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

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Animal ‘personality’ – the phenomenon of consistent individual differences in behaviour within populations – has been documented widely, yet its functional significance and the reasons for its persistence remain unclear. One possibility is that among-individual behavioural variation is linked to fitness-determining traits via effects on resource acquisition. In this study, we test this idea, using rockpool prawns (*Palaemon elegans*) to test for a correlation between ‘high-risk exploration’ and the ability to monopolise a limited resource. Modified open field trials (OFTs) confirmed that consistent among-individual (co)variation in high-risk exploratory behaviours does exist in this species, and multivariate analysis shows trait variation is consistent with a major axis of personality variation. Subsequent feeding trials in size-matched groups where competition was possible revealed a high repeatability of feeding duration, used here as a proxy for RHP (resource holding potential). We found significant negative correlations between feeding duration and two ‘risky’ behaviours, such that individuals that took fewer risks fed more. Our results are not consistent with the widely hypothesised idea of a ‘proactive syndrome’ in which bolder, risk-taking personalities are positively associated with RHP. Rather they suggest the possibility of a trade-off, with some individuals successful at monopolising limited, high-value resources, while others are more willing to engage in potentially risky exploration (which may increase the likelihood of encountering novel resource patches). We speculate that alternative strategies for acquiring limited resources might thereby contribute to the maintenance of personality variation observed in wild populations.
The existence of consistent among-individual differences in behaviour, or ‘animal personality’, has been documented widely in many types of behaviours and in a variety of organisms (Bell, Hankinson, & Laskowski, 2009; Réale, Dingemanse, Kazem, & Wright, 2010; Japyassú & Malange, 2014). A key question arising from these findings is why personality persists in wild populations (Sih, Bell, & Johnstone, 2004). Superficially, complete flexibility of behaviour would appear to be the optimal strategy when the local environment is changeable. However, studies of other trait types have emphasised the need to understand costs and limits associated with plasticity (Scheiner, 1993; DeWitt, Sih, & Wilson, 1998) that are, in general, not well characterised for behaviour (Ghalambor, Angeloni, & Carroll, 2010). Such costs (including the machinery required to make accurate predictions in fluctuating environments) are likely to limit the extent of behavioural plasticity as an adaptive strategy (Dall, Houston, & McNamara, 2004), yet the functional significance of consistent individual differences remains obscure: does personality provide adaptive advantages, act as an evolutionary constraint, or is it some combination of the two (Dall et al., 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf & Weissing, 2010)? Theoretical treatments have proposed multiple adaptive explanations for the emergence and maintenance of personality variation (e.g., Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010; Wolf & McNamara, 2012), and researchers are beginning to respond to the call for empirical investigations into links between behavioural types and traits that could contribute to an individual’s overall fitness (Dingemanse & Réale, 2005; Smith & Blumstein, 2008).

A comprehensive explanation for the existence and maintenance of personality variation is thus likely to depend (at least in part) upon how behavioural differences contribute to life history variation (Stamps, 2007). Correlations between personality variation and life history traits have been shown in invertebrates (Sinn, Apiolaza, & Moltschaniwskyj, 2006; Niemelä, Lattenkamp, & Dingemanse, 2015), fish (Adriaenssens et al., 2010; Ballew, Mittelbach, & Scribner, 2017), birds (Dingemanse, Both, Drent, & Tinbergen, 2004; Patrick & Wiemerskirch, 2014), and mammals (Boon, Réale, & Boutin, 2007; Seyfarth, Silk, & Cheney, 2012). While the interpretation of any such
correlations is complicated by the fact that within-individual trade-offs between different life-history traits largely determine fitness variation (Simpson, 1955; Stearns, 1989), a universal limiting factor to life-history trait expression is resource availability (Zera & Harshman, 2001). An increased ability to acquire a limited resource would allow an individual to invest more in all traits, and thereby increase its overall fitness (van Noordwijk & de Jong, 1986; Reznick, Nunney, & Tessier, 2000; Bolnick et al., 2011). Where intraspecific competition over a limited resource occurs, an individual’s capacity to monopolise that resource also provides an indication of its competitive ability, or ‘resource holding potential’ (RHP; Parker, 1974; Lindström, 1992). Observations of some measure of RHP might therefore provide insights into fitness variation (Parker, 1974; Smith, 1974), and can also be used at the individual level to determine associations with other traits of interest. While studies have typically focused on the effects of morphological differences (in particular, body size) on competitive outcomes (Tricarico, Benvenuto, Buccianti, & Gherardi, 2008; Briffa, Sneddon, & Wilson, 2015; Ida & Wada, 2017), there is increasing recognition that consistent individual behavioural differences may play a role in determining individual success (Rudin & Briffa, 2012; Camerlink, Arnott, Farish, & Turner, 2016; Lane & Briffa, 2017).

Here, we set out to test for the existence of a link between personality and the ability to monopolise a limited food resource using the Rockpool Prawn, *Palaemon elegans*. One of the most frequently studied personality traits is ‘boldness’, usually defined as an axis of variation in tendency to engage in risky behaviours (e.g. exploration of novel environments; Wilson, Clark, Coleman, & Dearstyne, 1994). A previous study on this species used a variety of assays that each recorded a single behaviour nominally considered a distinct personality trait, finding some evidence of consistent individual differences and correlations across time and situations (Chapman, Hegg, & Ljunberg, 2013). However, the explanatory importance of single behaviours can vary between contexts and species (Carter, Feeney, Marshall, Cowlishaw & Heinsohn, 2013). As a consequence, empirical investigations of personality are increasingly seeking to infer personality variation by placing individuals on axes of variation defined from repeated observations of multiple behaviours (e.g.,
Carter & Feeney, 2012; White, Kells, & Wilson, 2016; Houslay, Vierbuchen, Grimmer, Young, & Wilson, 2017). We follow that trend in this study, where we observed individuals repeatedly in modified open field trials (OFT; Walsh & Cummins, 1976), measuring movement behaviours in a novel and ‘risky’ environment. At the end of the OFT period we created small groups of these individuals for repeated group resource acquisition trials. In crustaceans, a limited food resource is expected to induce intraspecific competition for its acquisition (e.g. Barki, Karplus, & Goren, 1992; Sneddon, Huntingford, & Taylor, 1997; Stewart, McKenzie, Simon, & Baker, 2010). Since the ability to monopolise a limited resource is already known to be influenced by size in P. elegans (Evans & Shehadi-Moacdieh, 1988), we size-matched individuals in these groups in order to better identify any additional influence of among-individual behavioural variation as measured by the OFTs.

We predicted that (1) there would be consistent individual differences among multiple exploratory and/or risk-related behaviours assayed in the modified OFTs, (2) those behaviours would be correlated in such a way as to be consistent with a continuum of parameters traditionally described as being ‘shy-bold’ (Wilson et al., 1994), and (3) there would be a clear association between these correlated risk-related behaviours and an individual’s repeatable RHP (measured as the among-individual variation in feeding duration in group resource acquisition trials). We did not, however, have a clear prediction for the direction of such an association. Boldness is commonly positively correlated with resource acquisition (Biro & Stamps, 2008) and/or competitive ability (e.g. Sih, Cote, Evans, Fogarty, & Pruitt, 2012), a relationship that suggests the presence of a ‘proactive syndrome’ (reviewed in Briffa et al., 2015). However, there is increasing recognition that the sign of such correlations may be dependent on the details of the study system in question (Briffa et al., 2015). In P. elegans, alternative strategies for resource acquisition may be present and maintained through balancing selection (Wolf & McNamara, 2012). For instance, individuals that take more risks through exploration might find new resources quickly but be unable to defend them, while more socially dominant individuals may be better able to monopolise existing resources. In such a scenario, individuals with higher RHP could be seen to exhibit nominally ‘shy’ behaviours such as increased
refuge use, when in fact this ‘shyness’ is borne out of an ability to control limited shelter space and thus a reduced necessity to take risks. This would be in line with the results of Evans & Shehadi-Moacdieh (1988), who found that shelter residents are more likely to repel intruders, suggesting that refuge space itself is a limited resource in this species. It would also support their prediction that it appears to be ‘more adaptive’ for weaker *P. elegans* to avoid direct confrontation, as competitive scenarios produce fewer agonistic interactions when individuals are competitively asymmetrical. In their case weaker individuals were smaller, but in our size-matched trials other competitive asymmetries could arise. In this case, we predict a negative correlation between nominally ‘bold’ tendencies (to engage in risky exploration when shelter was available) and RHP.

**METHODS**

*Capture and Tagging*

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

After a 24-hour acclimatisation period we weighed and tagged the prawns. We used coloured implant elastomer for tagging (Northwest Marine Technology, [http://www.nmt.us/products/vie/vie.shtml](http://www.nmt.us/products/vie/vie.shtml)), allowing us to differentiate between individuals during data-collection blocks and when taking pre and post-mortem measurements. Tagging involved the
injection of a small amount of elastomer under the left and right sides of the third tail carapace segment. By using 6 colours and injecting two tags for each individual (one on either side of the tail) it was possible to uniquely tag 36 prawns. The 4 other individuals were retained for use in case of mortality. Pre-trial weight was also recorded during tagging, for use when size-matching individuals.

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

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

Open Field Trials (OFTs)

We used a modified form of the standard OFT paradigm, a commonly used test for boldness (Burns, 2008; Toms, Echevarria, & Jouandot, 2010), in which our arena also included a shelter (Fig. 1a), to characterise among-individual (co)variation in several putatively correlated behaviours. We carried out 3 trials per individual over consecutive days. On each day individuals were transferred in a haphazard order to a 45.5 cm x 19 cm x 29.5 cm experimental tank, filled to a depth of 6 cm. The experimental tank was lit from above, and surrounded by opaque barriers to minimise the effects of
outside stimuli on an individual’s behaviour. We included a shelter at one end of the tank that was graduated in height, from 3 cm above the floor at the tank end and 6 cm (i.e. surface level) at the distal edge. Viewed from above the shelter extends 6 cm from the wall, although for tracking purposes we included another 3 cm of horizontal distance in a ‘shelter zone’. We then defined additional edge (near to shelter and/or tank wall) and central zones.

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

Resource Acquisition Trials

For each block, after all OFTs were completed, we grouped individuals into five groups of 6 animals for use in competitive feeding trials. Individuals were approximately size-matched (Appendix A2 and Table A1) within each group in order to limit the effect of a prawn’s morphology on RHP and increase the likelihood of agonistic interactions (Evans & Shehadi-Moacdieh, 1988). The largest 6 individuals were placed into one group irrespective of actual size because the variance within the largest individuals was far greater, meaning size-matching within 0.1g was unfeasible. We felt it was
important for these individuals to be included as the nature of the limited resource made the feeding trials better suited to larger individuals as fewer could feed simultaneously. In other groups, where possible, size-matching was carried out so that an individual would weigh within 0.1g of its conspecifics within a group.

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

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

Note that feeding trials were conducted within groups in RATs because our pilot investigations showed that animals were unwilling to feed in dyadic trials after transfer to novel environments. We were unable to measure actual food intake, as our pilot studies showed that easily quantifiable food items (crustacean pellets) were too large and satiated prawns too quickly. We were also unable to distinguish competitive interactions between specific individuals, as pilot investigations found too many (often simultaneous) competitive interactions to track in real time using JWatcher 2.0. Video
recordings were not a viable solution to this as elastomer tags were only distinguishable by the naked eye. While this design means winners and losers are not identified in the dyadic context typical of RHP studies, time spent feeding actually provides a continuous – and possibly more informative – measure of competitive ability within the group.

Limited food supplies are widely used to predict resource competition in a range of species (e.g. Wise, 2006; Dennenmoser & Thiel, 2007; Pafilis, Meiri, Foufopoulos, & Valakos, 2009). In crustaceans, the introduction of a novel food resource, such as the one we presented here, is highly likely to elicit aggressive interactions and interference competition between individuals (Evans & Shehadi-Moacdieh, 1988; Barki et al., 1992; Dennenmoser & Thiel, 2007). In our study, the parcelling of the food source meant that only 1-2 prawns (or, in the case of the smallest individuals <0.5g, sometimes 3 prawns) could feed simultaneously. Moreover, factors such as the length of time spent in a potentially competitive setting have previously been shown to be a good predictor of the frequency of competitive interactions (Richter, Gras, Hodges, Ostner, & Schülke, 2015). Time at or near a food resource and number of feeding events have also been used as an effective measure of competitive success in crustaceans at high experimental group densities (Barki et al., 1992; Tran, O’Grady, Colborn, Van Ness, & Hill, 2014). High population densities have themselves also often been used as proxies for competition in other species (Tuck, Chapman, & Atkinson, 1997; Bolnick, 2004; Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016). These factors, coupled with the fact that competitive interactions in *P. elegans* often occur without any obvious physical contact (Evans & Shehadi-Moacdieh, 1988), suggest that time spent feeding should be a useful measure of RHP.

Post-hoc, this assessment appeared to hold true; of the 120 individuals we assayed, only one did not feed across any of its three resource-acquisition trial repeats, and only 56 of the 360 observations across all trials and repeats were of non-feeding individuals. Competitive displacements and charging behaviours were also frequently observed (pers. obs.), as indicated in our feeding frequency data (Appendix A4 & Fig. A2), where individuals that spent more time feeding also had
more feeding events, often leaving a resource to exclude another individual before returning and continuing to feed.

**Statistical Analyses**

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

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

We fitted a series of nested models to partition multivariate OFT behavioural variation (area covered, TIC, TIS and tracklength) into a between-individual covariance matrix (subsequently denoted $\mathbf{I}_D$) and a corresponding within-individual (i.e. residual) component. Each model included trait-specific fixed effects of repeat and experimental block. Our nested models featured different covariance specifications to test the expectation that there would be among-individual variance and covariance structure consistent with the presence of an axis of variation in nominally ‘bold’ tendencies.
**Model 1A** has no random effects, such that all phenotypic variance (conditional on the fixed effects) is allocated to the residual component \( R \) (which can be considered ‘within-individual’ here). We specified \( R \) as a ‘diagonal’ matrix, where variances for each behavioural trait are estimated but all among-trait covariance terms are set to zero. **Model 1B** includes individual ID as a random effect, with among-individual component \( ID \) also specified as a diagonal matrix. **Model 1C** allows among-trait covariance in \( R \) (i.e. estimating the off-diagonals in the residual covariance matrix). **Model 1D** extends 1C by also allowing among-trait covariance in \( ID \). We then used likelihood ratio tests to provide global tests (i.e. across all traits) for i) among-individual behavioural variation (1B vs 1A), ii) among-trait covariation (1C vs 1B), and iii) significant contribution of individual differences to this among-trait covariation (1D versus 1C).

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

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

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

Among-individual correlation between OFT behaviours and feeding duration

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

We again used parametric bootstrapping to estimate 95% confidence intervals around each element of the ID matrix from Model 2. While this allows statistical inferences to be made on individual variance/covariance/correlation estimates within the matrix, we caution that the confidence intervals estimated are necessarily approximate and based on assumed multivariate normality (see Boulton et al., 2014; Houle & Meyer, 2015 for discussion). Given our particular interest in the
strength of relationships between feeding duration and each of the OFT behaviours, we also used bivariate models to directly test significance for each of that subset of among-individual correlations. Finally, to check for any effects of within-group size differences on among-individual (co)variation in feeding duration, we re-ran those univariate and bivariate models in which feeding duration was a response variable, incorporating relative carapace length (i.e. centred at the mean of each size-matched feeding trial group) as an additional covariate on this trait.

**Ethical Note**

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

**RESULTS**

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

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

The among-individual variance-covariance matrix \( \mathbf{I}_D \) (as estimated from Model 2) is given in Table 2, in which the \( V_i \) estimates for each trait (analogous to behavioural repeatabilities) are on the diagonal of the matrix and range from 0.22-0.38. All are nominally significant based on approximate 95% CI. Table 3 shows adjusted repeatabilities (i.e. repeatability calculated after controlling for confounding effects; Nakagawa & Schielzeth, 2010) estimated separately for each trait, which are very similar.
We found a number of significant pairwise relationships between OFT behaviours in ID (r; Table 2, above-diagonals), and the results of our eigen analysis revealed that the first eigenvector (EV1) captured 68% of the among-individual (co)variation. This result suggests that a ‘latent variable’ described the majority of the (co)variation in the behavioural traits that we measured, consistent with the idea of a single underlying axis of variation. Figure 2 summarises the trait loadings, along with 95% confidence intervals from the parametric bootstrap, for both EV1 and EV2, which accounts for a further 24% of the observed variation (although noting that EV2 must be orthogonal to EV1, and therefore any interpretation of the EV2 loadings comes with the caveat that they are to some extent dependent upon those of EV1). For EV1, area covered and tracklength load heavily in the same direction, with TIS loading strongly in the other direction. The estimate of trait loading for TIC is in the same direction as area covered and tracklength, but the confidence intervals cross zero. These loadings mean that individuals could be placed along an axis of variation, with those that spend a lot of time in the shelter at one end (covering little to no area and travelling little to no distance), and individuals that covered a lot of area and travelled a greater distance at the other (spending little to no time in the shelter).

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

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

We found that feeding duration was highly repeatable (adjusted repeatability = 0.54 SE 0.05) over the course of the resource acquisition trials in size-matched groups (Table 3), and that there was a significant overall relationship between among-individual variation in feeding and exploratory behaviours as measured in the OFTs ($\chi^2_4 = 15.0, P = 0.005$). From the results shown in Table 2, this appeared to be driven primarily by a negative relationship between TIC and feeding duration.
Likelihood ratio tests from bivariate models showed that this was indeed statistically significant ($r_{\text{TIC,RHP}} = -0.41 \ SE 0.05, \chi^2_1 = 6.4, P = 0.011$; Figure 3a), as was the negative relationship between area 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 bootstrapped 95% confidence intervals shown in Table 2 do (just) span zero for $r_{\text{Area,Feeding}}$, we reiterate that these are approximate indicators of nominal significance at $\alpha=0.05$ and therefore do not represent strongly contradictory results.

Incorporating relative carapace length as a fixed effect in the univariate and bivariate models featuring feeding duration (to control for any effects of size variation within size-matched groups) showed only minor effects on among-individual (co)variation. Relative carapace length has a positive, though marginally non-significant, effect on feeding duration (estimate $= 0.93 \ SE 0.50$, $F_{1,99} = 3.46, P = 0.066$), and has a negligible effect on the proportion of variation explained by among-individual differences (adjusted repeatability $= 0.53 \ SE 0.05$, $\chi^2_{0.1} = 86.2, P < 0.001$). In the bivariate model of feeding duration and area covered, the correlation remains similar but becomes marginally non-significant ($r_{\text{Area,RHP}} = -0.32 \ SE 0.16, \chi^2_1 = 3.2, P = 0.068$). The correlation between feeding duration and TIC remained significant and strongly negative after the inclusion of relative carapace length as an additional covariate on feeding duration ($r_{\text{TIC,RHP}} = -0.39 \ SE 0.15, \chi^2_1 = 5.6, P = 0.017$).

**DISCUSSION**

We found strong support for the existence of among-individual behavioural (co)variation, and thus personality, in this species. Our investigation of the ID matrix among behaviours assayed in the open field trials (OFTs) also suggests a single underlying major axis of variation, consistent with our predictions. Finally, we found that variation in repeatable exploratory behaviours is related to individual differences in our measure of RHP. Specifically, greater feeding duration was associated with lower time spent in the centre and lower area covered in the OFT, indicating that individuals
that consistently appeared more risk-averse and less exploratory were actually more able to monopolise a food resource in the group feeding trials.

Having assayed multiple exploratory behaviours in the modified OFT (all of which demonstrated significant repeatabilities with estimates in line with previous work on exploratory and bold-type behaviours; Bell et al., 2009), our eigen analysis shows that the majority of the among-individual (co)variation in these behaviours falls on a single axis (EV1). Trait loadings suggest that we could describe this axis as the predicted single ‘shyness-boldness’ continuum (Wilson et al., 1994), where the ‘behavioural type’ ranges from those that remain in the shelter (travelling a shorter distance, and covering little area) to those that travel further and cover more of their surrounding area (and staying outside of the shelter). The second axis (EV2) might plausibly reflect variation in the degree or ‘styles’ (Koolhaas et al., 1999) of coping with stress induced by being away from the shelter (and thus putatively at higher predation risk). EV2 suggests that – when outside of the shelter – some individuals travel a long distance but stay in (apparently) safer zones nearer the wall. Meanwhile, other individuals explore the arena more fully, covering a greater area and spending more time in the centre. However, we suggest caution is warranted here as EV2 is necessarily dependent on EV1 (as these axes must be orthogonal to one another), and captures only 24% of variance in ID.

Nonetheless – in the context of the loadings of EV1 – the strong loading of TIC and area covered opposite tracklength and the lack of loading of TIS on EV2 provide some indication that high values of TIC and area covered generally denote exploratory, risky behaviour, while high values of tracklength and low values of TIS might not.

Our results also provide a clear indication that among-individual behavioural variation has its own impact on RHP (as measured by the duration spent feeding in an environment where competition was possible), independent of morphology. OFT behaviours are not themselves correlated with morphological traits, while the link between OFT behaviour and RHP was found in the presence of experimental (i.e. size-matching) and statistical (to account for remaining within-group variation)
controls for morphological variation. We note, however, that body size is expected to be a strong
determinant of RHP in crustaceans in general (e.g. Barki et al., 1992; Renison, Boersma, & Martella,
2002; Palaoro, Dalosto, Costa, & Santos, 2014) and in *P. elegans* specifically (Evans & Shehadi-
Moacdieh, 1988). The regular dispersal of intertidal species caused by high levels of disturbance
(Günther, 1992) should make both morphology and behavioural type relevant to an individual’s
ability to monopolise resources, as similarly sized individuals might often find themselves competing
to exclude one-another when their location on shore changes.

While OFT behaviour and RHP thus appear to be coupled in this species, the associations detected
are not consistent with the idea of a ‘proactive syndrome’ in *P. elegans*. Specifically, TIC and area
covered had statistically significant negative correlations with feeding time. While TIC did not load
significantly on EV1, it did load in the same direction as area covered, and these traits are
significantly positively correlated with one another. Both of these behaviours are therefore likely to
indicate an individual’s propensity to engage in high-risk exploration, with higher values representing
nominally ‘bolder’ individuals. Furthermore, the small additional (co)variation explained by EV2,
possibly indicative of stress, could provide some indication of why only TIC and area covered show a
significant association with feeding time. Again, interpretation of EV2 must be cautious, but given its
possible implications that tracklength and TIS might not be purely associated with high-risk
exploration, we would not expect the bivariate correlation between those behaviours and feeding
duration to be significant. It is important to note that our resource acquisition trials also included a
shelter component, which could allow ‘bolder’ individuals to simply emerge from shelter first and
thus monopolise the resource. In such a situation we would expect a negative correlation between
TIS and feeding duration (i.e. individuals that spend less time in the shelter during the OFT would
spend more time feeding in the group feeding trials), yet this correlation was close to zero (with a
very small positive estimate).
The range of behavioural phenotypes suggested by our analyses could potentially be maintained in natural populations by frequency-dependent selective processes (Dall et al., 2004; Wolf & McNamara, 2012), and/or life-history trade-offs leading to equal fitness returns for alternative strategies (Barta & Giraldeau, 1998; Taborsky & Brockmann, 2010). Recent work in other species also suggests that individuals that explore further afield take more risks (e.g. Stuber et al., 2013), but risk takers can be at a competitive disadvantage when living at higher population densities (e.g. Nicolaus et al., 2016). Trading off investment into competitive behaviours in favour of riskier strategies (as suggested by Biro & Stamps, 2008) could allow certain prawns to fill a behavioural niche largely uncontested by more dominant individuals, explaining the observed negative correlation between riskier exploration and feeding duration. This type of pattern has been shown in the hermit crab Pagurus bernhardus, where individuals trade off fecundity and boldness (Bridger, Bonner, & Briffa, 2015), and shyer individuals are also better able to defend their shells from eviction attempts (Courtene-Jones & Briffa, 2014). It is also consistent with the hypothesis presented by Wolf et al. (2007), where reduced future certainty of access to local resources (which could be brought about by lower RHP) should lead to an increased investment into risky behaviour (i.e. exploration in this instance). While an alternative explanation might be that some individuals feed less in order to invest in other fitness-related activities (such as finding mating opportunities) rather than risky behaviour, the correlations we find between feeding time and OFT behaviours are more indicative of an interaction between high-risk exploration and RHP.

If the propensity for high-risk exploratory behaviour is highly plastic as a 'strategy' for resource acquisition, we might also predict that exploratory risk-taking should be highly variable across longer periods. Individuals should then vary in how they invest into competition or risky exploration depending on their social environment (i.e. presence and phenotypes of conspecific competitors). There is ample evidence for the existence of individual-by-environment interactions (IxE) in behaviour (Japyassú & Malange, 2014), including reductions in individual repeatability in certain risk-related behaviours over longer time frames (e.g. Boulton et al., 2014), and variation...
among individuals in the extent to which social experience affects their level of boldness (e.g. Frost, Winfrow-Giffen, Ashley, & Sneddon, 2007). Future studies could investigate this by manipulating an individual’s hierarchical position across time-points, for example, by placing them in groups of disproportionately larger or smaller individuals and exploring how this affects their behavioural phenotype. We also acknowledge that one shortcoming of the methods presented here was our inability to measure actual food intake. As such, while time spent feeding provides one aspect of success in a potentially competitive environment, giving a good representation of an individual’s capacity to displace others and keep them away from a limited and valuable resource, it may not give a complete representation of RHP (or indeed of resource obtained).

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

**ACKNOWLEDGEMENTS**

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allowed us to steal some of their holding tanks for our second experiment. Furthermore, thanks
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A1: Gravid Status

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

A2: Size-matching

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

A3: Feeding trial housing and enrichment

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

A4: Feeding frequency measurement

A feeding event was deemed to have begun when an individual made extended contact with the food resource with either set of chela or its walking legs and to have ended when an individual had fully detached from the food source. This means that agonistic exchanges taking place on the food source itself (presenting large chela, locking large chela) are not captured in this data (although displacements arising from these interactions are). This measure of frequency was deemed appropriate as prawns could still have been feeding with their second, smaller periopods (secondary walking appendages) while still attached to the resource. We used our feeding frequency
measurements to help confirm that feeding duration was a reasonable proxy for RHP (see main
text). The strong relationship shown in Figure A2 lends support to this view. We also incorporated
feeding frequency into an earlier iteration of Model 2 but found that it did little to improve the
model fit due to its strong relationship with feeding duration.
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>
<thead>
<tr>
<th>Comparison</th>
<th>Testing</th>
<th>$\chi^2$</th>
<th>DF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1A vs 1B</td>
<td>Variance among individuals</td>
<td>123.0</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1B vs 1C</td>
<td>Among trait covariance</td>
<td>737.1</td>
<td>6</td>
<td>&lt;0.001</td>
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<tr>
<td>1C vs 1D</td>
<td>Among individual trait covariance</td>
<td>843.6</td>
<td>6</td>
<td>&lt;0.001</td>
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</table>

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 1. Among-individual variation

Among-individual (ID) variance-covariance matrices estimated from the full model including both open field and feeding trials (in italics). Among-individual variances (V, analogous to repeatabilities over the full range of behavioural measurements) are given on the diagonals (in bold), with among-individual between-trait covariances (COV) below and the corresponding correlations ($r$) 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).

**TABLES**

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Area</th>
<th>Centre</th>
<th>Shelter</th>
<th>Tracklength</th>
<th>Feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>0.22 (0.09,0.36)</td>
<td>0.62 (0.32,0.88)**</td>
<td>-0.64 (0.92, -0.36)**</td>
<td>0.60 (0.46,0.77)**</td>
<td>0.12 (0.68,0.02)**</td>
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<td>Centre</td>
<td>0.14 (0.03,0.26)</td>
<td><strong>0.24 (0.11,0.39)</strong></td>
<td>-0.27 (0.63,0.10)</td>
<td>0.06 (-0.31,0.40)</td>
<td>-0.40 (-0.73,0.08)**</td>
</tr>
<tr>
<td>Shelter</td>
<td>-0.17 (0.28, 0.66)</td>
<td>-0.07 (-0.18,0.03)</td>
<td><strong>0.31 (0.17,0.45)</strong></td>
<td>-0.04 (0.54,0.73)</td>
<td>0.07 (0.24,0.37)</td>
</tr>
<tr>
<td>Tracklength</td>
<td>0.20 (0.07,0.31)</td>
<td>0.02 (-0.06,0.12)</td>
<td>-0.29 (0.41,-0.16)</td>
<td><strong>0.38 (0.23,0.52)</strong></td>
<td>0.09 (0.17,0.35)</td>
</tr>
<tr>
<td>Feeding</td>
<td>-0.12 (0.23,0.01)</td>
<td>-0.11 (0.27,0.03)</td>
<td>0.01 (0.09,0.15)</td>
<td>0.04 (0.09,0.16)</td>
<td><strong>0.59 (0.37,0.78)</strong></td>
</tr>
</tbody>
</table>

Table 2. OFT and feeding covariance
Adjusted repeatabilities for each behaviour measured in the open field trials (OFTs) and feeding trials.

### Table 3. Repeatability

<table>
<thead>
<tr>
<th>Trial</th>
<th>Behaviour</th>
<th>Repeatability (SE)</th>
<th>$X^2_{3.1}$</th>
<th>$P$</th>
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<tr>
<td>Boldness</td>
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<td>0.22 (0.06)</td>
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<tr>
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<td>Centre</td>
<td>0.24 (0.06)</td>
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<td>Shelter</td>
<td>0.33 (0.06)</td>
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<td><strong>Tracklength</strong></td>
<td>0.41 (0.06)</td>
<td>54.7</td>
<td>&lt;0.001</td>
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<tr>
<td>Resource Acquisition</td>
<td>Feeding</td>
<td>0.54 (0.05)</td>
<td>1232.9</td>
<td>&lt;0.001</td>
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### Table A1. Morphology

<table>
<thead>
<tr>
<th>Block</th>
<th>Group</th>
<th>Mean Carapace Length (SE)</th>
<th>Mean Longest Chela (SE)</th>
<th>Mean Average Weight (SE)</th>
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<tr>
<td>1</td>
<td>1</td>
<td>49.98 (0.75)</td>
<td>26.08 (1.67)</td>
<td>1.58 (0.07)</td>
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<tr>
<td>1</td>
<td>2</td>
<td>45.79 (0.45)</td>
<td>18.72 (3.88)</td>
<td>1.21 (0.03)</td>
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<tr>
<td>1</td>
<td>3</td>
<td>44.12 (0.41)</td>
<td>21.87 (1.17)</td>
<td>1.11 (0.01)</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>41.98 (0.26)</td>
<td>20.41 (1.08)</td>
<td>0.98 (0.01)</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>40.04 (0.98)</td>
<td>16.98 (3.44)</td>
<td>0.86 (0.04)</td>
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<td>2</td>
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<td>21.17 (4.26)</td>
<td>1.57 (0.05)</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>47.03 (0.51)</td>
<td>23.03 (1.07)</td>
<td>1.31 (0.04)</td>
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<tr>
<td>2</td>
<td>8</td>
<td>43.95 (0.65)</td>
<td>21.14 (0.87)</td>
<td>1.11 (0.02)</td>
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<tr>
<td>2</td>
<td>9</td>
<td>45.31 (0.27)</td>
<td>21.75 (0.71)</td>
<td>1.01 (0.01)</td>
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<td>3</td>
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<tr>
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<td>20</td>
<td>42.24 (0.46)</td>
<td>19.55 (0.69)</td>
<td>0.98 (0.03)</td>
</tr>
</tbody>
</table>

With within-group means for morphological measures, with standard errors shown in parentheses.
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. 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).