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Bridger, D

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Individual quality and personality: Bolder males are less fecund in the hermit crab *Pagurus bernhardus*.

Danielle Bridger[1]

Simon J. Bonner[2]

Mark Briffa[1]

[1]Marine Biology & Ecology Research Centre, Plymouth University, Drake Circus, Plymouth, PL3 8AA, U.K.

[2]Department of Statistics, University of Kentucky, 725 Rose Street, Lexington KY 40536-0082.

Short title: Boldness and fecundity in hermit crabs

Summary

One explanation for animal personality is that different behavioural types derive from different life history strategies. Highly productive individuals, with high growth rates and high fecundity, are assumed to live life at a fast pace showing high levels of boldness and risk taking, compared to less productive individuals. Here we investigate among individual differences in mean boldness (the inverse of the latency to recover from a startling stimulus) and in the consistency of boldness, in male hermit crabs in relation to two aspects of life history investment. We assessed aerobic scope by measuring the concentration of the respiratory pigment haemocyanin, and we assessed fecundity by measuring spermatophore size. First, we found that individuals investing in large spermatophores also had high concentrations of haemocyanin. Using doubly hierarchical generalized linear models to analyse longitudinal data on startle responses we show that hermit crabs vary both in their mean response durations and in the consistency of their behaviour. Individual consistency was unrelated to haemocyanin concentration or spermatophore size but mean startle response duration increased with spermatophore size. Thus, counter to expectations it was the most risk-averse individuals, rather than the boldest and most risk prone, that were the most productive. We suggest that similar patterns should be present in other species, if the most productive individuals avoid risky behaviour.

Keywords: Fecundity, Boldness, Personality, Consistency, Intra-individual variation, Predictability

Introduction

Animal personality refers to among individual difference in behaviour that are consistent over time and in some cases across situations [1]. Recent studies have addressed the fact that these consistent differences are nested within a hierarchy of scales over which biological variation occurs. Westneat et al. [2], for example, describe variation among species, populations and individuals, and then at the finer level of behavioural plasticity, where individuals adjust their behaviour to match the current situation. We can then identify a yet finer level of residual variation within individuals that cannot be explained by plasticity. Similarly, Briffa et al. [3] described six categories of behavioural variation but again arrived at residual variation within individuals as the finest level of behavioural organisation. This fine scale residual variation [4] has also been described as consistency [5], stability [6,7] and recently as predictability and intra-individual variation (hereafter IIV) [3,8–11]. Although such hierarchies represent a useful framework for discussing the structure of behavioural variation, the levels are not isolated from one another. In-fact, animal personality, frequently quantified by calculating repeatability estimates, is dependent upon two of the levels described above; relatively high levels of among individual variance coupled with relatively low levels of within individual variance [12]. Even when environments are consistent across individuals, we may still see among individual differences in IIV [2,3,9–11,13,14]. In order to fully understand the causes and consequences of animal personality attention should therefore be paid to both of these levels of variation that contribute to the observed personality effect.

Personality has been documented in diverse animal taxa but, despite the fact that it has been clearly defined (as described above), its causes are still unclear. A range of approaches have been used to address this question. First we may look directly or indirectly [15] at the heritability [16] and fitness consequences [17–19] of personality variation. Second, we might determine what environmental parameters contribute to animal personality, and

under what conditions the personality effect tends to be eroded or promoted [3,20,21]. Indeed, plasticity can be demonstrated in both mean level responses and in IIV, so both components have the potential to vary among environments [3,9,14]. Another approach is to determine what other traits co-vary with personality. In some cases a personality trait might vary with another behavioural trait to form a behavioural syndrome [22]. Personality traits may also vary with physical traits including physiology (e.g. metabolic rate [23]) or morphology (e.g. size [24,25]) and it has been hypothesised that consistent behavioural differences derive from life-history trade-offs [24,26–28]. In particular, the Pace of Life Syndrome [27] explanation for animal personality is that such trade-offs could lead to divergent strategies represented by fast and slow individuals. Fast individuals are characterised by high metabolic rates and heavy investment in reproduction compared to slow individuals. Behaviourally, fast individuals are more explorative, bold and aggressive compared to reactive slow individuals. Slow individuals, on the other hand, may accumulate resources less quickly but accrue fitness over increased lifespans. Such trade-offs could derive from the need to balance behaviours that minimise exposure to risk against behaviours that allow acquisition of the resources required to maintain high metabolic rates [29] or high life-history productivity [30]. Productivity is defined as investment in biomass or fecundity [30]. As there are many traits that will influence individual patterns of investment in biomass and fecundity, point estimates of any single trait are unlikely to fully capture among-individual variance in life-history productivity. Indeed, the ability to acquire resources should vary with performance capacities. Therefore, in addition to assays of biomass and fecundity, we might also include investment in any physiological system that enhances performance as a key component of life-history productivity. Endurance capacity (stamina) for example requires investment in ventilation systems and oxygen transport systems, which define an individual's aerobic scope. This trait is known to influence success in demanding interactions [31–34]. In aggressive displays, for

example, high quality individuals that win fights tend to have greater stamina [33] and similar links between stamina and positive outcomes can also be seen in courtship behaviour [35] and in foraging [31,32].

While life history productivity is best quantified by measuring rates (e.g. the rate of biomass accumulation) it is still possible to gain insights into the links between behaviour and life history by obtaining point estimates of traits that are indicative of productivity. Thus the fecundity of jumping spiders *Dolomedes triton* has been assessed by counting the number of spiderlings emerging of the egg sacs of females, and their body mass was used as a proxy for investment in biomass [36]. Similarly, fledgling success in relation to provisioning behaviour and other personality traits has been assessed in birds [15,37]. Fecundity, the potential for reproductive output, can also be assessed by quantifying investment in gametes, usually eggs in females. In the codling moth, *Cydia pomonella* the number of eggs shows negative correlation with activity rate, indicating a trade-off between these two traits [38]. In the Atlantic silverside, *Menidia menidia*, egg volume was the measure of fecundity and in this case there was a positive association with boldness [39]. Although fecundity is most usually assessed in females, it can also vary among males, especially in species where males package their sperm up into costly spermatophores, as in the spiny lobster *Panulirus argus* [40] and the bush cricket *Gryllodes supplicans* [41]. Interestingly, the links between gamete packaging and male fecundity are not restricted to animals. In sea beet, *Beta vulgaris* ssp. *maritima*, male fecundity is directly linked to the quality of their pollen [42]. Thus, the question of how male fecundity might be traded-off against investment in other life history traits is relevant to a broad range of organisms.

We can therefore partition life history investment into traits that maximise day to day performance (enhancing growth and survival) and those that influence fecundity (enhancing reproductive success). Here we investigate the links between consistent among individual

differences in boldness and markers of these two aspects of life history, in the hermit crab *Pagurus bernhardus*. These decapod crustaceans occupy empty gastropod shells and when threatened they withdraw rapidly into them before slowly re-emerging. The duration of this startle response is directly analogous to that shown by other animals that retreat into a refuge upon being disturbed and usually described as 'boldness' (see [30,39,43] for examples). Here, we first look at boldness in relation to investment in haemocyanin the respiratory pigment of crustaceans, which varies among individuals and contributes to their capacity for demanding aerobic activity [44]. Second, we investigate boldness in relation to investment in spermatophore production quantified by the size of spermatophores, which are produced continuously in males. Previous studies on *P. bernhardus* have shown that individual mean level boldness and IIV in boldness vary among individuals and that both are sensitive to environmental effects such as temperature [3] and predation risk [9,45]. However, it is not known how either aspect might vary with investment in physiological condition or reproductive potential. To the best of our knowledge this is the first time that the potential for links between personality and life history traits representing (i) investment in performance capacity and (ii) investment in fecundity have been investigated simultaneously, at both mean and IIV levels of variation. We include individuals from two populations known to differ in mean startle response durations [45] such that the effect sizes of the life history parameters can be compared to the known population differences.

In the following experiment, we ask whether haemocyanin and spermatophore size are positively or negatively associated. A positive correlation would indicate that both traits are related to individual quality, with high quality individuals able to invest heavily in both day to day performance and fecundity. A negative correlation would indicate that the two traits are traded off, such that short term performance is sacrificed for enhanced fecundity. Furthermore, if animal personality in hermit crabs represents underlying differences in pace

of life we would expect to see a positive association between boldness and investment in large spermatophores and in haemocyanin. Thus individuals that have high concentrations of haemocyanin and large spermatophores should recover from a startling stimulus more quickly than those that show lower investment.

Materials and methods

Collection of animals and behavioural observations

Hermit crabs were collected from the rocky intertidal at Mount Batten (SX 48718 52888) and Hannafore Point (SX 25792 52533), UK, during March 2011. The crabs from both locations were bought to the laboratory at Plymouth and held in site-specific batches of 100 individuals in tanks containing aerated sea water at 15°C. Crabs were then removed from their gastropod shells, by carefully cracking the shell in a bench vice. We selected 27 males from Hannafore (mean mass = 0.516 ± S.E. = 0.07g) and 26 males from Mount Batten (Mount Batten mean mass = 0.49 ± S.E. = 0.07g), with data collected concurrently for crabs from the two sites. All crabs occupied *Littorina littorea* shells, and thus we avoided using the smallest size classes of intertidal hermit crabs, which occupy other shells such as *L. obtusata*. The total size range was 0.11g to 1.39g, which represents ca. 1.4% of the total size range of mature *P. bernhardus*, with sub-tidal individuals attaining masses in excess of 90.0g [46]. Body size correlates with age in hermit crabs [47] and estimates of the post-larval lifespan of *P. bernhardus* and other members of the genus range from 3 [48] to 10 years [49]. All males used in the experiment were free of obvious parasites and missing appendages. Females and discarded males were supplied with new shells and returned to the sea. Each male selected for the experiment was weighed and supplied with a new *Littorina littorea* shell of 100% of its preferred shell mass. The appropriate shell mass was calculated from regression lines, obtained from a previous

shell selection experiment [50]. This step is essential because numerous experiments (e.g. see the review in [51]) have shown that shell optima affect the behaviour of hermit crabs, including their startle response durations [52]. Crabs were then housed individually in 20 cm diameter opaque white plastic dishes containing continuously aerated sea water at 15°C to a depth of 5 cm, and fed white fish flesh *ad libitum*. During the experiment we did not collect dish-specific temperatures. However, we did assess temperature variation across the approximately 1.5m length of bench space over which dishes were distributed and found no significant variation in temperature across this space [3].

Startle response assay

Following a 24 hour acclimation period, a startle response was induced in each crab every day for eight days. The startle response was induced by removing the crab from its tank, inverting the crab for five seconds, which causes it to withdraw into its shell and then returning it to the tank with the aperture facing upwards. All startle responses were undertaken by a single observer (DB). Immediately prior to this, aeration was switched off so that the crab could be clearly observed and so that the air bubbles did not disturb the crab as it emerged from its shell. Aeration was switched back on again after observation. Startle responses were induced between 9am and 12pm each day and the observation order was randomised between days. The duration of the startle response was timed from when the crab was replaced in the tank until the walking legs first contacted the floor of the dish [45].

Analysis of haemocyanin and spermatophores

At the end of the final observation period a haemolymph sample was extracted from each crab. An insulin syringe was inserted into the infrabranchial sinus, via the arthrodial membrane at the base of the third pereiopod. A 10µl aliquot of the sample was immediately

added to a semi-micro cuvette containing 690µl of double distilled water. Following mixing, the absorbance was measured at 337nm in a spectrophotometer. The haemocyanin concentration was then determined for each crab following Nickerson & Van Holde [53], using the extinction coefficient (*E*): $E_{1\mathrm{cm}}^{\mathrm{mM/l}}$= 17.26. After taking the haemolymph sample each crab was humanely euthanized by placing it in a saturated solution of magnesium chloride. The *vas deferens* was then dissected out and a distal section joined to the gonopore, of ca 1mm length, was cut away and placed on a microscope slide with a drop of seawater and broken up to release the spermatophores. In hermit crabs spermatophores consist of a cylindrical sperm containing ampulla, which is tapered towards the distal end, the proximal end being attached to a basal plate by a solid peduncle [54]. In *P. bernhardus* the basal plates usually carry a line of four to six spermatophores. For each crab spermatophores, taken from five different basal plates were selected at random and photographed using a binocular confocal microscope (Leica MZ12) equipped with a Lumenera Infinity 1 camera connected to a computer. We measured the spermatophore ampulla lengths (henceforth 'spermatophore length') using point-to-point measurements in Lumenera Infinity Analyze 5.0.3 software. As in previous studies of hermit crab spermatophore size variation, only mature spermatophores from the distal section of the vas deferens were measured and an individual's spermatophore length was defined as the mean ampulla length of 5 selected spermatophores [55].

Statistical methods

Mean and IIV level variation can be assessed by first using a general linear mixed effects models to assess sample and individual mean level effects, and then deriving from this model a measure of residual individual standard deviation (riSD) [8]. An alternative approach taken by Westneat *et al*. [2] is to use a doubly hierarchical generalised linear model (DHGLM) fit

using Bayesian methods via Markov chain Monte Carlo (MCMC) sampling. This method allows the simultaneous modelling of mean and variance level effects. These two components are termed the mean and standard deviation (henceforth 'SD') models respectively. This approach has the advantages of (a) combining both steps into a single model such that uncertainty in our parameter estimates can be accounted for in each part of the analysis, and (b) the ability to cope with non-heterogeneous residual errors, allowing fixed effects to be assessed more robustly in comparison to LMM (although this is only likely to be of concern if there are greatly uneven sample sizes between groups). One of the differences between Bayesian statistics and more familiar methods is that Bayesian analyses allow the formal incorporation of prior information into the statistical model. If no prior information is available, non-informative or weakly informative prior distributions may be specified in order that the prior distribution has little effect on the results [56] and we adopted this approach here.

For the mean model we included fixed effects for spermatophore length, haemocyanin concentration, crab mass, population and observation number. For each crab we allowed a random intercept effect and a random slope effect with respect to occasion. Data were Log_{10} transformed to improve normality. Our initial mean model (see ESM1 for detailed descriptions) assumed a linear association between the predictors and the response. However, subsequent assessment of goodness of fit for this model suggested that the associations were more complex. Visual inspection of the data suggested a quadratic association would provide a better fit, so the mean portion of the model was configured to include quadratic terms for spermatophore length and haemocyanin concentration. For the SD model we included fixed effects for spermatophore length, haemocyanin concentration, crab mass and population. For each crab we allowed a random intercept. The fixed effects allow us to ask, at the population level, whether IIV correlates with haemocyanin and spermatophores and whether it differs

between the two populations. The random intercept allows us to ask whether individuals differ in IIV. Including a random slope effect in the SD model would have tested the idea that individuals might differ in how the level of IIV that they express varies across occasions. Since there was only 1 observation per occasion this was not an appropriate question to ask with this data set, although such an analysis could be attempted with a 'multiple burst' experiment. Sampling from the posterior distributions of the model parameters was conducted using the freely available software JAGS [57], which we controlled from within the R statistical computing environment using the package RJAGS (3.13) [58] (See ESM 2 and 3 for the RJAGS and JAGS code). Following the usual MCMC setup, the parameters in each model were updated conditional on the remaining parameters to generate random draws from their posterior distribution. The standard deviations of the random effects and error terms in both the mean and SD models were assigned weakly informative scaled half-t prior distribution with 3 df [59] while the fixed effects parameters were assigned non-informative normal prior distributions (See ESM1). Three chains were run in parallel so that convergence could be assessed and each chain was run with an adaptive phase ('burn in') of 10000 iterations and a sampling phase of 15000 iterations. We made inferences about the parameters in each model based on their posterior means and 95% credible intervals. As in the study by Westneat et al. [2], we based the primary assessment of the significance of each predictor on whether or not the 95% credible intervals for the corresponding parameter covered zero. In the case of fixed effects we are also able to judge significance by generating values analogous to classical *P*-values. These pseudo *P*-values (hereafter '*P*') are obtained by calculating the tail probability for each fixed parameter. They express, as a value between 0 and 1, the probability over the set of all equal tailed credible intervals that cover zero. Thus if the 95% CI abuts zero, $P = 0.05$ but if the 95.5% CI abuts zero, $P = 0.045$ indicating a significant effect. Smaller values indicate that the posterior mean is further from zero (relative to the

level of uncertainty) and provide stronger evidence for a significant effect. This calculation was not possible for random effects as they are constrained to be positive. In cases where the posterior mean effect size was very low (< 0.02) we considered that there was no evidence of a biologically meaningful effect, irrespective of whether the 95% credible intervals crossed or abutted zero.

Results

There was no difference between populations in crab weight (t_{51} = 0.34, P = 0.74), haemocyanin concentration (t_{51} = 0.91, P = 0.37) or average spermatophore length (t_{51} = 1.6, P = 0.11). There was no correlation between crab mass and average spermatophore length (r_{51} = -0.2, P = 0.15) or haemocyanin concentration (r_{51} = -0.148, P = 0.28) but there was a significant correlation between haemocyanin concentration and average spermatophore length (r_{51} = 0.7, P < 0.0001) (Figure 1). Note that it is still valid to include both of these covariates in the main DHGLM analysis reported below. Unlike classical stepwise procedures, *P*-values are not computed by removing variables and the order of variable entry into the model has no bearing on the calculation of parameter estimates or probability. By retaining both predictors and allowing them to compete in the same model we may assess the contribution of each conditional on the contribution of the other and thus assess which is more strongly associated with variation in startle response durations.

The parameter estimates from the DHGLM and their 95% credible intervals are presented in Table 1 (See ESM1 for a visual representation). The fixed effects component of the mean model provided strong evidence that mean startle response duration was greater in crabs from Mount Batten compared to those at Hannafore (P < 0.0001) and that, on average, startle response duration increased with spermatophore length (P < 0.0001) (Figure 2). This

positive association was non-linear, the effect of changes in spermatophore length on startle response duration being more marked in crabs with small spermatophores than in crabs with large spermatphores. There was no significant effect of haemocyanin concentration after controlling for spermatophore length (P = 0.9) indicating that although haemocyanin and spermatophores co-vary, it is variation in spermatophore length that is most closely associated with startle response duration. In the case of occasion there was a very small effect size and the upper 95% credible interval abutted zero, indicating no significant sample mean level change with occasion (P = 0.11). There was no evidence that mean startle time varied with mass (P = 0.32). The random effects components of the mean model provide strong evidence for variation on the mean startle response duration among individuals that is not explained by the covariates in the model (Table 1). This effect denotes significant repeatability in startle response duration. There was no evidence, however, that the pattern of change in mean startle time across occasions varies among individuals; the lower 95% credible interval of the random slope effect abutted zero and the effect size was very small.

The fixed effects components of the SD model indicate that IIV in startle response duration increased with crab mass (P = 0.03). In the case of population (P = 0.96), spermatophopre length (P = 0.17), and haemocyanin concentration (P = 0.44) the 95% credible intervals clearly overlapped zero and thus there was no evidence that IIV was influenced by these predictors. However, the 95% credible intervals for the random effects component were clearly distinct from zero providing strong evidence for significant variation in IIV of the startle time among individuals that was not explained by the covariates in the model (Table 2). The mean startle response duration was 16.3s ± S.E. = 0.5s.

Discussion

As in previous studies the data clearly show that hermit crabs exhibit animal personality in terms not only of consistent among individual differences in mean level behaviour but also in terms of significant among individual differences in IIV. We also found, similar to previous studies, that crab mass had no effect on the mean duration of startle responses [45]. Although we have controlled for mass in previous analyses of IIV [3,8,9] this is the first time that we have tested the possibility that IIV varies with mass and there was a clear effect for larger crabs to be less consistent in their behaviour than smaller ones. While crab mass is likely to vary with age [47] the size range of crabs used in this study represents only a small proportion of the size and hence age range of sexually mature males. Thus ontogenetic variation is unlikely to underpin this trend for increasing unpredictability with crab mass. A previous study [9] demonstrated that IIV can undergo facultative adjustment in the presence of risk so that animals in a high risk situation behave less predictably than those in a low risk situation. Perhaps then the perception of risk increases systematically with increasing body mass in hermit crabs. Larger individuals, for instance, might be more obvious, or more valuable, to predators and therefore experience a greater baseline level of risk. Similarly, greater energetic requirements might entail elevated foraging compared to smaller crabs, which would again expose larger individuals to greater risk. The main aim of this study, however, was to ask whether these patterns of among individual variation in startle responses might be linked to variation in investment in spermatophores and haemocyanin. These traits did not vary with crab mass but were positively correlated with one another, indicating that individuals that invest in high fecundity also have high haemocyanin, a result which we would expect if highly fecund animals are also those with the greatest performance capacity as predicted by the pace of life hypothesis. Surprisingly, however, spermatophore length showed a negative association with boldness. That is, individuals with high fecundity (and

therefore high haemocyanin) are on average slower to recover from the startling stimulus than are those that invest less in spermatophores and haemocyanin. Although we did not measure metabolic rate, a key process for the pace of life syndrome, this result seems counter to the idea that the most productive individuals should also be the boldest [27]. The links between behaviour and pace of life are not necessarily straightforward and there are various ecological factors that may disrupt the expected associations between behaviour and fecundity [27,30,60]. Thus, while some studies have provided clear support for the pace of life explanation for animal personality (e.g. *M. menidia* [39], domestic dogs, *Canis lupus familiaris* [61]) others have been more equivocal. Two other recent studies indicate a tendency for physiological but not behavioural traits to form syndromes [62,63].

Long startle responses reduce the time available for other activities but provide a mechanism for avoiding risk. Thus, in hermit crabs startle responses increase in duration under conditions of high risk [9,45,52]. Similar positive associations between risk level and hiding time are also seen in other species (e.g. grey mouse lemur, *Microcebus murinus* [64], rock agama *Agama planiceps* [65], nutmeg manikin, *Lonchura punctulata* [66]) suggesting that, despite the presence of personality variation, plasticity in boldness is a widespread strategy. In hermit crabs long hiding times can also be advantageous in the context of fighting behaviour [67]. While long hiding times may be beneficial, there is a potential physical constraint on the maximum time for which a hermit crab may remain withdrawn into its shell. In the withdrawn position, a crab's access to fresh well-aerated seawater is restricted, which can constrain ventilation and hence aerobic respiration [68]. Some oxygen, however, will be available as oxyhaemocyanin (i.e. the oxygenated form of the respiratory pigment) and the amount available will be proportional to an individual's haemocyanin concentration. Therefore it is conceivable that aerobic scope might contribute to hiding times by imposing an upper limit on the duration of hiding. On the other hand, hermit crabs in this study were

unlikely to have reached an upper threshold of hiding times imposed by constraints on aerobic respiration. The mean hiding time in this study (16s) was far shorter than the typical time that crabs spend withdrawn into their shell whilst defending it from an attack during a 'shell fight' (447s ± S.E. = 77s, calculated using data from [67]). Defending a shell by hiding inside it for a prolonged period (and possibly undergoing repeated tensioning of the abdominal muscles at the same time) leads to elevated lactic acid, a marker of anaerobic respiration. Accumulated lactate, however, does not appear to constrain the ability of defending hermit crabs to stay in their shell whereas it does limit the performance of attacking crabs that perform vigorous agonistic displays [33]. Thus hiding duration in the context of a fight, for periods far in excess of those observed in the current study, is not constrained by aerobic scope and it is therefore unlikely that the durations of the much shorter startle responses seen here were constrained by aerobic scope. Indeed, although haemocyanin concentration and spermatophore length co-vary, it was spermatophore length, rather than haemocyanin, that explained the variance in startle response durations in our model.

In studies of aggression and reproductive investment, individuals that show enhanced performance capacity and high fecundity are typically regarded as being of high mate quality (see [69] for a review). It appears that in hermit crabs, high quality individuals that have invested heavily in reproduction, by making large spermatophores, are the most risk averse. Until their spermatophores are provided to females the pay-off from their investment has not been secured. This effect, where males that expect high reproductive success in the future take fewer risks, has also been demonstrated in the three spine stickleback, *Gasterosteus aculeatus* [70]. Low quality males, on the other hand, may emerge more quickly in an attempt to maximise their chance of mating, or because they need to return more quickly to foraging, or through a combination of these causes. Interestingly, variation in haemocyanin among

individuals is thought to be partly driven by exposure to environmental conditions such as food availability and long term exposure to hypoxia [71], which could in turn derive from differences in individual behaviour, such that there is the potential for feedback between haemocyanin and boldness. In this experiment, however, all animals were maintained in identical conditions in the laboratory, there was no difference in haemocyanin concentration between animals from the two populations and haemocyanin did not explain variation in boldness. Nevertheless, animals in their natural setting will be exposed to a range of different microhabitats that could lead to greater variation in haemocyanin compared to what is seen under laboratory conditions. Thus, in future studies an investigation of boldness and physiology under natural conditions is warranted.

In contrast to the significant mean level effect of spermatophore length, there was no evidence that IIV is linked to spermatophore length or to haemocyanin concentration, even though it showed significant variation among individuals. Previous studies indicate that IIV in hermit crab hiding times varies with ambient risk level [3,9]. We suggested that individuals might have an optimal way of behaving but depart from this at times of high risk [8], in an attempt to reduce predictability (see also [72–74]). Therefore we might also expect IIV to co-vary with individual traits if these traits influence the amount of risk that individuals are likely to be exposed to. Perhaps then, the traits measured here do not directly affect risk exposure and IIV co-varies other unmeasured traits, in addition to mass. Although haemocyanin concentration is indicative of high performance, we did not measure metabolic rate directly and IIV might co-vary with metabolic rate since high activity rates are expected to correlate with risk exposure [23,27,29]. Another possibility is that IIV variation might reflect among individual differences in ability to accurately perceive risk levels [4]. The data currently available suggest that IIV is sensitive to environmental information [3,9] but not to

internal state. This suggests a plastic trait that allows animals to adjust their behaviour in order to cope with heterogeneous environments.

Our results highlight the complexities of unpicking the underlying causes of personality in animals. An overall trend seen across study systems seems to be that high boldness enhances reproductive success at the cost of elevated mortality risk [18], a pattern that clearly matches explanations such as the pace of life syndrome. Here we have uncovered a different pattern where, although investment in aerobic scope and fecundity are positively associated, the more fecund individuals take longer to recover form a startling stimulus compared to low quality individuals. The link between fecundity and startle response duration was very clear and of a similar magnitude to the difference in mean startle responses seen between the two populations. Overall, our data point to a situation where differences in in investment in reproduction and aerobic scope contribute to consistent among individual variation in behaviour. Furthermore, these differences appear to persist under conditions of *ad libitum* feeding and optimal environmental conditions in the lab. This suggests the presence of persistent underlying among individual differences in life-history productivity investment. The mechanistic causes of such variation remain to be elucidated but may, for instance, be related to consistent differences in metabolic rate and the baseline costs of resting metabolism. Further analyses integrating metabolism, fecundity, eventual reproductive success, performance capacity and personality are therefore warranted. It would also be interesting to examine a greater age range of hermit crabs because pertinent differences in spermatophore investment might emerge between individuals close to the beginning and end of their reproductive life. Indeed, in *D. dama* Jennings et al. [11] found a quadratic relationship between IIV and mating success (although this may be distinct from fecundity). In this study the full size range of sexually mature males was available, in contrast to the current study on a specific size class of hermit crabs. The current analysis, however,

suggests that for crabs of a similar age and size, variation in startle response duration might represent a strategy whereby the most fecund individuals attempt to safeguard their investment in future reproduction through low boldness at the cost of reduced time allocated to other activities.

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Data sharing

Data are available at: http://dx.doi.org/10.5061/dryad.bh980

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Table 1: Posterior summary statistics for the mean model.

Parameter name		**Mean**	**SD**	**95% CI Lower**	**95% CI Upper**	***P***
Intercept	β_1	0.11	0.09	-0.06	0.30	0.14
Crab mass	β_2	-0.04	0.04	-0.13	0.04	0.32
Population	β_3	0.40	0.09	0.22	0.56	<0.0001
Spermatophore length	β_4	0.70	0.08	0.56	0.87	0.08
Spermatophore length^2	B_5	-0.31	0.05	-0.42	-0.20	<0.0001
Haemocyanin concentration	B_6	0.11	0.07	-0.05	0.24	0.14
Haemocyanin concentration^2	B_7	0.00	0.05	-0.09	0.11	0.91
Occasion	B_8	-0.01	0.01	-0.02	0.00	0.11
Crab ID (intercept)	$\tau_{\mu,0}$	0.28	0.03	0.22	0.34	
Crab ID (occasion)	$\tau_{\mu,1}$	0.02	0.01	0.00	0.03	

(Mean effect sizes of the standardised factor and covariates with their standard deviations and lower and upper 95% credible intervals. Note that for quadratic terms the parameter estimate indicates the direction and degree of curvature in the trend.)

Table 2: Posterior summary statistics for the standard deviation model, used to assess intra-individual variation (IIV) in startle response durations.

Parameter name		Mean	SD	95% CI Lower	95% CI Upper	*P*
Intercept	γ_1	-2.06	0.14	-2.33	-1.78	<0.0001
Crab mass	γ_2	0.21	0.10	0.02	0.41	0.03
Population	γ_3	0.01	0.20	-0.38	0.40	0.96
Spermatophore length	γ_4	-0.22	0.15	-0.52	0.08	0.17
Haemocyanin concentration	γ_5	0.12	0.15	-0.18	0.42	0.44
Crab ID (intercept)	$\tau_{\sigma,0}$	0.64	0.08	0.50	0.81	

(Mean effect sizes of the standardised factor and covariates with their standard deviations and lower and upper 95% credible intervals)

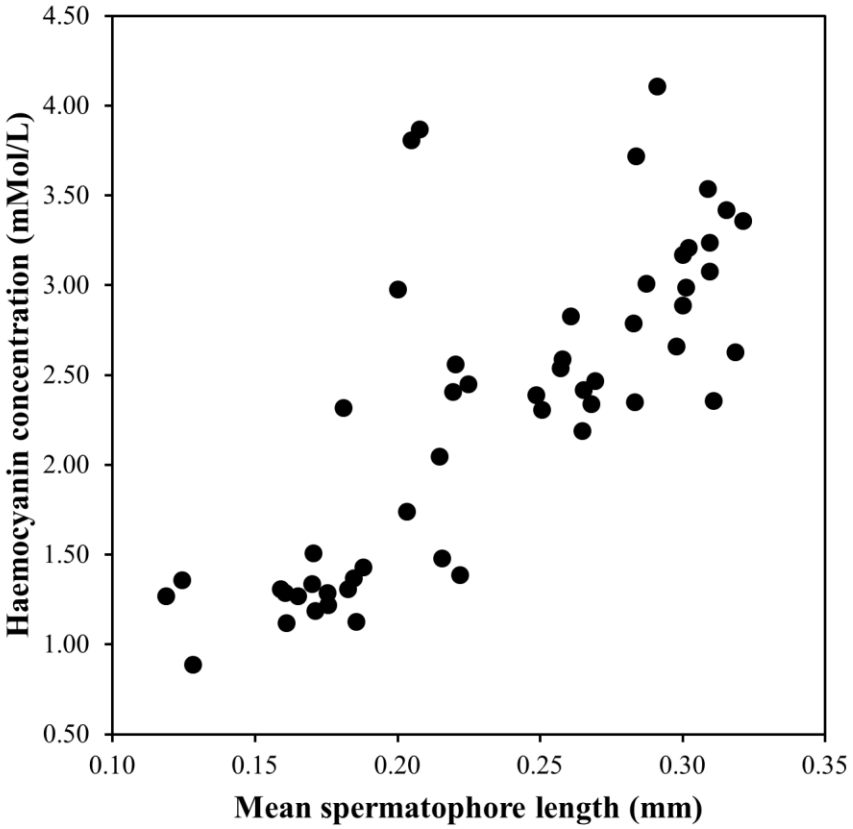

Figure 1: The positive association between mean spermatophore length and haemocyanin concentration.

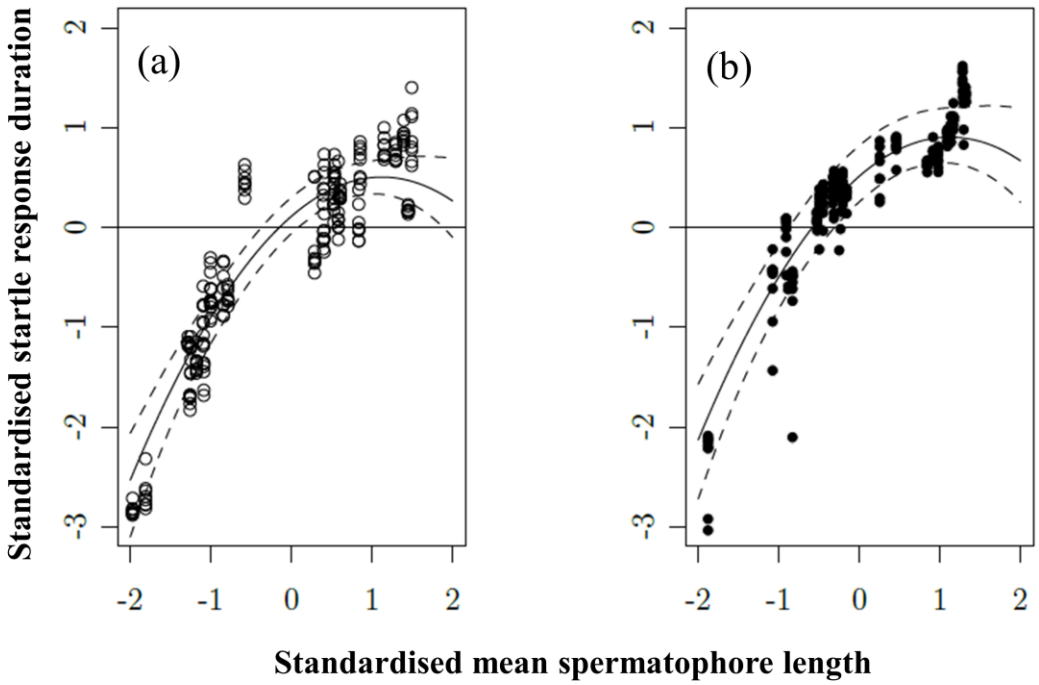

Figure 2: The quadratic relationships fitted to the association between standardised mean spermatophore length and standardised startle response duration, for data from (a) Mount Batten, open circles and (b) Hannafore, closed circles.