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

Daniel K Maskrey* [a,b], Stephen J White [a], Alastair J Wilson [a], Thomas M Houslay [a]

[a] Centre for Ecology and Conservation, Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Treliever Road, Penryn, Cornwall, TR10 9EZ, UK.**

[b] Nicholson Building, Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK.*

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*Corresponding author (current address)
E: D.Maskrey@liverpool.ac.uk
T: +447775091284

** Affiliate address

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, Buccianti, & 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, Cowlishaw & 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 16th April and 12th 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 χ^2_{nDF} as twice the

235   difference in model log likelihoods, with the number of degrees of freedom (*n*DF) 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 χ^2_0 and χ^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: χ^2_4 = 1.9, P = 0.76; body weight: χ^2_4 = 3.4, P =

339   0.49; longest periopod: χ^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 (χ^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   ($r_{TIC,RHP}$ = -0.41 SE 0.05, χ^2_1 = 6.4, P = 0.011; Figure 3a), as was the negative relationship between area

348   covered and feeding duration ($r_{Area,RHP}$ = -0.35 SE 0.16, χ^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 $r_{Area,Feeding}$, we

350   reiterate that these are approximate indicators of nominal significance at α=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 ($r_{Area,RHP}$ = -0.32 SE 0.16, χ^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 ($r_{TIC,RHP}$ = -0.39 SE 0.15, χ^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   Winrow-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.

463   **ACKNOWLEDGEMENTS**

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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 periopods (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	χ^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	**0.22 (0.09,0.36)**	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)	**0.24 (0.11,0.39)**	-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)	**0.31 (0.17,0.45)**	-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)	**0.38 (0.23,0.52)**	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)	**0.58 (0.37,0.78)**

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
	Tracklength	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.
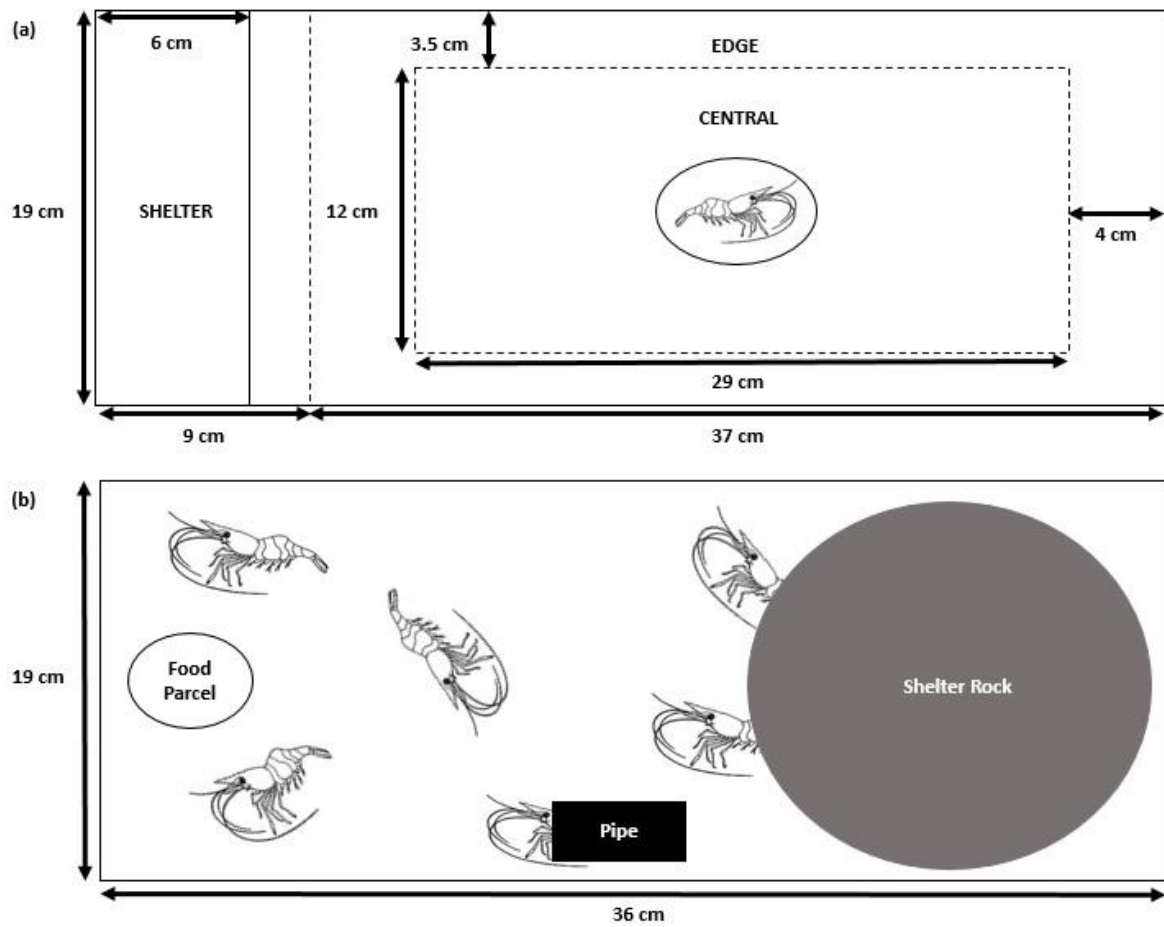
FIGURE 1

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).

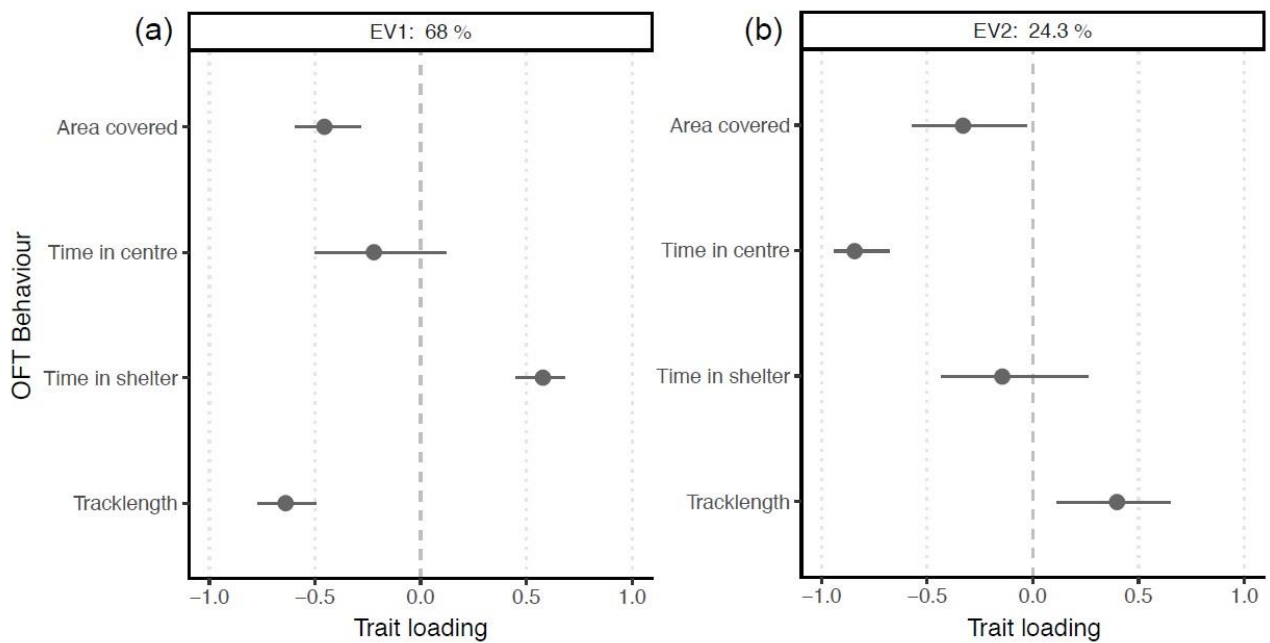(b) (below) shows the setup at the start of each competitive feeding trial.

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).
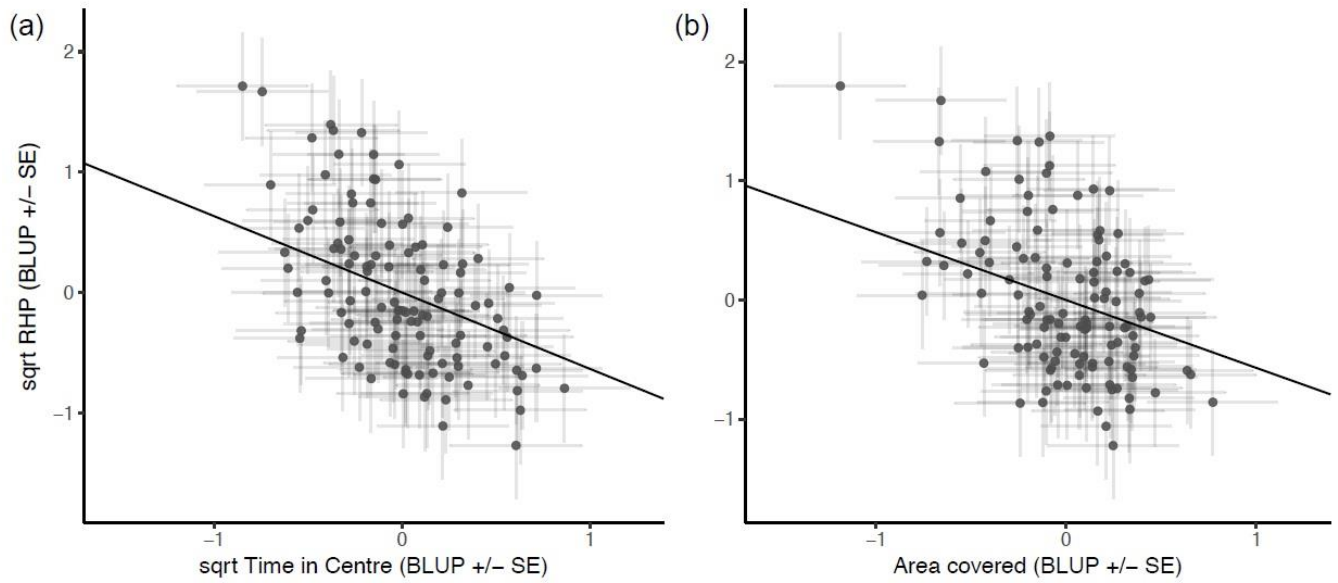
FIGURE 3

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.
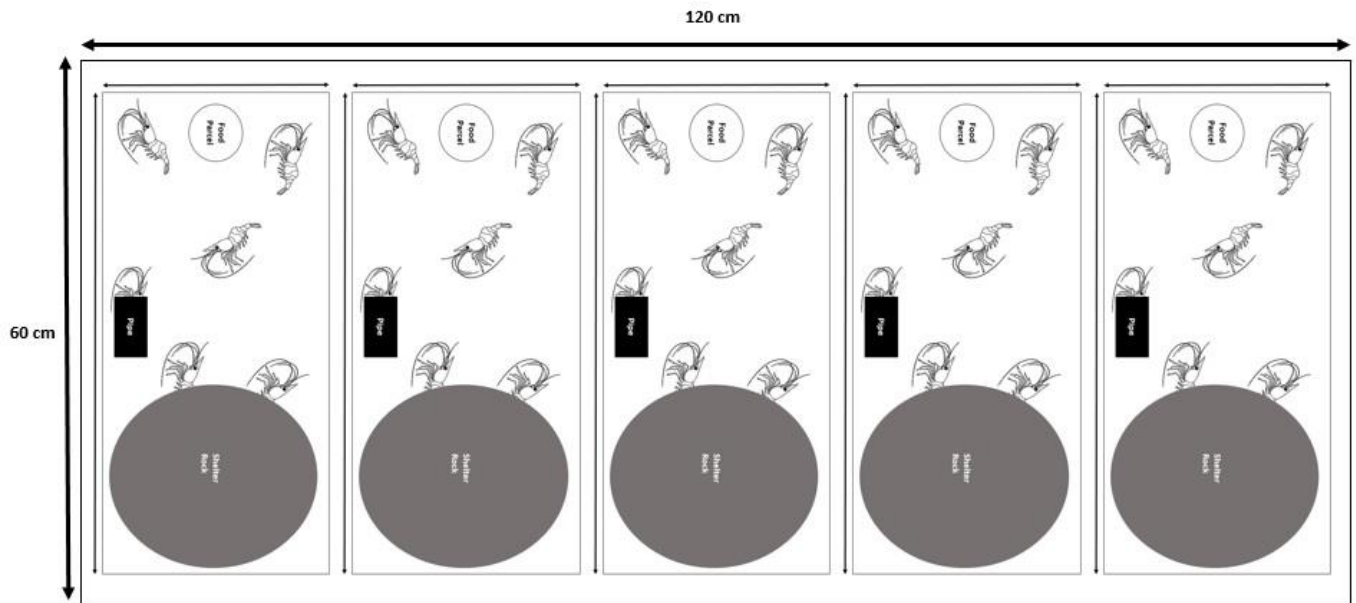
FIGURE A1

Figure A1. Prawn housing within resource acquisition tanks (RATS) in the main home tank during feeding trials.
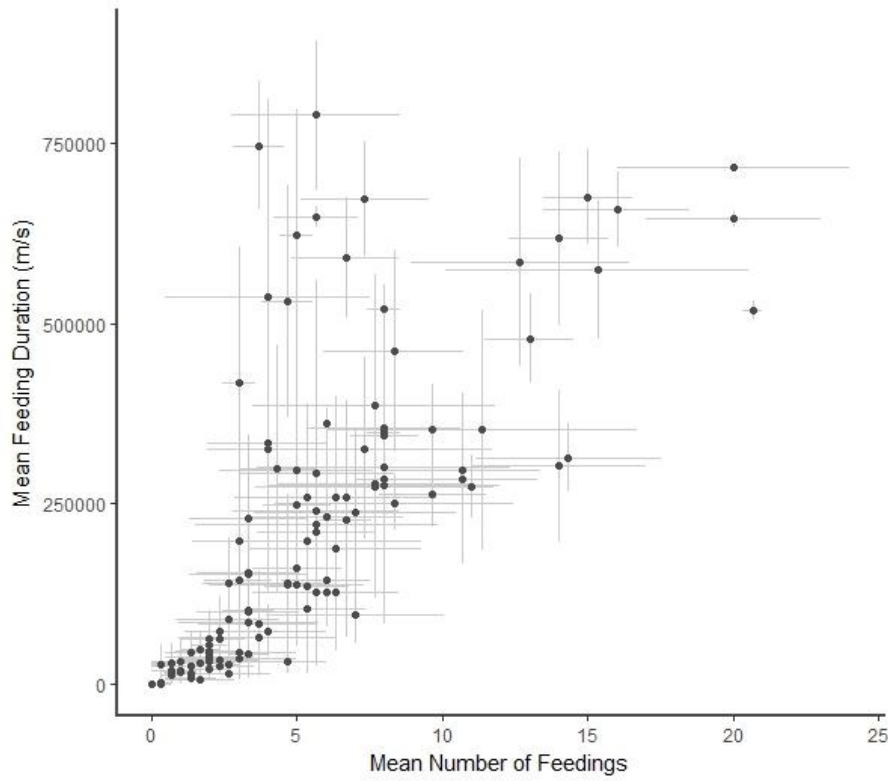
Figure A2. Mean values for feeding duration and number of feedings demonstrate the strong trend towards individuals who fed for longer also having more feeding events. Light grey lines show the standard errors around mean feeding duration (vertical) and mean number of feedings (horizontal).

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