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

3
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25 **ABSTRACT**

26 Attempts to unravel the proximate and ultimate causes of individual behavioural and life
27 history variation have often pointed to predicted correlations between behavioural,
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
35 conditions using a longitudinal repeated measures design. After accounting for the effects of
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,
40 simultaneously studying its three key components (behaviour, energetics and life history), the
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
52 highlighted the importance of links between behaviour, physiology and life-history
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
60 maintenance of consistent behavioural phenotypes (*aka* animal personalities) subsequently led
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
65 LH productivity (growth and reproduction) could act as proximate constraints on behaviour
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,
68 2008, 2010; Careau, Thomas, Humphries, & Réale, 2008; Wolf & Weissing, 2010). Further
69 theoretical development then brought together an even greater suite of physiological,
70 behavioural and life-history traits (Réale et al., 2010).

71 In essence, these POLS hypotheses predict that individuals with faster LH should also
72 have higher metabolic rates, fast growth, more active and bolder behaviour, and lower stress
73 responsiveness. While early literature reviews provided substantial evidence for positive
74 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
86 environmental variation (Beckmann & Biro, 2013; Biro, Adriaenssens, & Sampson, 2014;
87 Carter, Feeney, Marshall, Cowlshaw, & 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,

100 2018). This has led to calls for more stringent empirical research testing the predictions made
101 by 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 Klun, 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

125 provide reliable assessments of the relationships between them (see e.g. Careau, Beauchamp,
126 Bouchard, & Morand-Ferron, 2019; Eium, 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*

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

150 and a mean low water of 0.05m in this area results in the upper intertidal range experiencing
151 daily 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
153 a 5m² area of high-marsh, adjacent to the ESL (37°36'31.2"N 75°41'09.3"W) in July 2016.
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 (0.30m²) ($N = 4$), 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.

174 Within each plot, plant biomass density (biomass $\text{m}^{-2} \pm \text{SD}$, $215.3 \pm 2.1\text{g}$) and *S.*
175 *alterniflorus* height (mean $\pm \text{SD}$, $143 \pm 12.83\text{cm}$) were comparable to that of the nearby natural
176 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
177 plot, snail density (18 snails per plot ≈ 60 snails m^{-2}) was also comparable to the densities
178 found in and around the point of material collection (85 ± 15 snails m^{-2}). Individuals were
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,
183 permitted us to quantify growth variation among individuals under semi-natural conditions,
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 $28.5\text{ }^{\circ}\text{C}$) comparable to that experienced outdoors (mean $\pm \text{SD}$, $28.6 \pm 0.90\text{ }^{\circ}\text{C}$) under high
195 tide conditions.

196

197 ***Growth rates***

198 Shell length was measured after 24 hours of acclimation to the marsh plots, and again
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 (± 0.001 mm). 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***

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

223 hours after the behavioural trials undertaken on days 3, 6 and 9 (between 2-8pm). Feeding
224 was prevented after behavioural observations, allowing for clearance of any food consumed
225 prior to behavioural trials (Killen et al., 2011). Furthermore, snails generally remained
226 stationary during respirometry trials, and thus the minimum MR measurement achieved
227 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. Regensburg, Germany). Respirometers were supplied from a
231 central reservoir with fully aerated, filtered seawater; maintained at a constant $28 \pm 0.5^\circ\text{C}$ 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
234 preliminary set of experiments determined 1-2h as the acclimation time required for stress-
235 related metabolic elevation to subside and for subsequent stable measures of O_2 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.

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

248 To control for any background O₂ fluctuations during the experiment, oxygen
249 consumption was also measured in a control respirometer (sans snail) during each trial.
250 Residual declines in O₂ from the control respirometers (due to microbial, algal activity) were
251 accounted for during the final calculations. As a further control, individual snail shells were
252 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 ± 16.06 s, mean \pm SD) were first inverse ($1/\text{latency}$) 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 ± 10.82 $\mu\text{molO}_2/\text{h}$, 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
265 mean of 0 and a variance of 1 (z-transformed) to facilitate convergence (Schielzeth, 2010).

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

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

275 We included two unstructured variance-covariance matrices. The first (the ‘I-matrix’)
 276 accounts for among individual variation in each trait (random intercept effect of individual
 277 ‘ID’), estimating the among-individual variance of boldness, RMR and growth (VAR_{ind}) and
 278 the covariances between them (COV_{ind}). The second (‘R-matrix’) accounts for the residual
 279 variation (within-individual variance; VAR_r) and provides an estimate of covariance between
 280 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.

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

297
$$(r_{ind} = COV_{ind} / (\text{sqrt}(VAR_{ind}) * \text{sqrt}(VAR_{ind})))$$

298
$$(r_e = \text{COV}_e / (\text{sqrt}(\text{VAR}_e) * \text{sqrt}(\text{VAR}_e)))$$

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:

305
$$(R_j = \text{VAR}_{ind} / (\text{VAR}_{ind} + \text{VAR}_r))$$

306 The posterior modes of the random effects were then used, following a very informative
 307 tutorial by Houslay and Wilson (2017), to create graphical representations of r_{ind} to illustrate
 308 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
 314 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 ;
 316 -0.045]). There was no detectable effect of sex for any of the three traits (see Table 1).

317 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).

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

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

355 The high among-individual correlation between boldness and overall growth ($r_{\text{ind}} =$
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
369 correlation between boldness and growth, especially given the high r_{ind} observed here
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 ($r_{\text{ind}} = 0.13$). 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.

394 Our results also indicate moderate among-individual repeatability in boldness ($R_j =$
 395 0.49) and RMR ($R_j = 0.44$), corresponding with previous findings of invertebrate organisms
 396 tested under controlled laboratory conditions (Bell, Hankison, & Laskowski, 2009; Nespolo
 397 & 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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445 **REFERENCES**

- 446 Adolph, S. C., & Hardin, J. S. (2007). Estimating phenotypic correlations: Correcting for
 447 bias due to intra-individual variability. *Functional Ecology*, *21*, 178–184.
 448 <https://doi.org/10.1111/j.1365-2435.2006.01209.x>
- 449 Ariyomo, T. O., & Watt, P. J. (2012). The effect of variation in boldness and aggressiveness
 450 on the reproductive success of zebrafish. *Animal Behaviour*, *83*(1), 41–46.
 451 <https://doi.org/10.1016/j.anbehav.2011.10.004>
- 452 Auer, S. K., Killen, S. S., & Rezende, E. L. (2017). Resting vs. active: a meta-analysis of the
 453 intra- and inter-specific associations between minimum, sustained, and maximum
 454 metabolic rates in vertebrates. *Functional Ecology*, *31*(9), 1728–1738.
 455 <https://doi.org/10.1111/1365-2435.12879>
- 456 Auer, S. K., Salin, K., Anderson, G. J., & Metcalfe, N. B. (2016). Flexibility in metabolic
 457 rate and activity level determines individual variation in overwinter performance.
 458 *Oecologia*, *182*(3), 703–712. <https://doi.org/10.1007/s00442-016-3697-z>
- 459 Beckmann, C., & Biro, P. A. (2013). On the validity of a single (boldness) assay in
 460 personality research. *Ethology*, *119*(11), 937–947. <https://doi.org/10.1111/eth.12137>
- 461 Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a
 462 meta-analysis. *Animal Behaviour*, *77*(4), 771–783.
 463 <https://doi.org/10.1016/j.anbehav.2008.12.022>
- 464 Bell, A. M., & Peeke, H. V. S. (2012). Individual variation in habituation: Behaviour over
 465 time toward different stimuli in threespine sticklebacks (*Gasterosteus aculeatus*).
 466 *Behaviour*, *149*(13–14), 1339–1365. <https://doi.org/10.1163/1568539X-00003019>
- 467 Binder, T. R., Wilson, A. D. M., Wilson, S. M., Suski, C. D., Godin, J. G. J., & Cooke, S. J.
 468 (2016). Is there a pace-of-life syndrome linking boldness and metabolic capacity for
 469 locomotion in bluegill sunfish? *Animal Behaviour*, *121*(1), 175–183.

- 470 <https://doi.org/10.1016/j.anbehav.2016.09.006>
- 471 Bingham, F. O. (1972). Shell growth in the gastropod *Littorina irrorata*. *Nautilus*, 85(4),
472 136–141. Retrieved from
473 <https://www.biodiversitylibrary.org/item/34851#page/162/mode/1up>
- 474 Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2006). Behavioural trade-offs
475 between growth and mortality explain evolution of submaximal growth rates. *Journal*
476 *of Animal Ecology*, 75(5), 1165–1171. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2006.01137.x)
477 2656.2006.01137.x
- 478 Biro, P. A., Adriaenssens, B., & Sampson, P. (2014). Individual and sex-specific differences
479 in intrinsic growth rate covary with consistent individual differences in behaviour.
480 *Journal of Animal Ecology*, 83(5), 1186–1195. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2656.12210)
481 2656.12210
- 482 Biro, P. A., Garland Jr, T., Beckmann, C., Ujvari, B., Thomas, F., & Post, J. R. (2018).
483 Metabolic scope as a proximate constraint on individual behavioral variation: effects on
484 ‘personality’, plasticity, and predictability. *The American Naturalist*, 192(2), 142–154.
485 <https://doi.org/https://dx.doi.org/10.1086/697963>
- 486 Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history
487 productivity? *Trends in Ecology and Evolution*, 23(7), 361–368.
488 <https://doi.org/10.1016/j.tree.2008.04.003>
- 489 Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate
490 promote consistent individual differences in behavior? *Trends in Ecology and*
491 *Evolution*, 25(11), 653–659. <https://doi.org/10.1016/j.tree.2010.08.003>
- 492 Boulding, E. G., & Hay, T. K. (1993). Quantitative genetics of shell form of an intertidal
493 snail: Constraints on short-term response to selection. *Evolution*, 47(2), 576–592.
494 <https://doi.org/10.2307/2410072>

- 495 Briffa, M., Jones, N., & Macneil, C. (2016). Responses to threat in a freshwater invader:
496 Longitudinal data reveal personality, habituation, and robustness to changing water
497 temperatures in the “killer shrimp” *Dikerogammarus villosus* (Crustacea: Amphipoda).
498 *Current Zoology*, 62(1), 45–51. <https://doi.org/10.1093/cz/zov001>
- 499 Brzek, P., Gebczyński, A. K., Ksiazek, A., & Konarzewski, M. (2016). Effect of calorie
500 restriction on spontaneous physical activity and body mass in mice divergently selected
501 for basal metabolic rate (BMR). *Physiology and Behavior*, 161(1), 116–122.
502 <https://doi.org/10.1016/j.physbeh.2016.04.022>
- 503 Careau, V., Beauchamp, P. P., Bouchard, S., & Morand-Ferron, J. (2019). Energy
504 metabolism and personality in wild-caught fall field crickets. *Physiology & Behavior*,
505 199, 173–181. <https://doi.org/10.1016/J.PHYSBEH.2018.11.023>
- 506 Careau, V., & Garland, T. (2012). Performance, personality, and energetics: Correlation,
507 causation, and mechanism. *Physiological and Biochemical Zoology*, 85(6), 543–571.
508 <https://doi.org/10.1086/666970>
- 509 Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and
510 animal personality. *Oikos*, 117, 641–653. [https://doi.org/10.1111/j.2008.0030-](https://doi.org/10.1111/j.2008.0030-1299.16513.x)
511 [1299.16513.x](https://doi.org/10.1111/j.2008.0030-1299.16513.x)
- 512 Careau, V., Thomas, D., Pelletier, F., Turki, L., Landry, F., Garant, D., & Réale, D. (2011).
513 Genetic correlation between resting metabolic rate and exploratory behaviour in deer
514 mice (*Peromyscus maniculatus*). *Journal of Evolutionary Biology*, 24(10), 2153–2163.
515 <https://doi.org/10.1111/j.1420-9101.2011.02344.x>
- 516 Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013).
517 Animal personality: What are behavioural ecologists measuring? *Biological Reviews*,
518 88(2), 465–475. <https://doi.org/10.1111/brv.12007>
- 519 Cornwell, T. O., McCarthy, I. D., Snyder, C. R. A., & Biro, P. A. (2019). The influence of

- 520 environmental gradients on individual behaviour: Individual plasticity is consistent
521 across risk and temperature gradients. *Journal of Animal Ecology*, 88(4), 511–520.
522 <https://doi.org/10.1111/1365-2656.12935>
- 523 Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life
524 syndromes: a framework for the adaptive integration of behaviour, physiology and life
525 history. *Behavioral Ecology and Sociobiology*, 72(3), 62.
526 <https://doi.org/10.1007/s00265-018-2473-y>
- 527 Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C.,
528 Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural
529 plasticity across four populations of the great tit *Parus major*. *Journal of Animal*
530 *Ecology*, 81(1), 116–126. <https://doi.org/10.1111/j.1365-2656.2011.01877.x>
- 531 Dingemanse, N. J., Dochtermann, N. A., & Wright, J. (2010). A method for exploring the
532 structure of behavioural syndromes to allow formal comparison within and between
533 data sets. *Animal Behaviour*, 79(2), 439–450.
534 <https://doi.org/10.1016/j.anbehav.2009.11.024>
- 535 Dochtermann, N. A. (2011). Testing Cheverud’s conjecture for behavioral correlations and
536 behavioral syndromes. *Evolution*, 65(6), 1814–1820. [https://doi.org/10.1111/j.1558-
537 5646.2011.01264.x](https://doi.org/10.1111/j.1558-5646.2011.01264.x)
- 538 Dushoff, J., Kain, M. P., & Bolker, B. M. (2019). I can see clearly now: Reinterpreting
539 statistical significance. *Methods in Ecology and Evolution*, 10(6), 756–759.
540 <https://doi.org/10.1111/2041-210X.13159>
- 541 Einum, S., Fossen, E. I. F., Parry, V., & Pélabon, C. (2019). Genetic variation in metabolic
542 rate and correlations with other energy budget components and life history in *Daphnia*
543 *magna*. *Evolutionary Biology*, 46(2), 170–178. [https://doi.org/10.1007/s11692-019-
544 09473-x](https://doi.org/10.1007/s11692-019-09473-x)

- 545 Gębczyński, A. K., & Konarzewski, M. (2009). Locomotor activity of mice divergently
546 selected for basal metabolic rate: A test of hypotheses on the evolution of endothermy.
547 *Journal of Evolutionary Biology*, 22(6), 1212–1220. <https://doi.org/10.1111/j.1420->
548 9101.2009.01734.x
- 549 Geverink, N. A., Heetkamp, M. J. W., Schouten, W. G. P., Wiegant, V. M., & Schrama, J.
550 W. (2004). Backtest type and housing condition of pigs influence energy metabolism.
551 *Journal of Animal Science*, 82(4), 1227–1233.
- 552 Hadfield, J. D. (2010). MCMCglmm: MCMC Methods for Multi-Response GLMMs in R.
553 *Journal of Statistical Software*, 33(2), 1–22. <https://doi.org/10.1002/ana.22635>
- 554 Hamilton, P. V. (1978). Intertidal distribution and long-term movements of *Littorina*
555 *irrorata* (Mollusca: Gastropoda). *Marine Biology*, 46(1), 49–58.
556 <https://doi.org/10.1007/BF00393820>
- 557 Hemsworth, P. H., Coleman, G. J., Barnett, J. L., & Jones, R. B. (1994). Behavioural
558 responses to humans and the productivity of commercial broiler chickens. *Applied*
559 *Animal Behaviour Science*, 41(1–2), 101–114. <https://doi.org/10.1016/0168->
560 1591(94)90055-8
- 561 Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural
562 ecology. *Behavioral Ecology*, 28(4), 948–952. <https://doi.org/10.1093/beheco/ax023>
- 563 Johnsson, J. I., & Abrahams, M. V. (1991). Interbreeding with domestic strain increases
564 foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*):
565 An experimental study. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(2),
566 243–247. <https://doi.org/10.1139/f91-033>
- 567 Johnsson, J. I., Petersson, E., Jonsson, E., & Jarvi, T. (1996). Domestication and growth
568 hormone alter antipredator behaviour and growth patterns in juvenile brown trout,
569 *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(7), 1546–1554.

- 570 Killen, S. S., Marras, S., & Mckenzie, D. J. (2011). Fuel, fasting, fear: Routine metabolic
571 rate and food deprivation exert synergistic effects on risk-taking in individual juvenile
572 European sea bass. *Journal of Animal Ecology*, 80(5), 1024–1033.
573 <https://doi.org/10.1111/j.1365-2656.2011.01844.x>
- 574 Killen, S. S., Marras, S., Ryan, M. R., Domenici, P., & Mckenzie, D. J. (2012). A
575 relationship between metabolic rate and risk-taking behaviour is revealed during
576 hypoxia in juvenile European sea bass. *Functional Ecology*, 26(1), 134–143.
577 <https://doi.org/10.1111/j.1365-2435.2011.01920.x>
- 578 Klun, E., Siitari, H., & Brommer, J. E. (2013). Testing for between individual correlations
579 of personality and physiological traits in a wild bird. *Behavioral Ecology and*
580 *Sociobiology*, 68(2), 205–213. <https://doi.org/10.1007/s00265-013-1635-1>
- 581 Krams, I. A., Kivleniece, I., Kuusik, A., Krama, T., Freeberg, T. M., Mänd, R., ... Mänd, M.
582 (2013). Predation selects for low resting metabolic rate and consistent individual
583 differences in anti-predator behavior in a beetle. *Acta Ethologica*, 16(3), 163–172.
584 <https://doi.org/10.1007/s10211-013-0147-3>
- 585 Krams, I. A., Niemelä, P. T., Trakimas, G., Krams, R., Burghardt, G. M., Krama, T., ...
586 Kortet, R. (2017). Metabolic rate associates with, but does not generate covariation
587 between, behaviours in western stutter-trilling crickets, *Gryllus integer*. *Proceedings of*
588 *the Royal Society B: Biological Sciences*, 284(1851), e20162481.
589 <https://doi.org/10.1098/rspb.2016.2481>
- 590 Ksiazek, A., Konarzewski, M., & Lapo, I. B. (2004). Anatomic and energetic correlates of
591 divergent selection for basal metabolic rate in laboratory mice. *Physiol Biochem Zool*,
592 80(5), 491–499. <https://doi.org/PBZ030084> [pii]\r10.1086/425190
- 593 Mas-Muñoz, J., Komen, H., Schneider, O., Visch, S. W., & Schrama, J. W. (2011). Feeding
594 behaviour, swimming activity and boldness explain variation in feed intake and growth

- 595 of sole (*Solea solea*) reared in captivity. *PLoS ONE*, 6(6), e21393.
596 <https://doi.org/10.1371/journal.pone.0021393>
- 597 Mathot, K. J., & Frankenhuis, W. E. (2018). Models of pace-of-life syndromes (POLS): a
598 systematic review. *Behavioral Ecology and Sociobiology*, 72(3), 41.
599 <https://doi.org/10.1007/s00265-018-2459-9>
- 600 McCarthy, I. D. (2000). Temporal repeatability of relative standard metabolic rate in
601 juvenile Atlantic salmon and its relation to life history variation. *Journal of Fish*
602 *Biology*, 57(1), 224–238. <https://doi.org/10.1006/jfbi.2000.1313>
- 603 McKenzie, D. J., Belao, T. C., Killen, S. S., & Rantin, F. T. (2015). To boldly gulp: standard
604 metabolic rate and boldness have context-dependent influences on risk-taking to
605 breathe air in a catfish. *Journal of Experimental Biology*, 218(23), 3762–3770.
606 <https://doi.org/10.1177/0019464616651161>
- 607 Metcalfe, N. B., Taylor, A. C., & Thorpe, J. E. (1995). Metabolic rate, social status and life
608 history strategies in Atlantic salmon. *Animal Behaviour*, 49, 431–436.
609 <https://doi.org/10.1006/anbe.1995.0056>
- 610 Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in
611 metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology*,
612 88(1), 298–321. <https://doi.org/10.1111/jfb.12699>
- 613 Monceau, K., Dechaume-Moncharmont, F. X., Moreau, J., Lucas, C., Capoduro, R.,
614 Motreuil, S., & Moret, Y. (2017). Personality, immune response and reproductive
615 success: an appraisal of the pace-of-life syndrome hypothesis. *Journal of Animal*
616 *Ecology*, 86(4), 932–942. <https://doi.org/10.1111/1365-2656.12684>
- 617 Nespolo, R. F., & Franco, M. (2007). Whole-animal metabolic rate is a repeatable trait: a
618 meta-analysis. *Journal of Experimental Biology*, 210, 2000–2005.
619 <https://doi.org/10.1242/jeb.013110>

- 620 Niemelä, P. T., & Dingemanse, N. J. (2018). Meta-analysis reveals weak associations
621 between intrinsic state and personality. *Proceedings of the Royal Society B: Biological*
622 *Sciences*, 285(1873), e20172823. <https://doi.org/10.1098/rspb.2017.2823>
- 623 NOAA. (2018). Wachapreague, VA - Station ID: 8631044. Retrieved October 27, 2018,
624 from <https://tidesandcurrents.noaa.gov/stationhome.html?id=8631044>
- 625 Rasband, W. S. (2011). ImageJ, U.S. National Institutes of Health, Bethesda, Maryland,
626 USA. <Http://Imagej.Nih.Gov/Ij/>. Retrieved from <https://ci.nii.ac.jp/naid/10030139275/>
- 627 Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O.
628 (2010). Personality and the emergence of the pace-of-life syndrome concept at the
629 population level. *Philosophical Transactions of the Royal Society B*, 365(1560), 4051–
630 4063. <https://doi.org/10.1098/rstb.2010.0208>
- 631 Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male
632 personality, life-history strategies and reproductive success in a promiscuous mammal.
633 *Journal of Evolutionary Biology*, 22(8), 1599–1607. <https://doi.org/10.1111/j.1420->
634 [9101.2009.01781.x](https://doi.org/10.1111/j.1420-9101.2009.01781.x)
- 635 Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in*
636 *Ecology and Evolution*, 17(10), 462–468. <https://doi.org/10.1016/S0169->
637 [5347\(02\)02578-8](https://doi.org/10.1016/S0169-5347(02)02578-8)
- 638 Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). PACELESS LIFE? A
639 meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and*
640 *Sociobiology*, 72(3), 64. <https://doi.org/10.1007/s00265-018-2472-z>
- 641 Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural
642 mediators of genetic life-history trade-offs: A test of the pace-of-life syndrome
643 hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*,
644 284(1865), e1567. <https://doi.org/10.1098/rspb.2017.1567>

- 645 Schielzeth, H. (2010). Simple means to improve the interpretability of regression
 646 coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113.
 647 <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- 648 Selman, C., Lumsden, S., Bünger, L., Hill, W. G., & Speakman, J. R. (2001). Resting
 649 metabolic rate and morphology in mice (*Mus musculus*) selected for high and low food
 650 intake. *The Journal of Experimental Biology*, *204*, 777–784.
- 651 Stagg, C. L., & Mendelsohn, I. A. (2012). *Littoraria irrorata* growth and survival in a
 652 sediment-restored salt marsh. *Wetlands*, *32*(4), 643–652.
 653 <https://doi.org/10.1007/s13157-012-0297-5>
- 654 Stamps, J. A. (2007). Growth-mortality tradeoffs and “personality traits” in animals.
 655 *Ecology Letters*, *10*(5), 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>
- 656 Stamps, J. A., Briffa, M., & Biro, P. A. (2012). Unpredictable animals: Individual
 657 differences in intraindividual variability (IIV). *Animal Behaviour*, *83*(6), 1325–1334.
 658 <https://doi.org/10.1016/j.anbehav.2012.02.017>
- 659 Sundström, L. F., & Devlin, R. H. (2011). Increased intrinsic growth rate is advantageous
 660 even under ecologically stressful conditions in coho salmon (*Oncorhynchus kisutch*).
 661 *Evolutionary Ecology*, *25*(2), 447–460. <https://doi.org/10.1007/s10682-010-9406-1>
- 662 Van Dijk, P. L. M., Staaks, G., & Hardewig, I. (2002). The effect of fasting and refeeding on
 663 temperature preference, activity and growth of roach, *Rutilus rutilus*. *Oecologia*,
 664 *130*(4), 496–504. <https://doi.org/10.1007/s00442-001-0830-3>
- 665 Vaughn, C. C., & Fisher, F. M. (1988). Vertical migration as a refuge from predation in
 666 intertidal marsh snails: A field test. *Journal of Experimental Marine Biology and*
 667 *Ecology*, *123*(2), 163–176. [https://doi.org/10.1016/0022-0981\(88\)90167-0](https://doi.org/10.1016/0022-0981(88)90167-0)
- 668 Vaughn, C. C., & Fisher, F. M. (1992). Dispersion of the salt-marsh periwinkle *Littoraria*
 669 *irrorata*: Effects of water level, size, and season. *Estuaries*, *15*(2), 246–250.

- 670 <https://doi.org/10.2307/1352699>
- 671 Velasque, M., & Briffa, M. (2016). The opposite effects of routine metabolic rate and
 672 metabolic rate during startle responses on variation in the predictability of behaviour in
 673 hermit crabs. *Behaviour*, *153*(13–14), 1545–1566. [https://doi.org/10.1163/1568539X-](https://doi.org/10.1163/1568539X-00003371)
 674 [00003371](https://doi.org/10.1163/1568539X-00003371)
- 675 Vermeij, G. J., & Signore, P. W. (1992). The geographic, taxonomic and temporal
 676 distribution of determinate growth in marine gastropods. *Biological Journal of the*
 677 *Linnean Society*, *47*(3), 233–247. <https://doi.org/10.1111/j.1095-8312.1992.tb00668.x>
- 678 Walsh, M. R., Munch, S. B., Chiba, S., & Conover, D. O. (2006). Maladaptive changes in
 679 multiple traits caused by fishing: Impediments to population recovery. *Ecology Letters*,
 680 *9*(2), 142–148. <https://doi.org/10.1111/j.1461-0248.2005.00858.x>
- 681 Ward, A. J. . W., Thomas, P., Hart, P. J. B., & Krause, J. (2004). Correlates of boldness in
 682 three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and*
 683 *Sociobiology*, *55*, 561–568. <https://doi.org/10.1007/s00265-003-0751-8>
- 684 West, D. L., & Williams, A. H. (1986). Predation by *Callinectes sapidus* (Rathbun) within
 685 *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and*
 686 *Ecology*, *100*(1–3), 75–95. [https://doi.org/10.1016/0022-0981\(86\)90156-5](https://doi.org/10.1016/0022-0981(86)90156-5)
- 687 White, S. J., Kells, T. J., & Wilson, A. J. (2016). Metabolism, personality and pace of life in
 688 the Trinidadian guppy, *Poecilia reticulata*. *Behaviour*, *153*(13–14), 1517–1543.
 689 <https://doi.org/10.1163/1568539x-00003375>
- 690 Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs
 691 favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584.
 692 <https://doi.org/10.1038/nature05835>
- 693 Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality
 694 differences. *Philosophical Transactions of the Royal Society B*, *365*(1560), 3959–3968.

695 <https://doi.org/10.1098/rstb.2010.0215>

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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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726 **List of figures**

727

728 **Figure 1** The saltmarsh periwinkle, *Littoraria irrorata*.

729

730 **Figure 2** Metabolic rate ($\mu\text{mol O}_2/\text{L}$) traces of three representative *L. irrorata* during
731 preliminary respirometry trials. Each dot represents O_2 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.

734

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

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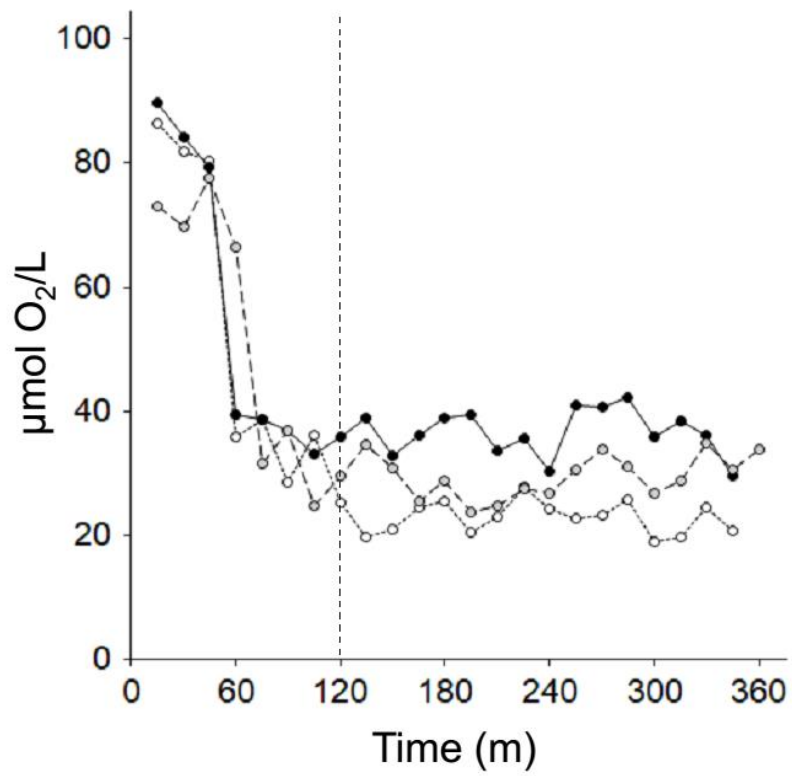
750

751 **Figure 1**



762

763 **Figure 2**



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765 **Figure 3**

