Monceau et al., 2017).

Until recently, the majority of research has focussed on testing associations between one behavioural trait and one life-history trait (e.g. Ariyomo & Watt, 2012; Biro et al., 2014; Klun, Siitari, & Brommer, 2013; Mas-Muñoz, Komen, Schneider, Visch, & Schrama, 2011; Monceau et al., 2017; Niemelä & Dingemanse, 2018; Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009; Ward, Thomas, Hart, & Krause, 2004) or between a behavioural trait and metabolism (e.g. Auer et al., 2016; Binder et al., 2016; Killen et al., 2011; Killen, Marras, Ryan, Domenici, & McKenzie, 2012; Krams et al., 2013, 2017; McKenzie, Belao, Killen, & Rantin, 2015; Réale et al., 2010; Velasque & Briffa, 2016; White, Kells, & Wilson, 2016). However, given the multidimensional nature of individual variation (Réale et al., 2010), interpreting pairwise correlations of individual traits can be problematic (Dingemanse, Dochtermann, & Wright, 2010; Mathot & Frankenhuys, 2018), and do not allow for the testing of hypotheses related to causation (Santostefano, Wilson, Niemelä, & Dingemanse, 2017). Therefore, it is important to consider the associations between multiple traits in order to

provide reliable assessments of the relationships between them (see e.g. Careau, Beauchamp, Bouchard, & Morand-Ferron, 2019; Einum, Fossen, Parry, & Pélabon, 2019).

Here, the multidimensional associations between risk-taking propensity, metabolism and growth are examined together in a controlled laboratory experiment, using a marine gastropod, *Littoraria irrorata* (Figure 1). We aimed to examine (a) the repeatability of these behavioural and physiological traits, and (b) the among-individual associations between boldness, RMR, and overall growth, as well as the within-individual association between boldness and RMR using a multivariate mixed model approach. Due to the hypothesised functional role played by risk-taking behaviour in mediating life-history trade-offs (Biro & Stamps, 2008; Stamps, 2007; Wolf, Van Doorn, Leimar, & Weissing, 2007), we expected to observe faster overall growth in those individuals most prone to risk-taking behaviour. Further, where risk-taking behaviour may be necessary during foraging to satisfy the higher energy demands of individuals with higher metabolism (Biro & Stamps, 2010; Careau & Garland, 2012; Killen et al., 2011; Monceau et al., 2017), we also expected that individual propensity for risk-taking (boldness) would covary with RMR in a positive direction. Based on these predictions, and the idea that higher relative growth should associate with higher RMR (e.g. Biro & Stamps, 2010), we also expected to observe that individuals with relatively high RMR would exhibit faster overall growth.

METHODS

Collection and husbandry

Data collection was undertaken at the Virginia Institute of Marine Science (VIMS), Eastern Shore Laboratory (ESL), Wachapreague, VA, USA. All living materials were obtained from the adjacent, *Sporobolus alterniflorus* (formerly *Spartina alterniflora*) dominated saltmarsh system, sheltered by the U.S Atlantic barrier island system. The mean high water of 1.28m

and a mean low water of 0.05m in this area results in the upper intertidal range experiencing daily tidal inundation to a height of approximately 0.3 m (NOAA, 2018).

We haphazardly collected $N = 72$ adult snails, 17-28mm shell length, at low tide from a 5m² area of high-marsh, adjacent to the ESL (37°36'31.2"N 75°41'09.3"W) in July 2016. Since Littorinids are known to exhibit indeterminate growth (Boulding & Hay, 1993; Vermeij & Signore, 1992) estimates of individual life stage were based on field observations made by Hamilton (1978). All snails were transported to the laboratory and excess water was removed from the shells prior to being individually marked (1-72) using acrylic paint covered with a thin layer of non-toxic aquarium glue (Cornwell, McCarthy, Snyder, & Biro, 2019; Stagg & Mendelssohn, 2012). Individual snails were then sexed, by visual assessment for the presence or absence of the male reproductive organ (42 females and 30 males). Only animals with fully intact shells, and without any obvious parasites, were included in the study.

Experimental design

Snails were initially allocated (randomly) to one of four outdoor ‘replica marsh plots’ (0.30m²) ($N = 4$), where conditions were comparable with that of the adjacent natural marsh. Marsh plots (60 x 50 x 5cm) were constructed using marsh cores taken from the nearby saltmarsh (37°36'31.2"N 75°41'09.3"W), each including *S. alterniflorus* roots and intact standing stems. The plots were positioned in water tables (248cm x 61cm x 20cm), each connected to a flow through-system, circulating water from and back to the nearby Wachapreague channel. Within each water table, tidal inundations were simulated daily by replicating the tidal patterns in the natural marsh, at the point of material collection. Daily changes in water level were also replicated, approximately, by referring to a guide measure placed in the natural marsh, visible from the marsh plots.

Within each plot, plant biomass density (biomass $\text{m}^{-2} \pm \text{SD}$, $215.3 \pm 2.1\text{g}$) and *S. alterniflorus* height (mean $\pm \text{SD}$, $143 \pm 12.83\text{cm}$) were comparable to that of the nearby natural marsh (biomass m^{-2} $255.3 \pm 103.1\text{g}$; stem height $178\text{cm} \pm 32.83$, mean $\pm \text{SD}$). In each marsh plot, snail density (18 snails per plot ≈ 60 snails m^{-2}) was also comparable to the densities found in and around the point of material collection (85 ± 15 snails m^{-2}). Individuals were housed outdoors in these plots for 30 days to allow them to feed, *ad-libitum*, on plant stems and marsh detritus. Animals were monitored daily to ensure all individuals were present, and throughout the experiment all snails remained in marsh plots or within the water tables. This 30 day interval, plus the additional 12d during which we observed behaviour and metabolism, permitted us to quantify growth variation among individuals under semi-natural conditions, over a total duration of 42d; on average, snails increased in length by 0.6% over this interval, representing an estimated increase in mass of 1.62%.

After the initial 30-day period, marsh plots were transported into the laboratory where they were maintained, in ambient conditions for a further twelve days, where feeding could continue *ad-libitum*. Previous work on this species has highlighted the influence of both temperature and tidal cycle on individual behaviour (Cornwell et al., 2019), and thus, we controlled for both tide and temperature during subsequent behavioural trials and metabolic rate measurements. Consequently, snails were measured under high tide conditions, representing conditions indicative of high predation risk (Cornwell et al., 2019; Vaughn & Fisher, 1988, 1992; West & Williams, 1986), and within a consistent temperature range (28-28.5 °C) comparable to that experienced outdoors (mean $\pm \text{SD}$, 28.6 ± 0.90 °C) under high tide conditions.

Growth rates

Shell length was measured after 24 hours of acclimation to the marsh plots, and again before release on the final day of the experiment 42d later. Measurement time was approximately equal across individuals and took no longer than 1 minute. Digital photographs were taken of all individuals prior to being returned to their designated marsh plots, and again at the end of the experiment. Images were later used to re-measure original and final shell length with ImageJ (Image processing and Analysis in Java - Rasband 2011) to provide more accurate measures of individual length ($\pm 0.001\text{mm}$). All shell measurements were undertaken by the same observer.

Risk taking propensity

Once in the laboratory, and after 24 hours of acclimation to controlled conditions, individual boldness was scored as the inverse of latency to emerge from a hiding response as done previously (Cornwell et al., 2019). Briefly, each snail was held over a white photo tray whilst pressure was applied to the animal's foot, using a blunt-ended seeker (dissection probe), eliciting a retraction of the body and closure of the operculum over the shell aperture. Once fully retracted, the snail was placed, aperture facing upward, onto the tray and the time taken for the operculum to re-open and for the first antennae to become visible (response latency) was recorded. To ensure consistency, all observations were conducted by a single observer. Response latencies were recorded in a random order, once daily (between 9am and 12pm), for nine consecutive days, yielding a total behavioural sample size of 648 (= 72 individuals x 9 repeats).

Resting metabolic rate

Resting metabolic rate (RMR, $\mu\text{molO}_2/\text{h}$) was calculated using oxygen uptake measurements obtained for aquatic respiration, using stop-flow respirometry, at least five

hours after the behavioural trials undertaken on days 3, 6 and 9 (between 2-8pm). Feeding was prevented after behavioural observations, allowing for clearance of any food consumed prior to behavioural trials (Killen et al., 2011). Furthermore, snails generally remained stationary during respirometry trials, and thus the minimum MR measurement achieved during a trial was defined as its resting MR, hereafter its RMR.

Each respirometer (volume = 140ml) contained a stirring bar, to prevent the formation of oxygen partial pressure (pO_2) gradients during trials and was fitted with an oxygen sensitive optode (Fibox 4, PreSens Gmbh. Regensburg, Germany). Respirometers were supplied from a central reservoir with fully aerated, filtered seawater; maintained at a constant $28 \pm 0.5^\circ\text{C}$ and a salinity of 34ppt. The respirometers were covered with a dark, opaque plastic sheet to create a darkened environment and to reduce disturbance during acclimation and during trials. A preliminary set of experiments determined 1-2h as the acclimation time required for stress-related metabolic elevation to subside and for subsequent stable measures of O_2 uptake in the study animals (see Figure 2). Using this information, each snail was placed in an individual respirometer and was conservatively given 2h to acclimate and settle into the experimental environment prior to any measurements being taken. During these preliminary trials, no faecal matter was present in the respirometry chambers indicating that animals were indeed in a post-absorptive state after feeding ceased at least 5h prior.

After each initial acclimation period, water flow to respirometers (12 + 1 control) was stopped and the decline in $\mu\text{mol } O_2/\text{Litre}$ was measured every 15 minutes, over a 60-minute period, for each animal. Respirometry chambers were not flushed between measures, however O_2 did not fall below 70% during trials. O_2 decline was measured using the Fibox 4 fiber optic oxygen meter (PreSens Gmbh. Regensburg, Germany), which automatically standardises barometric pressure, temperature and salinity during trials. RMR was recorded as the lowest measure for each individual over the 60-minute period.

To control for any background O₂ fluctuations during the experiment, oxygen consumption was also measured in a control respirometer (sans snail) during each trial. Residual declines in O₂ from the control respirometers (due to microbial, algal activity) were accounted for during the final calculations. As a further control, individual snail shells were scrubbed to remove debris and algae prior to respirometry trials.

Statistical analysis

We used a single multivariate mixed model (MMM) to simultaneously estimate the following: adjusted repeatability of boldness and RMR, correlations among boldness, RMR and growth at the among-individual level, and the correlation between boldness and RMR at the within-individual (residual) level. Residual correlation between growth and other traits is not possible because it is a single value representing growth over 42d. Response latencies (24.39 ± 16.06 s, mean $\pm$ SD) were first inverse ($1/\text{latency}$) transformed to create boldness scores (larger numbers = bolder responses). Boldness values were then ln-transformed to meet the assumptions of normality. RMR (31.98 ± 10.82 $\mu\text{molO}_2/\text{h}$, mean $\pm$ SD) was also ln-transformed to meet the assumption of normality and to ensure a linear relationship with shell length. The response variables boldness and RMR were then centred and standardised to a mean of 0 and a variance of 1 (z-transformed) to facilitate convergence (Schielzeth, 2010).

Fixed effects of trial, sex and initial shell length (t_0) (mm) were fitted for all three traits. To facilitate the interpretation of these fixed effects, sex was treated as a continuous variable (female = 0, male = 1) and centred on the mean, trial number (effect of time) was mean-centred, and initial shell length (t_0) (22.6 ± 2.64 mm, mean $\pm$ SD) was ln-transformed, then centred and standardised to a mean of 0 and a variance of 1 (Houslay & Wilson, 2017). Finally, individual 'ID' was included as a random (intercept) effect. We also fitted a random slope effect of trial number in an initial model; however, the estimated effect was zero, and

its inclusion affected model convergence, making inferences on trait covariance unstable, and thus was omitted from the final analysis.

We included two unstructured variance-covariance matrices. The first (the ‘I-matrix’) accounts for among individual variation in each trait (random intercept effect of individual ‘ID’), estimating the among-individual variance of boldness, RMR and growth (VAR_{ind}) and the covariances between them (COV_{ind}). The second (‘R-matrix’) accounts for the residual variation (within-individual variance; VAR_r) and provides an estimate of covariance between the residual repeated measures of boldness and RMR (COV_e).

Parameters were estimated using the Marko chain Monte Carlo (MCMC) method. To ensure convergence and adequate chain mixing, the posterior distributions and autocorrelation plots of five independent chains were compared, each with a total of 750,000 iterations, 60,000 burn-ins and a thinning interval of 275 iterations (R package 'MCMCglmm' 2.21, Hadfield 2010). Before running the MMM, an ‘uninformative’, parameter-expanded, model prior was specified appropriate for trait error distributions (gaussian for all three traits). This included a prior mean ($\alpha.\mu$) of 0 for each random effect, and a (co)variance matrix ($\alpha.V$) of 1000. For the within-individual variance, it must be noted that since only a single measure of overall growth was recorded for each individual, growth has no residual (within-individual) variance and as such, within-individual correlations involving this trait must be 0. However, specified variances must be positive, so we fixed the within-individual variance for growth at a small positive number (0.0001); fixing the residual variance in this way thus means all variance in growth is expressed only at the among-individual level in the I-matrix.

Model (co)variances were used to estimate among-individual (r_{ind}) and within-individual (r_e) correlations between response variables by dividing the corresponding covariance between two variables by the product of the square root of their variances:

$$(r_{ind} = COV_{ind} / (\sqrt{VAR_{ind}} * \sqrt{VAR_{ind}}))$$

$$(r_e = \text{COV}_e / (\text{sqrt}(\text{VAR}_e) * \text{sqrt}(\text{VAR}_e)))$$

Since these correlations can be either positive or negative, we were able to use the 95% credible intervals (CI) to assess statistical clarity (Dushoff, Kain, & Bolker, 2019), and only correlations with a CI excluding zero were considered statistically clear.

Adjusted repeatability (R_j) for boldness and RMR (i.e. conditioned on the fixed effects) were estimated by dividing their respective among-individual variance estimates by the sum of their among-individual and residual variances:

$$(R_j = \text{VAR}_{ind} / (\text{VAR}_{ind} + \text{VAR}_r))$$

The posterior modes of the random effects were then used, following a very informative tutorial by Housley and Wilson (2017), to create graphical representations of r_{ind} to illustrate associations between each of the variables of interest (see Figure 3).

RESULTS

On average, snails showed a tendency for increased boldness (β [95%CI] = 0.026, [0.005 ; 0.047]) and increased RMR (β [95%CI] = 0.032, [0.008 ; 0.054]) across trials. Initial shell length had a clear effect on boldness, RMR and overall growth, with larger individuals tending towards higher RMR (β [95%CI] = 0.841, CI [0.737 ; 0.944]), longer response times (β [95%CI] = -0.249, CI [-0.414 ; -0.073]) and slower growth (β [95%CI] = -0.097, CI [-0.148 ; -0.045]). There was no detectable effect of sex for any of the three traits (see Table 1).

After accounting for the fixed effects of trial, sex and mass, both boldness (R_j = 0.49, CI [0.394 ; 0.592]) and RMR (R_j = 0.44 CI [0.303 ; 0.588]) were moderately repeatable, meaning that covariance among the traits was possible. Indeed, the multivariate mixed effects model revealed clear, positive covariance between boldness and RMR at both the among-individual (COV_{ind} = 0.081, CI [0.001 ; 0.154]), and at the within-individual (COV_e = 0.064, CI [0.010 ; 0.116]) levels. These estimates provided moderate correlations at both the among-individual

($r_{\text{ind}} = 0.32$, CI [0.023 ; 0.549]) (Figure 3) and within-individual levels ($r_e = 0.22$, CI [0.042 ; 0.382]). Finally, there was also a clear positive covariance between boldness and growth ($\text{COV}_{\text{ind}} = 0.091$, CI [0.051 ; 0.138]), but no clear covariance between RMR and growth ($\text{COV}_{\text{ind}} = 0.011$, CI [-0.013 ; 0.035]) at the among-individual level. These estimates indicated a strong, positive correlation between boldness and growth ($r_{\text{ind}} = 0.58$, CI [0.398 ; 0.730]) (Figure 3) but not between RMR and growth ($r_{\text{ind}} = 0.13$, CI [-0.146 ; 0.391]) (Figure 3).

DISCUSSION

Our aim was to examine correlations between boldness, RMR and somatic growth in *L. irrorata*, in order to test predictions made by the POLS hypothesis. Our results revealed among-individual correlations between boldness and RMR ($r_{\text{ind}} = 0.32$), and between boldness and growth ($r_{\text{ind}} = 0.58$). Simply put, those with relatively high growth rates had shorter anti-predator response times and thus were considered bolder; bolder individuals also had relatively higher RMR. Thus, our results provide rare and compelling evidence for among-individual covariation between boldness and RMR, and between boldness and growth, commensurate with the predictions made by the POLS hypothesis (Biro & Stamps, 2010; Careau et al., 2008; Réale et al., 2010; Ricklefs & Wikelski, 2002; Stamps, 2007; Wolf & Weissing, 2010).

The clear, positive association between behaviour and metabolism (RMR), at both the among- and within-individual levels reinforces previous suggestions that individual behavioural variation may be underpinned by energetic constraints (Biro et al., 2018; Biro & Stamps, 2010; Careau et al., 2008; Van Dijk, Staaks, & Hardewig, 2002). In particular, RMR may reflect differences in the idling cost of the ‘metabolic machinery’ required for periods of maximal energy expenditure (Auer, Killen, & Rezende, 2017; Biro & Stamps, 2010), such as those experienced during predator avoidance. In this case, relatively high RMR animals may

be generating higher energy output whilst also requiring more energy to sustain themselves. Therefore, boldness affecting foraging and food intake rates would be expected to covary with RMR to pay the cost of higher overall RMR. Further, given that food was available *ad libitum* and that conditions were standardised, observed links between metabolism and behaviour may reflect developmental plasticity in a common direction, or they may be genetically correlated (Brzek, Gebczyński, Ksiazek, & Konarzewski, 2016; Careau et al., 2011; Gębczyński & Konarzewski, 2009), an underlying premise of the POLS hypothesis (Réale et al., 2010).

The high among-individual correlation between boldness and overall growth ($r_{\text{ind}} = 0.59$), along with the general observation that study animals spent much of their time foraging, indicates that boldness plays a functional role in resource acquisition in *L. irrorata*, as predicted by the POLS hypothesis (Biro & Stamps, 2008; Stamps, 2007). Further, this also provides support for the suggestion that consistently high levels of behaviours affecting food intake rates should be exhibited by intrinsically productive individuals (Biro & Stamps, 2008; Stamps, 2007), and adds to the currently limited evidence for among-individual covariation between boldness and growth rate (e.g. Biro et al., 2014). It is also possible (as previously suggested, Biro et al., 2014) that motivation to feed is, for those with higher than average growth rates, a proximate driver for higher levels of boldness, which would be consistent with previous work reporting higher risk-taking and higher food intake as a result of artificial selection or gene manipulation for growth enhancement (Johnsson & Abrahams, 1991; Johnsson, Petersson, Jonsson, & Jarvi, 1996; Sundström & Devlin, 2011). This, along with the correlation(s) persisting despite *ad libitum* food availability may indicate a genetic correlation between boldness and growth, especially given the high r_{ind} observed here (Dochtermann, 2011).

Despite a positive trend for higher overall growth in individuals with higher RMR, our findings indicate that RMR and overall growth were likely not correlated ($r_{\text{ind}} = 0.13$). This

might be contrary to the idea that increased growth rates (and thus higher food intake) should be associated with morphological and physiological systems geared towards processing more food per unit time (Biro & Stamps, 2008). Nevertheless, increased growth has been shown to associate with morphological and physiological traits that improve digestive efficiency in different taxa (Biro, Abrahams, Post, & Parkinson, 2006; Geverink, Heetkamp, Schouten, Wiegant, & Schrama, 2004; Hemsworth, Coleman, Barnett, & Jones, 1994; Selman, Lumsden, Bünger, Hill, & Speakman, 2001; Walsh, Munch, Chiba, & Conover, 2006), and some studies suggest that higher productivity might require higher RMR (Ksiazek, Konarzewski, & Lapo, 2004; McCarthy, 2000; Metcalfe, Taylor, & Thorpe, 1995), likely related to larger morphological structures (e.g. digestive organs, liver, heart etc), which have higher intrinsic mass-specific rates (Ksiazek et al., 2004). It is also possible, given the relatively low growth rates reported here (~0.6% average length gain), that our results could reflect changes in growth rate with individual size in *L. irrorata*, where growth declines with size (and age) (Bingham, 1972). Since the majority of our specimens (shell length; 17-28.3mm) were adult, it is possible that further growth would not increase fecundity to the degree that it might in younger individuals. Thus, energy is likely being channelled to activity, rather than reproductive output. In order to test our assumptions relating to the lack of a clear correlation between growth and RMR, future studies should consider quantifying associations between growth and RMR in different size classes to determine whether younger individuals, yet to reach maturity exhibit higher growth with higher RMR, as predicted by the POLS hypothesis.

Our results also indicate moderate among-individual repeatability in boldness ($R_j = 0.49$) and RMR ($R_j = 0.44$), corresponding with previous findings of invertebrate organisms tested under controlled laboratory conditions (Bell, Hankison, & Laskowski, 2009; Nespolo & Franco, 2007), adding to existing evidence of consistent boldness (personality) in *L.*

irrorata (Cornwell et al., 2019). Further, the observed (co)variance structure suggests that the model of a risk-prone, risk-averse (bold-shy) continuum appears to be valid for this population, under stable temperature and at high tide situations. Both of which have previously been shown to influence among- and within-individual repeatability in this species (Cornwell et al., 2019). Although individual differences in behavioural changes over time are a common observation, indicating varying levels of habituation to experimental protocols (Bell & Peeke 2012; Dingemanse *et al.* 2012; Stamps, Briffa & Biro 2012; Briffa, Jones & Macneil 2016), we observed no evidence for individual behavioural changes in boldness or RMR over time (i.e. temporal plasticity). This finding is similar to that reported previously for this species (Cornwell et al., 2019), and suggests that individual predicted mean values were consistent over time, and thus we provide further evidence of consistent individual behaviour (personality) in *L. irrorata*.

In summary, we identified clear positive correlations between behaviour (boldness) and metabolism (RMR), and between boldness and growth, with a detectable trend towards increased overall growth in relatively high MR animals. Importantly, the association between RMR and boldness was found to be clear at both the among- and within-individual levels. Overall, we provide rare support of a pace-of-life syndrome between boldness, metabolism and somatic growth, which are particularly important given the recent limited support for among-individual correlations between behaviour, physiology, and life-history traits presented recently (Niemelä & Dingemanse, 2018; Royauté et al., 2018). Further, we feel these results also highlight the importance of a combination of careful control, longitudinal repeated measures, and rigorous analysis accounting for the among- and within-individual patterns of variation and covariance in unravelling these associations. Finally, based on assumptions made in previous work on individual behaviour in *L. irrorata* (Cornwell et al., 2019), these results further reinforce the idea that behavioural variation in this species is

influenced by factors associated with individual state, in this case, individual metabolism
(Biro et al., 2018; Biro & Stamps, 2010; Careau et al., 2008; Van Dijk et al., 2002).

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Table 1 Fixed effects fitted to the multivariate mixed model for scaled response variables RMR, boldness and for overall growth in *L. irrorata*.

Trait	Post.mean	l-95% CI	u-95% CI	pMCMC
RMR				
Intercept	-0.0387	-0.1497	0.0591	
Shell length	0.8412	0.7369	0.9442	<0.001
Sex	0.0359	-0.1897	0.2419	0.7578
Trial	0.0315	0.0077	0.0543	0.0080
Boldness				
Intercept	-0.0013	-0.1693	0.1595	
Shell length	-0.2491	-0.4139	-0.0733	0.0016
Sex	0.2428	-0.1075	0.5686	0.1841
Trial	0.0255	0.0052	0.0474	0.0167
Growth				
Intercept	0.9999	0.9496	1.0532	
Shell length	-0.0968	-0.1476	-0.0446	<0.001
Sex	0.0500	-0.0524	0.1629	0.3457

Note that growth was only measured once and thus, trial number was not fitted for this variable. Shown are Posterior means, lower and upper 95% confidence intervals and pMCMC (pMCMC values ($P < 0.01$) are in bold).

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List of figures

Figure 1 The saltmarsh periwinkle, *Littoraria irrorata*.

Figure 2 Metabolic rate ($\mu\text{mol O}_2/\text{L}$) traces of three representative *L. irrorata* during preliminary respirometry trials. Each dot represents O_2 consumption over a 15-minute period. Vertical dashed line indicates minimum acclimation time (2h) used in subsequent trails as the pre-trial acclimation period.

Figure 3 Representation of the among-individual correlations between (a) boldness and RMR, (b) boldness and growth, and (c) growth and RMR in *L. irrorata*. Data are based on the posterior modes of the random effects (equivalent to best linear unbiased predictions, BLUPs) from the multivariate linear mixed model. Error bars denote 95% CIs.

751 **Figure 1**

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763 **Figure 2**

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765 **Figure 3**