

2023-07

Boldness is not associated with dynamic performance capacity in hermit crabs.

Briffa, Mark

<https://pearl.plymouth.ac.uk/handle/10026.1/21022>

10.1098/rsbl.2023.0224

Biology Letters

The Royal Society

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1 **Boldness is not associated with dynamic performance capacity in hermit crabs.**

2

3 Winne Courtene-Jones

4 Mark Briffa

5

6 School of Biological and Marine Sciences,

7 University of Plymouth,

8 Drake Circus,

9 PL4 8AA.

10 U.K.

11

12 Author for correspondence: mark.briffa@plymouth.ac.uk

13 *Accepted manuscript – published in *Biology Letters**

14

15

16 Boldness, the way an individual reacts to risk, is a commonly studied personality trait in
17 animals. Consistent among-individual differences in startle response durations (latency to
18 recover from a startling stimulus) are frequently assumed to reflect variation in boldness. An
19 alternative explanation is that these latencies are not directly driven by variation in responses
20 to information on risk, but by underlying differences in dynamic performance capacities. Here
21 we investigate this possibility by analysing relations between locomotory speed, a measure of
22 whole-body dynamic performance capacity in hermit crabs, and startle response duration, a
23 repeatable latency measure used as an index of boldness. Individuals differed in mean startle
24 response duration, in the consistency of their startle responses, in their reaction norms across
25 repeated observations, and mean startle responses increased with crab mass. However, there
26 were no relations between startle responses and locomotory speed. This indicates that startle
27 responses do not reflect underlying performance capacities and suggests that they provide
28 insight into differences in how individuals respond to risky situations. Since similar latencies
29 are used as measures of boldness in other animals, we suggest that potential relations between
30 apparent boldness and performance capacity should be tested.

31

32

33

34

35

36 INTRODUCTION

37 Animal personality in its narrowest sense refers to the presence of significant differences
38 among individuals in their behavioural means derived from repeated observations, typically
39 quantified by repeatability and its confidence intervals. Formally, repeatability, is the
40 proportion of variance due to differences between individuals (between individual variance;
41 V_{BA}) out of the total variance including that within individuals (V_{WA}), the latter also called
42 unpredictability [1], predictability [2], residual [3] or intra-individual behavioural variance [4].
43 Within-individual variance itself can differ among individuals and thus can be considered
44 another aspect of animal personality, along with differences between individuals in how their
45 behaviour changes plastically over time or across gradients, where individuals show different
46 behavioural reaction norms [5]. Demonstrating the presence of narrow sense animal personality
47 does not in itself provide insight into its underlying proximate or evolutionary causes [6] but
48 the terms used to describe behaviours, once demonstrated as repeatable, can carry connotations
49 of particular causal factors [7]. For instance, of the five major axes of animal personality, as
50 adapted from human psychology [8], ‘boldness’ has received particular attention. In lay-terms
51 boldness equates to ‘confidence’ and biologically it has been defined as “an individual’s
52 reaction to any risky situation” [8]. Thus boldness, as generally understood, implies differences
53 in how individuals react to information on risk, i.e. their ‘risk-coping strategy’. When
54 confronted with a potentially dangerous event animals may either flee or hide, which includes
55 adopting a protective posture. In this latter case, bolder individuals re-emerge from hiding, and
56 resume ongoing activity, more quickly compared with shyer individuals at the opposite end of
57 a bold-shy continuum. An untested alternative to different risk-coping strategies is that among-
58 individual differences in apparent boldness, instead primarily result from variation in dynamic
59 performance capacities, defined as the ability to perform sustained and rapid movement [9].
60 The latter could be indirectly compatible with differences in risk-coping, if boldness covaries
61 with performance capacities as suggested by the pace of life syndrome hypothesis (POLS) [7,
62 10] for example. However, risk-coping and performance capacities do not necessarily covary
63 and performance capacities could directly drive consistent differences in apparent boldness if
64 they constrain reaction times. Testing for a link between putative measures of boldness and
65 dynamic performance is therefore a potentially important step in interpreting apparent
66 boldness, particularly when measures used as indices of boldness are based on behavioural
67 latencies that could be influenced by speed of movement.

68 A commonly used index of boldness is latency to recover from a startling stimulus, e.g.
69 resumption of ongoing activities after a protective posture has been adopted [1, 11] or re-
70 emergence from a shelter [4, 12-13]. European hermit crabs, *Pagurus bernhardus*, show both
71 fleeing (from a visual cue [14]) and repeatable startle response durations when handled directly
72 [12], measured as time spent tightly retracted into their empty gastropod shell, which hermit
73 crabs use as portable shelters when threatened. This otherwise repeatable behaviour shows
74 plasticity across gradients of risk, lasting longer and [12] and being less predictable [2] in the
75 presence of a predator. Collectively, these results are compatible with underlying differences
76 in risk-coping strategies, but they do not rule out the possibility that they are driven (or driven
77 in part) by underlying differences in performance capacity, particularly as startle responses
78 correlate with metabolic rate [15, 16]. Locomotion speed (measured as time taken to cover a
79 set distance) has been validated an energetically significant activity [17] and a measure of
80 dynamic performance capacity in a previous study on *P. bernhardus*, where slower moving

81 individuals also performed energetically demanding ‘shell rapping’ (which engages the same
82 abdominal muscles used during startle responses) more slowly during subsequent agonistic
83 contests [18]. While the role of abdominal musculature during locomotion remains to be fully
84 elucidated it is likely that these muscles are engaged in order to adjust shell position, so as to
85 maintain a posture where the shell will not interfere with locomotion [17]. Here we ask whether
86 startle response durations are associated with this measure of dynamic performance capacity.
87 If the speed of re-emergence is directly constrained by dynamic performance capacity, or if
88 boldness covaries with performance as predicted by POLS, we should see a positive correlation
89 between mean startle response duration and time taken to walk a set distance (i.e. slower
90 walking individuals hide for longer). A negative correlation (i.e. faster moving individuals hide
91 for longer) is unexpected if latency reflects dynamic performance but could be present for other
92 reasons, for example if investment in high movement speed is part of a wider risk-avoidance
93 syndrome. In this case we would also expect a negative correlation between movement speed
94 and within individual variance in startle response duration, on the assumption that less
95 predictable startle responses mitigate risk [2]. A lack of any correlation in either direction
96 would indicate that startle response durations vary independently of dynamic performance and
97 may instead differ across individuals for other reasons including differences in ability to detect
98 or process information on risk, or differences in sensitivity to such information, i.e. differences
99 in risk-coping strategy .

100

101 **METHODS**

102 Hermit crabs were hand-collected from Hannafore Point, Cornwall UK between February-July
103 2013 (see ESM.1). Following transport back to the lab in Plymouth, crabs were held in groups
104 of ~100 individuals in constantly aerated and filtered seawater at 15°C to a depth of 30cm, in
105 a controlled 12:12 h light:dark environment, and fed *ad libitum* on small pieces of white fish.
106 Prior to observation crabs were removed from their shells by carefully cracking the shell open
107 using a bench vice, then sexed and weighed. Females were given new shells and returned to
108 the sea and only males free of obvious injury or parasites were used in the experiment [19].
109 See ESM section 1 for further details. Male crabs were provided with a new *Littorina littorea*
110 shell 50% of its optimal shell mass, calculated from a previous shell selection experiment,
111 reduced shell size ensuring that continuous locomotion could be stimulated [18]. Males were
112 then individually allocated to white plastic flat-bottomed dishes (20cm diameter), filled with a
113 5cm depth of aerated 15°C seawater. Startle responses were evoked by manually lifting a crab
114 out of the seawater, causing it to retract into its shell [20], and replacing the shell, aperture
115 upwards on the base of the dish. The duration of the response was timed using a stopwatch,
116 until the crab re-emerged to the point where its second pair of walking legs contacted the
117 substrate [12, 20]. In 52 males 8 startle responses were recorded per crab, over a period of 4
118 days, alternating between 16- and 5-hour intervals between successive observations. Following
119 this, each crab was placed into a clear plastic circular raceway (3.25m in outer circumference,
120 6cm wide raceway) filled to a depth of 5cm with aerated 15°C seawater. Each crab was
121 stimulated to walk by a series of light taps on its shell using a wooden probe. Once in motion
122 the crab was followed by the probe at its own speed at a distance of one body length. If a crab
123 stopped moving it immediately received an additional light tap, which caused walking to
124 resume throughout the trial, and did not cause crabs to withdraw into their shell. We obtained
125 two measures of locomotory performance: The time taken to cover 13m (4 laps), a measure of

126 overall performance, and the duration of the fastest lap of the four, a measure of maximum
127 exertion [18]. Due to some data exclusions (see ESM section 2) a final sample size of 407
128 startle responses across 51 crabs was obtained.

129 *Statistical methods*

130 To determine whether variance in startle response durations differed among individuals we
131 conducted an initial Levene's test. This revealed the presence of significant among individual
132 differences in V_{WI} (see below), so prior to further analysis we $\text{Log}_{10}(1+x)$ transformed the data,
133 which yielded homogeneity of variance across individuals, and improved the normality of
134 residuals in subsequent models. There were no correlations between either measure of dynamic
135 performance capacity and mass (see ESM section 2), so we then ran a linear mixed effects
136 model to determine the effects of crab mass, time taken to complete 4 laps, and observation
137 number, on the duration of startle responses. Time taken to complete the fastest lap was used
138 as a predictor in a further model. Random effects included in the initial model were individual
139 specific intercepts and slopes across observations 1-8, with an assumed correlation between
140 them. The model was first fitted using ML estimation so that it could be compared to alternative
141 models were (a) random intercepts and slopes were uncorrelated and (b) only random intercepts
142 were included, using ΔAICc values, where a more complex model was favoured over a simpler
143 one if its AICc value was at least three points lower. Once the appropriate random effects
144 structure was established we re-ran the model using REML estimation to test the fixed effects,
145 using the Satterthwaite method to calculate degrees of freedom. Finally, we calculated (LMM
146 based) repeatability of startle response duration. See ESM section 3 for details of the code and
147 R packages used.

148

149 **RESULTS**

150 Individuals differed in within-individual variance (Levene's test: $F_{50,356} = 3.2$, $P < 0.0001$) but
151 startle responses were still repeatable ($R = 0.61$ [95% CI = 0.473, 0.699], $P_{\text{LRT}} < 00001$). The
152 model including correlated random intercepts and slopes provided the better fit for the data
153 compared with the model containing uncorrelated random effects ($\Delta\text{AICc} = 3.7$) or random
154 intercepts only ($\Delta\text{AICc} = 16.9$), indicating significant variation among individuals in how their
155 startle responses changed across observations (**Figure 1**). Startle response duration did not vary
156 across observations ($F_{1,50.04} = 1.3$, $P = 0.26$) or correlate with time to complete four laps ($F_{1,48}$
157 $= 2.85$, $P = 0.1$; **Figure 2a**) but the duration increased on average with crab mass ($F_{1,48} = 5.26$,
158 $P = 0.026$; **Figure 2b**). Results using time taken to complete the fastest lap were qualitatively
159 identical and are reported in ESM section 2, which also outlines an alternative analytical
160 approach.

161

162 **DISCUSSION**

163 Startle response duration is frequently used as an index of boldness (e.g. [1, 4, 11-14]), and for
164 probing motivational states (e.g. [21, 22]). Here there was no association in either direction
165 between locomotion speed and mean startle responses. Thus, it is unlikely that locomotive
166 performance contributes to repeatable variation in startle response duration in hermit crabs,
167 either as a constraint on dynamic performance capacity, or as an alternative strategy to hiding.

168 In a previous study [23] we found a link between startle response duration and a potential casual
169 factor for dynamic performance capacity, haemocyanin concentration, the respiratory pigment
170 that determines oxygen carrying capacity. In this case, the correlation was in the opposite
171 direction to the expectation under constraints on performance limiting the speed of re-
172 emergence because startle response duration increased rather than decreased with haemocyanin
173 concentration. Thus, it appeared that individuals in good physiological condition behaved in a
174 more risk averse way rather than being more risk prone, perhaps because greater oxygen
175 storage allowed them to tolerate a longer period of respiratory limitation while withdrawn into
176 the shell [23], or because (as suggested above) investment in haemocyanin is part of a wider
177 risk-mitigation syndrome.

178 The current null result for dynamic performance provides further evidence to support
179 the view that startle response duration in hermit crabs provides a direct index of boldness, i.e.
180 variation in risk-coping, albeit one where oxygen carrying capacity may contribute to an upper
181 limit of hiding times [23]. While there was no relation with dynamic performance, other
182 patterns in the current analysis are consistent with previous studies of boldness in hermit crabs.
183 Boldness was repeatable [12, 20, 23], it increased with crab mass [24] and individuals differed
184 in variance around their means [2, 4, 25]. Individuals also differed in how their startle responses
185 changed over repeated observation [4]. Visual inspection of individual slopes indicates that
186 some crabs sensitised (i.e. startle response durations increased with observation number), some
187 habituated (i.e. startle response durations decreased with observation number) but for most
188 crabs there was limited overall change in either direction.

189 Similar patterns are seen in other animal personality studies focussed on boldness and
190 using startle responses or analogous latency measures (e.g. see [4]). We suggest that testing for
191 links between such measures and dynamic performance would clarify the extent to which these
192 patterns represent variation in boldness *per se*. The presence of a correlation where latency
193 decreases as performance capacity increases (note that in the current experiment this would
194 equate to a positive correlation between startle response duration and time taken to complete
195 the locomotory task) could be due to an indirect link between the repeatable behaviour and
196 risk-coping. Alternatively, such a correlation could be present because the repeatable behaviour
197 under test primarily relates to dynamic performance capacity rather than risk-coping. Thus,
198 additional data would then be needed to determine the underpinnings of repeatable latency
199 behaviour. One potential approach would be to collect repeated measures of dynamic
200 performance per individual, ideally time-matched with the collection of repeated startle
201 response data. This would enable between- and within- individual covariation to be
202 distinguished [25] across different conditions of risk exposure (e.g. a predator cue absent and
203 present) and energetic state (which will impact on dynamic performance). Then the relative
204 contribution of each to the means and variances of startle response duration could be assessed.
205 Furthermore, an interaction between risk-level and performance capacity could be tested for.
206 For instance, in systems where dynamic performance capacities do impose constraints on
207 recovery time, such constraints might be greater under low-risk situations where latencies are
208 expected to be relatively short in species that show behavioural plasticity over gradients of risk.
209 In contrast, under high-risk situations with elevated hiding times, we would not expect
210 performance capacity to constrain latency to recover. In the current study though, we found no
211 evidence that startle responses covary with dynamic performance capacity indicating that
212 latency of re-emergence is independent of this measure. This allows us to be less “agnostic”

213 [6] in our interpretation of repeatable startle response durations and lends more confidence to
214 the assumption that they represent consistent differences in risk-coping strategy, or ‘boldness’
215 in terms of how this phrase is generally understood.

216

217 **Acknowledgements**

218 We are grateful to Mark Laidre and an anonymous reviewer for their constructive comments,
219 which helped us to improve the manuscript.

220

221

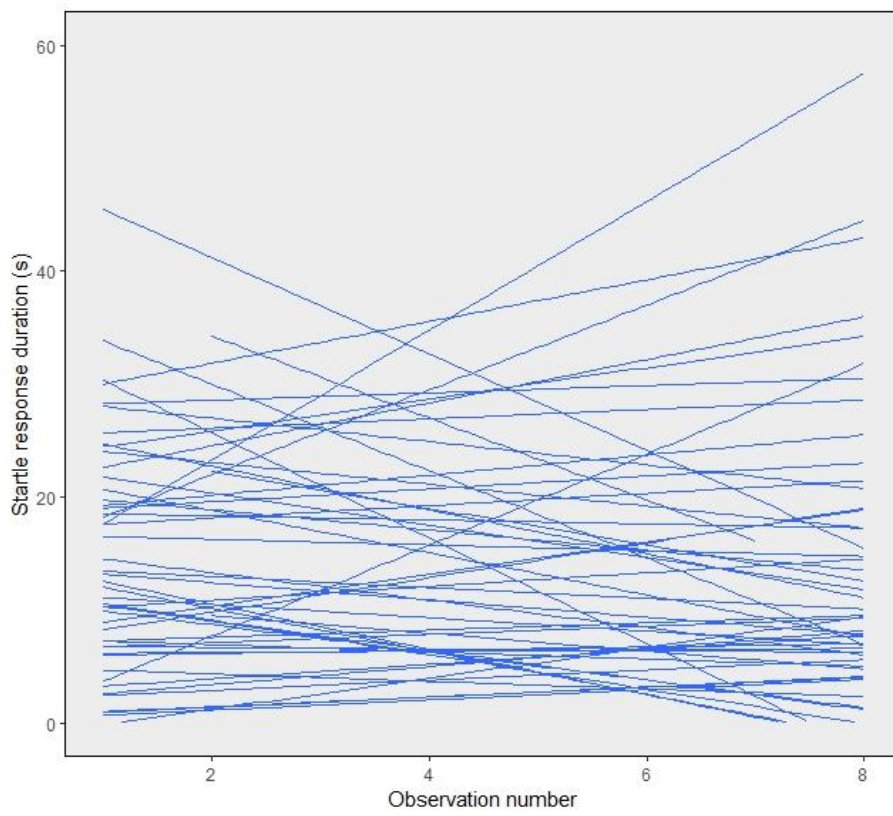
222

223 **REFERENCES**

- 224 1. Maskrey DK, Sneddon LU, Arnold KE, Wolfenden DCC, Thomson JS. 2021.
225 Temperature-driven changes in behavioural unpredictability and personality in the
226 beadlet sea anemone, *Actinia equina*. *Anim. Behav.* **181**, 13-27.
- 227 2. Briffa M. 2013. Plastic proteans: reduced predictability in the face of predation risk in
228 hermit crabs. *Biol. Letts.* **9**, 20130592-20130592.
- 229 3. Westneat DF, Wright J, Dingemanse NJ. 2014. The biology hidden inside residual
230 within-individual phenotypic variation. *Biol. Rev.* **90**, 729-743.
- 231 4. Stamps JA, Briffa M, Biro PA. 2012 Unpredictable animals: individual differences in
232 intraindividual variability (IIV). *Anim. Behav.* **83**, 1325-1334.
- 233 5. Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms:
234 animal personality meets individual plasticity. *TREE* **25**, 81-89.
- 235 6. Bell AM. 2017. There is no special sauce: a comment on Beekman and Jordan. *Behav.*
236 *Ecol.* **28**, 626-627.
- 237 7. Careau V, Garland T. 2012. Performance, Personality, and Energetics: Correlation,
238 Causation, and Mechanism. *Physiol. Biochem. Zool.* **85**, 543-571.
- 239 8. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal
240 temperament within ecology and evolution. *Biol. Rev.* **82**, 291-318.
- 241 9. Jerry F. Husak, Duncan J. Irschick, Stephen D. McCormick, Ignacio T. Moore. 2009.
242 Hormonal regulation of whole-animal performance: Implications for selection. *Integr.*
243 *Comp. Biol.* **49**, 349-353.
- 244 10. Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010.
245 Personality and the emergence of the pace-of-life syndrome concept at the population
246 level. *Phil. Trans. R. Soc. B* **365**, 4051-4063.
- 247 11. Briffa M, Greenaway J. 2011. High *In Situ* Repeatability of Behaviour Indicates Animal
248 Personality in the Beadlet Anemone *Actinia equina* (Cnidaria). *PLoS ONE* **6**, e21963-
249 e21963.
- 250 12. Briffa M, Rundle SD, Fryer A. 2008. Comparing the strength of behavioural plasticity
251 and consistency across situations: animal personalities in the hermit crab *Pagurus*
252 *bernhardus*. *Proc. R. Soc. B* **275**, 1305-11.
- 253 13. Dalesman S, Inchley C. (2008). Interaction between olfactory and visual cues affects flight
254 initiation and distance by the hermit crab, *Pagurus bernhardus*. *Behaviour* **145**, 1479-
255 1492.
- 256 14. Brown C, Jones F, Braithwaite V. 2005. *In situ* examination of boldness–shyness traits
257 in the tropical poeciliid, *Brachyrhaphis episcopi*. *Anim. Behav.* **70**, 1003-1009.

- 258 15. Velasque M, Briffa M. 2016. The opposite effects of routine metabolic rate and
259 metabolic rate during startle responses on variation in the predictability of behaviour in
260 hermit crabs. *Behaviour* **153**, 13-14.
- 261 16. Velasque M, Denton JA, Briffa M. 2023. Under the influence of light: How light
262 pollution disrupts personality and metabolism in hermit crabs. *Environ. Pollut.* **316**,
263 120594.
- 264 17. Herreid CF, Full RJ. 1986. Energetics of hermit crabs during locomotion: the cost of
265 carrying a shell. *J. Exp. Biol.* **120**: 297–308.
- 266 18. Mowles SL, Cotton PA, Briffa M. 2010. Whole-organism performance capacity
267 predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Anim.*
268 *Behav.* **80**, 277-282.
- 269 19. Elwood RW, Neil SJ. 1992. *Assessments and decisions: A study of information*
270 *gathering by hermit crabs*. London: Chapman & Hall.
- 271 20. Briffa M, Bibost A-L. 2009. Effects of shell size on behavioural consistency and
272 flexibility in hermit crabs. *Can. J. Zool.* **87**,. 597-603.
- 273 21. Briffa M, Elwood RW. 2001. Motivational change during shell fights in the hermit crab
274 *Pagurus bernhardus*. *Anim. Behav.* **62**, 505-510.
- 275 22. Moorhouse JE, Fosbrooke IH, Ludlow AR. 1987. Stopping a walking locust with
276 sound: an analysis of variation in behavioural threshold. *Exp. Biol.* **46**, 193-201.
- 277 23. Bridger D, Bonner SJ, Briffa M. 2015. Individual quality and personality: bolder males
278 are less fecund in the hermit crab *Pagurus bernhardus*. *Proc. R. Soc B* **282**, 20142492.
- 279 24. Briffa M, Archer R. 2022. Size specific boldness associated with differences in resource
280 requirements and habitat use: a cross-sectional study in hermit crabs. *Curr. Zool.* p.
281 zoac049.
- 282 25. Niemelä PT, Dingemanse NJ. 2018. On the usage of single measurements in
283 behavioural ecology research on individual differences. *Anim. Behav.* **145**, 99-105.
- 284

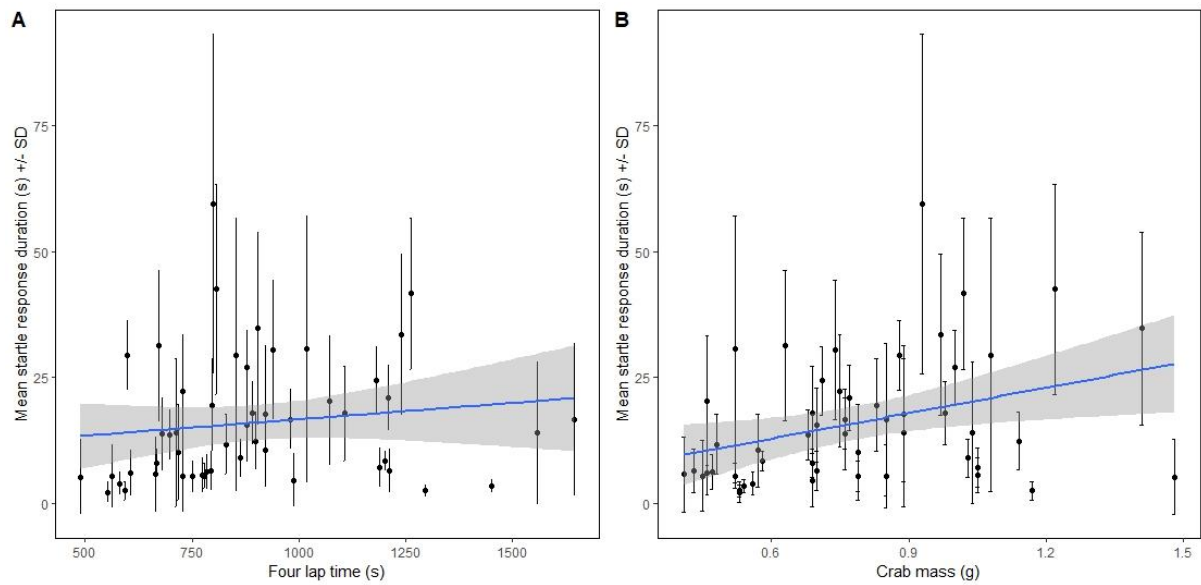
285



286

287 **Figure 1:** Fitted lines representing individual norms of reaction in startle response duration
288 across repeated observations.

289



290

291 **Figure 2:** Individual means (black circles) with standard deviations (black vertical lines) of
 292 startle response durations plotted against (A) time taken to walk 13m and (B) crab mass. Blue
 293 lines represent OLS linear regressions of mean startle response durations against (A) time taken
 294 to complete four laps and (B) crab mass, and shaded areas show the standard error of the
 295 regression.

296

297 **ELECTRONIC SUPPLEMENTARY MATERIAL**

298 **Boldness is not associated with dynamic performance capacity in hermit crabs.**

299

300 Winne Courtene-Jones

301 Mark Briffa

302

303

304 **ESM. 1 STRANGE statement**

305 Hermit crabs were collected from all areas of rockpools, which were searched across open
306 water areas, under algae, in cervices and around the periphery of each pool, to reduce the
307 chance of collection biases for certain behavioural types, which may select different
308 microhabitats and be differently trappable, due to unquantified variation in social experience,
309 age, genetic make-up or preferred environment [1]. Although it is not possible to age hermit
310 crabs data included in the analysis contained only contained crabs of a single size class defined
311 by the preferred species of occupied gastropod shell, *Littorina littorea* [2]. As crabs were wild-
312 caught rather than lab-reared we did not consider potential sampling biases due to differences
313 in rearing history.

314

315 **ESM. 2 Data exclusions and supplementary analyses**

316 Initial inspection of the data indicated that one crab was of a different size class to the rest of
317 the sample (mean mass with large individual removed = 0.79g, SD = 0.25g) and because shell
318 preferences and startle responses vary across size class [2] this single large individual (mass =
319 2.66g) was excluded from the analyses. Additionally, one crab produced a single startle
320 response of unusually long duration (392s) compared to the average (mean with long response
321 removed = 16.05s, SD = 16.28s) and Grubb's test confirmed that this was an outlying value (G
322 = 15.17, $P < 0.0001$). To check whether this outlying value exerted undue leverage on any
323 effects in the LMM, we analysed the data with this data point both included and excluded. The
324 results of both analyses were qualitatively identical (and quantitatively similar) but we chose
325 to report the analysis with the outlying data point excluded in the main Results section (see
326 Table 1), to aid visualisation of the results (in Figure 1). The version of the analysis including
327 the outlier is reported below in Table ESM 1, along with versions of the analysis using time
328 taken to complete the fastest lap, rather than time taken to complete four laps. As mentioned in
329 the main text, prior to these analyses we checked for a correlation between crab mass and the
330 two measures of locomotory performance. To do this we used a pair of linear models where
331 crab mass was the predictor and locomotion was the response. There was no effect of crab mass
332 on the time taken to complete the fastest lap ($F_{1,49} = 0.07$, $P = 0.79$) or on the time taken to
333 complete four laps ($F_{1,49} = 0.06$, $P = 0.81$).

334 In previous studies we analysed similar data using a different analysis approach, doubly
335 hierarchical general linear models (DHGLM), implemented using Bayesian techniques. The
336 advantage of these is that the effects of predictors can be simultaneously modelled on the mean

337 and variance of the response variable, and random effects can be specified for both levels of
 338 analysis, in this way streamlining the analysis. Here we were able to implement such a model
 339 that achieved convergence but (on the basis of the Raftery-Lewis diagnostic) it was not possible
 340 to generate 95% confidence intervals of the posterior means with sufficient accuracy, and
 341 therefore the results of this analysis would need to be interpreted cautiously. Nevertheless, the
 342 results of this version of the analysis are congruent with those obtained via LMM, reported in
 343 the main text. Briefly, there was no effect of dynamic performance or observation number on
 344 mean startle response duration but there was a positive association between crab mass and
 345 startle response duration. There were no effects of dynamic performance or mass on the
 346 variance of startle response durations. It was not possible to include random slopes in mean
 347 model (due to convergence issues) but 95% credible intervals of the random intercept in the
 348 mean model did not cross zero, congruent with the finding of significant repeatability.
 349 Furthermore, 95% credible intervals of the random intercept in the dispersal model did not
 350 cross zero, analogous to the significant Levene’s test showing heterogenous variance among
 351 individuals, reported in the main text. For comparison of results yielded by the two approaches
 352 we include below the results of a DHGLM, where time taken to complete 4 laps was used as a
 353 predictor, and the single outlying startle response duration was excluded from the data (Table
 354 *ESM 2*). As with the LMMs, further analyses including the outlying data point and using fastest
 355 lap time as a predictor produced qualitatively identical results.

356

357 **Table ESM 1.** Supplementary analyses of fixed effects using LMM. (a) LMM using total time
 358 to complete 4 laps of the race way as a predictor and including the outlying startle response
 359 datapoint in the analysis. (b) LMM using time to complete the quickest single lap of the race
 360 way as a predictor and excluding the outlying startle response datapoint from the analysis. (c)
 361 LMM using time to complete the quickest single lap of the race way as a predictor and
 362 including the outlying startle response datapoint from the analysis. All three supplementary
 363 analyses retained the random effects structure of the model reported in the main text.

364

	<i>F</i>	<i>df</i>	<i>P</i>
<i>Model (a)</i>			
Four lap time	3.40	1,48	0.07
Crab mass	6.04	1,48	0.02
Observation	1.83	1,50	0.18
<i>Model (b)</i>			
Fastest lap time	1.84	1,48	0.18
Crab mass	5.11	1,48	0.03
Observation	1.30	1,50	0.23
<i>Model (c)</i>			
Fastest lap time	2.17	1,48	0.15
Crab mass	5.82	1,48	0.02
Observation	1.83	1,50	0.18

365 **Table ESM 2:** Posterior summary statistics for each component of a supplementary DHGLM
 366 analysis.

	Posterior mean	SD	Lower 95% CI	Upper 95% CI
Mean model				
<i>Fixed effects</i>				
Intercept	1.19	0.51	0.18	2.19
Four lap time	0.06	0.04	-0.02	0.14
Crab mass	0.92	0.42	0.08	1.75
Observation	0.00	0.01	-0.03	0.02
<i>Random effect</i>				
Intercept (Crab ID)	0.70	0.08	0.68	0.88
Dispersion model				
<i>Fixed effects</i>				
Intercept	-1.08	0.50	-2.04	-0.09
Four lap time	-0.04	0.04	-0.12	0.03
Crab mass	0.40	0.42	-0.44	1.19
<i>Random effect</i>				
Intercept (Crab ID)	0.53	0.12	0.31	0.78

367

368

369

370 **ESM 3. Details of LMM analysis**

371 *Software used*

372 All analyses were conducted using R 4.2 [3] and using the following packages:

- 373 outliers [4]: Grubb’s to check for outliers.
- 374 lmerTest [5]: Provides df and P for fixed effects in models fitted using lme4.
- 375 lme4 [6]: Fitting mixed effects models.
- 376 AICcmodavg [7]: Calculating AICc values.
- 377 rptR [8]: Estimating LMM based repeatability.
- 378 car [9]: Levene’s Test.

379

380 *Code*

```

381 data <-read.csv("DPSR_LM data.csv")
382 #re-scaling dynamic performance predictor to optimise convergence
383 four.lap.sc <-data$Four.lap.s/100
384 fast.lap.sc <-data$Fastest.lap.s/100

```

```

385
386 newdata<- data.frame(data$ID,data$DURATION, data$Wt, data$Occasion,
387 data$Four.lap.s, four.lap.sc, fast.lap.sc)
388 #(Retains unscaled versions for use in figures)
389
390 #Outlier test and version of data frame excluding it
391 grubbs.test(newdata$data.DURATION)
392
393 newdata.2 <- newdata[!newdata$data.DURATION > 390,]
394 names (newdata.2)
395
396 #Can 4 lap speed and mass both be included as predictors? (Do they
397 correlate)
398 newdata.3 <- newdata[!newdata.2$data.Occasion > 1.1,]
399 plot(newdata.3$four.lap.sc,newdata.3$data.Wt)
400 lm1<-lm(newdata.3$four.lap.sc~newdata.3$data.Wt)
401 lm2<-lm(newdata.3$fast.lap.sc~newdata.3$data.Wt)
402 anova(lm1)
403 anova(lm2)
404 # no correlation, they may both be included.
405
406 #Initial random slopes models, Log10(X+1) and raw
407 m1<-lmer(log(1+data.DURATION) ~ four.lap.sc + data.Wt +
408 data.Occasion + (data.Occasion|data.ID), data = newdata.2)
409 m2<-lmer(data.DURATION ~ four.lap.sc + data.Wt + data.Occasion +
410 (data.Occasion|data.ID), data = newdata.2)
411
412
413 #diagnostics log version m1
414 plot(m1)
415 leveneTest(log(1+data.DURATION)~data.ID, data = newdata.2)
416 par(mfrow=c(1,3))
417 eij=residuals(m1)
418 qqnorm(residuals(m1))

```

```

419 hist(eij,main="Histogram of residuals")
420 plot(density(eij),main="Density plot of
421 residuals",ylab="Density",xlab="Residuals")
422 par(mfrow=c(1,1))
423 #Diagnostics raw version m2
424
425 plot(m2)
426 leveneTest(data.DURATION~data.ID, data = newdata.2)
427
428 par(mfrow=c(1,3))
429 eij=residuals(m2)
430 qqnorm(residuals(m2))
431 hist(eij,main="Histogram of residuals")
432 plot(density(eij),main="Density plot of
433 residuals",ylab="Density",xlab="Residuals")
434 par(mfrow=c(1,1))
435
436 ## choose Log10 model
437 #Random slopes v random intercepts
438
439 m1a<-lmer(log(1+data.DURATION) ~ four.lap.sc + data.Wt +
440 data.Occasion + (data.Occasion|data.ID), data = newdata.2, REML = F)
441 m1b<-lmer(log(1+data.DURATION) ~ four.lap.sc + data.Wt +
442 data.Occasion + (1|data.ID) + (0+data.Occasion|data.ID), data =
443 newdata.2, REML = F)
444 m1c<-lmer(log(1+data.DURATION) ~ four.lap.sc + data.Wt +
445 data.Occasion + (1|data.ID), data = newdata.2, REML = F)
446
447 random_slopes_and_intercept_corrleated <- AICc(m1a)
448 random_slopes_and_intercept_uncorrleated <- AICc(m1b)
449 random_intercept_only <- AICc(m1c)
450
451 AICc <-
452 c(random_slopes_and_intercept_corrleated,random_slopes_and_intercept
453 _uncorrleated,random_intercept_only)

```

```

454 AICc
455 delta.AICc.a.c = random_slopes_and_intercept_corrleated [1] -
456 random_intercept_only [1]
457 delta.AICc.a.b = random_slopes_and_intercept_corrleated [1] -
458 random_slopes_and_intercept_uncorrleated [1]
459 delta.AICc.a.c
460 delta.AICc.a.b
461
462 ## choose random slopes + intercepts
463 anova(m1)
464
465 #Supplementary analyses
466 mSa<-lmer(log(1+data.DURATION) ~ four.lap.sc + data.Wt +
467 data.Occasion + (data.Occasion|data.ID), data = newdata)
468 anova(mSa)
469 mSb<-lmer(log(1+data.DURATION) ~ fast.lap.sc + data.Wt +
470 data.Occasion + (data.Occasion|data.ID), data = newdata.2)
471 anova(mSb)
472 mSc<-lmer(log(1+data.DURATION) ~ fast.lap.sc + data.Wt +
473 data.Occasion + (data.Occasion|data.ID), data = newdata)
474 anova(mSc)
475
476 #Repeatability
477 rpt(log(1+data.DURATION) ~ (1 | data.ID), grname = "data.ID", data =
478 newdata.2, datatype = "Gaussian",
479     nboot = 1000, npermut = 1000)
480 #supplementary version with outlier included
481 rpt(data.DURATION ~ (1 | data.ID), grname = "data.ID", data =
482 newdata.2, datatype = "Gaussian",
483     nboot = 1000, npermut = 1000)
484
485
486
487
488

```


489 **ESM References**

- 490 1. Hills A, Webster MM. 2022. Sampling biases and reproducibility: experimental design
491 decisions affect behavioural responses in hermit crabs. *Anim. Behav.* **194**, 101-110.
492 2. Briffa M, Archer R. 2022. Size specific boldness associated with differences in resource
493 requirements and habitat use: a cross-sectional study in hermit crabs. *Curr. Zool.*
494 p. zoac049. <https://doi.org/10.1093/cz/zoac049>
495 3. R Core Team . 2023. R: A Language and Environment for Statistical Computing}. R
496 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
497 4. Komsta L. 2022. outliers: Tests for Outliers. R package version 0.15.
498 <https://CRAN.R-project.org/package=outlier>.
499 5. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest Package: Tests in Linear
500 Mixed Effects Models. *J. Stat. Softw.* **82**, 1-26. doi:10.18637/jss.v082.i13
501 6. Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using
502 lme4. *J. Stat. Softw.* **67**, 1-48. doi:10.18637/jss.v067.i01.
503 7. Mazerolle MJ. 2020 AICcmodavg: Model selection and multimodel inference based on
504 (Q)AIC(c). R package version 2.3-1. <https://cran.r-project.org/package=AICcmodavg>.
505 8. Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance
506 decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639-
507 1644.
508 9. Fox J, Weisberg S. 2019. *An {R} Companion to Applied Regression*, Third Edition. Thousand
509 Oaks CA: Sage. URL: <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
510

511