

# Who dares doesn't always win: risk-averse rockpool prawns are better at controlling a limited food resource.

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2 *Potential, Risk.*

3 Animal ‘personality’ – the phenomenon of consistent individual differences in behaviour within  
4 populations – has been documented widely, yet its functional significance and the reasons for its  
5 persistence remain unclear. One possibility is that among-individual behavioural variation is linked to  
6 fitness-determining traits via effects on resource acquisition. In this study, we test this idea, using  
7 rockpool prawns (*Palaemon elegans*) to test for a correlation between ‘high-risk exploration’ and the  
8 ability to monopolise a limited resource. Modified open field trials (OFTs) confirmed that consistent  
9 among-individual (co)variation in high-risk exploratory behaviours does exist in this species, and  
10 multivariate analysis shows trait variation is consistent with a major axis of personality variation.  
11 Subsequent feeding trials in size-matched groups where competition was possible revealed a high  
12 repeatability of feeding duration, used here as a proxy for RHP (resource holding potential). We  
13 found significant negative correlations between feeding duration and two ‘risky’ behaviours, such  
14 that individuals that took fewer risks fed more. Our results are not consistent with the widely  
15 hypothesised idea of a ‘proactive syndrome’ in which bolder, risk-taking personalities are positively  
16 associated with RHP. Rather they suggest the possibility of a trade-off, with some individuals  
17 successful at monopolising limited, high-value resources, while others are more willing to engage in  
18 potentially risky exploration (which may increase the likelihood of encountering novel resource  
19 patches). We speculate that alternative strategies for acquiring limited resources might thereby  
20 contribute to the maintenance of personality variation observed in wild populations.

21 The existence of consistent among-individual differences in behaviour, or ‘animal personality’, has  
22 been documented widely in many types of behaviours and in a variety of organisms (Bell, Hankinson,  
23 & Laskowski, 2009; Réale, Dingemanse, Kazem, & Wright, 2010; Japyassú & Malange, 2014). A key  
24 question arising from these findings is why personality persists in wild populations (Sih, Bell, &  
25 Johnstone, 2004). Superficially, complete flexibility of behaviour would appear to be the optimal  
26 strategy when the local environment is changeable. However, studies of other trait types have  
27 emphasised the need to understand costs and limits associated with plasticity (Scheiner, 1993;  
28 DeWitt, Sih, & Wilson, 1998) that are, in general, not well characterised for behaviour (Ghalambor,  
29 Angeloni, & Carroll, 2010). Such costs (including the machinery required to make accurate  
30 predictions in fluctuating environments) are likely to limit the extent of behavioural plasticity as an  
31 adaptive strategy (Dall, Houston, & McNamara, 2004), yet the functional significance of consistent  
32 individual differences remains obscure: does personality provide adaptive advantages, act as an  
33 evolutionary constraint, or is it some combination of the two (Dall et al., 2004; Réale, Reader, Sol,  
34 McDougall, & Dingemanse, 2007; Wolf & Weissing, 2010)? Theoretical treatments have proposed  
35 multiple adaptive explanations for the emergence and maintenance of personality variation (e.g.,  
36 Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010; Wolf & McNamara, 2012), and  
37 researchers are beginning to respond to the call for empirical investigations into links between  
38 behavioural types and traits that could contribute to an individual’s overall fitness (Dingemanse &  
39 Réale, 2005; Smith & Blumstein, 2008).

40 A comprehensive explanation for the existence and maintenance of personality variation is thus  
41 likely to depend (at least in part) upon how behavioural differences contribute to life history  
42 variation (Stamps, 2007). Correlations between personality variation and life history traits have been  
43 shown in invertebrates (Sinn, Apiolaza, & Moltschaniwskyj, 2006; Niemelä, Lattenkamp, &  
44 Dingemanse, 2015), fish (Adriaenssens et al., 2010; Ballew, Mittelbach, & Scribner, 2017), birds  
45 (Dingemanse, Both, Drent, & Tinbergen, 2004; Patrick & Wiemerskirch, 2014), and mammals (Boon,  
46 Réale, & Boutin, 2007; Seyfarth, Silk, & Cheney, 2012). While the interpretation of any such

47 correlations is complicated by the fact that within-individual trade-offs between different life-history  
48 traits largely determine fitness variation (Simpson, 1955; Stearns, 1989), a universal limiting factor to  
49 life-history trait expression is resource availability (Zera & Harshman, 2001). An increased ability to  
50 acquire a limited resource would allow an individual to invest more in all traits, and thereby increase  
51 its overall fitness (van Noordwijk & de Jong, 1986; Reznick, Nunney, & Tessier, 2000; Bolnick et al.,  
52 2011). Where intraspecific competition over a limited resource occurs, an individual's capacity to  
53 monopolise that resource also provides an indication of its competitive ability, or 'resource holding  
54 potential' (RHP; Parker, 1974; Lindström, 1992). Observations of some measure of RHP might  
55 therefore provide insights into fitness variation (Parker, 1974; Smith, 1974), and can also be used at  
56 the individual level to determine associations with other traits of interest. While studies have  
57 typically focused on the effects of morphological differences (in particular, body size) on competitive  
58 outcomes (Tricarico, Benvenuto, Bucciatti, & Gherardi, 2008; Briffa, Sneddon, & Wilson, 2015; Ida &  
59 Wada, 2017), there is increasing recognition that consistent individual behavioural differences may  
60 play a role in determining individual success (Rudin & Briffa, 2012; Camerlink, Arnott, Farish, &  
61 Turner, 2016; Lane & Briffa, 2017).

62 Here, we set out to test for the existence of a link between personality and the ability to monopolise  
63 a limited food resource using the Rockpool Prawn, *Palaemon elegans*. One of the most frequently  
64 studied personality traits is 'boldness', usually defined as an axis of variation in tendency to engage  
65 in risky behaviours (e.g. exploration of novel environments; Wilson, Clark, Coleman, & Dearstyne,  
66 1994). A previous study on this species used a variety of assays that each recorded a single  
67 behaviour nominally considered a distinct personality trait, finding some evidence of consistent  
68 individual differences and correlations across time and situations (Chapman, Hegg, & Ljunberg,  
69 2013). However, the explanatory importance of single behaviours can vary between contexts and  
70 species (Carter, Feeney, Marshall, Cowlshaw & Heinsohn, 2013). As a consequence, empirical  
71 investigations of personality are increasingly seeking to infer personality variation by placing  
72 individuals on axes of variation defined from repeated observations of multiple behaviours (e.g.,

73 Carter & Feeney, 2012; White, Kells, & Wilson, 2016; Houslay, Vierbuchen, Grimmer, Young, &  
74 Wilson, 2017). We follow that trend in this study, where we observed individuals repeatedly in  
75 modified open field trials (OFT; Walsh & Cummins, 1976), measuring movement behaviours in a  
76 novel and 'risky' environment. At the end of the OFT period we created small groups of these  
77 individuals for repeated group resource acquisition trials. In crustaceans, a limited food resource is  
78 expected to induce intraspecific competition for its acquisition (e.g. Barki, Karplus, & Goren, 1992;  
79 Sneddon, Huntingford, & Taylor, 1997; Stewart, McKenzie, Simon, & Baker, 2010). Since the ability to  
80 monopolise a limited resource is already known to be influenced by size in *P. elegans* (Evans  
81 & Shehadi-Moacdieh, 1988), we size-matched individuals in these groups in order to better identify  
82 any additional influence of among-individual behavioural variation as measured by the OFTs.

83 We predicted that (1) there would be consistent individual differences among multiple exploratory  
84 and/or risk-related behaviours assayed in the modified OFTs, (2) those behaviours would be  
85 correlated in such a way as to be consistent with a continuum of parameters traditionally described  
86 as being 'shy-bold' (Wilson et al., 1994), and (3) there would be a clear association between these  
87 correlated risk-related behaviours and an individual's repeatable RHP (measured as the among-  
88 individual variation in feeding duration in group resource acquisition trials). We did not, however,  
89 have a clear prediction for the direction of such an association. Boldness is commonly positively  
90 correlated with resource acquisition (Biro & Stamps, 2008) and/or competitive ability (e.g. Sih, Cote,  
91 Evans, Fogarty, & Pruitt, 2012), a relationship that suggests the presence of a 'proactive syndrome'  
92 (reviewed in Briffa et al., 2015). However, there is increasing recognition that the sign of such  
93 correlations may be dependent on the details of the study system in question (Briffa et al., 2015). In  
94 *P. elegans*, alternative strategies for resource acquisition may be present and maintained through  
95 balancing selection (Wolf & McNamara, 2012). For instance, individuals that take more risks through  
96 exploration might find new resources quickly but be unable to defend them, while more socially  
97 dominant individuals may be better able to monopolise existing resources. In such a scenario,  
98 individuals with higher RHP could be seen to exhibit nominally 'shy' behaviours such as increased

99 refuge use, when in fact this 'shyness' is borne out of an ability to control limited shelter space and  
100 thus a reduced necessity to take risks. This would be in line with the results of Evans & Shehadi-  
101 Moacdieh (1988), who found that shelter residents are more likely to repel intruders, suggesting  
102 that refuge space itself is a limited resource in this species. It would also support their prediction  
103 that it appears to be 'more adaptive' for weaker *P. elegans* to avoid direct confrontation, as  
104 competitive scenarios produce fewer agonistic interactions when individuals are competitively  
105 asymmetrical. In their case weaker individuals were smaller, but in our size-matched trials other  
106 competitive asymmetries could arise. In this case, we predict a negative correlation between  
107 nominally 'bold' tendencies (to engage in risky exploration when shelter was available) and RHP.

## 108 **METHODS**

### 109 ***Capture and Tagging***

110 We collected data in 4 blocks between the 16<sup>th</sup> April and 12<sup>th</sup> June 2016. Each block comprised a 2-  
111 week period during which wild-caught animals were housed in the laboratory and subjected to  
112 behavioural trials and morphological measurements. At the start of each data collection block we  
113 captured 40 prawns (N = 160 in total) from rock pools on Gyllyngvase Beach, Falmouth, on the south  
114 coast of Cornwall, UK (lat: 50.144116, long: -5.068408) and transported them to the laboratory in a  
115 sealed container filled with seawater and enriched with rock shelters. In the laboratory prawns were  
116 kept in a 120 cm x 60 cm x 30 cm aerated home tank, filled to a depth of 25 cm, which was  
117 maintained at a constant temperature of 11.5°C and a salinity of 33-35 parts per thousand. The  
118 home tank was kept in a regular 7am-7pm day-night cycle and was enriched with rocks and sections  
119 of 3 cm diameter plastic piping for prawns to use as refuges.

120 After a 24-hour acclimatisation period we weighed and tagged the prawns. We used coloured  
121 implant elastomer for tagging (Northwest Marine Technology,  
122 <http://www.nmt.us/products/vie/vie.shtml>), allowing us to differentiate between individuals during  
123 data-collection blocks and when taking pre and post-mortem measurements. Tagging involved the

124 injection of a small amount of elastomer under the left and right sides of the third tail carapace  
125 segment. By using 6 colours and injecting two tags for each individual (one on either side of the tail)  
126 it was possible to uniquely tag 36 prawns. The 4 other individuals were retained for use in case of  
127 mortality. Pre-trial weight was also recorded during tagging, for use when size-matching individuals.

128 We then allowed a further 24 hours for recovery before starting behavioural trials. Trials consisted  
129 of a 'boldness' testing phase followed by assays of resource acquisition (described below). Prawns  
130 were fed twice daily on commercial fish food during acclimatisation and open field trials. Morning  
131 feeds (9am) consisted of cyclops (Ocean Nutrition) accompanied by crustacean pellets (Tetra-  
132 Crusta). Evening feeds (4:30pm) consisted of bloodworm (Tropical Marine Centre), again  
133 accompanied by crustacean pellets.

134 At the end of each data collection block, we euthanised individuals through rapid cooling to induce  
135 torpor, followed by transfer to a sealed plastic bag and freezing at -20°C for later examination. We  
136 took post-mortem morphological measurements from all individuals after euthanasia. We measured  
137 and recorded carapace length (measured as the tip of the rostrum to the furthest point of the tail),  
138 weight, and the length of each first periopod (measured as the full length of each clawed  
139 appendage) post-mortem. For analysis, we calculated average weight (from the initial live weight  
140 taken during tagging and the post-mortem weight) across the two-week experimental period. We  
141 also recorded the gravid status of each individual (Appendix A1).

#### 142 ***Open Field Trials (OFTs)***

143 We used a modified form of the standard OFT paradigm, a commonly used test for boldness (Burns,  
144 2008; Toms, Echevarria, & Jouandot, 2010), in which our arena also included a shelter (Fig. 1a), to  
145 characterise among-individual (co)variation in several putatively correlated behaviours. We carried  
146 out 3 trials per individual over consecutive days. On each day individuals were transferred in a  
147 haphazard order to a 45.5 cm x 19 cm x 29.5 cm experimental tank, filled to a depth of 6 cm. The  
148 experimental tank was lit from above, and surrounded by opaque barriers to minimise the effects of

149 outside stimuli on an individual's behaviour. We included a shelter at one end of the tank that was  
150 graduated in height, from 3 cm above the floor at the tank end and 6 cm (i.e. surface level) at the  
151 distal edge. Viewed from above the shelter extends 6 cm from the wall, although for tracking  
152 purposes we included another 3 cm of horizontal distance in a 'shelter zone'. We then defined  
153 additional edge (near to shelter and/or tank wall) and central zones.

154 At the beginning of each trial we placed the individual in a clear plastic cylinder in the centre of the  
155 central zone. We removed the cylinder after 30 seconds, then allowed a further 30 seconds of  
156 acclimation before recording 270 seconds of subsequent activity using a Sunkwang C160 video  
157 camera suspended above the tank. After every 5 behavioural trials we replaced a litre of water in the  
158 experimental tank with a litre from the home-tank to limit any build-up of specific chemical cues (a  
159 variation on the method used in Chapman et al., 2013; see also Warren & Calaghan, 1975; Houslay  
160 et al., 2017 for similar methods). After the completion of each trial we transferred the animal to a  
161 holding tank, where they were kept until all 36 tagged individuals had been trialled and could be  
162 returned to the home tank. We extracted data on the following behaviours from each of the videos  
163 using the tracking software Viewer II (BIOBSERVE Behavioural Research): the time spent in the  
164 central zone (TIC), the time spent in the shelter zone (TIS), tracklength (i.e. the distance the  
165 individual travelled during the trial), and the percentage area of the experimental space (excluding  
166 the shelter zone) that the individual covered.

### 167 ***Resource Acquisition Trials***

168 For each block, after all OFTs were completed, we grouped individuals into five groups of 6 animals  
169 for use in competitive feeding trials. Individuals were approximately size-matched (Appendix A2 and  
170 Table A1) within each group in order to limit the effect of a prawn's morphology on RHP and  
171 increase the likelihood of agonistic interactions (Evans & Shehadi-Moacdieh, 1988). The largest 6  
172 individuals were placed into one group irrespective of actual size because the variance within the  
173 largest individuals was far greater, meaning size-matching within 0.1g was unfeasible. We felt it was



174 important for these individuals to be included as the nature of the limited resource made the  
175 feeding trials better suited to larger individuals as fewer could feed simultaneously. In other groups,  
176 where possible, size-matching was carried out so that an individual would weigh within 0.1g of its  
177 conspecifics within a group.

178 Space constraints meant that it was only possible to house 5 groups simultaneously, so we retained  
179 the other 6 individuals (comprising of those which did not clearly fit into any one group, and the  
180 smallest individuals) in case of mortality. We placed each group into a separate enriched 36 cm x 19  
181 cm x 23 cm tank within the main home tank (Appendix A3 and Fig. A1). Groups were housed in these  
182 resource acquisition tanks (RATs) for the duration of the feeding trials (Fig. 1b). We gave groups 48  
183 hours to acclimatise to their new surroundings and social groups before feeding trials commenced.

184 We carried out 3 feeding trials per group, with a 24-hour rest spell between each trial. At each  
185 feeding trial, we lowered a mesh parcel containing a fully defrosted 5g cube of brine shrimp (JMC  
186 Aquatics, <http://www.jmc-aquatics.co.uk/product/jmc-frozen-fish-food-100gm-pack/>) into the  
187 group's RAT at the opposite end from the shelter rock (Fig. 1b). Once the food parcel had been  
188 placed in the tank, we observed the tank for 15 minutes and used the keylogging software JWatcher  
189 2.0 (Blumstein, Daniel, & Evans, 2012) to record the amount of time each individual (identifiable  
190 from tags by the naked eye) spent feeding. We provided all animals with brine shrimp (unparcelled)  
191 at the end of their group's trial in an attempt to minimise differing levels of satiation between  
192 prawns across trials. Prawns were not fed again between trials.

193 Note that feeding trials were conducted within groups in RATs because our pilot investigations  
194 showed that animals were unwilling to feed in dyadic trials after transfer to novel environments. We  
195 were unable to measure actual food intake, as our pilot studies showed that easily quantifiable food  
196 items (crustacean pellets) were too large and satiated prawns too quickly. We were also unable to  
197 distinguish competitive interactions between specific individuals, as pilot investigations found too  
198 many (often simultaneous) competitive interactions to track in real time using JWatcher 2.0. Video

199 recordings were not a viable solution to this as elastomer tags were only distinguishable by the  
200 naked eye. While this design means winners and losers are not identified in the dyadic context  
201 typical of RHP studies, time spent feeding actually provides a continuous – and possibly more  
202 informative – measure of competitive ability within the group.

203 Limited food supplies are widely used to predict resource competition in a range of species (e.g.  
204 Wise, 2006; Dennenmoser & Thiel, 2007; Pafilis, Meiri, Foufopoulos, & Valakos, 2009). In  
205 crustaceans, the introduction of a novel food resource, such as the one we presented here, is highly  
206 likely to elicit aggressive interactions and interference competition between individuals (Evans &  
207 Shehadi-Moacdieh, 1988; Barki et al., 1992; Dennenmoser & Thiel, 2007). In our study, the parcelling  
208 of the food source meant that only 1-2 prawns (or, in the case of the smallest individuals <0.5g,  
209 sometimes 3 prawns) could feed simultaneously. Moreover, factors such as the length of time spent  
210 in a potentially competitive setting have previously been shown to be a good predictor of the  
211 frequency of competitive interactions (Richter, Gras, Hodges, Ostner, & Schülke, 2015). Time at or  
212 near a food resource and number of feeding events have also been used as an effective measure of  
213 competitive success in crustaceans at high experimental group densities (Barki et al., 1992; Tran,  
214 O’Grady, Colborn, Van Ness, & Hill, 2014). High population densities have themselves also often  
215 been used as proxies for competition in other species (Tuck, Chapman, & Atkinson, 1997; Bolnick,  
216 2004; Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016). These factors, coupled with the fact  
217 that competitive interactions in *P. elegans* often occur without any obvious physical contact (Evans  
218 & Shehadi-Moacdieh, 1988), suggest that time spent feeding should be a useful measure of RHP.  
219 Post-hoc, this assessment appeared to hold true; of the 120 individuals we assayed, only one did not  
220 feed across any of its three resource-acquisition trial repeats, and only 56 of the 360 observations  
221 across all trials and repeats were of non-feeding individuals. Competitive displacements and  
222 charging behaviours were also frequently observed (pers. obs.), as indicated in our feeding  
223 frequency data (Appendix A4 & Fig. A2), where individuals that spent more time feeding also had

224 more feeding events, often leaving a resource to exclude another individual before returning and  
225 continuing to feed.

## 226 ***Statistical Analyses***

227 We analysed all data using linear mixed effects models fitted in ASreml-R 3.0 (Butler, Cullis, Gilmour,  
228 & Gogel, 2009) in R version 3.4.1 (R Core Team, 2017). TIC and feeding duration were square root-  
229 transformed, after which visual inspection of residuals from all models suggested all behaviours  
230 conformed to the assumption of residual normality. For multivariate analyses, behavioural  
231 measurements were scaled to standard deviation units prior to analysis (following transformation if  
232 necessary), enabling more meaningful comparison of effect sizes across traits and assisting  
233 multivariate model fitting (described below). For testing the significance of random effects we  
234 compared nested models using likelihood ratio tests (LRTs), in which we estimated  $\chi^2_{nDF}$  as twice the  
235 difference in model log likelihoods, with the number of degrees of freedom ( $nDF$ ) equal to the  
236 number of additional parameters in the more complex model. When testing a single random effect,  
237 we assumed the test statistic to be asymptotically distributed as an equal mix of  $\chi^2_0$  and  $\chi^2_1$  (denoted  
238 as  $\chi^2_{0,1}$ ; Visscher, 2006). Fixed effects (described below) were included as statistical controls only and  
239 are not directly relevant to hypotheses being tested so no statistical inference is presented.

### 240 *Among-individual behavioural (co)variation in OFT behaviours*

241 We fitted a series of nested models to partition multivariate OFT behavioural variation (area  
242 covered, TIC, TIS and tracklength) into a between-individual covariance matrix (subsequently  
243 denoted **ID**) and a corresponding within-individual (i.e. residual) component. Each model included  
244 trait-specific fixed effects of repeat and experimental block. Our nested models featured different  
245 covariance specifications to test the expectation that there would be among-individual variance and  
246 covariance structure consistent with the presence of an axis of variation in nominally 'bold'  
247 tendencies.

248 **Model 1A** has no random effects, such that all phenotypic variance (conditional on the fixed effects)  
249 is allocated to the residual component **R** (which can be considered ‘within-individual’ here). We  
250 specified **R** as a ‘diagonal’ matrix, where variances for each behavioural trait are estimated but all  
251 among-trait covariance terms are set to zero. **Model 1B** includes individual ID as a random effect,  
252 with among-individual component **ID** also specified as a diagonal matrix. **Model 1C** allows among-  
253 trait covariance in **R** (i.e. estimating the off-diagonals in the residual covariance matrix). **Model 1D**  
254 extends **1C** by also allowing among-trait covariance in **ID**. We then used likelihood ratio tests to  
255 provide global tests (i.e. across all traits) for i) among-individual behavioural variation (1B vs 1A), ii)  
256 among-trait covariation (1C vs 1B), and iii) significant contribution of individual differences to this  
257 among-trait covariation (1D versus 1C).

258 Note that since behaviours were scaled to standard deviation units prior to analysis, the among-  
259 individual variance ( $V_I$ ) terms on the diagonal of **ID** can be viewed as analogous to repeatabilities  
260 (since repeatability =  $V_I/V_P$ , and the observed phenotypic variance  $V_P$  is 1). We also estimated the  
261 ‘adjusted repeatability’ of each behavioural trait from separate univariate models, where  $V_P$  in this  
262 case is the sum of among-individual and residual variance after having conditioned on fixed effects  
263 (Nakagawa & Schielzeth, 2010).

264 To aid the interpretation of covariance terms contained in **ID**, we calculated the corresponding  
265 among-individual correlations  $r_i$ . We also subjected **ID** to eigen decomposition to determine the  
266 proportion of among-individual variation captured by each principal component (see Houslay &  
267 Wilson, 2017 for further discussion of this approach). We used this eigen decomposition to assess  
268 whether a single major axis of variation could indeed explain most of the among-individual variation  
269 (consistent with the expectation of a nominal ‘shy-bold’ axis of personality). We estimated  
270 uncertainty on the trait loadings associated with each principal component (eigenvector) using a  
271 parametric bootstrap approach (as described by Boulton, Grimmer, Rosenthal, Walling, & Wilson,  
272 2014, Houslay et al., 2017).

273 *Testing correlations between OFT behaviours and morphology*

274 We extended model **1D** by adding an additional morphological response variable to test whether  
275 aspects of morphological variation were significantly correlated with among-individual differences in  
276 OFT behaviours. Residual (co)variances involving morphology were not identifiable as they were  
277 measured only once, so these were constrained to be zero. We then fitted a reduced model where  
278 we also constrained the among-individual correlations between behaviour and the morphological  
279 trait to zero, and compared these models using a likelihood ratio test on 4 degrees of freedom. We  
280 repeated this process for carapace length, body weight, and the size of the individual's longest  
281 periopod (walking appendage).

282 *Among-individual correlation between OFT behaviours and feeding duration*

283 We fitted a further multivariate mixed model (**Model 2**) that enabled us to investigate the  
284 relationship between feeding duration and OFT behaviours. Fixed effects were repeat and  
285 experimental block for all traits, and also the effect of group tank for feeding duration. **Model 2**  
286 extends model 1D by the inclusion of feeding duration as an additional response, fitting a fully  
287 unstructured covariance matrix at the among-individual level (**ID**). As feeding duration was not  
288 measured in the same trial as other behaviours, observation level (residual or within-individual)  
289 correlations involving feeding are not statistically identifiable and therefore were constrained to be  
290 zero. To test the overall significance of the among-individual correlations between feeding duration  
291 and the 4 OFT behaviours, we fitted a reduced model where we also constrained these to zero, and  
292 compared these models using a likelihood ratio test on 4 degrees of freedom.

293 We again used parametric bootstrapping to estimate 95% confidence intervals around each element  
294 of the **ID** matrix from **Model 2**. While this allows statistical inferences to be made on individual  
295 variance/covariance/correlation estimates within the matrix, we caution that the confidence  
296 intervals estimated are necessarily approximate and based on assumed multivariate normality (see  
297 Boulton et al., 2014; Houle & Meyer, 2015 for discussion). Given our particular interest in the

298 strength of relationships between feeding duration and each of the OFT behaviours, we also used  
299 bivariate models to directly test significance for each of that subset of among-individual correlations.  
300 Finally, to check for any effects of within-group size differences on among-individual (co)variation in  
301 feeding duration, we re-ran those univariate and bivariate models in which feeding duration was a  
302 response variable, incorporating relative carapace length (i.e. centred at the mean of each size-  
303 matched feeding trial group) as an additional covariate on this trait.

#### 304 ***Ethical Note***

305 The study was subject to ethical review and approval at the University of Exeter. No additional  
306 permits or licences were required. Numbers of individuals captured, housed and euthanised were  
307 kept to a minimum without compromising the explanatory power of the study. Tagging was carried  
308 out using the least invasive method possible by injecting tags between the carapace and the muscle.  
309 Outside of trials, prawns were housed in diverse, enriched environments and disturbance was kept  
310 to a minimum. Euthanasia was carried out as humanely as possible: noting that the concentration of  
311 MS222 (Tricain mesylate) required for anaesthesia would suffocate this species, induction of torpor  
312 before freezing was deemed the best way to minimise welfare impact on the animals.

#### 313 **RESULTS**

##### 314 ***Among-Individual (co)Variation in OFT Behaviours***

315 Our comparisons of models 1A-1D showed evidence of among-individual variance in multivariate  
316 phenotype, as well as covariance structure driven in part by individual-level effects (Table 1).

317 The among-individual variance-covariance matrix **ID** (as estimated from Model 2) is given in Table 2,  
318 in which the  $V_i$  estimates for each trait (analogous to behavioural repeatabilities) are on the diagonal  
319 of the matrix and range from 0.22-0.38. All are nominally significant based on approximate 95% CI.

320 Table 3 shows adjusted repeatabilities (i.e. repeatability calculated after controlling for confounding  
321 effects; Nakagawa & Schielzeth, 2010) estimated separately for each trait, which are very similar.

322 We found a number of significant pairwise relationships between OFT behaviours in **ID** ( $r_i$ ; Table 2,  
323 above-diagonals), and the results of our eigen analysis revealed that the first eigenvector (EV1)  
324 captured 68% of the among-individual (co)variation. This result suggests that a ‘latent variable’  
325 described the majority of the (co)variation in the behavioural traits that we measured, consistent  
326 with the idea of a single underlying axis of variation. Figure 2 summarises the trait loadings, along  
327 with 95% confidence intervals from the parametric bootstrap, for both EV1 and EV2, which accounts  
328 for a further 24% of the observed variation (although noting that EV2 must be orthogonal to EV1,  
329 and therefore any interpretation of the EV2 loadings comes with the caveat that they are to some  
330 extent dependent upon those of EV1). For EV1, area covered and tracklength load heavily in the  
331 same direction, with TIS loading strongly in the other direction. The estimate of trait loading for TIC  
332 is in the same direction as area covered and tracklength, but the confidence intervals cross zero.  
333 These loadings mean that individuals could be placed along an axis of variation, with those that  
334 spend a lot of time in the shelter at one end (covering little to no area and travelling little to no  
335 distance), and individuals that covered a lot of area and travelled a greater distance at the other  
336 (spending little to no time in the shelter).

337 We found no evidence of among-individual correlations between these OFT behaviours and any of  
338 the morphological traits measured (carapace length:  $\chi^2_4 = 1.9$ ,  $P = 0.76$ ; body weight:  $\chi^2_4 = 3.4$ ,  $P =$   
339  $0.49$ ; longest periopod:  $\chi^2_4 = 1.0$ ,  $P = 0.91$ ).

#### 340 ***Among-Individual Correlations between Feeding Trial and OFT Traits***

341 We found that feeding duration was highly repeatable (adjusted repeatability = 0.54 SE 0.05) over  
342 the course of the resource acquisition trials in size-matched groups (Table 3), and that there was a  
343 significant overall relationship between among-individual variation in feeding and exploratory  
344 behaviours as measured in the OFTs ( $\chi^2_4 = 15.0$ ,  $P = 0.005$ ). From the results shown in Table 2, this  
345 appeared to be driven primarily by a negative relationship between TIC and feeding duration.

346 Likelihood ratio tests from bivariate models showed that this was indeed statistically significant  
347 ( $r_{\text{TIC,RHP}} = -0.41$  SE 0.05,  $\chi^2_1 = 6.4$ ,  $P = 0.011$ ; Figure 3a), as was the negative relationship between area  
348 covered and feeding duration ( $r_{\text{Area,RHP}} = -0.35$  SE 0.16,  $\chi^2_1 = 4.2$ ,  $P = 0.040$ ; Figure 3b). While the  
349 bootstrapped 95% confidence intervals shown in Table 2 do (just) span zero for  $r_{\text{Area,Feeding}}$ , we  
350 reiterate that these are approximate indicators of nominal significance at  $\alpha=0.05$  and therefore do  
351 not represent strongly contradictory results.

352 Incorporating relative carapace length as a fixed effect in the univariate and bivariate models  
353 featuring feeding duration (to control for any effects of size variation within size-matched groups)  
354 showed only minor effects on among-individual (co)variation. Relative carapace length has a  
355 positive, though marginally non-significant, effect on feeding duration (estimate = 0.93 SE 0.50,  $F_{1,99}$   
356 = 3.46,  $P = 0.066$ ), and has a negligible effect on the proportion of variation explained by among-  
357 individual differences (adjusted repeatability = 0.53 SE 0.05,  $\chi^2_{0,1} = 86.2$ ,  $P < 0.001$ ). In the bivariate  
358 model of feeding duration and area covered, the correlation remains similar but becomes marginally  
359 non-significant ( $r_{\text{Area,RHP}} = -0.32$  SE 0.16,  $\chi^2_1 = 3.2$ ,  $P = 0.068$ ). The correlation between feeding  
360 duration and TIC remained significant and strongly negative after the inclusion of relative carapace  
361 length as an additional covariate on feeding duration ( $r_{\text{TIC,RHP}} = -0.39$  SE 0.15,  $\chi^2_1 = 5.6$ ,  $P = 0.017$ ).

## 362 **DISCUSSION**

363 We found strong support for the existence of among-individual behavioural (co)variation, and thus  
364 personality, in this species. Our investigation of the **ID** matrix among behaviours assayed in the open  
365 field trials (OFTs) also suggests a single underlying major axis of variation, consistent with our  
366 predictions. Finally, we found that variation in repeatable exploratory behaviours is related to  
367 individual differences in our measure of RHP. Specifically, greater feeding duration was associated  
368 with lower time spent in the centre and lower area covered in the OFT, indicating that individuals



369 that consistently appeared more risk-averse and less exploratory were actually more able to  
370 monopolise a food resource in the group feeding trials.

371 Having assayed multiple exploratory behaviours in the modified OFT (all of which demonstrated  
372 significant repeatabilities with estimates in line with previous work on exploratory and bold-type  
373 behaviours; Bell et al., 2009), our eigen analysis shows that the majority of the among-individual  
374 (co)variation in these behaviours falls on a single axis (EV1). Trait loadings suggest that we could  
375 describe this axis as the predicted single 'shyness-boldness' continuum (Wilson et al., 1994), where  
376 the 'behavioural type' ranges from those that remain in the shelter (travelling a shorter distance,  
377 and covering little area) to those that travel further and cover more of their surrounding area (and  
378 staying outside of the shelter). The second axis (EV2) might plausibly reflect variation in the degree  
379 or 'styles' (Koolhaas et al., 1999) of coping with stress induced by being away from the shelter (and  
380 thus putatively at higher predation risk). EV2 suggests that – when outside of the shelter – some  
381 individuals travel a long distance but stay in (apparently) safer zones nearer the wall. Meanwhile,  
382 other individuals explore the arena more fully, covering a greater area and spending more time in  
383 the centre. However, we suggest caution is warranted here as EV2 is necessarily dependent on EV1  
384 (as these axes must be orthogonal to one another), and captures only 24% of variance in ID.  
385 Nonetheless – in the context of the loadings of EV1 – the strong loading of TIC and area covered  
386 opposite tracklength and the lack of loading of TIS on EV2 provide some indication that high values  
387 of TIC and area covered generally denote exploratory, risky behaviour, while high values of  
388 tracklength and low values of TIS might not.

389 Our results also provide a clear indication that among-individual behavioural variation has its own  
390 impact on RHP (as measured by the duration spent feeding in an environment where competition  
391 was possible), independent of morphology. OFT behaviours are not themselves correlated with  
392 morphological traits, while the link between OFT behaviour and RHP was found in the presence of  
393 experimental (i.e. size-matching) and statistical (to account for remaining within-group variation)

394 controls for morphological variation. We note, however, that body size is expected to be a strong  
395 determinant of RHP in crustaceans in general (e.g. Barki et al., 1992; Renison, Boersma, & Martella,  
396 2002; Palaoro, Dalosto, Costa, & Santos, 2014) and in *P. elegans* specifically (Evans & Shehadi-  
397 Moacdieh, 1988). The regular dispersal of intertidal species caused by high levels of disturbance  
398 (Günther, 1992) should make both morphology and behavioural type relevant to an individual's  
399 ability to monopolise resources, as similarly sized individuals might often find themselves competing  
400 to exclude one-another when their location on shore changes.

401 While OFT behaviour and RHP thus appear to be coupled in this species, the associations detected  
402 are not consistent with the idea of a 'proactive syndrome' in *P. elegans*. Specifically, TIC and area  
403 covered had statistically significant negative correlations with feeding time. While TIC did not load  
404 significantly on EV1, it did load in the same direction as area covered, and these traits are  
405 significantly positively correlated with one another. Both of these behaviours are therefore likely to  
406 indicate an individual's propensity to engage in high-risk exploration, with higher values representing  
407 nominally 'bolder' individuals. Furthermore, the small additional (co)variation explained by EV2,  
408 possibly indicative of stress, could provide some indication of why only TIC and area covered show a  
409 significant association with feeding time. Again, interpretation of EV2 must be cautious, but given its  
410 possible implications that tracklength and TIS might not be purely associated with high-risk  
411 exploration, we would not expect the bivariate correlation between those behaviours and feeding  
412 duration to be significant. It is important to note that our resource acquisition trials also included a  
413 shelter component, which could allow 'bolder' individuals to simply emerge from shelter first and  
414 thus monopolise the resource. In such a situation we would expect a negative correlation between  
415 TIS and feeding duration (i.e. individuals that spend less time in the shelter during the OFT would  
416 spend more time feeding in the group feeding trials), yet this correlation was close to zero (with a  
417 very small positive estimate).

418 The range of behavioural phenotypes suggested by our analyses could potentially be maintained in  
419 natural populations by frequency-dependent selective processes (Dall et al., 2004; Wolf &  
420 McNamara, 2012), and/or life-history trade-offs leading to equal fitness returns for alternative  
421 strategies (Barta & Giraldeau, 1998; Taborsky & Brockmann, 2010). Recent work in other species  
422 also suggests that individuals that explore further afield take more risks (e.g. Stuber et al., 2013), but  
423 risk takers can be at a competitive disadvantage when living at higher population densities (e.g.  
424 Nicolaus et al., 2016). Trading off investment into competitive behaviours in favour of riskier  
425 strategies (as suggested by Biro & Stamps, 2008) could allow certain prawns to fill a behavioural  
426 niche largely uncontested by more dominant individuals, explaining the observed negative  
427 correlation between riskier exploration and feeding duration. This type of pattern has been shown in  
428 the hermit crab *Pagurus bernhardus*, where individuals trade off fecundity and boldness (Bridger,  
429 Bonner, & Briffa, 2015), and shyer individuals are also better able to defend their shells from eviction  
430 attempts (Courtene-Jones & Briffa, 2014). It is also consistent with the hypothesis presented by Wolf  
431 et al. (2007), where reduced future certainty of access to local resources (which could be brought  
432 about by lower RHP) should lead to an increased investment into risky behaviour (i.e. exploration in  
433 this instance). While an alternative explanation might be that some individuals feed less in order to  
434 invest in other fitness-related activities (such as finding mating opportunities) rather than risky  
435 behaviour, the correlations we find between feeding time and OFT behaviours are more indicative of  
436 an interaction between high-risk exploration and RHP.

437 If the propensity for high-risk exploratory behaviour is highly plastic as a 'strategy' for resource  
438 acquisition, we might also predict that exploratory risk-taking should be highly variable across longer  
439 periods. Individuals should then vary in how they invest into competition or risky exploration  
440 depending on their social environment (i.e. presence and phenotypes of conspecific  
441 competitors). There is ample evidence for the existence of individual-by-environment interactions  
442 (IxE) in behaviour (Japyassú & Malange, 2014), including reductions in individual repeatability in  
443 certain risk-related behaviours over longer time frames (e.g. Boulton et al., 2014), and variation

444 among individuals in the extent to which social experience affects their level of boldness (e.g. Frost,  
445 Winfrow-Giffen, Ashley, & Sneddon, 2007). Future studies could investigate this by manipulating an  
446 individual's hierarchical position across time-points, for example, by placing them in groups of  
447 disproportionately larger or smaller individuals and exploring how this affects their behavioural  
448 phenotype. We also acknowledge that one shortcoming of the methods presented here was our  
449 inability to measure actual food intake. As such, while time spent feeding provides one aspect of  
450 success in a potentially competitive environment, giving a good representation of an individual's  
451 capacity to displace others and keep them away from a limited and valuable resource, it may not  
452 give a complete representation of RHP (or indeed of resource obtained).

453 Overall, our study shows strong support for consistent individual differences in behaviour in  
454 *P.elegans*, adding to the growing body of literature supporting the existence of complex behavioural  
455 variation across a variety of invertebrate phyla (Kralj-Fišer & Schuett, 2014). Our results provide  
456 compelling evidence for a link between personality and RHP in this species and, specifically, for a  
457 negative relationship between putatively high-risk exploration behaviour and the ability to  
458 monopolise a limited food resource. The sign of this association is consistent with the hypothesis  
459 that alternative strategies for obtaining food resources may contribute to the maintenance of  
460 consistent individual differences in behaviour. More generally, our results highlight the importance  
461 of delving more extensively into associations between personality and fitness-related traits,  
462 including performance in competition, across a wide range of species.

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665 **APPENDIX**

666 ***A1: Gravid Status***

667 Although sex could not be readily determined, many females were carrying eggs (including all  
668 individuals in our last block) and so gravid status was recorded and its effects analysed. Preliminary  
669 models indicated that gravid status had no impact on OFT behaviours or feeding time.

670 ***A2: Size-matching***

671 Table A1 shows that our size-matching was highly successful in controlling for carapace length and  
672 average weight, with variation in morphological traits within feeding groups showing very little  
673 deviation from the group mean. We were somewhat less successful in controlling for chela length,  
674 but preliminary analyses showed this trait and average weight had no significant effect on RHP and  
675 that both were strongly correlated with carapace length.

676 ***A3: Feeding trial housing and enrichment***

677 We deemed it appropriate to house prawns in 5 separate 36 cm x 19 cm x 23 cm tanks during the  
678 feeding trials because the higher depth of water in the home tank meant each smaller tank  
679 experienced the same conditions and because preliminary analysis found that tank identity had no  
680 impact on feeding time. See figure A1 for detail.

681 ***A4: Feeding frequency measurement***

682 A feeding event was deemed to have begun when an individual made extended contact with the  
683 food resource with either set of chela or its walking legs and to have ended when an individual had  
684 fully detached from the food source. This means that agonistic exchanges taking place on the food  
685 source itself (presenting large chela, locking large chela) are not captured in this data (although  
686 displacements arising from these interactions are). This measure of frequency was deemed  
687 appropriate as prawns could still have been feeding with their second, smaller pereopods (secondary  
688 walking appendages) while still attached to the resource. We used our feeding frequency

689 measurements to help confirm that feeding duration was a reasonable proxy for RHP (see main  
690 text). The strong relationship shown in Figure A2 lends support to this view. We also incorporated  
691 feeding frequency into an earlier iteration of **Model 2** but found that it did little to improve the  
692 model fit due to its strong relationship with feeding duration.

## TABLES

**Table 1.** Among-individual variation

Comparison	Testing	$\chi^2$	DF	P
1A vs 1B	Variance among individuals	123.0	4	<0.001
1B vs 1C	Among trait covariance	737.1	6	<0.001
1C vs 1D	Among individual trait covariance	843.6	6	<0.001

Multivariate model comparisons showing tests of among-individual variation, among-trait covariance, and among-individual trait covariance. Models were fitted as described in main text and compared by likelihood ratio test.

**Table 2.** OFT and feeding covariance

	Area	Centre	Shelter	Tracklength	Feeding
Area	<b>0.22 (0.09,0.36)</b>	0.62 (0.32,0.88)**	-0.64 (-0.92,-0.36)**	0.69 (0.46,0.87)**	-0.32 (-0.68,0.02)**
Centre	0.14 (0.03,0.26)	<b>0.24 (0.11,0.39)</b>	-0.27 (-0.63,0.10)	0.06 (-0.32,0.40)	-0.40 (-0.73,-0.08)**
Shelter	-0.17 (-0.28,-0.06)	-0.07 (-0.18,0.03)	<b>0.31 (0.17,0.45)</b>	-0.84 (-0.94,-0.73)	0.07 (-0.24,0.37)
Tracklength	0.20 (0.07, 0.31)	0.02 (-0.08, 0.12)	-0.29 (-0.41,-0.16)	<b>0.38 (0.23,0.52)</b>	0.09 (-0.17,0.39)
Feeding	-0.12 (-0.23,0.01)	-0.15 (-0.27,-0.03)	0.03 (-0.09,0.15)	0.04 (-0.09,0.16)	<b>0.58 (0.37,0.78)</b>

Among-individual (ID) variance-covariance matrices estimated from the full model including both open field and feeding trials (in italics). Among-individual variances ( $V_i$ , analogous to repeatabilities over the full range of behavioural measurements) are given on the diagonals (in bold), with among-individual between-trait covariances ( $COV_i$ ) below and the corresponding correlations ( $r_i$ ) above. 95% confidence intervals in parentheses are based on 5000 bootstrapped ID matrices. Correlations are marked with \*\* where the proportion of parametric bootstrap samples that did not have the same sign as our estimate was <0.05 (equivalent to the p-value from a one-tailed test).



**Table 3.** Repeatability

Trial	Behaviour	Repeatability (SE)	$\chi^2_{0,1}$	P
Boldness	Area	0.22 (0.06)	16.0	<0.001
	Centre	0.24 (0.06)	18.4	<0.001
	Shelter	0.33 (0.06)	33.9	<0.001
	<u>Tracklength</u>	0.41 (0.06)	54.7	<0.001
Resource Acquisition	Feeding	0.54 (0.05)	1232.9	<0.001

Adjusted repeatabilities for each behaviour measured in the open field trials (OFTs) and feeding trials.

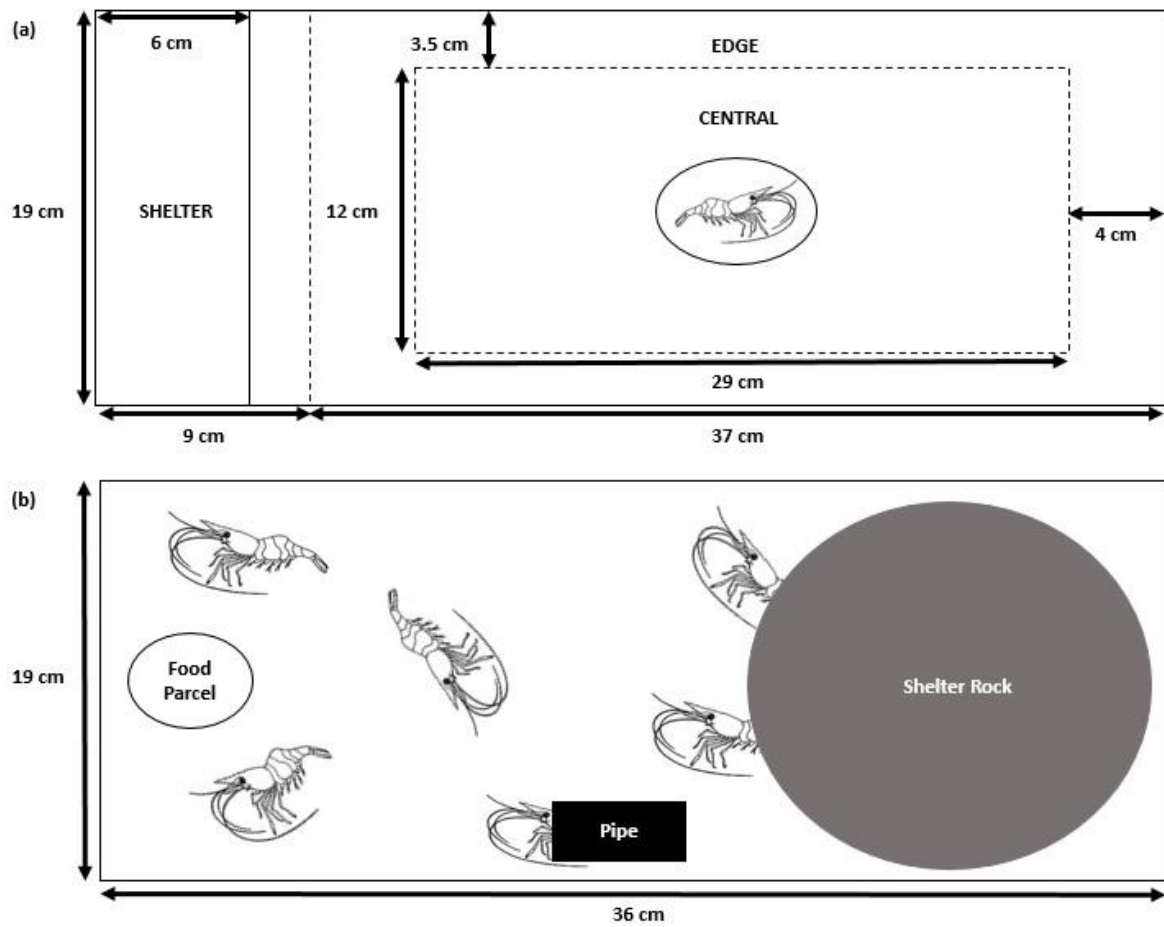
693

**Table A1.** Morphology

Block	Group	Mean Carapace Length	Mean Longest Chela	Mean Average Weight
1	1	49.38(0.75)	26.08(SE=1.67)	1.58(SE=0.07)
1	2	45.79(0.45)	18.72(SE=3.88)	1.21(SE=0.03)
1	3	44.12(0.41)	21.87(SE=1.17)	1.1(SE=0.01)
1	4	41.98(0.26)	20.41(SE=1.08)	0.98(SE=0.01)
1	5	40.04(0.98)	16.98(SE=3.44)	0.86(SE=0.04)
2	6	48.35(0.67)	21.17(SE=4.26)	1.57(SE=0.05)
2	7	47.03(SE=0.51)	23.03(SE=1.07)	1.31(SE=0.04)
2	8	43.95(SE=0.65)	21.14(SE=0.87)	1.11(SE=0.02)
2	9	43.31(SE=0.27)	21.75(SE=0.71)	1.01(SE=0.01)
2	10	42.24(SE=0.6)	18.11(SE=3.63)	0.95(SE=0.01)
3	11	50.05(SE=0.85)	21.64(SE=4.36)	1.75(SE=0.14)
3	12	46.27(SE=0.93)	22.23(SE=1.35)	1.26(SE=0.04)
3	13	43.26(SE=0.24)	16.94(SE=3.42)	1.03(SE=0.01)
3	14	41.4(SE=0.82)	19.66(SE=1.13)	0.87(SE=0.03)
3	15	32.52(SE=0.78)	12.4(SE=2.59)	0.46(SE=0.01)
4	16	49.88(SE=0.92)	24.83(SE=1.07)	1.59(SE=0.06)
4	17	46.5(SE=0.41)	18.57(SE=3.75)	1.27(SE=0.02)
4	18	44.27(SE=0.58)	20.35(SE=0.73)	1.12(SE=0.05)
4	19	43.77(SE=0.12)	20.08(SE=0.62)	1.03(SE=0.02)
4	20	42.24(SE=0.46)	19.55(SE=0.69)	0.98(SE=0.03)

Within-group means for morphological measures, with standard errors shown in parentheses.

**FIGURE 1**

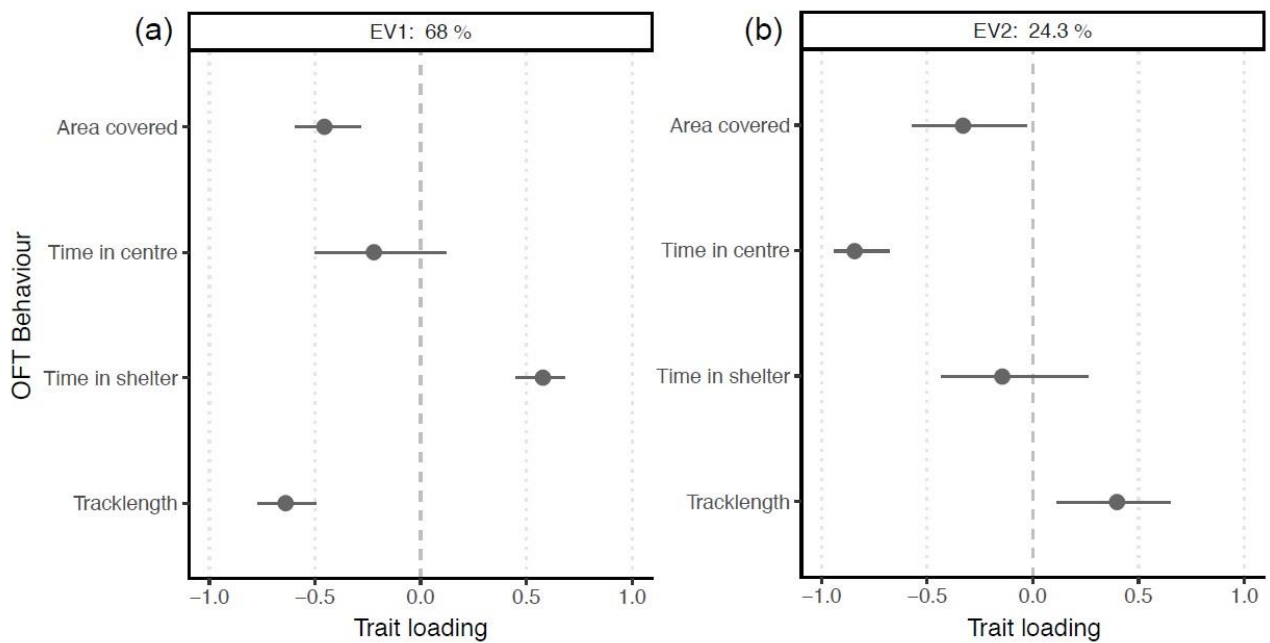


**Figure 1.** Tank set-ups for each set of trials.

(a) (above) shows the starting set-up for each open field trial showing the dimensions of each of the zones (denoted by the dashed lines) and a prawn in the central cylinder. Due to the nature of the tracking software the shelter zone necessarily extended 3 cm beyond the actual shelter (the end of which is denoted by the solid line).

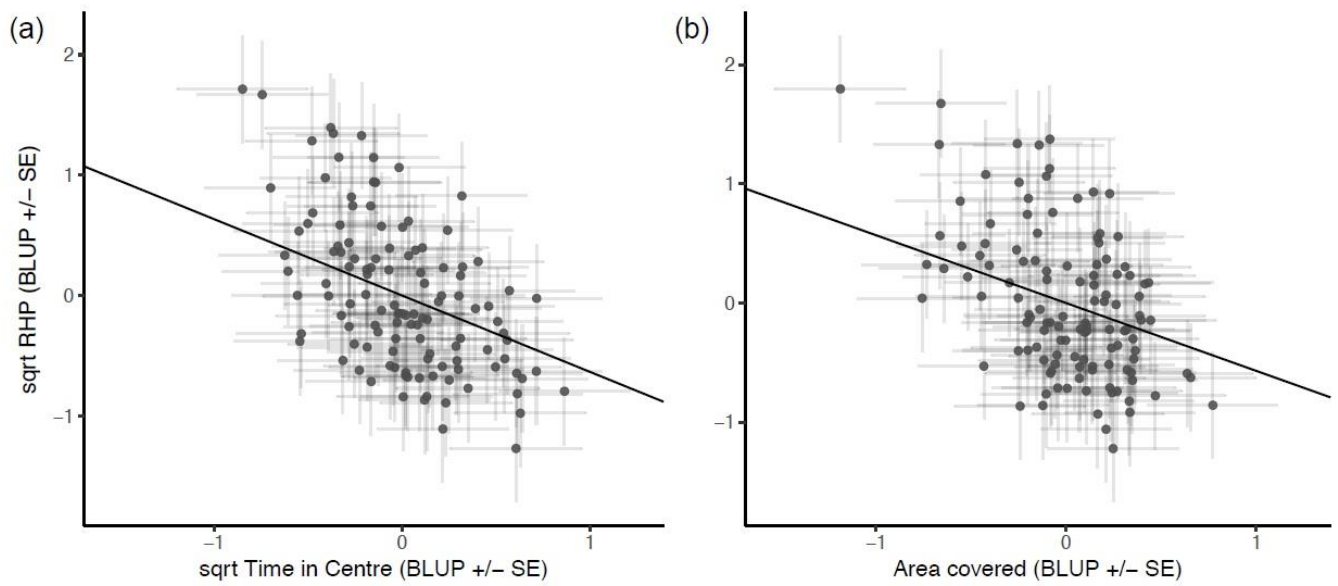
(b) (below) shows the setup at the start of each competitive feeding trial.

**FIGURE 2**



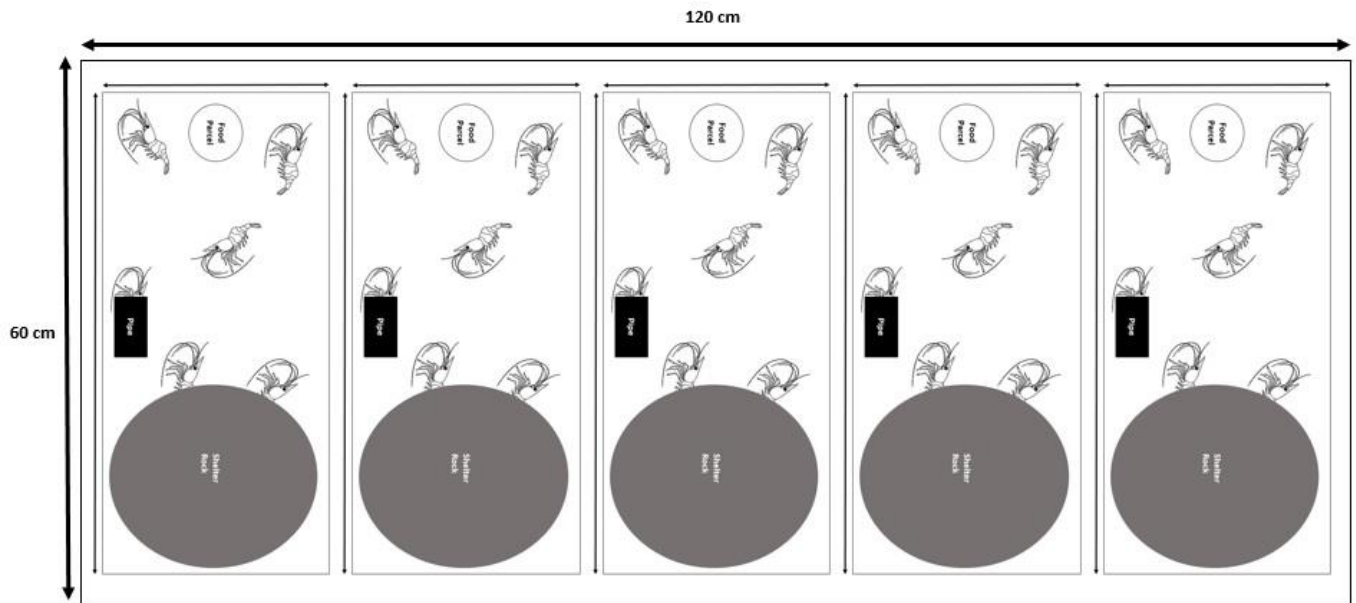
**Figure 2.** Trait loadings on the first two eigenvectors (EV1, left; EV2, right), from the I matrix for open field trial (OFT) behavioural variation. Lines represent 95% confidence intervals, calculated from 5000 bootstrapped replicates. Loadings are considered nominally significant if CIs do not cross zero (dashed vertical line). Arithmetic sign of loading denotes groups of behaviours that load in opposing directions (i.e., EV1 represents an axis where one extreme features individuals that cover more area, travel greater distance and spend less time in the shelter; the other extreme those that spend greater time in the shelter, covering less area and travelling a lower distance).

**FIGURE 3**

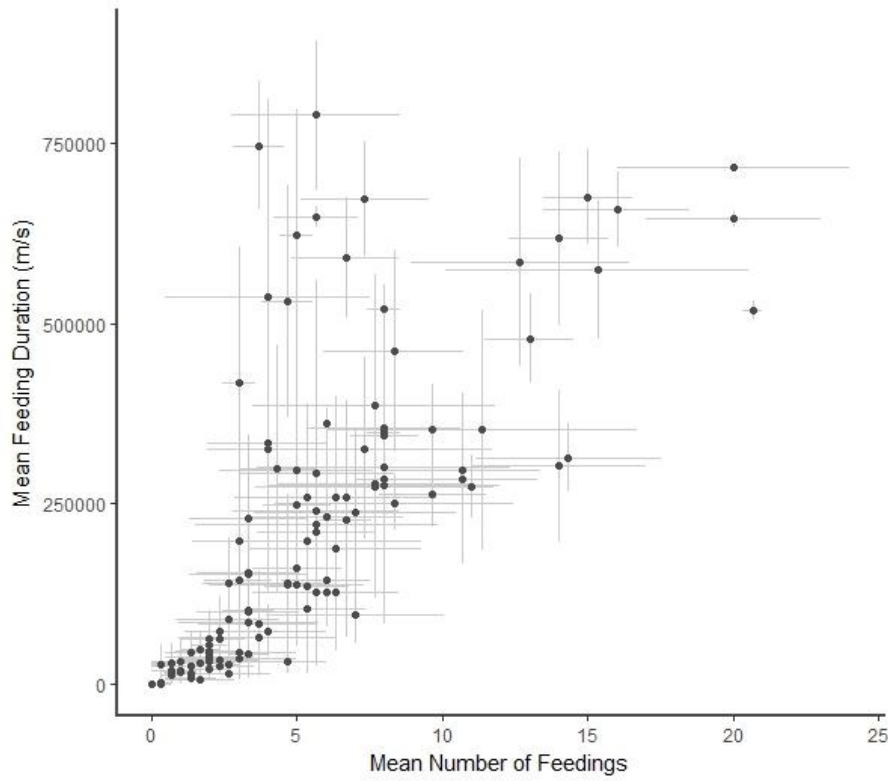


**Figure 3.** Individual-level predictions (BLUPs) from separate bivariate models demonstrate the relationship between among-individual variation in resource holding potential (the ability to monopolise a limited resource, or RHP) and (a) time in the centre (TIC), (b) area covered. All traits were centred at zero and divided by their standard deviation prior to analysis (note also that RHP and time in the centre were square root-transformed before this standardisation step, to ensure that model residuals met the assumption of multivariate normality). In both panels, the plotted regression slope (black line) was calculated directly from the (co)variance estimates from the bivariate model. Light grey lines show the standard errors around the predicted value for each trait.

**FIGURE A1**



**Figure A1.** Prawn housing within resource acquisition tanks (RATs) in the main home tank during feeding trials.



**Figure A2.** Mean values for feeding duration and number of feedings demonstrate the strong trend towards individuals who fed for longer also having more feeding events. Light grey lines show the standard errors around mean feeding duration (vertical) and mean number of feedings (horizontal).

