

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

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1	Integration of physiology, behaviour and life-history traits:
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25 ABSTRACT

Attempts to unravel the proximate and ultimate causes of individual behavioural and life 26 history variation have often pointed to predicted correlations between behavioural, 27 28 physiological and life-history traits, forming pace-of-life syndromes (POLS). The POLS 29 hypothesis predicts that high levels of production (growth, fecundity) require high levels of 30 foraging effort and risk-taking, supported by high metabolism. Despite tremendous interest in 31 this topic, the POLS hypothesis still has limited empirical support, which has led to calls for 32 more stringent empirical tests of the hypothesis and its assumptions. To that end, we examined 33 the associations between risk-taking behaviour (boldness), resting metabolic rate (RMR) and 34 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 35 36 sex, size, and time (trial number), a multivariate mixed model revealed that bolder individuals 37 had higher RMR, and grew faster, whereas RMR and growth were not strongly correlated. 38 Further, if individuals were bolder than their average on a given day, then their RMR was also 39 higher. Our study represents rare and compelling support for the POLS hypothesis, simultaneously studying its three key components (behaviour, energetics and life history), the 40 41 success of which we attribute to careful control, concurrent sampling of each trait, and 42 rigorous analysis of the among- and within-individual patterns of variation and covariance.

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

50 **INTRODUCTION**

51 Recent attempts to explain the evolution of life history and behavioural diversification have highlighted the importance of links between behaviour, physiology and life-history 52 53 characteristics, which are predicted to form pace-of-life syndromes (POLS; Ricklefs & 54 Wikelski 2002). The POLS hypothesis highlights that individuals within single populations 55 align along a gradient of slow to fast life history (LH) — in particular, it emphasises 56 physiological constraints as being key to constraining life-history variation along this 57 continuum, and points to the integration and co-evolution of behavioural, physiological and 58 life-history characteristics (Ricklefs & Wikelski, 2002).

59 Keen interest by behavioural ecologists to understand the development and maintenance of consistent behavioural phenotypes (aka animal personalities) subsequently led 60 61 to similar hypotheses being proposed, and refined. For example, Stamps (2007) suggested that 62 trade-offs between growth and mortality could explain the existence of personality trait 63 variation for behaviours related to resource acquisition, such as activity, boldness or 64 territoriality. Later theoretical developments included how resting metabolic rate (RMR) and LH productivity (growth and reproduction) could act as proximate constraints on behaviour 65 66 to explain animal personality, where behavioural variation is maintained as a result of trade-67 offs between productivity and mortality, or present and future reproduction (Biro & Stamps, 2008, 2010; Careau, Thomas, Humphries, & Réale, 2008; Wolf & Weissing, 2010). Further 68 69 theoretical development then brought together an even greater suite of physiological, 70 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

75 energy (Biro & Stamps, 2010; Careau et al., 2008), and between behaviours that provide 76 energy for production of new biomass (Biro & Stamps, 2008), subsequent studies generally 77 have not (Dammhahn, Dingemanse, Niemelä, & Réale, 2018). Indeed, a recent meta-analysis 78 found little to no evidence for positive correlations among these traits as predicted by the 79 POLS hypothesis (Royauté, Berdal, Garrison, & Dochtermann, 2018). However, it did find 80 significant but weak correlations between behaviour and hormones (r = 0.18) and between 81 behaviour and growth rate (r = 0.23); the work concluded that a reason for weak or no 82 correlations may have resulted from methodological challenges associated with studying and 83 analysing individual behaviour (Royauté et al. 2018; see also Niemelä & Dingemanse 2018).

84 A challenge when studying this topic is the fact that behaviour and physiological 85 traits are highly labile, meaning they are sensitive to study protocols and methods, and to environmental variation (Beckmann & Biro, 2013; Biro, Adriaenssens, & Sampson, 2014; 86 87 Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). This is why it is important to study 88 this topic in controlled experiments, using many individuals and repeated measures, where 89 physiology, behaviour and life history are concurrently sampled (Biro et al., 2014; Biro & 90 Stamps, 2008, 2010; Careau et al., 2008). Unfortunately, about a third of recently reviewed 91 POLS studies had no repeated measures for the labile traits considered (Royauté et al., 2018), 92 which tends to downwardly bias any correlation that may be present (Adolph & Hardin, 2007). 93 Conversely, there is also the possibility of upward bias where studies use best linear unbiased 94 predictions (BLUPS) from separate univariate mixed-models to estimate correlations between 95 traits. An approach that fails to account for the error around individual-level predictions — 96 potentially leading to anticonservative hypothesis tests and small confidence intervals 97 (Houslay & Wilson, 2017). In addition, another recent meta-analysis also found little support 98 for correlations between behaviours and metabolism or hormones, and painted an even bleaker 99 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 madeby the POLS hypothesis (Biro et al., 2014; Dammhahn et al., 2018).

102 Of particular interest within the POLS hypothesis is the expected association between 103 behavioural traits and metabolic rate (Biro & Stamps, 2010; Careau et al., 2008; Metcalfe, 104 Van Leeuwen, & Killen, 2016; Réale et al., 2010). Proximate explanations for this relationship 105 centre on relatively expensive metabolic 'machinery' being necessary to support a 106 comparatively active, fast paced, productive and risky life style (Biro & Stamps, 2010; Careau 107 et al., 2008). Therefore, rapid growth, high fecundity and/or frequent reproduction should 108 require high levels of foraging activity and boldness all else being equal, and high RMR is 109 also expected as it likely reflects the underlying machinery needed to support this (Auer, Salin, 110 Anderson, & Metcalfe, 2016; Biro & Stamps, 2010; Careau & Garland, 2012; Killen, Marras, 111 & Mckenzie, 2011; Monceau et al., 2017).

112 Until recently, the majority of research has focussed on testing associations between 113 one behavioural trait and one life-history trait (e.g. Ariyomo & Watt, 2012; Biro et al., 2014; 114 Kluen, Siitari, & Brommer, 2013; Mas-Muñoz, Komen, Schneider, Visch, & Schrama, 2011; 115 Monceau et al., 2017; Niemelä & Dingemanse, 2018; Réale, Martin, Coltman, Poissant, & 116 Festa-Bianchet, 2009; Ward, Thomas, Hart, & Krause, 2004) or between a behavioural trait 117 and metabolism (e.g. Auer et al., 2016; Binder et al., 2016; Killen et al., 2011; Killen, Marras, 118 Ryan, Domenici, & Mckenzie, 2012; Krams et al., 2013, 2017; McKenzie, Belao, Killen, & 119 Rantin, 2015; Réale et al., 2010; Velasque & Briffa, 2016; White, Kells, & Wilson, 2016). 120 However, given the multidimensional nature of individual variation (Réale et al., 2010), 121 interpreting pairwise correlations of individual traits can be problematic (Dingemanse, 122 Dochtermann, & Wright, 2010; Mathot & Frankenhuis, 2018), and do not allow for the testing 123 of hypotheses related to causation (Santostefano, Wilson, Niemelä, & Dingemanse, 2017). 124 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).

127 Here, the multidimensional associations between risk-taking propensity, metabolism 128 and growth are examined together in a controlled laboratory experiment, using a marine 129 gastropod, Littoraria irrorata (Figure 1). We aimed to examine (a) the repeatability of these 130 behavioural and physiological traits, and (b) the among-individual associations between 131 boldness, RMR, and overall growth, as well as the within-individual association between 132 boldness and RMR using a multivariate mixed model approach. Due to the hypothesised 133 functional role played by risk-taking behaviour in mediating life-history trade-offs (Biro & 134 Stamps, 2008; Stamps, 2007; Wolf, Van Doorn, Leimar, & Weissing, 2007), we expected to 135 observe faster overall growth in those individuals most prone to risk-taking behaviour. 136 Further, where risk-taking behaviour may be necessary during foraging to satisfy the higher 137 energy demands of individuals with higher metabolism (Biro & Stamps, 2010; Careau & 138 Garland, 2012; Killen et al., 2011; Monceau et al., 2017), we also expected that individual 139 propensity for risk-taking (boldness) would covary with RMR in a positive direction. Based 140 on these predictions, and the idea that higher relative growth should associate with higher 141 RMR (e.g. Biro & Stamps, 2010), we also expected to observe that individuals with relatively 142 high RMR would exhibit faster overall growth.

143

144 **METHODS**

145 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 experiencingdaily tidal inundation to a height of approximately 0.3 m (NOAA, 2018).

152 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. 153 154 Since Littorinids are known to exhibit indeterminate growth (Boulding & Hay, 1993; Vermeij 155 & Signore, 1992) estimates of individual life stage were based on field observations made by 156 Hamilton (1978). All snails were transported to the laboratory and excess water was removed 157 from the shells prior to being individually marked (1-72) using acrylic paint covered with a 158 thin layer of non-toxic aquarium glue (Cornwell, McCarthy, Snyder, & Biro, 2019; Stagg & 159 Mendelssohn, 2012). Individual snails were then sexed, by visual assessment for the presence 160 or absence of the male reproductive organ (42 females and 30 males). Only animals with fully 161 intact shells, and without any obvious parasites, were included in the study.

162

163 Experimental design

164 Snails were initially allocated (randomly) to one of four outdoor 'replica marsh plots' 165 $(0.30m^2)$ (N = 4), where conditions were comparable with that of the adjacent natural marsh. 166 Marsh plots (60 x 50 x 5cm) were constructed using marsh cores taken from the nearby 167 saltmarsh (37°36'31.2"N 75°41'09.3"W), each including S. alterniflorus roots and intact 168 standing stems. The plots were positioned in water tables (248cm x 61cm x 20cm), each 169 connected to a flow through-system, circulating water from and back to the nearby 170 Wachapreague channel. Within each water table, tidal inundations were simulated daily by 171 replicating the tidal patterns in the natural marsh, at the point of material collection. Daily 172 changes in water level were also replicated, approximately, by referring to a guide measure 173 placed in the natural marsh, visible from the marsh plots.

Within each plot, plant biomass density (biomass $m^{-2} \pm SD$, 215.3 \pm 2.1g) and S. 174 *alterniflorus* height (mean \pm SD, 143 \pm 12.83cm) were comparable to that of the nearby natural 175 marsh (biomass m⁻² 255.3 \pm 103.1g; stem height 178cm \pm 32.83, mean \pm SD). In each marsh 176 plot, snail density (18 snails per plot ≈ 60 snails m⁻²) was also comparable to the densities 177 found in and around the point of material collection $(85 \pm 15 \text{ snails m}^{-2})$. Individuals were 178 179 housed outdoors in these plots for 30 days to allow them to feed, *ad-libitum*, on plant stems 180 and marsh detritus. Animals were monitored daily to ensure all individuals were present, and 181 throughout the experiment all snails remained in marsh plots or within the water tables. This 182 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, 183 184 over a total duration of 42d; on average, snails increased in length by 0.6% over this interval, 185 representing an estimated increase in mass of 1.62%.

186 After the initial 30-day period, marsh plots were transported into the laboratory where 187 they were maintained, in ambient conditions for a further twelve days, where feeding could 188 continue *ad-libitum*. Previous work on this species has highlighted the influence of both 189 temperature and tidal cycle on individual behaviour (Cornwell et al., 2019), and thus, we 190 controlled for both tide and temperature during subsequent behavioural trials and metabolic 191 rate measurements. Consequently, snails were measured under high tide conditions, 192 representing conditions indicative of high predation risk (Cornwell et al., 2019; Vaughn & 193 Fisher, 1988, 1992; West & Williams, 1986), and within a consistent temperature range (28-194 28.5 °C) comparable to that experienced outdoors (mean \pm SD, 28.6 \pm 0.90 °C) under high 195 tide conditions.

196

197 *Growth rates*

Shell length was measured after 24 hours of acclimation to the marsh plots, and again 198 199 before release on the final day of the experiment 42d later. Measurement time was 200 approximately equal across individuals and took no longer than 1 minute. Digital photographs 201 were taken of all individuals prior to being returned to their designated marsh plots, and again 202 at the end of the experiment. Images were later used to re-measure original and final shell 203 length with ImageJ (Image processing and Analysis in Java - Rasband 2011) to provide more 204 accurate measures of individual length (±0.001mm). All shell measurements were undertaken 205 by the same observer.

206

207 Risk taking propensity

208 Once in the laboratory, and after 24 hours of acclimation to controlled conditions, 209 individual boldness was scored as the inverse of latency to emerge from a hiding response as 210 done previously (Cornwell et al., 2019). Briefly, each snail was held over a white photo tray 211 whilst pressure was applied to the animal's foot, using a blunt-ended seeker (dissection probe), 212 eliciting a retraction of the body and closure of the operculum over the shell aperture. Once 213 fully retracted, the snail was placed, aperture facing upward, onto the tray and the time taken 214 for the operculum to re-open and for the first antennae to become visible (response latency) 215 was recorded. To ensure consistency, all observations were conducted by a single observer. 216 Response latencies were recorded in a random order, once daily (between 9am and 12pm), for 217 nine consecutive days, yielding a total behavioural sample size of 648 (= 72 individuals x 9 218 repeats).

219

220 Resting metabolic rate

Resting metabolic rate (RMR, μmolO₂/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.

228 Each respirometer (volume = 140ml) contained a stirring bar, to prevent the formation 229 of oxygen partial pressure (pO_2) gradients during trials and was fitted with an oxygen sensitive 230 optode (Fibox 4, PreSens Gmbh. Regenburg, Germany). Respirometers were supplied from a 231 central reservoir with fully aerated, filtered seawater; maintained at a constant $28 \pm 0.5^{\circ}$ C and 232 a salinity of 34ppt. The respirometers were covered with a dark, opaque plastic sheet to create 233 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-234 235 related metabolic elevation to subside and for subsequent stable measures of O₂ uptake in the 236 study animals (see Figure 2). Using this information, each snail was placed in an individual 237 respirometer and was conservatively given 2h to acclimate and settle into the experimental 238 environment prior to any measurements being taken. During these preliminary trials, no faecal 239 matter was present in the respirometry chambers indicating that animals were indeed in a post-240 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 µmol O₂/Litre was measured every 15 minutes, over a 60-minute period, for each animal. Respirometry chambers were not flushed between measures, however O₂ did not fall below 70% during trials. O₂ decline was measured using the Fibox 4 fiber optic oxygen meter (PreSens Gmbh. Regenburg, 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 O_2 fluctuations during the experiment, oxygen consumption was also measured in a control respirometer (sans snail) during each trial. Residual declines in O_2 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.

253

254 Statistical analysis

255 We used a single multivariate mixed model (MMM) to simultaneously estimate the 256 following: adjusted repeatability of boldness and RMR, correlations among boldness, RMR 257 and growth at the among-individual level, and the correlation between boldness and RMR at 258 the within-individual (residual) level. Residual correlation between growth and other traits is 259 not possible because it is a single value representing growth over 42d. Response latencies 260 $(24.39 \pm 16.06s, \text{mean} \pm \text{SD})$ were first inverse (1/latency) transformed to create boldness 261 scores (larger numbers = bolder responses). Boldness values were then ln-transformed to meet 262 the assumptions of normality. RMR (31.98 \pm 10.82 µmolO₂/h, mean \pm SD) was also ln-263 transformed to meet the assumption of normality and to ensure a linear relationship with shell 264 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). 265

Fixed effects of trial, sex and initial shell length (t0) (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 (t0) (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, andthus 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*}).

281 Parameters were estimated using the Marko chain Monte Carlo (MCMC) method. To 282 ensure convergence and adequate chain mixing, the posterior distributions and autocorrelation 283 plots of five independent chains were compared, each with a total of 750,000 iterations, 60,000 284 burn-ins and a thinning interval of 275 iterations (R package 'MCMCglmm' 2.21, Hadfield 285 2010). Before running the MMM, an 'uninformative', parameter-expanded, model prior was 286 specified appropriate for trait error distributions (gaussian for all three traits). This included a 287 prior mean (alpha.mu) of 0 for each random effect, and a (co)variance matrix (alpha.V) of 288 1000. For the within-individual variance, it must be noted that since only a single measure of 289 overall growth was recorded for each individual, growth has no residual (within-individual) 290 variance and as such, within-individual correlations involving this trait must be 0. However, 291 specified variances must be positive, so we fixed the within-individual variance for growth at 292 a small positive number (0.0001); fixing the residual variance in this way thus means all 293 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 withinindividual (r_e) correlations between response variables by dividing the corresponding covariance between two variables by the product of the square root of their variances:

297
$$(\mathbf{r_{ind}} = \text{COV}_{ind} / (\text{sqrt}(\text{VAR}_{ind}) * \text{sqrt}(\text{VAR}_{ind})))$$

298
$$(\mathbf{r}_{e} = \text{COV}_{e} / (\text{sqrt}(\text{VAR}_{e}) * \text{sqrt}(\text{VAR}_{e})))$$

299 Since these correlations can be either positive or negative, we were able to use the 95% 300 credible intervals (CI) to assess statistical clarity (Dushoff, Kain, & Bolker, 2019), and only 301 correlations with a CI excluding zero were considered statistically clear.

302 Adjusted repeatability (R_j) for boldness and RMR (i.e. conditioned on the fixed 303 effects) were estimated by dividing their respective among-individual variance estimates by 304 the sum of their among-individual and residual variances:

$$(\mathbf{R}_{j} = \text{VAR}_{ind} / (\text{VAR}_{ind} + \text{VAR}_{r}))$$

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

309

310 **RESULTS**

311 On average, snails showed a tendency for increased boldness (β [95%CI] = 0.026, [0.005 ;

312 0.047]) and increased RMR (β [95%CI] = 0.032, [0.008; 0.054]) across trials. Initial shell

313 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

315 [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]

318 ; 0.592]) and RMR ($R_j = 0.44$ CI [0.303; 0.588]) were moderately repeatable, meaning that

319 covariance among the traits was possible. Indeed, the multivariate mixed effects model

320 revealed clear, positive covariance between boldness and RMR at both the among-individual

321 ($COV_{ind} = 0.081$, CI [0.001; 0.154]), and at the within-individual ($COV_e = 0.064$, CI [0.010;

322 0.116]) levels. These estimates provided moderate correlations at both the among-individual

323 $(r_{ind} = 0.32, CI [0.023; 0.549])$ (Figure 3) and within-individual levels ($r_e = 0.22, CI [0.042;$ 324 0.382]). Finally, there was also a clear positive covariance between boldness and growth 325 $(COV_{ind} = 0.091, CI [0.051; 0.138])$, but no clear covariance between RMR and growth 326 $(COV_{ind} = 0.011, CI [-0.013; 0.035])$ at the among-individual level. These estimates indicated 327 a strong, positive correlation between boldness and growth ($r_{ind} = 0.58$, CI [0.398; 0.730]) 328 (Figure 3) but not between RMR and growth ($r_{ind} = 0.13$, CI [-0.146; 0.391]) (Figure 3). 329

330 **DISCUSSION**

331 Our aim was to examine correlations between boldness, RMR and somatic growth in L. 332 irrorata, in order to test predictions made by the POLS hypothesis. Our results revealed 333 among-individual correlations between boldness and RMR ($r_{ind} = 0.32$), and between boldness 334 and growth ($r_{ind} = 0.58$). Simply put, those with relatively high growth rates had shorter anti-335 predator response times and thus were considered bolder; bolder individuals also had 336 relatively higher RMR. Thus, our results provide rare and compelling evidence for among-337 individual covariation between boldness and RMR, and between boldness and growth, 338 commensurate with the predictions made by the POLS hypothesis (Biro & Stamps, 2010; 339 Careau et al., 2008; Réale et al., 2010; Ricklefs & Wikelski, 2002; Stamps, 2007; Wolf & 340 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).

355 The high among-individual correlation between boldness and overall growth (r_{ind} = 356 0.59), along with the general observation that study animals spent much of their time foraging, 357 indicates that boldness plays a functional role in resource acquisition in L. irrorata, as 358 predicted by the POLS hypothesis (Biro & Stamps, 2008; Stamps, 2007). Further, this also 359 provides support for the suggestion that consistently high levels of behaviours affecting food 360 intake rates should be exhibited by intrinsically productive individuals (Biro & Stamps, 2008; 361 Stamps, 2007), and adds to the currently limited evidence for among-individual covariation 362 between boldness and growth rate (e.g. Biro et al., 2014). It is also possible (as previously 363 suggested, Biro et al., 2014) that motivation to feed is, for those with higher than average 364 growth rates, a proximate driver for higher levels of boldness, which would be consistent with 365 previous work reporting higher risk-taking and higher food intake as a result of artificial 366 selection or gene manipulation for growth enhancement (Johnsson & Abrahams, 1991; 367 Johnsson, Petersson, Jonsson, & Jarvi, 1996; Sundström & Devlin, 2011). This, along with 368 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 369 370 (Dochtermann, 2011).

371 Despite a positive trend for higher overall growth in individuals with higher RMR, our 372 findings indicate that RMR and overall growth were likely not correlated ($r_{ind} = 0.13$). This

373 might be contrary to the idea that increased growth rates (and thus higher food intake) should 374 be associated with morphological and physiological systems geared towards processing more 375 food per unit time (Biro & Stamps, 2008). Nevertheless, increased growth has been shown to 376 associate with morphological and physiological traits that improve digestive efficiency in 377 different taxa (Biro, Abrahams, Post, & Parkinson, 2006; Geverink, Heetkamp, Schouten, 378 Wiegant, & Schrama, 2004; Hemsworth, Coleman, Barnett, & Jones, 1994; Selman, 379 Lumsden, Bünger, Hill, & Speakman, 2001; Walsh, Munch, Chiba, & Conover, 2006), and 380 some studies suggest that higher productivity might require higher RMR (Ksiazek, 381 Konarzewski, & Lapo, 2004; McCarthy, 2000; Metcalfe, Taylor, & Thorpe, 1995), likely 382 related to larger morphological structures (e.g. digestive organs, liver, heart etc), which have 383 higher intrinsic mass-specific rates (Ksiazek et al., 2004). It is also possible, given the 384 relatively low growth rates reported here (~0.6% average length gain), that our results could 385 reflect changes in growth rate with individual size in *L. irrorata*, where growth declines with 386 size (and age) (Bingham, 1972). Since the majority of our specimens (shell length; 17-387 28.3mm) were adult, it is possible that further growth would not increase fecundity to the 388 degree that it might in younger individuals. Thus, energy is likely being channelled to activity, 389 rather than reproductive output. In order to test our assumptions relating to the lack of a clear 390 correlation between growth and RMR, future studies should consider quantifying associations 391 between growth and RMR in different size classes to determine whether younger individuals, 392 yet to reach maturity exhibit higher growth with higher RMR, as predicted by the POLS 393 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*. 398 *irrorata* (Cornwell et al., 2019). Further, the observed (co)variance structure suggests that the 399 model of a risk-prone, risk-averse (bold-shy) continuum appears to be valid for this 400 population, under stable temperature and at high tide situations. Both of which have previously 401 been shown to influence among- and within-individual repeatability in this species (Cornwell 402 et al., 2019). Although individual differences in behavioural changes over time are a common 403 observation, indicating varying levels of habituation to experimental protocols (Bell & Peeke 404 2012; Dingemanse et al. 2012; Stamps, Briffa & Biro 2012; Briffa, Jones & Macneil 2016), 405 we observed no evidence for individual behavioural changes in boldness or RMR over time 406 (i.e. temporal plasticity). This finding is similar to that reported previously for this species 407 (Cornwell et al., 2019), and suggests that individual predicted mean values were consistent 408 over time, and thus we provide further evidence of consistent individual behaviour 409 (personality) in L. irrorata.

410 In summary, we identified clear positive correlations between behaviour (boldness) 411 and metabolism (RMR), and between boldness and growth, with a detectable trend towards 412 increased overall growth in relatively high MR animals. Importantly, the association between 413 RMR and boldness was found to be clear at both the among- and within-individual levels. 414 Overall, we provide rare support of a pace-of-life syndrome between boldness, metabolism 415 and somatic growth, which are particularly important given the recent limited support for 416 among-individual correlations between behaviour, physiology, and life-history traits 417 presented recently (Niemelä & Dingemanse, 2018; Royauté et al., 2018). Further, we feel 418 these results also highlight the importance of a combination of careful control, longitudinal 419 repeated measures, and rigorous analysis accounting for the among- and within-individual 420 patterns of variation and covariance in unravelling these associations. Finally, based on 421 assumptions made in previous work on individual behaviour in L. irrorata (Cornwell et al., 422 2019), these results further reinforce the idea that behavioural variation in this species is

423	influenced by factors associated with individual state, in this case, individual metabolism
424	(Biro et al., 2018; Biro & Stamps, 2010; Careau et al., 2008; Van Dijk et al., 2002).
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Trait	Post.mean	I-95% CI	u-95% Cl	рМСМС
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

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

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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726 List of figures

728	Figure 1	The sa	ltmarch	neriwinkle	Littoraria	irrorata
120	rigure I	The sc	uunaisn	periwilikie,	Liioraria	irroraia.

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730 Figure 2 Metabolic rate (µmol O<sub>2</sub>/L) traces of three representative L. irrorata during
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731 preliminary respirometry trials. Each dot represents O₂ consumption over a 15-minute period.

732 Vertical dashed line indicates minimum acclimation time (2h) used in subsequent trails as the

- 733 pre-trial acclimation period.

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Figure 3 Representation of the among-individual correlations between (a) boldness and RMR,
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(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.

Figure 1



Figure 2



