The causes and consequences of personality variation in the red cherry shrimp, *Neocaridina heteropoda*.

Submitted by

Rosie Ann Rickward

to the University of Exeter as a thesis for the degree of Masters by Research in Biological Sciences May 2024.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

(Signature) ……… Rosie Rickward ………

Thesis Abstract

Behaviour is arguably the most flexible aspect of the phenotype. It is also an important determinant for vital components of fitness including survival, reproduction, and growth. When the local environment is changeable, complete behavioural flexibility (or plasticity) might seem as though it is the optimal strategy, allowing for rapid phenotypic responses to maintain fitness. However, this level of behavioural flexibility is not typically found, perhaps indicating such a strategy would have costs arising from other adaptive evolutionary processes or is constrained by the genetics underlying behavioural traits and plasticity. Such costs and constraints could also help to explain the phenomenon of animal personality, which is defined as among-individual differences in behaviour that are repeatable across time and/or context. Although animal personality is now widely studied, the empirical literature remains dominated by work on vertebrates and much less is known about this phenomenon in invertebrates, which represents >90% of the Earth's animal diversity. This creates an exciting research opportunity that I address in this thesis, using the red cherry shrimp as a model for personality research in decapod crustaceans. I present two empirical studies focussing on shy-bold variation and explore possible mechanisms underpinning both behavioural consistency and plasticity. Firstly (Chapter 2), I use a repeated measures design coupled to multivariate behavioural phenotyping to investigate personality structure. I find significant individual-level variation in, and covariation among, behaviours putatively indicative of boldness, although my results do not align fully with *a priori* predictions for a simple shy-bold personality axis. I also show sexual dimorphism and size dependence do not make important contributions to among-individual variation. Secondly (Chapter 3), I take advantage of the short generation time and ease of breeding to conduct a quantitative genetic study, using a full-sib/half-sib breeding design to estimate the genetic contribution to personality and test the interplay of (heritable) personality and plasticity in the presence of predator cues. I find behavioural responses are weakly plastic to perceived predation risk and estimate a moderate heritability of time in refuge (used as a measure of boldness), although the significance in the additive genetic contribution, is marginally non-significant. I further find no support for genotype-by-environmental interactions (GxE), the presence of which would imply plasticity was also heritable. My research demonstrates behavioural differences among individual shrimp which are repeatable across two simple testing paradigms. Although some statistical caveats apply, it shows that boldness-related traits (e.g. time in the refuge) have moderate heritability and should evolve if under directional selection. Conversely, any further adaptive evolution of behavioural plasticity may be constrained. My description of personality and plasticity in the red cherry shrimp further adds to the growing picture of these phenomena in decapod crustaceans. While this research certainly sets the foundations for more fundamental studies, improved knowledge of personality may also have applications for welfare, management, and conservation efforts in decapods.

List of Contents

Chapter 1: Thesis Introduction

Chapter 2: Among-individual behavioural variation in the ornamental red cherry shrimp, *Neocaridina heteropoda*

2.3: Methods

2.4: Results

Chapter 3: Investigating heritability, plasticity and genotype-by-environmental interactions for boldness in the red cherry shrimp, *Neocaridina heteropoda*

3.3: Methods

Chapter 4: General Discussion

List of Tables and Figures

List of Appendix Tables and Figures

Acknowledgements

The following research protocols and discussions have only been made possible through the collaborative efforts by a range of people. I am grateful for all of the help from Dr Francesca Santostefano whose efforts have been instrumental to the development of my thesis, data analysis and subsequent publication of my first paper. Francesca’s contribution and guidance has massively assisted with my further advances in academia. I must, of course, further thank Professor Alastair Wilson for firstly, taking me on as a master’s student but also allowing me to tackle complicated statistical analysis and his instruction on scientific writing. Without Alastair, I would still be grappling with data formatting in RStudio I’m sure. Both Alastair and Francesca have been crucial in directing and maintaining the momentum of my research and merits significant recognition for their approachable and professional assistance over the entire duration of my research. Gratitude must also be extended to Dr Sam Green who provided me with invaluable knowledge based on his experience with the behavioural tracking software. Thanks also to all of the laboratory technicians for explaining the particulars of the study system and for help with all aspects of husbandry to maintain shrimp populations. A special thanks to Dr Tom Black for keeping me sane during months of extensive data collection and all of his efforts in undertaking the arrangement of new tanks to house shrimp families with continual monitoring and maintenance. A massive thanks also to the students who are responsible for collecting data, either used in this thesis or for preliminary analysis. I would like to extend my thanks to all PGR support staff at the University of Exeter in Penryn especially Monique Clark and Heather Platt who have personally dealt with several PGR and SRS issues I have had. Finally, I would like to extend my gratitude to members of the IT help desk at the University of Exeter both on the Penryn and Streatham campus (including but not limited to) Jo Parker and Zelin Ozturk who tenaciously tackled and resolved a long running IT issue I had over my MScbyRes programme duration.

Author’s Declaration

Rosie Rickward declares that all literature searches, manuscript writing and predominant data curation and presentation consisting of the thesis composition contributing directly to the work submitted here was carried out only by Rosie Rickward. Professor Alastair Wilson and Dr Francesca Santostefano provided feedback and advice on drafts for this work throughout the entirety of the MScbyRes programme. All raw data used was collected by Rosie Rickward and students at the University of Exeter, Penryn campus. Dr Santostefano further provided guidance on the particulars of data repositories and data visualisation for paper publications and open scientific access.

Chapter 1: Thesis Introduction

1.1: What is animal personality and why should we study it?

Animal personality is defined as the presence of behavioural differences among individuals within populations that are repeatable across time and context (Gosling, 2001; Réale et al., 2007). Theoretical studies in behavioural ecology have proposed a number of adaptive explanations for the emergence, and subsequent maintenance of this variation, proposing that among-individual differences (personality variation) have important functional significance and thus impact fitness (Dall et al., 2004; Sih et al., 2004). But are personality differences broadly adaptive, do they act as evolutionary constraints or might both possibilities be true (Dall et., al 2004)? Over the last two decades empirical work on personality has been burgeoned. However, while we now know personality variation is quite ubiquitous in animals, we are only just beginning to understand its functional and fitness consequences (Smith & Blumstein, 2008). In other words, just how does natural selection act on personality variation? This has become an important and active topic of research in behavioural ecology, with many unanswered questions remaining about why personality variation persists in animal populations.

While many researchers are focused on the *consequences* of personality variation for fitness, there are also important questions about its *causes*. Behavioural variation among individuals will certainly reflect differences in underlying physiological and neurological processes, which in turn are structured by both genes and environments (Snell-Rood, 2013). Determining the magnitude of genetic variation relative to the amount of among-individual variance caused by environmental effects is important to understand the evolution of personality (Dochtermann et al., 2019; Laine & van Oers, 2017). This is because while selection depends on how personality impacts fitness, any response to selection depends on the contribution of genes to among-individual differences. In fact, individuals can differ not just in their average behaviour (i.e. personality), but in the extent to which they respond plastically to environmental cues. Such among-individual variation in plasticity can itself be heritable, a phenomenon known as genotype-by-environment interaction (GxE). Its presence means that genotypes differ in their sensitivity to environmental change and thus elicit differing plastic responses (Nussey et al., 2007). In general, behaviours are highly plastic (West-Eberhard, 2003) but this is not incompatible with personality. For example, the expression of risk-related behaviours may be reduced on average in a high predation environment, but some individuals will consistently take more risks than others. However, if GxE is widespread this could lead to instability of individual personality across environmental contexts (e.g. if a particular genotype increases aggression under some, but not all conditions), and also cause changes in the amount of (heritable) personality variation present (Japyassú & Malange, 2014).Thus to predict the evolution of personality, we need to determine how much of this variation is explained by genes, how much by the environmental context, and potentially, how much is dependent on interactions between the two.

1.2: Research objectives and structure of thesis

In this thesis, I use the red cherry shrimp (*Neocaridina heteropoda*), as a model system to investigate an aspect of animal personality known as ‘shy-bold’ variation or simply ‘boldness’. Boldness is one of the most studied personality traits in behavioural ecology and can be defined as a variation among individuals in their tendency to engage in risk-taking behaviours (Wilson et al., 1993). Even though we might expect natural selection to favour a situation in which all individuals optimally vary their behaviour according to changes in immediate risk in the environment (Piersma & Drent, 2003), we commonly find that individuals within populations differ consistently in behaviour when observed repeatedly. This among-individual variation lies on a continuum from risk-averse (shy) individuals through to risk-prone (bold) ones (Briffa et al., 2015). Starting from this general idea, this thesis presents two empirical studies.

First, in Chapter 2, I explore personality variation in red cherry shrimp, with the goal of characterising the amount and structure of variation among-individuals for a set of behavioural traits putatively indicative of shy-bold differences. I use two distinct behavioural assays that are based on modifications of standard open field trials, and subject individuals to repeated trials using both assays. This allows me to test for among-individual behavioural differences in shy-bold type behaviours that are repeatable across both time (repeated observations) and context (i.e. assay). I also investigate the correlation structure among-traits at the individual level and ask whether the multivariate ‘shape’ of personality variation revealed by the assays matches expectations for an underlying continuum of shy-bold variation.

Building upon this study in Chapter 3, I also assess the stability of personality variation across contexts in a more ecologically informed way. I test shrimp in the presence and absence of predator (fish) cues to alter the perceived risk-reward balance of engaging in risky (bold) behaviour. I use a shelter-seeking behaviour as a measure of boldness and test the hypothesis that shrimp will increase shelter-use in response to heightened (perceived) predation risk. This follows from the idea that personality (consistent differences among individuals) and plasticity (within individual change across context) are not mutually exclusive. However, perhaps the main goal of Chapter 3 is to investigate the importance of genetic factors for personality variation. To investigate this, I conduct the behavioural trials on shrimp from known families produced in full-sib/half-sib breeding design. I then conduct behavioural assays similar to those described in Chapter 2. Although only a single observation per individual was obtained in this study, each family was split across the two treatments. I then used quantitative genetic models to test for behavioural plasticity to predator cues, estimate heritability of shelter use, and test for genotype-by-environment interactions (GxE).

1.3: Why study personality variation in decapods?

Animal personality has been shown in several hundred species. However, while most animals are invertebrates (10 million or more species (Kellert, 1993)), empirical personality research has been heavily biased towards vertebrates (Horvath et al., 2013). The extent to which ideas and patterns generalise across diverse taxa remains unclear, such that increasing our understanding of invertebrate personality variation is important. Historically, behaviour in invertebrates has often been viewed as ‘simple’ when contrasted with that of ‘higher’ vertebrates. Similarities have been used to infer the capacity of invertebrate species to obtain analogous experiences to vertebrates (including ourselves). Conversely, inconsistencies and differences have sometimes been taken as support for the premise that invertebrates are insentient (or at least, less sentient than vertebrates (Gherardi, 2009; Sherwin, 2001)) or cognitively limited and display largely ‘pre-programmed’ behavioural patterns (e.g. some insects continue feeding whilst being eaten by predators or, as in the case for the male praying mantis, by their sexual partners (Eisemann et al.,1984)). Whilst these views no longer dominate behavioural research, it remains true that vertebrate behaviour receives far more attention. However, empirical work on invertebrate behaviour and personality is growing. This is needed firstly, to understand the evolutionary and behavioural ecology of understudied groups, and secondly, because behavioural variation is increasingly relevant to more applied fields including, for example, toxicology, welfare science, and ecosystem management (Horvath et al., 2013).

Decapod crustaceans provide one good example of an understudied invertebrate group. Many species in this order are commercially important in food production, while others are playing an increasing role as models for pharmaceutical and ecotoxicological studies. Despite this, decapods have not been widely considered in the recent surge of personality research. Moreover, studies that have been done have focussed on only a small sample of species such as the mud crab, the swimming crab and the hermit crab (see examples; Hazlett, 1981; Su et al., 2022; Wall et al., 2009). Many billions of wild-caught or aquaculturally raised decapod crustaceans such as prawns, crabs, crayfish and shrimp are reared for the purpose of human consumption annually (Elwood, 2012), and paucity of behavioural data in decapod crustacean studies may well limit our ability to improve both production and welfare traits. For example, feed conversion depends on individuals being attracted to a potential food resource, and then how they feed given extrinsic factors (e.g. perceived predation risk, competition with conspecifics) that are known to depend on personality (Bardera et al., 2019). Personality and related concepts (e.g. stress coping style) are recognised in finfish aquaculture and becoming incorporated into selective breeding regimes (Castanheira et al., 2013; Ibarra-Zatarain et al., 2016). Consequently, it seems likely that increased understanding of decapod personality could provide feeding efficiency gains that support the expanding crustacean aquaculture sector (Barki et al., 2010; FAO, 2016).

1.4: The study system - *Neocaridina heteropoda*

Neocaridina is a genus of Atydid shrimp in the sub order Caridea. It consists of twenty-six species of freshwater shrimp native to Japan, China, Taiwan, Korea, and Vietnam. Many of these species have become popular in the aquatic pet trade, none more so than the red cherry shrimp, *Neocaridina heteropoda*

(Yixiong, 1996). Commercial cultivation of this species is viable and occurs globally due to aesthetic appeal (with many selected colour morphs now available), small size (<30mm in length), adaptability to captive environments, and fast development. In 2009 international trade values for global ornamental production of animals was approximately US $717 million with average growth increases of 14% approximately a year (FAO, 2014).

Despite its growing economic importance within the ornamental trade, there is very little information on this species available in the peer-reviewed scientific literature. Almost nothing is known about their basic biology and ecology in the wild, and only a few studies on growth and reproductive performance in relation to environmental parameters in captivity have been published (Tropea et al., 2015). There is however growing evidence that cherry shrimp can successfully invade habitats outside their native range. *Neocaridina* can tolerate a wide range of water and temperature parameters, and careless release by aquarists can therefore be followed by rapid establishment and dispersal. Feral populations are now known in Japan, USA, and several European countries. Consequences for native freshwater invertebrate communities are expected to follow (Klotz et al., 2013; Pantaleao et al., 2017; Weber & Traunspurger, 2016). For instance, a recent laboratory study demonstrated the top-down control of *Neocaridina davidi* can have on meiofaunal assemblages due to its omnivorous nature (Weber & Traunspurger, 2016). Of relevance for my work is that personality traits have been linked to invasion success in signal crayfish (Daniels & Kemp, 2022; Galib et al., 2022; Taylor, 2016) and thus are plausibly important in this species too. Therefore, understanding personality trait biases that enhance decapod establishment success, native species interactions, and dispersal within ecosystems is crucial (Brodin & Drotz, 2014; Daniels & Kemp, 2022).

Although basic knowledge is limited, red cherry shrimp are nevertheless emerging as a model system for studies in quantitative genetics, pharmaceutical, reproductive, and toxicological research (Hu et al., 2019; Razekenari et al., 2023; Sung et al., 2011). This is largely because of convenience. They are exceptionally easy to house in captivity and are amenable to experimental manipulation of environmental conditions (e.g. social contexts, food availability, predator cues and abiotic factors). They are also relatively short-lived but also reach maturity quickly which facilitates genetic studies and means trait inheritance across generations can be studied in a reasonable time frame (Kralj-Fišer & Schuett, 2014; Passantino et al., 2021). Usefully, mature animals are sexually dimorphic, females being larger, darker in colouration and having a curved lower abdomen shape. Females also have a visible "saddle", which is the name given to the appearance of eggs in the ovaries situated behind the head (Oh et al., 2003; Serezli et al., 2017; Vazquez et al., 2017). Females carry their eggs after fertilisation and, since the species shows direct development, these then hatch into fully formed juvenile 'shrimplets' rather than going through a nauplius larval stage.

In all these respects*, Neocaridina heteropoda* makes an ideal laboratory model system in which to investigate the causes and consequences of personality variation even if we don't yet know anything about if, or how, selection acts on behaviour in the wild.

Chapter 2: Among-individual behavioural variation in the ornamental red cherry shrimp, *Neocaridina heteropoda*

2.1: Abstract

Personality variation, defined as among-individual differences in behaviour that are repeatable across time and context, is widely reported across animal taxa. From an evolutionary perspective, characterising the amount and structure of this variation is useful since differences among individuals are the raw material for adaptive behavioural evolution. However, behavioural variation among individuals also has implications for more applied areas of evolution and ecology from invasion biology to ecotoxicology and selective breeding in captive systems. Here, I investigate the structure of personality variation in the red cherry shrimp, *Neocaridina heteropoda*, a popular ornamental species that is readily kept and bred under laboratory conditions and is emerging as a decapod crustacean model across these fields, but for which basic biological, ecological, and behavioural data are limited. Using two assays and a repeated measures approach, I quantify behaviours putatively indicative of shy–bold variation and test for sexual dimorphism and/or size-dependent behaviours (as predicted by some state-dependent models of personality). I find moderate-to-high behavioural repeatabilities in most traits. Although strong individual-level correlations across behaviours are consistent with a major personality axis underlying these observed traits, the multivariate structure of personality variation does not fully match a priori expectations of a shy–bold axis. This may reflect ecological naivety with respect to what really constitutes bolder, more risk-prone behaviour in this species. I find no evidence for sexual dimorphism and only weak support for size-dependent behaviour. My study contributes to the growing literature describing behavioural variation in aquatic invertebrates. Furthermore, it lays a foundation for further studies harnessing the potential of this emerging model system. In particular, this existing behavioural variation could be functionally linked to life-history traits and invasive success and serve as a target of artificial selection or bioassays. It thus holds significant promise in applied research across ecotoxicology, aquaculture and invasion biology.

2.2: Introduction

Within populations, individual animals often exhibit behavioural differences that are consistent across time and context (Réale et al., 2007; Réale et al., 2010a; Sih et al., 2004). Although this phenomenon, widely referred to as animal personality (Gosling, 2001), has been demonstrated across very diverse animal taxa (Bell et al., 2009), the empirical literature is dominated by vertebrate studies (Kralj-Fišer & Schuett, 2014; Mather & Logue, 2013). In comparison, personality variation in invertebrates generally, and aquatic invertebrates in particular, has been less well studied (Gherardi et al., 2012). This omission matters because understanding personality variation is not only central to fundamental research on animal behaviour, but also increasingly relevant across more applied fields such as welfare (Prentice et al., 2022), ecotoxicology (Bertram et al., 2022; Ford et al., 2021) and invasion biology (Juette et al., 2014).

From a fundamental perspective, among-individual variation in behaviour is widely assumed to have functional importance, impacting fitness via effects on survival and/or reproduction (Bertram et al., 2022; Briffa & Weiss 2010; Moiron et al., 2020; Smith & Blumstein, 2008). While quantitative genetic studies have also shown that among-individual differences are often heritable (Charmantier et al., 2014; Dochtermann et al., 2019; Stirling et al., 2002), understanding the evolutionary causes and consequences of this variation remains a challenge. Why does variation persist? Are among-individual differences adaptive, or do they reflect evolutionary constraints (e.g. trade-offs)? Why can’t all individuals adjust behaviour plastically to be optimal for the conditions they find themselves in? Hypothesised answers to these questions often invoke state-dependence, predicting that personality will covary with other traits (e.g. metabolic rate, body size) or intrinsic variables (e.g. age, sex) as a consequence of feedback between behaviour and state (Biro & Stamps, 2008; Dingemanse & Wolf, 2010; Ferderer et al., 2022; Luttbeg & Sih, 2010; Wolf & Weissing, 2010). For example, if small individuals face greater starvation risk, they may need to be ‘bolder’ (less risk averse) and more explorative to find resources faster, even if this behaviour increases predation risk (Biro & Stamps, 2010; Sih et al., 2015). State-dependence means behaviour is likely to be integrated within broader life history strategies (Dammhahn et al., 2018; Mathot & Frankenhuis, 2018; Réale et al., 2010b), and differ systematically between sexes (Patrick & Weimerskirch, 2014). For example, in some systems males, on average, need to adopt riskier behaviour than females in order to obtain mating opportunities (Harris et al., 2010; Nathan et al., 2008). Conversely, female behaviour may be selected for to reduce costs from male harassment (Clutton-Brock et al., 1995).

Although evolutionarily motivated studies dominate the literature on animal personality (Briffa & Weiss, 2010), this phenomenon is increasingly recognised as having wider implications and applications. For example, Prentice et al. (2022) argues how the integration of personality traits with stress physiology means artificial selection on behavioural biomarkers could be used to improve welfare in fish aquaculture (see also e.g. Castanheira et al., 2013; Ibarra-Zatarain et al., 2016). Ecotoxicology is another applied field in which the potential importance of among-individual differences in behaviour has been recently highlighted (Bertram et al., 2022). For example, great tits (*Parus major*) with high levels of lead in their blood and high levels of multiple metals in their feathers, should lower explorative behaviours on average (Grunst et al., 2019), while insecticide exposure lowered behavioural repeatabilities in spiders (Royauté et al., 2015), reducing the relative importance of among-individual differences. Furthermore, Polverino et al. (2021) found long-term fluoxetine exposure in guppies (*Poecilia reticulata*) erodes variation in activity levels between individuals. Ubiquitous contamination may therefore impair behaviour and future adaptive potential of phenotypic variation to anthropogenic-induced alterations within both terrestrial and aquatic landscapes.

In decapod crustaceans, such as the species I investigate here, several applications of personality variation have been suggested. First, just as in fishes, personality traits may be relevant to welfare outcomes in captivity, which are under increasing scrutiny following recognition of sentience (Birch et al., 2021; Gherardi, 2009). Second, decapod behavioural change following sub-lethal exposure to environmental pollutants could contribute to bioassays relevant for monitoring ecosystem health and susceptibility of benthic and/or sediment dwelling invertebrates to pollutants (Razekenari et al., 2023). Third, since decapods demonstrate trait-biased dispersal, with bolder individuals outcompeting conspecifics, variation in boldness and activity may link to invasive success (Galib et al., 2022; Malmqvist, 2002). Furthermore, many billions of decapod crustaceans are harvested from wild fisheries and raised in aquaculture systems for human consumption annually (Elwood, 2012). Personality differences have been shown to predict trappability in decapods (Biro & Sampson, 2015; Moland et al., 2019) just as in vertebrates (Garamszegi et al., 2009; Vanden et al., 2021), and this differential trappability may exert selection pressures on behaviour in wild populations. Finally, behavioural differences are also expected to be integrated with life-history traits important for production in aquaculture, where, for example, traits associated with foraging can affect growth rates (Bardera et al., 2019; Daly et al., 2021).

Here I investigate the presence and structure of among-individual variation in the red cherry shrimp *Neocaridina heteropoda* (syn. *N. davidi*), a small (<30mm) caridean species. This is a popular ornamental species that, being easy to maintain and breed under laboratory conditions, is an emerging model for pharmaceutical and ecotoxicological research, with relevance to ecosystem stability (Bardera et al., 2019; Horvath et al., 2013; Hu et al., 2019; Pantaleão et al., 2017; Razekenari et al., 2023.; Sung et al., 2011; Weber & Traunspurger, 2016). A short generation time and fast development also make it amenable to genetic studies and potentially a convenient model system for decapod aquaculture (Bondad-Reantaso et al., 2012; Hauton, 2012). Cherry shrimp are of commercial aquaculture importance themselves as an ornamental species (Heerbrandt & Lin, 2006). Unfortunately, release by aquarists combined with a wide tolerance of water and temperature parameters means they have become invasive outside their native range (Klotz et al., 2013; Pantaleão et al., 2017; Weber & Traunspurger, 2016). Despite this, basic biological information on this species is scarce (but see e.g. Pantaleão et al., 2017; Razekenari et al., 2023). In particular there is a lack of baseline behavioural data that may, for example, impede use of ‘behavioural endpoints’ in ecotoxicology (Ågerstrand et al., 2020; Faimali et al., 2017; Melvin & Wilson, 2013). Very little is currently known about the amount or structure of behavioural variation among-individuals. Nor is it known whether state-dependent behavioural variation, if present, is linked to intrinsic variables such as size or sex.

I focus specifically on ‘shy-bold’ variation (Wilson et al., 1993), an aspect of personality that describes differences in behavioural response to (perceived) risk (Toms et al., 2010). I use two simple testing paradigms, Open field trials

(OFT) and Food and shelter trials (FST), coupled with multivariate behavioural phenotyping and a repeated measures design. My specific aims are to (i) test for repeatable among-individual differences of the behavioural measures of boldness across the OFT and FST, (ii) determine whether the structure of multivariate behavioural variation observed is consistent with expectations given an underlying shy-bold among-individual axis (i.e. “bold” individuals explore more actively the arena, show less thigmotaxis and stress response, and are more willing to feed than “shy” individuals), and (iii) determine whether size and/sex explains behavioural variation among-individuals.

2.3: Methods

2.3.1: Study animals and husbandry

All shrimp used were from a captive-bred colony sourced from the aquarium pet trade in February 2022 and subsequently maintained in the Freshwater Laboratory of the Animal Facility in Penryn, Cornwall. The founding colony consisted of 200 red morph adult shrimp, with unknown sex ratio. On arrival in the laboratory, adult shrimp were housed in large breeding stock tanks (28cm x 19.5cm x 18.5cm) for several months to establish the breeding colony. Behavioural data for this study were collected during October and November 2022 under the local ethical approval (University of Exeter approval ID 517031). Forty-eight individuals were taken from stock tanks and moved to individual housing containers (22cm x 8.5cm x 15cm) connected to a shared recirculating water supply. Each individual tank contained a short piece of black plastic (3.5cm x 3.5cm) and a plastic plant to provide refuge. Shrimp moved to these containers were sampled haphazardly from stock, but with the condition that they needed to have a body length of at least 6mm. These were presumed to be adult females and males since individuals with a total length of >7mm can be sexed (De Silva, 1988; Pantaleão et al., 2017; Schoolmann & Arndt, 2018) and to ensure the effective tracking of behaviour in the experimental set-up (described below). Water temperature was maintained at 25 °C and shrimp were fed every two days on commercial ORGANIX granulate shrimp pellets. A constant light:dark cycle was enforced (lighting hours 07:00-19:00).

2.3.2: Overview of experimental design

To test for and characterise among-individual variation in *N. heteropoda*, I aimed to subject each of the 48 individuals to three repeats of two separate behavioural assays: an Open field trial (OFT) and a Food and shelter trial (FST). The order of assays was held constant, with all individuals completing 3 x OFT followed by 3 x FST over a five-week period, with a minimum of 48 hours between any two successive trials. This design would have yielded 288 trials (48 individuals x3 repeats x2 assays). However, some mortalities occurred during the investigation period. In some cases, I opportunistically replaced mortalities with new stock shrimp such that my final data set analysed actually comprised 273 trials on 53 shrimp, with a mean of 2.5 OFT and 2.6 FST per individual. In my final sample, 43 individuals were tested in both assays (41 of which had at least 2 repeats for each assay), 5 only in the OFT, and 5 only in the FST. I note that a small number of assays (5 OFT and 1 FST) took place but was discarded later for technical videotracking issues. Stress responses (e.g. to handling or changes in conditions due to the behavioural assays) can trigger moulting in crustaceans, which is known to affect behaviour (see Bacqué-Cazenaze et al,. 2019). Before each trial, I recorded the presence of an exuvia from moulting in the housing tank; 23 shrimp out of 273 moulted over the experimental period. However, because this was recorded only on the day of the assay, exuviae could be remains from moulting in previous days, and I do not know how long the possible behavioural changes may persist after moult.

Trials were run between 0900 and 1300 hours with individuals tested in a random order. On any given day, all trials conducted in the laboratory were of a single assay type, with duplicate experimental arena tanks allowing two shrimp to be tested simultaneously. These experimental tanks (30 cm x 20.5 cm x 21cm) were filled to 5cm^3 with water from the sump of the recirculating water system to which all individual housing units were connected. The water was changed every 6 trials to reduce any influence of conspecific cues that might be produced. Each tank was filmed from above using a Sunkwang C160 video camera mounted with a 5-50mm manual focus lens, and the tracking software Viewer II (BiObserve) used to measure behaviours putatively linked to shy-bold variation (described below for each assay). The experimental tanks were surrounded by cardboard screens to exclude external visual stimuli that might otherwise impact behaviour. Individuals were randomly assigned before each trial to one of the two arenas to minimize slight technical differences in setup, such as lighting and camera angle, that may affect the tracking, or possible differences e.g. in outside disturbance or other conditions that may affect the behaviour of the shrimp itself.

At the end of each trial, size and sex data were recorded and the shrimp was then returned to individual housing. For size both length was measured (mean: 15.77mm, SD: 2.28; from the tip of the rostrum to the posterior end of the telson using digital callipers to the nearest 0.01mm) and mass (mean: 0.07g, SD: 0.03; using a digital balance after dabbing the animal with a tissue to remove water droplets to the nearest 0.01g). However, length and mass measures were highly correlated across observations ($r=0.717$, $t_{268} = 16.843$, $P<0.001$), while mass was slightly more repeatable at the individual level ($R_{mass}= 0.768$ versus, $R_{length}= 0.581$). Assuming size was (approximately) constant for individuals over the study period then this suggests mass has a lower measurement error. I therefore used mass as my measure of size in all analyses. Sex was estimated from external morphology after each trial, and shrimp were scored as a male, female, or of unknown sex. On average, females are larger and more opaque than males, and have more rounded bellies and body plates (Vazquez et al., 2017). Females can sometimes be seen carrying eggs in their swimmerets and may show a distinctive ‘saddle’ marking (Serezli et al., 2017). Given uncertainty in sex determination, I elected to score it after each trial blind to any previous assessments of the same individual. After all observations were complete, I assigned a single sex determination of a male or female if ≥5/6 trial-specific assessments were in agreement. I assigned sex as ‘unknown’ if this criterion was not met. Following this criterion, my final sample consisted of 17 males, 14 females, and 22 shrimp of unknown sex.

Open field trials (OFT)

The OFT is a generic and simple assay widely used across taxa to measure shy-bold variation related aspects of personality (e.g. exploration in a novel environment, anxiety-like behaviour, stress coping-style) (Carter et al., 2013; Champagne et al., 2010; Dingemanse et al., 2002). In this assay, a shrimp was placed within a tube positioned in the centre of the tank (Figure 1a) and allowed to acclimate for 120 seconds. The tube was then lifted out and movement tracked for a subsequent 240 seconds using Viewer. I extracted four behavioural traits from tracking data: *Track Length, Area Covered, Wall Distance* and *Freezings* (see Table 1 for definitions). Based on OFT behaviour in other taxa, the prediction is that bolder individuals will tend to show higher values for the first three traits (i.e. more active exploration of the arena and less thigmotaxis) but lower values for freezing (Aparicio-Simón et al., 2010.; Perrot-Minnot et al., 2017). The latter prediction stems from the fact that freezing behaviour under perceived risk is a common component of behavioural stress response (e.g. the 'flight-fight-freeze' response) (Houslay et al., 2022). These behaviours are widely used in studies of shy-bold variation based on similar assays applied in fishes (Boulton et al., 2014; Polverino et al., 2016; Toms et al., 2010). I consider this an appropriate starting point, but fully acknowledge that *a priori* predictions are naïve with respect to decapod biology in general (and *N. heteropoda* specifically). Summary statistics for the original variables measured in the OFT assay are presented in Table S1.

Food and shelter trial (FST)

The FST used a modified arena into which I added (i) a shelter made of black-plastic (18cm x 5cm x 5.5cm), positioned at one end of the tank, and (ii) a food zone, comprising a black-plastic square (5cm x 5cm) with food glued to it at the other end (Figure 1b). The food was a mixture of Repashy Solient Green premix powder and ORGANIX shrimp granulate pellets (approximately 10) glued to the black-plastic square using aquarium safe glue (see Figure 1b) to prevent floating, but still accessible to the shrimp. The food zone was re-used between trials since the food consumption was minimal compared to the amount available but changed at the end of each day. Shrimp were introduced via the black acclimation tube at the centre of the tank for 120 seconds, then tracked for 240 seconds after being released. Four traits were measured: *Track Length*, *Time in Open*, *Food Latency*, and *Freezings*. Predictions for Track Length and Freezings are as described above but note that movement of shrimp could not be tracked once they were within the shelter and food zones, so these traits are recorded only for the portion of the observation period that they are outside these zones. The prediction is that bolder individuals will spend more time in the open (i.e. outside the shelter zone) and have a short latency to enter the food zone (used as a willingness to feed). Summary statistics for the original variables measured in the FST assay are presented in Table S1.

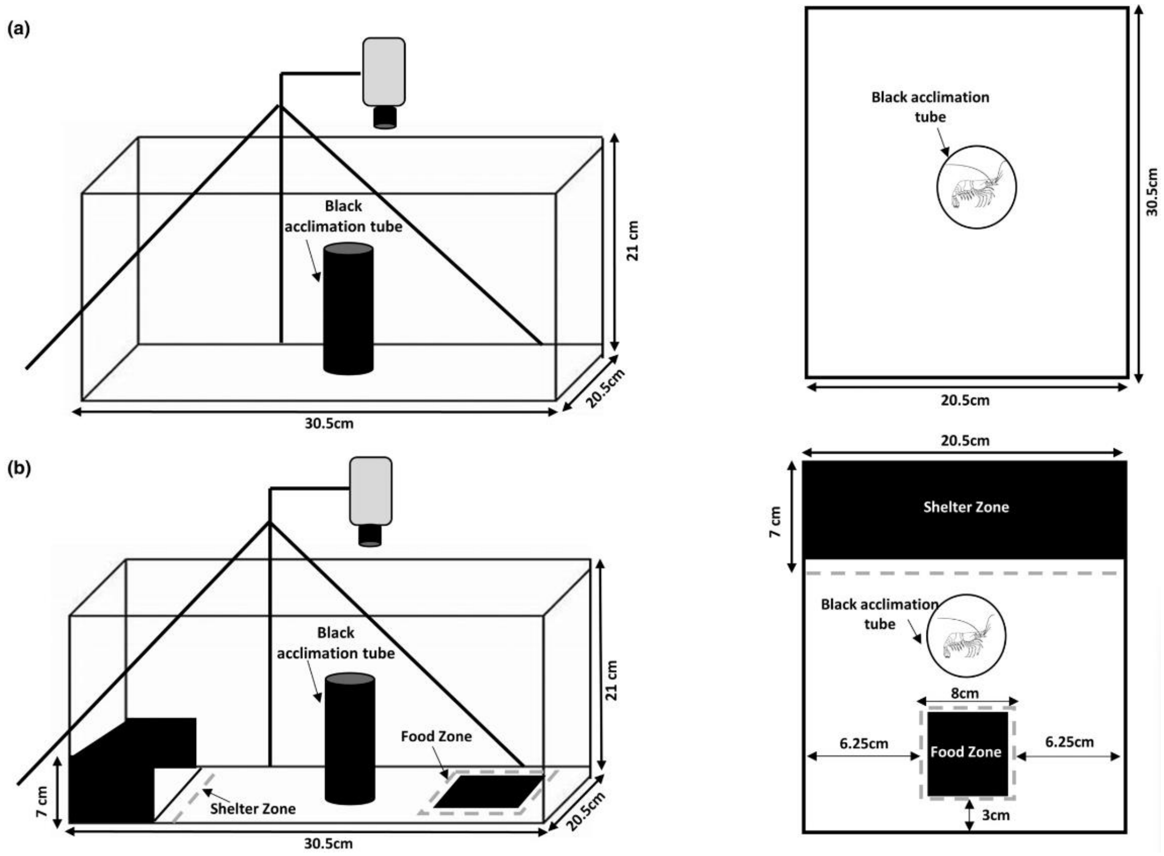


Figure 1: The tank set-ups used for (a) Open field trials (OFT) and (b) Food and shelter trials (FST) showing a side view on the left and an overhead view on the right. The starting set up for both assays has the shrimp to be tested placed inside the black acclimation tube.

Table 1: Behavioural traits recorded in Open field trial (OFT) and Food and shelter trials (FST)

Assay	**Trait**	**Definition of measured behaviour (before transformation)-**
OFT	*Track Length*	Total distance travelled (cm)
	Area Covered	Proportion of total arena (%)
	Wall Distance	Average distance away from tank walls (cm)
	-(Freezings)	Number of 'freezes' defined as speed dropping <4cm. s^{-1} for ≥2.5s
FST	*Track Length*	Distance travelled while outside shelter and food zones (cm)
	Time in Open	Time spent outside the shelter zone (s)
	-(Food Latency)	Time to first entry of the food zone (s)
	-(Freezings)	Number of 'freezes' (defined above) outside shelter and food zones

2.3.3: Statistical analyses

I used mixed effect models fitted with ASReml-R implemented in R version 4.1.1 (R Core Team, 2023). I applied log-transformations (OFT *Wall Distance;* FST *Food Latency*) and square root transformations (OFT *Track Length, Freezings*; FST *Track Length, Time in Open* and *Freezings*) to improve Gaussian assumptions, before scaling to standard deviation units which facilitates multivariate modelling. Finally, I also multiplied the transformed and scaled data for *Freezings* (both assays), and *Food Latency* (FST) by -1. This sign reversal was to simplify biological interpretation of results by making high values correspond to *a priori* expectation of 'bolder' behaviour in all cases. Following these transformations, model residuals were (approximately) Gaussian with the exception of *-(Food Latency)*, which showed major departures from residual normality that could not be resolved. Strictly Gaussian residuals are assumed in generating P values for inference, but, as shown in (Schielzeth et al., 2020), linear models have proven very robust to this, and therefore deviations from

Gaussian residuals should not cause bias in the parameter estimates presented.

Among-individual variance in behavioural traits

I tested for among-individual variation in each of the OFT and FST traits using a series of univariate linear mixed models. For each trait, I fitted a model with fixed effects of order (from 1-6 reflecting the order of individuals tested between experimental water changes), trial *repeat* number for the individual (from 1-3), time of day (in minutes after midnight) and experimental arena used (tank A versus B). The FST traits of *Track Length* and *-(Freezings)* are analogous to OFT traits but were only recorded for the portion of the observation period while shrimp were trackable outside the food and shelter zones. Since both traits were square root transformed for analysis, I included the square root of time spent in the trackable part of the arena as an additional fixed effect in the model of these traits. All these fixed effects were included simply to control for potential nuisance variables unrelated to my hypotheses. Each model also contained a random effect of individual identity (ID), allowing us to estimate among-individual variance $V_{I.}$ For each trait, I then estimated repeatability (R) conditional on fixed effects as the proportion of phenotypic variance (V_P) explained by individual differences. Thus $R=V_P/(V_I + V_R)$ where V_R is the residual (within-individual) variance. For each trait I compared my model to a reduced version of the same model without the random effect of individual identity by likelihood ratio test (LRT) to assess the significance of V_I. For testing a single variance component, I assumed twice the difference in log-likelihoods is distributed at a 50:50 mix of χ^2 on 0 and 1 DF following (Visscher, 2006).

Among individual covariance in behavioural traits

Next, I fitted a multivariate mixed model to estimate the among-individual behavioural co-variance matrix (**ID**) for the full set of 8 traits. Fixed and random effects on each trait were as described above for the univariate models. **ID** contains estimates of V_I for each trait on the diagonal, with off-diagonal elements corresponding to COV_I, the among-individual covariance for each pair of traits. Residual within-individual (co)variance was partitioned to the corresponding matrix **R**. However residual covariance (COV_R) is only identifiable between trait pairs observed simultaneously (i.e. in the same trial), so was fixed to zero between OFT and FST traits. To test the presence of among-trait covariance in **ID**, I compared the full model to one in which all COV_I were fixed to zero by LRT assuming twice the difference in model log-likelihoods as distributed as χ^2_{28}.

Having estimated **ID**, I then wanted to assess whether it was qualitatively consistent with a dominant underlying axis of shy-bold variation as predicted. To do this I (i) standardised among-individual covariance terms to the more intuitive correlation scale (where, for any pair of traits x,y the among-individual correlation $r_{I(x,y)} = COV_{I(x,y)} / \sqrt{(V_{Ix} \times V_{Iy})}$); and (ii) subjected the estimated matrix to eigen decomposition (principal component analysis). Since all traits were transformed such that high values indicated bolder behaviour, I predict correlations should be uniformly positive. I also predict that the leading eigen vector of **ID** (subsequently referred to as $\mathbf{id}_{\mathbf{max}}$) will explain a large proportion of among-individual variance and have same-sign loadings on all traits. I used a parametric bootstrap approach, following (Boulton et al., 2015) with a bootstrap sample size of 1000, to generate approximate 95% CI on the eigen values of **ID** and trait loadings on $\mathbf{id}_{\mathbf{max}}$.

Testing whether sex and size contribute to among-individual variation

To assess the extent of the contribution of sex and/or size to the among-individual variation in behaviour, I refitted all models described above but with additional fixed effects of sex (a 3 level factor: male, female, unknown), size (mass as a covariate) and their interaction sex:size. Using univariate models and conditional F-tests, I tested the significance of these effects on each trait. I compared estimates of V_I and R from these expanded models to those obtained above. I then refitted my multivariate model with the additional fixed effects and estimated $\mathbf{ID}_{\mathbf{sex:mass}}$, the among individual (co)variance matrix conditional on sex and mass. I scaled covariances to correlations, and subjected $\mathbf{ID}_{\mathbf{sex:mass}}$ to eigen decomposition as described above, allowing comparison to its structure to **ID**. I also checked for any clustering of personality visually by sex and/or size in a multivariate personality space, by predicting and plotting individual scores on $\mathbf{id}_{\mathbf{max}}$ for each shrimp.

2.4: Results

2.4.1: Among-individual behavioural variation

Our shrimp population shows significant among-individual differences in all behavioural traits measured in OFT and FST assays bar *-(Food Latency)* (Table 2). Thus, behaviours are repeatable with a median of R=0.353 (range 0.168 – 0.626) conditional on fixed effects (Figure 2, blue points). Fixed effect estimates from these models are not relevant to biological hypotheses but are presented in the Supplementary Material (Table S2). Of these, I note that replicate (i.e. number of repeat) affected OFT *Area Covered*, OFT *Wall Distance*, and FST *Freezings*, possibly indicating a habituation effect over time.

Table 2: Estimated variance components and repeatabilities (R) from univariate mixed-effect models of OFT and FST traits. V_I and V_R denote among-individual and residual variances respectively and standard errors are shown in parentheses. Also shown are X^2 and P derived from LRT to test the significance of V_I for each trait.

Assay	**Trait**	**V_I**	**V_R**	**R**	**$X^2_{0,1}$**	**P**
OFT	*Track Length*	0.616 (0.158)	0.368 (0.058)	0.626 (0.074)	48.884	<0.001
	Area Covered	0.529 (0.146)	0.413 (0.065)	0.562 (0.085)	33.988	<0.001
	Wall Distance	0.153 (0.100)	0.759 (0.118)	0.168 (0.102)	3.040	0.041
	-(Freezings)	0.456 (0.141)	0.546 (0.086)	0.455 (0.094)	22.633	<0.001
FST	*Track Length*	0.102 (0.060)	0.458 (0.069)	0.183 (0.098)	4.032	0.022
	Time in Open	0.365 (0.130)	0.668 (0.102)	0.353 (0.097)	14.207	<0.001
	-(Food Latency)	0.000*	0.995 (0.122)	0.000*	0.000	0.500
	-(Freezings)	0.109 (0.048)	0.306 (0.046)	0.263 (0.099)	8.056	0.002

*For this trait the estimate of V_I was bound to zero and no SE is estimable.

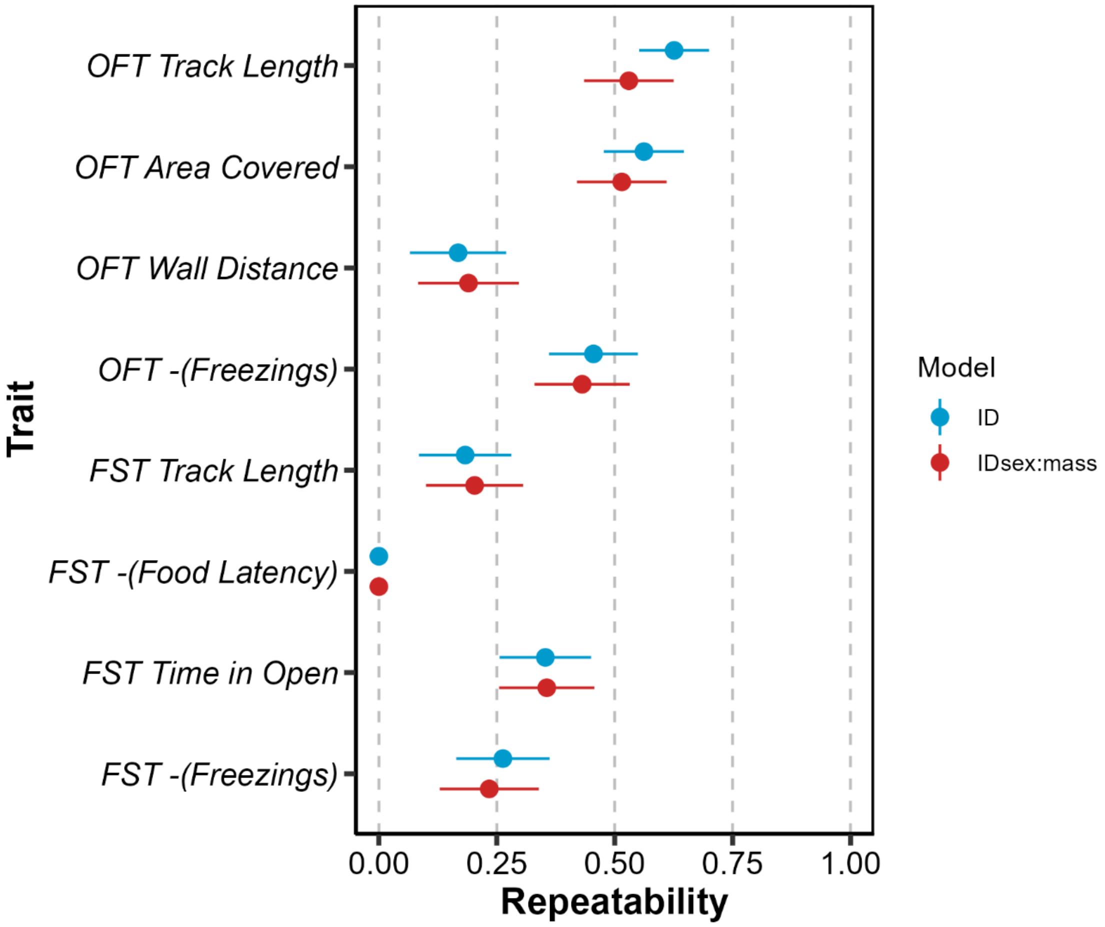
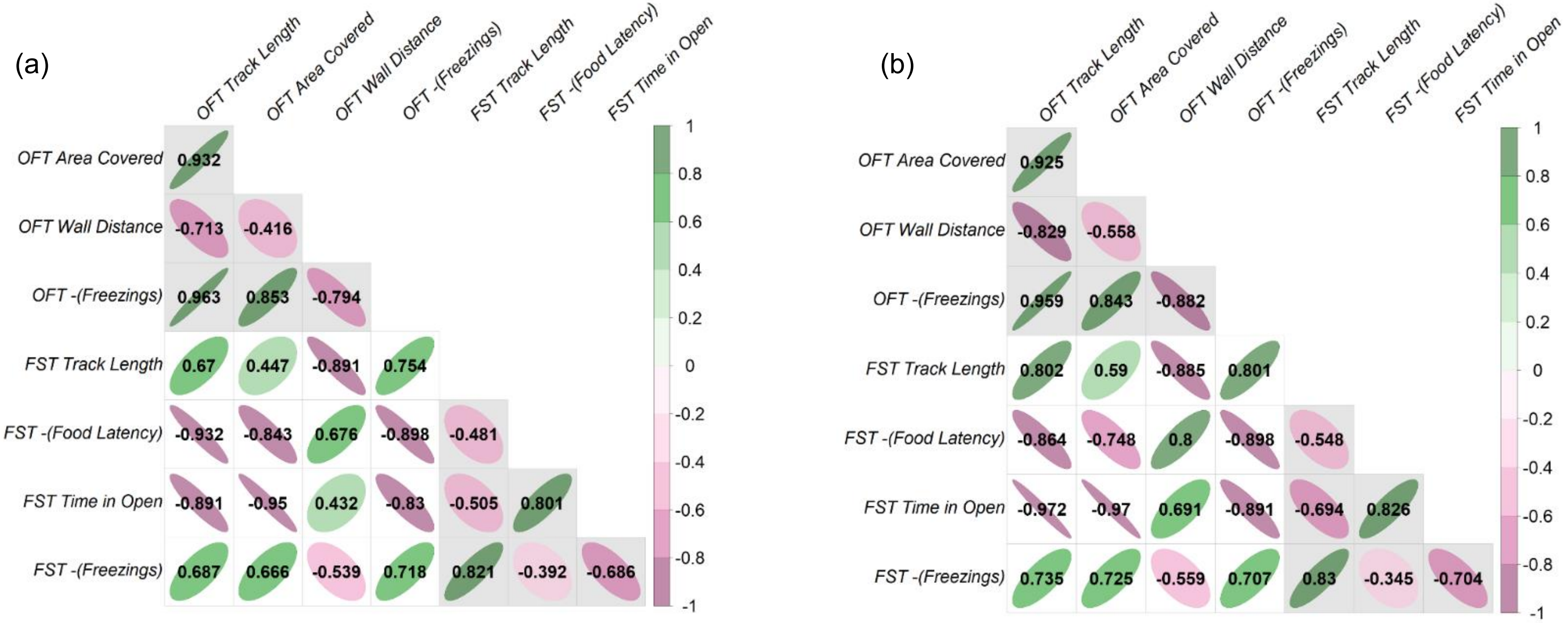


Figure 2: Repeatabilities for OFT and FST traits estimated from initial univariate models (blue points) and refitted models that condition on additional fixed effects of size and sex (red points). Error bars depict estimates ±1SE.

2.4.2: Among individual (co)variation

The multivariate model provides statistical support for individual-level covariance among the traits tested (LRT comparison of full model to one in which all COV_I terms fixed to zero; X^2_{28}=104.87, P<0.001). Pairwise correlations between traits in **ID** are generally strong (Figure 3a) with a median absolute magnitude of 0.736 (range -0.95 to 0.963). Furthermore, correlations among traits within- and across- assays are of similar magnitude. However, contrary to the prediction of a simple shy-bold axis of variation, the among-individual correlations between (transformed) trait pairs are not uniformly positive (Figure 3a). This result is also reflected in the eigen decomposition where $\mathbf{id}_{\mathbf{max}}$ captures 61% (95% CI, 46.82%-72.23%) of the among-individual (co)variance, consistent with a strong axis of personality underpinning the observed behaviours, but loads antagonistically on some traits (Figure 4, blue points). These loadings show that individuals appearing bolder than average as measured by most traits (e.g. OFT *Track Length*, OFT *-(Freezings)*), tend to appear less bold than average as measured by OFT *Wall Distance*, FST *-(Food Latency)*, and FST *Time in Open*. Of these traits, only FST *Time in Open* clearly loads significantly on $\mathbf{id}_{\mathbf{max}}$ (based on 95% CI not overlapping zero), but this is particularly notable as it indicates shrimp we might view as bolder based on most other criteria actually spend more time than average in the shelter during FST. I present the full **ID** variance-covariance matrix from which the correlations are derived in Table S3. I note that as V_I was small and non-significant for FST -(*Food Latency*), caution must be taken when interpreting correlations with this trait.



(a)

	OFT Track Length	OFT Area Covered	OFT Wall Distance	OFT -(Freezings)	FST Track Length	FST -(Food Latency)	FST Time in Open
OFT Area Covered	0.932						
OFT Wall Distance	-0.713	-0.416					
OFT -(Freezings)	0.963	0.853	-0.794				
FST Track Length	0.67	0.447	-0.891	0.754			
FST -(Food Latency)	-0.932	-0.843	0.676	-0.898	-0.481		
FST Time in Open	-0.891	-0.95	0.432	-0.83	-0.505	0.801	
FST -(Freezings)	0.687	0.666	-0.539	0.718	0.821	-0.392	-0.686

(b)

	OFT Track Length	OFT Area Covered	OFT Wall Distance	OFT -(Freezings)	FST Track Length	FST -(Food Latency)	FST Time in Open
OFT Area Covered	0.925						
OFT Wall Distance	-0.829	-0.558					
OFT -(Freezings)	0.959	0.843	-0.882				
FST Track Length	0.802	0.59	-0.885	0.801			
FST -(Food Latency)	-0.864	-0.748	0.8	-0.898	-0.548		
FST Time in Open	-0.972	-0.97	0.691	-0.891	-0.694	0.826	
FST -(Freezings)	0.735	0.725	-0.559	0.707	0.83	-0.345	-0.704

Figure 3: Among-individual correlation structure between traits as determined from multivariate model estimates of (a) **ID** the variance covariance matrix and **ID**$_{\mathbf{sex:mass}}$, the corresponding matrix conditional on sex and size. Ellipse shape and colour denote the strength and sign of each correlation. Light grey background shading indicates sets of correlations among-traits measured within each assay type (FST, OFT), while across-assay correlations have white backgrounds.

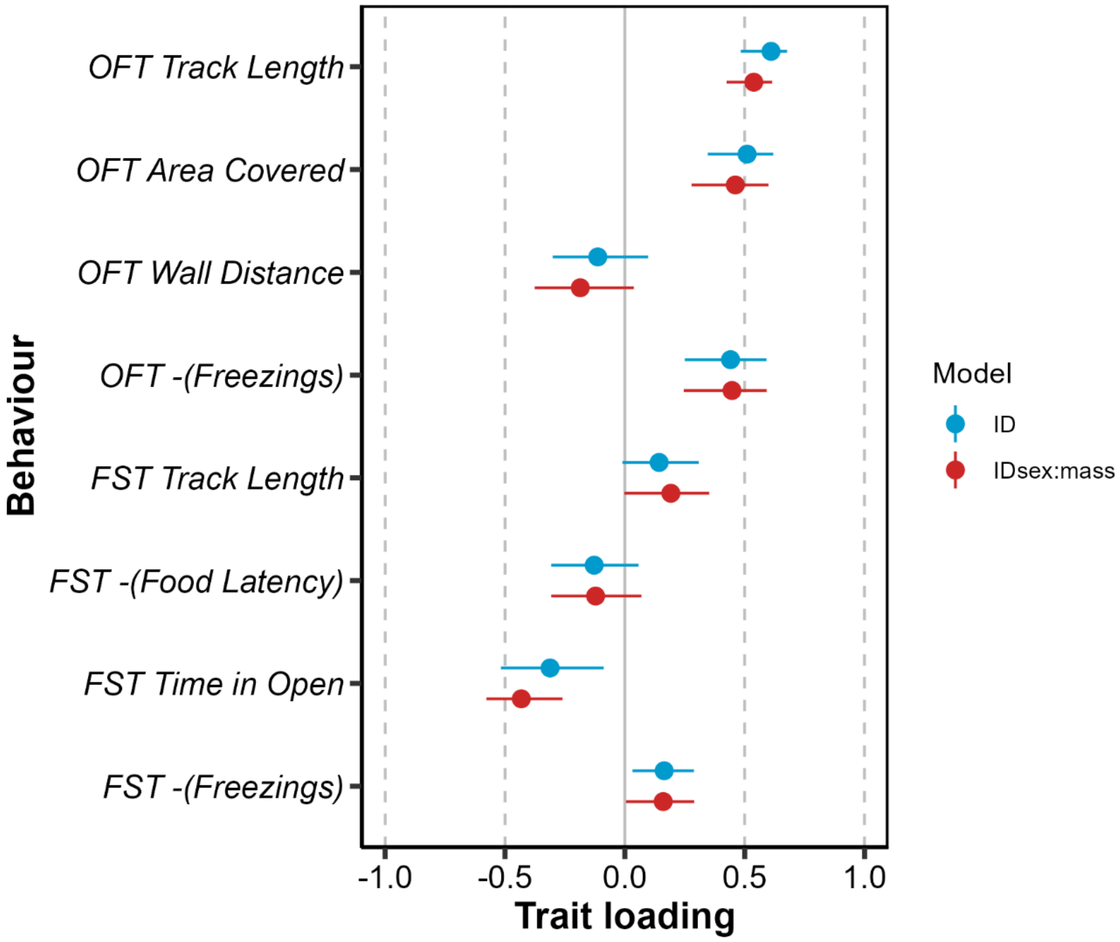


Figure 4: Trait loadings on the leading vectors of **ID** (blue points) and **ID$_{\mathbf{sex:mass}}$** (red points). Error bars denote 95% confidence intervals obtained using a parametric bootstrap (n=5000) and loadings can be considered nominally significant if CI do not cross zero (solid vertical line).

2.4.3: Effects of sex and mass

I find limited support for the hypothesis that among-individual behavioural differences are explained by sex and/or size (mass). Refitted univariate models provide no statistical support for differences in behavioural means between assigned sexes (Table 3), nor did I detect any significant sex:size interactions. However, I did detect significant main effects of size (mass) on OFT *Track Length* and OFT *Area Covered*. Both coefficients are positive meaning heavier individuals on average cover longer distances and a larger area in OFT trials.

Estimates of V_I and R from these refitted univariate models were very similar to those estimated unconditional on the extra fixed effects (Figure 2), providing further confirmation that neither sex nor size affects considerable among-individual behavioural variation in single traits. This same result also holds for the multivariate phenotype in that the correlation structure in $\mathbf{ID_{sex:mass}}$ is very similar to that in **ID** (Figure 3). Moreover, the first vector of $\mathbf{ID_{sex:mass}}$ captures 65% (95% CI 47.96%-73.26%) of multivariate variance and has trait loadings almost identical to those of $\mathbf{id_{max}}$ (Figure 4). Finally, plotting individual behavioural scores on $\mathbf{id_{max}}$ confirms the absence of clustering by sex (Figure 5). While a net positive association between mean weight and $\mathbf{id_{max}}$ can be seen, it is also clear that size accounts for only a small fraction of the variation present. I present the full table of fixed effects estimates in Table S4 and the full $\mathbf{ID_{sex:mass}}$ variance-covariance matrix from which the correlations are derived in Table S5.

Table 3: Estimated effects of sex and size on OFT and FST behavioural traits. Sex was fitted as 3 level factor (female, male, unknown) with unknown treated as the reference level. Size was measured as live mass (g). Estimates are from univariate models with significance tested using conditional F tests.

Assay	Trait	Effect	Level	Coefficient (SE)	F	DF	P
OFT	*Track Length*	sex	female	1.523 (0.862)	0.271	2,44.7	0.760
			male	1.246 (0.774)			
		mass		12.380 (6.131)	7.049	1,111.6	0.009
		sex:mass	female	-3.000 (10.140)	0.058	2,115.8	0.944
			male	0.792(11.610)			
	Area Covered	sex	female	-1.913 (0.876)	0.072	2,45.8	0.931
			male	-1.870 (0.788)			
		mass		18.400 (6.232)	4.608	1,110.4	0.034
		sex:mass	female	-17.090 (10.310)	2.073	2,115	0.130
			male	-19.430 (11.840)			
	Wall Distance	sex	female	-0.327 (0.885)	0.251	2,44.8	0.779
			male	-0.907 (0.853)			
		mass		1.9850 (6.303)	0.044	1,74.9	0.834

		sex:mass	female	-9.506 (10.490)	0.437	2,84.3	0.648
			male	-0.510 (13.020)			
	-(Freezings)	sex	female	2.735 (0.939)	0.192	2,46.5	0.826
			male	2.852 (0.860)			
		mass		12.195 (6.697)	0.764	1,101.1	0.384
		sex:mass	female	-13.750 (11.090)	1.612	2,108.1	0.204
			male	-21.000 (13.000)			
FST	*Time in Open*	sex	female	-0.717 (0.913)	2.076	2,49.1	0.136
			male	1.306 (0.996)			
		mass		-0.608 (5.973)	0.081	1,90.6	0.776
		sex:mass	female	11.770 (10.400)	1.528	2,95.6	0.222
			male	-15.540 (15.260)			
	-(Food Latency)	sex	female	-2.088 (0.775)	0.766	2,127	0.297
			male	0.343 (0.937)			
		mass		-0.939 (5.300)	0.025	1,127	0.874
		sex:mass	female	10.698 (8.915)	2.586	2,127	0.079
			male	-23.320 (14.520)			
	Track Length	sex	female	-3.449 (0.666)	0.157	2,49.3	0.855
			male	-2.915 (0.756)			
		mass		5.909 (4.441)	0.267	1,75.6	0.607
		sex:mass	female	-7.836 (7.673)	1.465	2,85.5	0.237
			male	-18.360 (11.650)			
	-(Freezings)	sex	female	0.187 (0.573)	0.818	2, 48.8	0.447
			male	0.028 (0.645)			
		mass		1.587 (3.804)	0.937	1,77.5	0.336
		sex:mass	female	2.223 (6.591)	0.203	2,87	0.817
			male	6.008 (9.930)			

Note: Sex was fitted as 3 level factor (female, male, unknown) with unknown treated as the reference level. Size was measured as live mass (g). Estimates are from univariate models with significance tested using conditional *F*-tests.

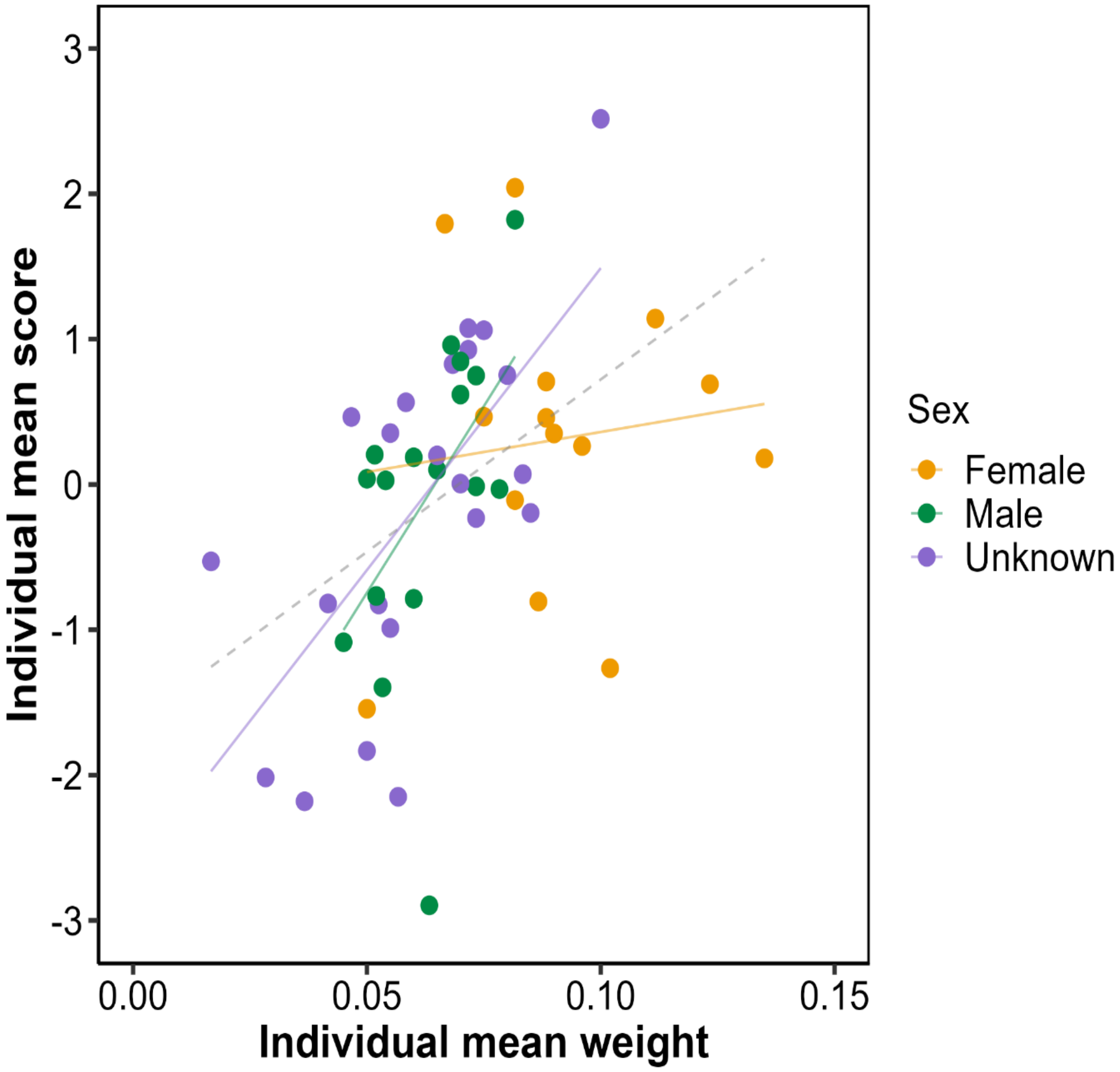


Figure 5**:** A graphical illustration of the relationship between multivariate personality, mass, and sex. Each point represents an individual's predicted behavioural score **id**$_{\mathbf{max}}$ plotted against mean weight with colours denoting assigned sex (female, male, unknown). Behavioural scores are calculated for each individual as $\mathbf{id}_{\mathbf{max}}.\mathbf{i}^{T}$ where **i** is a column vector containing the best linear unbiased predictions (BLUPs) of individual deviations from each trait mean. Also shown for illustrative purpose are overall (grey dashed) and sex-specific regressions of behavioural score on mean weight. Behavioural scores are (uncertain) model predictions and no statistical inference is intended.

2.5: Discussion

Our repeated measure design provided strong statistical support for consistent among-individual differences in behaviour across the Open field (OFT) and Food and shelter (FST) assays. As expected, multivariate analyses also yielded evidence of strong individual-level correlations among the specific traits assayed. However, in asking whether the structure of multivariate behavioural variation was consistent with *a priori* expectations of an underlying axis of shy-bold personality variation, my results provided a somewhat mixed picture. Specifically, I did find a dominant leading eigen vector of **ID** that explains most (61%) of individual level variation in, and covariation-among, traits. However, several of the behaviours measured load antagonistically on this axis, a pattern that does not match the *a priori* predictions for a simple shy-bold axis. Further analyses provided little statistical support for major contributions of size- or sex-effects to the personality variation described (though some size effects were found). Below I discuss each of these main results in the context of the existing literature and highlight some important caveats to my conclusions.

Behavioural repeatabilities were statistically significant in seven of the eight behavioural traits tested. This confirms the presence of personality variation in red cherry shrimp and shows it is readily detected using simple testing paradigms adapted from fish models. Estimates of R were lower than in the FST assay than in the OFT assay, notably for *Track Length*. This may result in some way from the greater environmental complexity of the FST or could conceivably be due to the set up that only allowed individual tracking outside the shelter (e.g. if individual activity was more repeatable in the shelter). It would be useful to develop an assay that allows tracking of animals in the shelter, and so determination of whether patterns of activity change systematically between being in the shelter and the open.

Although personality has yet to be widely tested in decapods, the repeatability estimates align with the conclusions of Bridger et al., (2015) who demonstrated among-individual variation in startle response duration (a proxy of boldness) in male hermit crabs (*Pagurus bernhardus)*. Repeatability in traits associated with shy-bold and/or exploratory personality variation has also been demonstrated in the European crayfish (*Astacus astacus*; Vainikka et al., 2011), and the rock pool shrimp (*Palaemon elegans*; Maskrey et al., 2018). In these latter examples, boldness was also negatively correlated with resource holding potential, suggesting a trade-off whereby bolder individuals may be better at finding resources but less able to defend them in competition (Maskrey et al., 2018). We do not yet know if similar relationships hold in *N. heteropoda* but investigating the functional significance of personality in relation to competition and other ecological processes (López et al., 2005) in this species would be useful. More generally, testing for associations of behavioural profiles with individual life histories would permit scrutiny of whether personality variation is maintained through adaptive processes (e.g., resource allocation trade-offs (Dingemanse & Wolf, 2010)), and/or arises through differences in resource acquisition coupled to state-dependent behaviour (Haave-Audet et al., 2022).

While estimates clearly varied among traits, some repeatabilities were notably high in comparison to the wider animal personality literature. For example, estimates of R=0.63 and R=0.56 for OFT *Track Length* and *Area Covered* are high compared to a median behavioural repeatability of 0.37 reported by Bell et al., (2009). This may, at least in part, reflect the use of a short inter-observation interval; R is known to decline as the time between observations increases (e.g., Boulton et al., 2014). However, high repeatabilities also have some implications worth noting. First, R sets an upper limit for heritability (and so potential rate of selection response) and facilitates more accurate selective breeding in aquaculture (Hill et al., 2004). Selection on behaviour has been suggested as a way to improve growth and other production traits in commercial shrimp cultivation (Bardera et al., 2019) and in this context, high repeatability of the selection target would be advantageous. In a study of Pacific white shrimp (*Litopenaeus vannamei*), Sanchez et al., (2005) found that individuals interacting more with feed had a lower latency of approach and consumed food more rapidly. In my FST assay, latency to enter the zone containing food in the FST was actually not repeatable (and so not heritable). However, if simple behavioural biomarkers of improved feeding could be identified, then selecting on these could be valuable in an industry where food waste is a major source of economic inefficiency (Cuzon et al., 2004; Sick et al., 1973). At the same time, boldness is often positively correlated with aggressiveness in animals generally (Garamszegi et al. 2013), and while agonistic behaviours appear rare in red cherry shrimp (personal observations) this is not generally true of decapods. Therefore, care must be taken that selection on behaviour to improve feeding efficiency does not exacerbate welfare and/or production costs by increasing aggression among conspecifics.

Although the implications are perhaps less clear at present, personality variation has been widely linked to the likelihood of establishment and/or invasive spreading of species following accidental or intentional introduction (Chapple et al., 2012; Rehage et al., 2016). For instance in the American signal crayfish (*Pacifastacus leniusculus*), Daniels et al., (2022) found repeatable differences in shy-bold type behaviour that predicted individual motivation to disperse by passing through weirs (though not successful at doing so). Invasion processes could therefore be considered a 'selective filter' whereby only individuals with appropriate combinations of personality and other traits can invade a novel environment successfully (Chapple et al., 2022). Working on the same species of crayfish, Pintor et al., (2008), found invasive populations were bolder and more aggressive on average than populations within their native range. However, this was only true where invasive populations were allopatric to native crayfish, and the extent to which differences were present prior to invasions, as opposed to emerging after as adaptations to a new environment is unclear. Moreover, whether population level repeatability to shy-bold type behaviours (as opposed to individual or population mean) influences invasive potential is unresolved. Low repeatability implies high plasticity- at least relative to 'fixed' individual differences- and there is a long-standing hypothesis that plasticity plays an important role in adaptation to novel environments following dispersal (Baldwin, 1896). A recent study found differences in behavioural repeatability between native and invasive species of nudibranchs that is consistent with this idea (Macali et al., 2023), but more empirical studies are needed to see if low behavioural repeatabilities reliably predict risk of invasive spread.

Although I found strong support for personality in red cherry shrimp, multivariate analyses show the structure of behavioural variation differs somewhat from the initial predictions. My eigen decomposition of the **ID** matrix is consistent with the presence of a latent personality axis that describes the majority of among-individual (co)variation in the measured behavioural traits (Houslay et al., 2018; White et al., 2020). This was expected: all traits analysed were chosen precisely because they are putatively measures of the same underlying shy-bold personality axis. Thus, the important result here is not the presence of correlation structure in **ID**, but the overall 'shape' of that structure. Specifically, because traits were scaled such that higher numbers denoted putatively bolder phenotypes, I had also predicted that covariances in **ID**, would be uniformly positive, and all traits would load on the main eigenvector with concordant signs. Some, but not all, relationships were as expected. For example, individuals that travelled further than average in the OFT, also have higher track length in the FST, cover more area (OFT), and freeze less (both assays). These behavioural characteristics meet *a priori* expectations for the bolder end of the shy-bold continuum indicating that exploratory individuals are associated with the propensity to take greater risks (Toms et al., 2010). However, the same individuals also tend to swim closer to the tank walls in the OFT (i.e. be more thigmotaxic) and take longer to visit the food zone in the FST, which are characteristics typically associated with shy personality types. Neither of these traits load significantly on $\mathbf{id}_{\mathbf{max}}$ (based on 95% CI not overlapping zero) and among-individual variance for FST *-(Food Latency)* was not statistically supported in the univariate model. However, FST *Time in Open* loads significantly on $\mathbf{id}_{\mathbf{max}}$ with a negative sign and is also moderately repeatable. This actually means individuals considered bolder and/or more exploratory in the OFT spend longer durations than average in the shelter during FST, a result that is counterintuitive. Very speculatively, it is possible that the shelter provided may have been perceived as a risky environment (rather than a safe one as intended). This could arise if, for instance, the shelter mimicked the type of structure used by drift-feeding and opportunistic foraging predatory fish (Nunn et al., 2011; Willis et al., 2019). With this considered, it would be interesting to investigate whether a refuge with greater structural complexity and/or smaller open spaces may be preferred (as demonstrated in mud crabs *Scylla serrata*; Mirera & Moksnes, 2013).

I find limited evidence for sex and size effects on behaviour and conclude that these aspects of state do not make a major contribution to personality (co)variation in the shrimp population. The absence of sex effects is perhaps somewhat surprising given the extensive evidence of behavioural sexual dimorphism in decapods. For example, male rock pool prawns (*Palaemon elegans*) are bolder and more active than females (Chapman et al., 2013), while aggression is sexually dimorphic in white shrimp (*Penaeus vannamei*; Chow & Sandifer, 1991), rock shrimp (*Rhynchocinetes typus*; Dennenmoser & Thiel, 2007) and American lobsters (*Homarus americanus*; Karavanich & Atema, 1998

). In these species, males tend to be more aggressive and able to monopolise food for longer durations relative to females. In finding an absence of sexual dimorphism here I acknowledge that uncertainty in sexing the shrimp reduces statistical power. Of the 53 shrimp tested, I ultimately classified 22 as being of unknown sex. These were, on average, smaller individuals than those assigned to male or female categories and likely to be younger (and potentially sexually immature). I therefore cannot exclude the possibility that my study partially conflates sex, age and maturation status in ways that mask any dimorphism, and thus interpret my results with caution. To check whether my findings may have been affected by the high number of unknown individuals, I re-run the univariate models with sex, mass, and their interaction, removing the individuals of unknown sex (noting that the sample size decreases considerably). For all the traits, sex and sex:mass interactions were not significant (results not shown). Nevertheless, I also note that several other decapod studies have reported an absence of sex effects on shy-bold type traits. For example, Brodin & Drotz (2014) found no difference in mean boldness or activity between male and female Chinese mitten crabs *Eriocheir sinensis*, while sex did not predict startle response duration in hermit crabs *Pagurus bernhardus* (Briffa et al., 2008).

I did find some evidence for size-dependent behaviour. Statistical support was limited to two traits in the OFT, with larger (heavier) individuals traveling slightly further and covering more area on average. These trait-specific effects drive a trend towards larger individuals having higher behaviour scores on $\mathbf{id}_{\mathbf{max}}$. This could potentially be explained by links between behavioural type and life-history strategy as proposed under heuristic frameworks such as the ‘Pace of Life Syndrome’ (Biro & Stamps, 2008; Réale et al., 2010b). For instance, high metabolic rate may be associated with bolder behaviour, increased resource acquisition, and faster growth leading to increased size (Careau et al., 2008), albeit at the likely cost of higher mortality risk (e.g. from predation; Wolf et al., 2007). At present I lack individual level data on life histories to test these hypothesised relationships. Also, there is a lack of sufficient ecological data to explore (arguably) simpler explanations for size-dependence. For instance, Toscano et al. (2014) argued size-dependent behaviour of mud crabs (*Panopeus herbstii*) was linked to size-dependent predation risk. Small crabs used refuges more than large crabs and also increased use in the presence of predators. Other mechanisms proposed for generating size-behaviour relationships in decapods are related to mating traits. For instance, male-male competition can drive size-dependent mating tactics (Correa & Thiel, 2003) with larger males engaging more in mate guarding (Knolton,1980) and contest behaviour (Jivoff & Hines, 1998; Wilber, 1989) while smaller rivals adopt exploratory mate searching tactics (Correa & Thiel, 2003). Although we cannot yet rule out similar processes in cherry shrimp, it is notable that I found no sex by size interactions on the behaviours assayed here (i.e. both larger males and females have higher *Track Length* and *Area Covered* in the OFT).

2.6: Conclusion

In conclusion, this is the first study to our knowledge that describes patterns of among-individual variation in putative measures of shy-bold variation in the cherry shrimp, *N. heteropoda.* Using simple assays widely applied to small fish models, my results are consistent with the verbal model of a single major personality axis underlying among-individual differences observed. However, the structure of this axis does not fully match *a priori* expectations of shy-bold. This could be because my initial assumptions of what constitutes ‘riskier’ behaviour in this species are incorrect. I also found no evidence for sexual dimorphism in behaviour and only limited support for size-behaviour relationships. This description of personality variation in red cherry shrimp adds to the growing picture of this phenomenon in invertebrates generally (Kralj-Fišer & Schuett, 2014) and decapod crustaceans specifically (Gherardi et al., 2012).

While in this study I investigated the structure of behavioural (co)variation over time and two experimental contexts, it will be interesting to assess this structure's stability over ecologically relevant factors, for example the presence of predator cues (i.e. perceived predation risk) and/or anthropogenic pollutants known to impact behaviour of aquatic organisms (e.g. pharmaceuticals; Bertram et al. 2022). Such factors are widely known to impact mean behaviour but can also alter the magnitude and stability of differences between individuals, resulting in environmental sensitivity of behavioural repeatabilities and the **ID** matrix (e.g. Polverino et al. 2021; Royaute et al. 2015). We have now initiated experimental work to test for this in red cherry shrimp. I therefore hope this study will set the foundations for future investigations of mechanism and functional significance in this emerging model system, as well as providing baseline data for more applied research across ecotoxicology, aquaculture, and invasion biology.

Chapter 3: Investigating heritability, plasticity and genotype-by-environment interactions for boldness in the red cherry shrimp, *Neocaridina heteropoda*

3.1: Abstract

Among-individual variation in behaviour is widely assumed to have fitness consequences, which means personality traits such as boldness (i.e. the propensity to engage in risk-taking behaviour) are subject to natural selection. If so, characterising the extent to which individual differences in behaviour arises from genetic effects is vital for understanding if, and how, boldness can evolve. Here, I conduct a quantitative genetic study of personality in the red cherry shrimp, *Neocaridina heteropoda*, to estimate the heritability of a boldness trait, specifically time spent in a refuge. I employ a full-sib/ half-sib breeding design and also split families across two different experimental treatments ('control' vs 'predator'). This allowed me to test for behavioural plasticity to increased risk (presence of predator cues in the water), but also for genotype-by-environment interaction (GxE) which is heritable variation in plasticity. I find some limited support for behavioural plasticity, with a small but marginal non-significant increase in average refuge use in 'predator' treatment. Overall, the data does support the presence of genetic variation for time spent in the refuge, but not GxE. This suggests there is adaptive evolutionary potential of boldness (time spent in the refuge) but that further evolution of behavioural plasticity may be constrained by a lack of genetic variation.

3.2: Introduction

Repeatable differences in behaviour are commonly referred to as animal personality (Dingemanse & Wolf, 2010; Gosling, 2001; Réale et al., 2007; Sih et al., 2004), and have been widely demonstrated across taxa. Variation among-individuals is the raw material for adaptation (Roche et al., 2016) and personality differences can have important fitness consequences (Bell et al., 2009; Briffa & Weiss, 2010; Moiron et al., 2020; Smith & Blumstein, 2008). Characterising the mechanisms that structure and maintain personality variation within populations is therefore important for understanding behavioural adaptation and generating evolutionary questions. For instance, we may intuitively expect selection in risky environments to reduce the propensity to engage in risk-taking behaviours over evolutionary time (Réale et al., 2007). Moreover, selection for a single optimal personality type should erode quantitative genetic variation (Ebert et al.,1993; Robertson, 1959). However, if this is the case, why do populations still contain personality types varying widely from risk-averse (shy) to risk-prone (bold) (Briffa et al., 2015)? Are there adaptive mechanisms that maintain personality variation? Or could it be that any selection present is ineffective at causing an evolutionary response? Determining exactly how constraints or costs might allow personality variation to persist has become an evolutionary conundrum we are yet to resolve (Dall et al., 2004; Sih et al., 2004; Wolf et al., 2008).

Although selection acts on variation among individuals (Houle, 1992), the evolutionary response to any selection depends on whether, and to what extent phenotypic differences among-individuals are caused by genes (Hill, 2010; Laine & van Oers, 2017). Quantitative genetic approaches address this question for any complex, polygenic phenotype (Falconer & Mackay, 1996; Kruuk et al., 2008; Lynch & Walsh, 1998) such as animal personality. Specifically, if behavioural variation is quantified among sets of individuals that include known relatives, it is possible to apply quantitative genetic methods such as the ‘animal model’ (Kruuk, 2004) to estimate genetic parameters of interest. Perhaps most importantly, we can estimate heritability (h^2), defined as the proportion of phenotypic variance explained by additive genetic effects, which determines the rate at which a trait under selection will evolve (Falconer & Mackay, 1996). Relative to other trait types (e.g. morphology), we know much less about levels of genetic variation for behaviours. Nonetheless, for personality traits in natural populations, studies to date have generally reported moderate h^2 estimates in the range of 0.2-0.5 (see examples; Brommer & Kluen, 2012; Dochtermann et al., 2014; Petelle et al., 2015). If this finding proves general, then it suggests abundant potential for further evolutionary change if it is broadly true that personality traits are under directional selection (Stirling et al., 2002). However, there remains a need to investigate the heritability of personality across more taxa, and in particular more invertebrate taxa. For instance, while pedigree-based analyses have explored genetic contributions to behavioural variation in insects (see examples on crickets; Rudin et al., 2018; Santostefano et al., 2017), little work has been done on other groups. Here I address this gap by investigating the quantitative genetics of risk-taking tendency in a decapod crustacean.

While the study of animal personality emphasises the importance of among-individual differences and the extent to which they arise from genes (Laine & van Oers, 2017), we also expect behavioural variation within-individuals as a consequence of phenotypic plasticity (Dingemanse & Wolf, 1998). Importantly, plasticity and personality are not exclusive (Dingemanse et al., 2010), so, for instance, even bold individuals will typically moderate risk-taking to some degree when there are cues indicating heightened danger (Houslay et al., 2018). Moreover, we now know plastic responses, as well as average behaviour (i.e. personality), can differ among-individuals. This means plasticity can itself be thought of as a trait that is potentially under selection and could evolve if heritable (Mathot et al., 2011; Nussey et al., 2005; Wolf et al., 2008). Genetic variation in plasticity is genotype-by-environment interaction (GxE), the presence of which means that different genotypes have different plastic responses to environmental changes (Nussey et al., 2007). An alternative, but equivalent view is that GxE means key evolutionary parameters such as h^2 will be sensitive to the environment. Recognising this may help us to understand the maintenance of among-individual variation (Wilson et al., 2006). For example, GxE could cause shy-bold personality to have high heritability only in environments when selection imposed by predators is weak (see; Dingemanse et al., 2012). Regardless of whether it is thought of as a heritable plasticity or environmental sensitivity of trait heritability, any GxE interaction present will play a vital role in shaping adaptive evolution in variable environments (Mulder & Bijma, 2005; Sartori et al., 2022; Toghiani et al., 2020).

Here, I conduct a quantitative genetic study of personality in the red cherry shrimp, *Neocaridina heteropoda*, that builds on my previous study of this species showing among-individual variation in shy-bold type behaviours (Rickward et al., 2024). My goals are to characterise the genetic contribution to personality variation, but also to investigate the interplay of (heritable) personality and plasticity. Specifically, I focus on behavioural plasticity to the presence of predator cues that indicate elevated risk in the environment. To do this, I employ a full-sib/ half-sib breeding design coupled to experimental manipulation of predator cues in the environment. My specific aims are to;

firstly, test for plasticity of behaviour under experimental manipulation of predator cues and so perceived predation risk; secondly, estimate the h^2 of shy-bold type variation, and thirdly, to test for genotype by environmental interactions (GxE).

3.3: Methods

3.3.1: Shrimp husbandry and breeding

This study used individuals from a captive colony of *Neocaridina heteropoda* housed in the Penryn Aquatic facility (see Chapter 2 for details on the source of animals and standard husbandry conditions). Maternal care coupled to direct development (i.e. absence of a planktonic stage) makes this species amenable to controlled breeding designs that permit subsequent quantitative genetic analysis (Correa & Thiel, 2003; Mahmoud et al., 2020; Oh et al., 2003). To create families in a known pedigree structure, I set up 41 breeding groups of adult shrimp, each comprising 1 male and 4 females haphazardly sampled from stock tanks 5.8l (28cm x 19.5cm x 18.5cm). After laying and fertilisation, females fix their eggs to their swimmerettes and carries them till hatching (approximately 15 days). I therefore checked groups at least once a week and any ovigerous females detected were transferred to separate 2.9l tanks (22cm x 8.5cm x 15cm). They were subsequently inspected approximately twice weekly until eggs hatched, after which the female was removed, and brood data (such as hatchling date) was recorded. Females were not re-used, but males remained in breeding groups and so could mate with multiple females. Where mortalities occurred in breeding groups I replaced, if possible, although availability of ‘unambigous’ females (see Chapter 2) was somewhat limiting.

Although up to 205 adults were housed in breeding groups at any given time, in total, 396 adults (M=54, F=342) were used over a period of 8 months. This was because where possible, mortalities were replaced, as were berried females removed from the groups in order to collect offspring. However, only 112 (75 female and 37 males individuals actually contributed to the offspring generation. Thus, here I present analyses based on the behaviour of 1111 individuals from 75 full-sibship families (mean ± se total offspring produced per brood: 15±1), nested within 37 paternal half-sibships. In fact the total offspring generation collected for phenotyping comprised 1191 individuals, but 80 were removed from the present study for a separate purpose.

Each family was raised in its own hatching tank with a recirculating water supply standardising conditions across families to minimise sources of common environment effects. Two recirculating water supplies were used, with approximately half the families on each water supply. Families were checked regularly to identify and remove any unwanted F2 shrimplets produced by sib-matings. This species is known to inbreed readily so I removed any F2 found before they could grow large enough to be mistaken for the F1 offspring. For analyses described below I treat my pedigree as known without error. This assumes no errors in paternity and that all stock adults used in breeding are unrelated.

3.3.2: Behavioural assays

Behavioural data was collected on the offspring generation from September to November 2023. Phenotyping commenced when shrimp in all families were of sufficient size for tracking. This means families necessarily differed in age at the time of behavioural data collection, a source of variation I control for statistically. Behavioural trials of individual shrimp were run between 0900-1600 hours using video tracking (Viewer). The assay used was similar to those described in Chapter 2 but with some modifications as shown in Figure 6. Most notably I created a ‘refuge zone’ that contained structure (artificial plants) that differed from the form of refuge provided in the experiments described in Chapter 2.

I tested four shrimps simultaneously using two duplicate ‘set-ups’, each comprising a single camera mounted over two replicate arenas filled to a depth of $5cm^3$. Two experimental treatments were used; a ‘control’ environment with water used to house shrimp, and a ‘predator’ treatment with water that had been used to house fish (specifically green swordtails, *Xiphophorus helleri*). Each individual experienced only a single trial, and so just one treatment level. However, families were split across treatment levels (as well as set-ups) and treatments used in each arena were alternated between ‘blocks’ of data collection. Each block was a set of 40 shrimp (10 consecutive trials x 2 set-ups x 2 arenas per set up), with two blocks (i.e. 80 trials) completed per day. Water was changed between blocks (i.e. after 10 trials in an arena).

At the end of each trial, length was measured and (putative) sex was recorded (as described in Chapter 2).

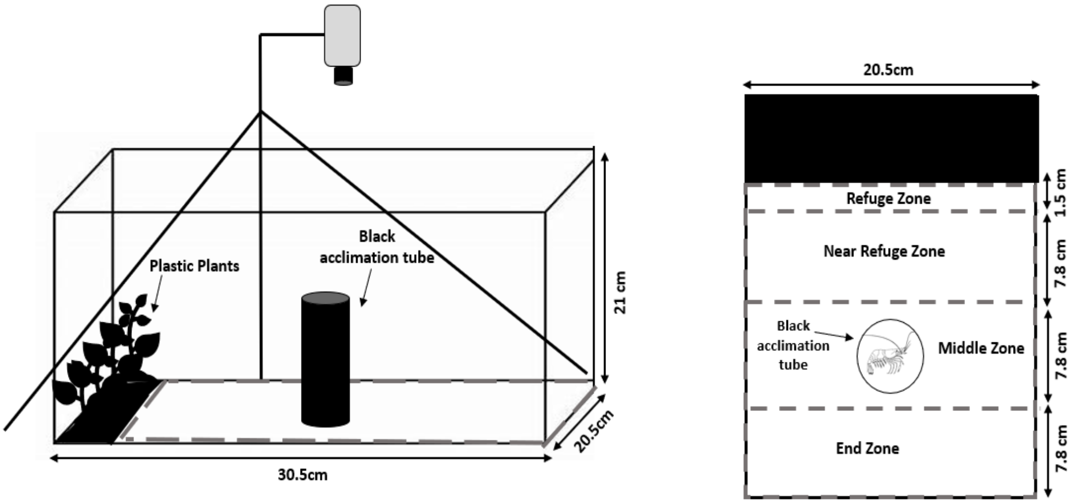


Figure 6: The tank set up used for ‘control’ and ‘predator’ trials, showing a side view on the left and an overhead view on the right. The starting set up has the shrimp to be tested inside the black acclimation tube positioned in the ‘Middle Zone’.

3.3.3: Statistical analyses

To test for plasticity, genetic variance, and GxE I analysed a single trait, namely time in the refuge zone (TIR), expected to indicate shy-bold personality (or risk-proneness). I fitted a series of univariate linear (mixed) models, including pedigree-based animal models in ASReml-R (R Core Team, 2023). I performed visual checks of model residuals to check the assumption of Gaussian residuals, and scaled TIR to standard deviation units before fitting models.

To test for behavioural plasticity to the increased perceived risk (presence of predator cues in the water) we fitted Model 1 which included: *order* (1-10 reflecting the order of individuals tested between water changes) as a fixed covariate and *arena* (tank 1-4) as a fixed factor. I also included a linear effect of *age at testing* (which ranged from 41 to 215 days) to account for this potentially important source of variation among families. Finally, I included a fixed factor of *treatment* (control vs predator water) to test for a plastic response to predator cues in the water. I predicted TIR would be higher on average in the predator treatment and used conditional F-statistics to test this (and all fixed effects). Model 1 also included a random effect of *family* to account for non-independence among full-sibs within tanks. Although family level variance (V_F) is expected to include the genetic effects under Model 1, it will also capture any maternal and/or common-environment effects. I tested the significance of V_F by likelihood ratio test (LRT) of Model 1 to a reduced formulation in which the random effect was not included. I assumed twice the difference in log-likelihoods is distributed at a 50:50 mix of x^2 on 0 and 1 DF (Visscher, 2006).

Next, Model 2 is fitted to test for and estimate the contribution of additive genetic variance and therefore allows for the estimate of heritability of shy-bold type variation. This model had identical fixed effects and the random effect of family but was formulated as an animal model (see Wilson et al., 2010) by addition of a second random effect of individual genetic merit. This allowed us to decompose phenotypic variance (VP) not explained by fixed effects into additive genetic (V_A), among-family (V_F) and residual (V_R) components. I tested the significance of V_A by likelihood ratio test (LRT), comparing Model 2 to Model 1 (as described above) to calculate the heritability (h^2) conditional on fixed effects (as $h^2=V_A/V_P$ where $V_P=V_A + V_F + V_R$).

Finally, to test for GxE under the character state approach, I formulated bivariate Model 3 in which TIR was treated as two treatment-specific traits or 'character states' ($TIR_{control}$, $TIR_{predator}$). Fixed effects were as described above and a random effect of *family* included on each trait. The additive genetic contribution was modelled as 2x2 genetic covariance matrix containing treatment-specific estimates of the additive genetic variance ($V_{A.control}$, $V_{A.predator}$), and the cross-treatment genetic covariance (COV_A), which was scaled to the corresponding genetic correlation r_G. Note that in the presence of GxE genetic effects are environment (i.e. treatment) dependent, meaning that genetic variances will differ between treatments and/or the cross-treatment genetic correlation will be less than +1. To test for statistically significant deviations from the null model of no GxE, I compared Model 3 to a reduced formulation in which I impose an absence of GxE (i.e. constraining the model such that that $V_{A.control}$, $= V_{A.predator}$ and $r_G=+1$) using a likelihood ratio test (LRT).

3.4: Results

Visual inspection of the raw data showed TIR observation varied across the full possible range of 0-300s. Family mean TIR ranged from 84.33-286.56s, while the ranking of families by mean TIR was broadly conserved across treatments. This is seen in Figure 7 with the trend across families ordered by mean TIR in the control treatment also being visually apparent with the same ordering applied to the predator treatment data.

Across all individual trials, mean TIR was slightly higher in the predator treatment as predicted, but the effect size is very small (Figure 7). Moreover, under Model 1 I find limited statistical support for the hypothesis that time in the refuge increases in the presence of water-born predator cues (Table 1). After controlling for other effects in the model, average time in the refuge was slightly higher in the predator treatment, although the difference between treatments was marginally non-significant under the two-tailed test applied (effect of predator presence on TIR, +0.103 ±0.053 SDU, P=0.050). In this model the among-family variance associated with the random effect was also significant (V_F= 0.222 ± 0.048, $\chi^2_{0,1}$= 172.665, P<0.001).

Under Model 2 (the animal model), the heritability (h^2) of TIR was estimated as 0.302 ± 0.195. Under this model the proportion of variance explained by among-family effects was much estimated as 0.069 as compares to the corresponding estimate of 0.222 under Model 1 (see Table 4). This strongly suggests the great majority of among-family variance detected in the simpler model can be attributed to genetic factors rather than maternal or common environment factors. Strictly however, the LRT comparisons of Models 1 and 2 is marginally non-significant ($\chi^2_{0,1}$ =2.386, P=0.061). Thus, while additive genetic variance explains approximately 30% of the phenotypic variance, I acknowledge that formal statistical support is therefore slightly equivocal. I do find significant among-family variation in behaviour (Model 1) that appears to come primarily from additive genetic effects (Model 2) but I am unable to completely exclude the possibility that among-family differences stem from non-genetic sources (e.g., maternal effects, common environment effects).

Model 3 provided no significant improvement on Model 2 (χ^2_2=0.358, P=0.836). Moreover, the cross-context genetic correlation between the normal and predator treatment was estimated at almost exactly +1 (r_G=1.0520 ± 0.127), and the two genetic variance estimates were also similar to each other ($V_{A.control}$ = 0.32, $V_{A.predator}$ =0.35). Thus, I find no support at all for genotype by environmental interactions (GxE), meaning there is no evidence for genetic variance in plasticity.

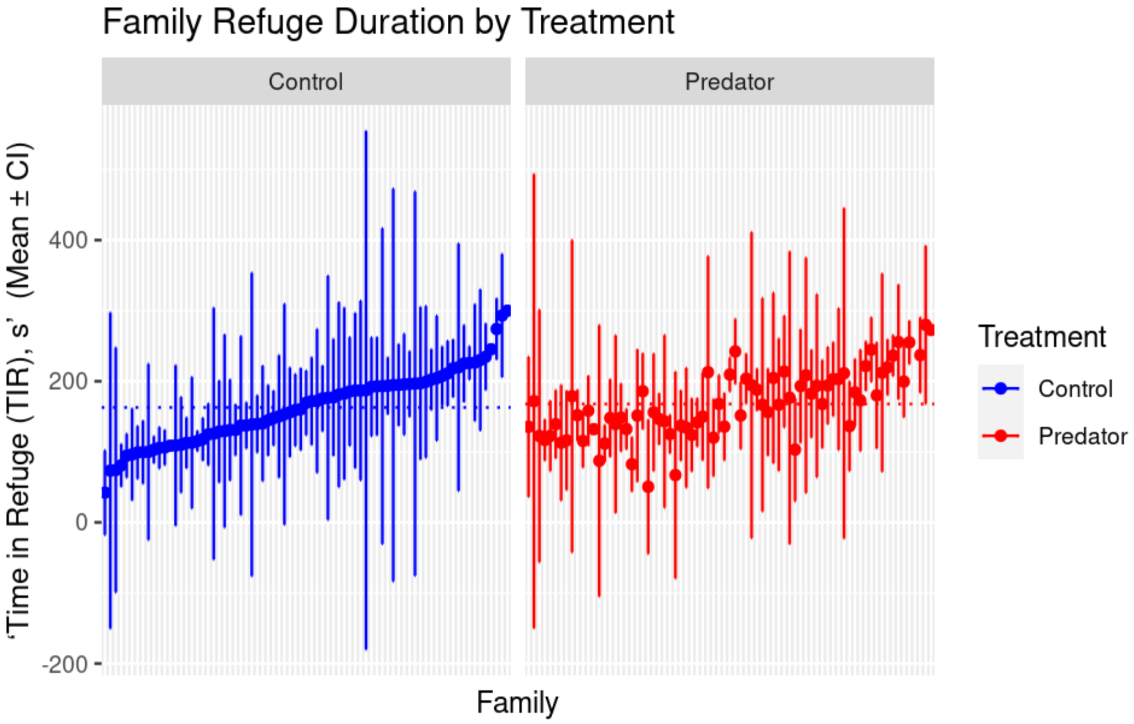


Figure 7: Mean TIR by family under control and predator treatments. In both plots families are ordered by increasing mean TIR in the control treatment with error bars denoting 95% confidence interval. Dashed horizontal lines denote the mean TIR among-individuals within each treatment.

Table 4: Estimated fixed and random effects from Model 1 and Model 2 of Time in Refuge (TIR). The significance of fixed effects is tested using conditional F-tests and influence on random effect by likelihood ratio test (LRT). Note that coefficients are in standard deviation units not seconds.

Model	**Fixed Effects**						**Random Effects**					
	Effect	**Level**	**Coefficient (SE)**	**F**	**DF**	**P**	**V_F (SE)**	**$X^2_{0,1}$**	**P**	**V_A (SE)**	**$X^2_{0,1}$**	**P**
1	Treatment	Normal	0.000 (-)	3.839	1, 1035.50	0.050	0.222 (0.048)	172.665	<0.001			
		Predator	0.103 (0.053)									
	Order		0.028 (0.011)	6.607	1, 1072.80	0.010						
	Tank	1	0.000 (-)	2.829	3, 1037.40	0.036						
		2	-0.074 (0.074)									
		3	-0.090 (0.074)									
		4	0.105 (0.074)									

	Age (days)		0.004 (0.002)	4.989	1, 86.8	0.028						
2	Treatment	Normal	0.000 (-)	3.857	1, 1036.5	0.050	0.069 (0.084)	0.584	0.222	0.294 (0.197)	2.386	0.061
		Predator	0.104 (0.053)									
	Order		0.028 (0.011)	6.752	1, 986.3	0.010						
	Tank	1	0.000 (-)	2.832	3, 1038.3	0.037						
		2	-0.073 (0.074)									
		3	-0.089 (0.074)									
		4	0.105 (0.074)									
	Age (days)		0.004 (0.002)	5.536	1, 82.1	0.021						

3.5: Discussion

I found some support for my first prediction that behaviour would be plastic to perceived predation risk in the red cherry shrimp. As predicted, average time in the refuge zone increases in the presence of water-born predator (fish) cues. Although the effect size was marginally non-significant. If the qualitative pattern is broadly robust, this would be consistent with the general finding that animals plastically reduce risk-taking behaviour in response to increased predation risk (see examples; Johnson & Sih, 2007; Kim, 2016; Sih et al., 2003). Studies of predator-induced plasticity remain limited in crustaceans but changes in behaviours thought to influence avoidance or escape have been reported (Gherardi et al., 2012). These include effects on catatonic postures in crabs (Hazlett & Mclay, 2005), locomotory tail flips in crayfish (Bouwma & Hazlett, 2001) and the duration of startle responses in hermit crabs (Briffa, et al., 2008).

Little is known about the ecology of wild *Neocaridina* species, but fish are known to be major predators of most shrimp populations (see reviews; Minello & Zimmerman, 1991; Salini et al., 1990). Consequently, increasing use of refuge areas in response to fish cues is likely an adaptive form of plasticity (Lima & Dill, 1990). If so, it is perhaps surprising that the average effect size of predator cues is so small. This may reflect the current choice of the specific trait or it may prove a general feature of shy-bold behaviours in system. In the latter case, low levels of plasticity could mean that the costs of plasticity (e.g. maintaining sensory capabilities, processing environmental cues) are high relative to expected benefits (e.g. reduced predation risk; Dall et al., 2004; Hazlett, 1995). Although, I have only analysed a single behaviour so far, the tracking data from this experiment will allow a more a multivariate approach (as used in Chapter 2) and characterising plastic responses across a wider set of traits putatively linked to boldness is an obvious next step.

In this experiment I did not obtain repeat observations on individuals so cannot directly assess individual consistency of the form (as demonstrated in Chapter 2). However, it is notable that, we do see variation among-families and also consistency of family mean behaviour across treatments. If family differences are genetic, this suggests that (i) there is underlying genetic basis of behavioural variation, and (ii) genetic effects are broadly similar in the control and predator treatments (i.e. any GxE present is of a limited effect size). However, ‘common environment’ effects (Kruuk & Hadfield, 2007) could increase phenotypic similarity between-full siblings and upwardly bias estimated genetic variance (see examples of brood effects in birds; MacColl & Hatchwell, 2003; Merilä & Sheldon, 2000). Here, I sought to control for common environment effects both experimentally (e.g. the use of recirculating systems to standardise water chemistry) and statistically (e.g. inclusion of age as a covariate in all models). Moreover, under the animal model (Model 2), the vast majority of among-family variance (as estimated under Model 1) was estimated as additive genetic. Nonetheless, additive genetic variance was estimated with quite high uncertainty, and I acknowledge that heritability was marginally non-significant. I suspect this reflects power limitations arising from the pedigree structure. Ideally, my breeding effort would have resulted in more paternal half-sibship structure (i.e. more females mated to each male) to improve this. Reiterating the above caveat about statistical significance, my model yielded an estimate of heritability of 0.3 for TIR. This is moderately high for a behavioural trait, but within the range of estimates reported in other animal studies (see examples; Brommer & Kluen, 2012; Dingemanse et al., 2002; Kralj-Fišer& Schneider, 2012; Prentice et al., 2023). Since heritability indicates the relative contribution of genes to behavioural variation (Dochtermann et al., 2019), the obtained estimate supports the view that boldness, as measured here by time spent in the refuge, could evolve under selection. Nothing is yet known about natural selection on personality in cherry shrimp populations, though boldness variation can have important fitness consequences in some systems (Rudin et al., 2019).

For labile behaviours, natural selection could potentially act on individual plasticity as well as average (across environment) trait value. This possibility arises if plasticity varies among-individuals (Laine & van Oers, 2017). Although we cannot directly test this here due to the absence of repeated observations on individuals, I was able to test for GxE (i.e. genetic variance in plasticity) using a character state approach. I found no support for differences in genetic variance in TIR between treatments and my estimate of the cross-treatment genetic correlation is (effectively) +1. From this I can conclude that there is no support for GxE on TIR across the two treatment environments tested. From an evolutionary perspective, this means genetic effects on the trait are independent of environmental context, or (equivalently) that plasticity of TIR to predator cues is not genetically variable and so would not be expected to evolve if selection does not act on plasticity. Tests of GxE for traits specifically associated with shy-bold personality variation remain rare (but see e.g. Prentice et al., 2023). However, more broadly, there is compelling evidence of GxE on labile animal behaviours across a range of environmental factors (e.g. see work done on male crickets; Callander et., 2013, Kasumovic et al., 2012; Rapkin et al., 2017). It would therefore be interesting to determine whether the current results hold true across a wider set of behavioural traits and/or a wider set of external environments (e.g. visual cues of predator) and internal states (e.g. hunger level) that may influence the costs and benefits of engaging in risk-taking behaviours.

3.6: Conclusion

In conclusion, I find some support for behavioural plasticity to the presence of water-born predator cues although the average effect size is small and marginally non-significant. Since I analyse only a single behaviour, I cannot yet conclude whether (putatively adaptive) plasticity to predator cues is an important driver of within-individual variation in shy-bold type behaviour for this species. I do find evidence for heritable genetic variation in TIR, but not for GxE. This implies that the trait could evolve under directional selection but that the scope for further adaptive evolution of behavioural plasticity may be limited. Currently, little is known about wild cherry shrimp and, as a consequence, how predation regimes select on behaviour in the field. Addressing this gap would provide valuable ecological context for these findings. In the meantime, the results provide insights into the genetics of personality variation in an emerging model for behaviour of decapod crustaceans.

Chapter 4: General Discussion

Characterising the amount and structure of behavioural variation in decapod crustaceans is an important step for investigating their behavioural and evolutionary ecology. Since among-individual differences act as the raw material for adaptive evolution, investigating behavioural variation will enrich our fundamental understanding of this invertebrate group, but also has potential to inform several areas of more applied science. For example, improved understanding of behavioural variation is useful for species management, conservation efforts and, for improving efficiency in aquaculture production. The red cherry shrimp is emerging as a valuable laboratory model for decapod biology, and my research has set the foundations for personality research in this species. In what follows, I briefly summarise the main findings of my thesis, providing some additional ecological and evolutionary context, and also suggest some future research avenues that I think would be valuable next steps.

4.1: Identifying among-individual variation in shy-bold type behaviours

In Chapter 2, my analyses of among-individual behavioural variation provided a key outcome of this thesis. Here, I showed statistically significant repeatabilities with moderate to high effect sizes for behaviours expected to *a priori* reflect shy-bold variation. This finding, together with, structure of individual-level (co)variation and correlation among traits, is consistent with the ideas of a single major personality axis underlying individual differences in the set of traits observed. Consideration of multiple behaviours and the (co)variance structure among them therefore gives a greater holistic portrayal of personality differences than would be obtained by using just one trait. In this chapter, I show the danger of the latter approach because the structure of personality uncovered did not fully match our predictions of how each indicator trait would be linked to boldness. This could be attributable to naïve assumptions of what exactly comprises risk-proneness in cherry shrimp. I also highlight the lack of among-individual variation for food latency. This means for example, if this trait alone had been used to investigate boldness, I would have erroneously concluded a lack of among-individual variation in this species. Decapod crustaceans perform feed-grabbing behaviours through pleopod beating to generate water currents (Bardera et al., 2019), so not visiting the food zone may not fully equate with not feeding. If so, then within-individual (across trial) changes in the extent of reliance on foraging movements versus feed-grabbing may have led to low among-individual variation in visits to the food zone, even if some shrimp consistently fed more than others. It was not possible to measure feed-grabbing through pleopod beating using video tracking, but this can potentially be scored from video in future studies.

I find no evidence for sex effects contributing to this personality variation and only limited support for size-behavioural relationships. This was perhaps surprising since many studies have argued state-dependent selection is argued to seemingly drive behavioural traits shared between sexes (Han et al., 2015). However, it is also the case that the direction of predictions is quite variable. For instance, in some species, smaller individuals are predicted to be bolder and more explorative because high metabolic rates increases proportional energy demands relative to larger individuals (Cooper & Frederick, 2007; Krause et al., 1998; Peters, 1986). Conversely, in cases, bigger individuals tend to be bolder, perhaps because predation risk decreases with size (Brown et al., 2007). Specifically, in caridean sexual system diversity, body size may particularly affect male mating and be linked to among-individual variation in ‘pure searching’ behaviour as evident for *Heptacarpus pictus* and *Palaemonetes pugio* (Bauer & Abdalla, 2001; Correa & Thiel, 2003). For instance, where size-dependent behaviour driven by mating competition does occur (Blenderman, 2020; Wolf & Weissing, 2010), larger decapod males are more likely to defend females and/or refuges whilst smaller ones ‘search’ for mates (see reviews; Correa & Thiel, 2003; Wickler & Seibt, 1981) and may therefore be perceived as more exploratory and bold.

In Chapter 2, I have thus provided a baseline description of among-individual behavioural variation in red cherry shrimp. There is now a need to investigate the functional role of personality in relation to predation risk, competition, mating tactics and individual life histories. This research is needed to understand what the consequences of personality differences are for evolutionary fitness, and so whether variation might be explained by trade-offs or other adaptive processes.

4.2: Identifying the genetic contribution to shy-bold type behaviours

If phenotypic selection is acting on personality traits in natural populations, then it may or may not be effective at causing any changes in behavioural response. This will depend on the role of genes in causing and maintaining personality (Jensen et al., 2008; Laine & van Oers, 2017). However, there is very little knowledge of the extent to which personality variation is genetically determined in decapods. In Chapter 3, I addressed this for the trait of 'time in the refuge', using this as an indicator of shy-bold personality. I also investigated plasticity in this trait, testing the prediction that shrimp would increase their average time in the refuge in the presence of predator cues. Whilst noting the effect size is small, I find some support for behavioural plasticity to predator exposure in the direction predicted. I also find some support for heritable genetic variation in time spent in the refuge, but no evidence for genotype-by-environment interactions (GxE). The evolution of behavioural plasticity may sometimes be constrained by costs (e.g. of maintaining sensory capabilities) that offset its advantages. In decapods, it has been argued that limited plasticity of behaviours that are risky but facilitate resource acquisition may also reflect genetic constraints (Gherardi et al., 2012). My analysis supports this because the absence of GxE indicates that plasticity is not heritable and so would not evolve further even if a stronger plastic response was selected for.

A limitation of Chapter 3 is that I have, thus far, only analysed a single behaviour putatively indicative of shy-bold variation. Fully investigating the interactions between genetic and plastic effects on behaviour will likely benefit from the more multivariate approach as employed in Chapter 2. Additional traits can be extracted from tracking records of individuals tested in Chapter 3. This will allow, for example, testing of whether perceived risk (i.e. presence of predator cues) impacts estimated genetic correlations among traits. Future work expanding the set of traits to include (e.g. aspects of physiology (Houslay et al., 2022)) would be useful, as would measuring traits at different ages or life stages. Together, this would facilitate a better understanding of how behavioural differences develop and provide insights into how physiological processes might stabilise personality (Stamps & Groothuis, 2010). To date few studies have investigated how among-individual and/or genetic correlations among behavioural traits change across ontogeny and little is known, for example, about whether early life experience can impact later life correlation structure (Bell, 2007; Frost et al., 2007; Groothuis & Carere, 2005).

4.3: Concluding Remarks

Despites its popularity in the aquatic trade and increasing use a biological model, currently, very little is known about the red cherry shrimp, *Neocaridina heteropoda.* The research presented here provides important behavioural data that I hope will further develop our appreciation of personality in decapod crustaceans and stimulates more research into the mechanisms that explain it. I have also set out several future research avenues that could build upon current findings to further explore the function, causation, and evolution of personality in this group of animals. My work demonstrates the presence of among-individual behavioural variation but also of among-family differences, in accordance with a contribution of genetic factors to behavioural profiles that are consistent across time and context. This holds promise for aquaculture where artificial selection on genetically-based behavioural profiles could improve welfare and productivity (e.g. if behaviours are genetically integrated with life-history traits such as growth). The cherry shrimp is also now being used as an ecotoxicology model, and work on sensitivity to pharmaceutical pollutants (including non-lethal effects on behaviour) has begun in our captive population. Thus, I hope that the data from this thesis will provide a useful baseline against which to assess environmental-sensitivity and impacts of environmental pollutants. However, perhaps the main contribution of this work will be in evolutionary and behavioural ecology. I have tried to highlight the value of cherry shrimp as a behavioural genetic model and provided a foundation for personality research in this species. More work is now needed to understand the functional significance of this behavioural variation and to determine if, and how, correlations with fitness related traits may promote or constrain evolutionary adaptation.

Appendix tables and figures

Table S1: Summary statistics for the OFT and FST untransformed behavioural traits observed in Chapter 2.

Assay	Trait	mean	sd	median	min	max
OFT	*Track Length*	707.99	365.15	703.90	58.5	1752.2
OFT	*Area*	38.78	16.29	39.90	0.7	71.2
OFT	*Wall Distance*	2.71	1.26	2.40	0.8	9.1
FST	*Freezings*	10.00	6.34	10.00	0	31.0
FST	*Track Length*	147.85	135.56	104.80	0	667.3
FST	*Time in Open*	84.83	75.09	53.45	0	240.0
FST	*Food Latency*	90.72	103.67	33.10	0	240.0
FST	*Freezings*	3.05	3.75	2.00	0	19.0
-	size (mm)	15.77	2.28	16.00	9.00	21.54
-	mass (g)	0.07	0.03	0.07	0.01	0.14

Table S2: Fixed effects from univariate models presented in Chapter 2. Estimated effects of experimental tank set up, order, replicate, and time of day on OFT and FST behavioural traits. Tank set up was fitted as a two-level factor (Tank A, Tank B) with Tank A being treated as the reference level. Order (1-6) reflects the order shrimp were tested between water changes. Replicate reflects the trial repeat number for the individual (from 1-3). Time of day is recorded as minutes after midnight. Estimates are derived from univariate models with significance tested using conditional F tests.

Assay	**Trait**	**Effect**	**Level**	**Coefficient (SE)**	**F**	**DF**	**P**
OFT	*Track Length*	Set Up	Tank A	1.884 (1.186)	0.154	1,94.5	0.695
			Tank B	1.836 (0.122)			
		Order		0.012 (0.038)	0.102	1, 92.6	0.750
		Replicate		-0.100 (0.067)	2.197	1, 86.5	0.142
		Time of Day		-0.003 (0.002)	2.044	1, 110.8	0.156
	Area Covered	Set Up	Tank A	-2.237 (1.231)	14.800	1, 96	0.000

			Tank B	-1.743 (0.128)			
		Order		-0.016 (0.039)	0.155	1, 93.8	0.695
		Replicate		0.210 (0.071)	8.728	1, 85.7	0.004
		Time of Day		0.002 (0.002)	1.658	1, 114.3	0.200
	Wall Distance	Set Up	Tank A	-0.975 (1.439)	8.881	1, 117.0	0.004
			Tank B	-1.454 (0.161)			
		Order		0.022 (0.050)	0.209	1, 114.1	0.648
		Replicate		-0.233 (0.094)	6.064	1, 89.2	0.016
		Time of Day		0.002 (0.002)	1.149	1, 127.9	0.286
	- *(Freezings)*	Set Up	Tank A	2.375 (1.367)	4.979	1, 101.7	0.028
			Tank B	2.700 (0.145)			
		Order		0.034 (0.045)	0.574	1, 99.1	0.451
		Replicate		-0.072 (0.081)	0.776	1, 87.6	0.381
		Time of Day		-0.004 (0.002)	3.170	1, 120.8	0.078
FST	*Time in Open*	Set Up	Tank A	-0.267 (1.782)	0.058	1, 122.9	0.810
			Tank B	-0.227 (0.167)			
		Order		-0.052 (0.053)	0.943	1, 120.8	0.333
		Replicate		0.025 (0.086)	0.088	1, 89.8	0.767
		Time of Day		0.001 (0.003)	0.041	1, 132.6	0.841
	-(Food Latency)	Set Up	Tank A	-0.143 (1.787)	1.974	1, 133	0.162
			Tank B	-0.393 (0.178)			
		Order		0.071 (0.057)	1.518	1, 133	0.220
		Replicate		-0.060 (0.103)	0.342	1, 133	0.560
		Time of Day		0.000 (0.003)	0.008	1, 133	0.930
	Track Length	Set Up	Tank A	-3.34 (1.360)	1.070	1, 130	0.303
			Tank B	-3.204 (0.131)			
		Time in Arena		0.159 (0.016)	99.480	1, 129.4	<0.001

	Order		-0.02 (0.042)	0.216	1, 129.8	0.643
	Replicate		0.067 (0.07)	0.903	1, 91.2	0.344
	Time of Day		0.003 (0.002)	2.224	1, 129.3	0.138
- *(Freezings)*	Set Up	Tank A	-0.078 (1.157)	4.372	1, 126.7	0.039
		Tank B	-0.308 (0.110)			
	Time in Arena		-0.181 (0.014)	178	1, 131.9	<0.001
	Order		0.046 (0.036)	1.634	1, 126.3	0.204
	Replicate		0.178 (0.058)	9.502	1, 90.2	0.003
	Time of Day		0.002 (0.002)	0.722	1, 131.7	0.397

Table S3: Variance-covariance **ID** matrix estimated from the multivariate model presented in the main text of Chapter 2. Variances and covariances with associated standard errors are presented on the diagonal and lower off diagonal respectively.

Trait	*OFT Track Length*	*OFT Area Covered*	*OFT Wall Distance*	*OFT -(Freezings)*	*FST Time in Open*	*FST -(Food Latency)*	*FST Track Length*	*FST -(Freezings)*
OFT Track Length	0.611 (0.154)	-	-	-	-	-	-	-
OFT Area Covered	0.470 (0.13)	0.488 (0.137)	-	-	-	-	-	-
OFT Wall Distance	-0.134 (0.087)	0.017 (0.081)	0.155 (0.099)	-	-	-	-	-
OFT -(Freezings)	0.373 (0.117)	0.284 (0.103)	-0.120 (0.081)	0.423 (0.133)	-	-	-	-
FST Time in Open	-0.239 (0.105)	-0.237 (0.099)	0.017 (0.079)	-0.149 (0.095)	0.371 (0.13)	-	-	-
FST -(Food Latency)	-0.134 (0.084)	-0.073 (0.077)	0.052 (0.065)	-0.090 (0.077)	0.081 (0.080)	0.069 (0.099)	-	-
FST Track Length	0.129 (0.073)	0.047 (0.066)	-0.104 (0.057)	0.123 (0.067)	-0.046 (0.070)	0.000 (0.058)	0.140 (0.066)	-
FST -(Freezings)	0.130 (0.065)	0.148 (0.061)	-0.004 (0.049)	0.120 (0.059)	-0.036 (0.061)	0.029 (0.050)	0.088 (0.042)	0.128 (0.051)

Table S4: Fixed effects from expanded univariate models including sex and size (mass) presented in Chapter 2. Estimated effects of experimental tank set up, order, replicate, time of day, sex, and size on OFT and FST behavioural traits. Tank set up was fitted as a two level factor (Tank A, Tank B) and sex as a 3 level factor (female, male, unknown). Tank A, unknown, and unknown:mass are treated as the reference level. Order (1-6) reflects the order shrimp were tested between water changes. Replicate reflects the trial repeat number for the individual (from 1-3). Time of day is recorded as minutes after midnight. Estimates are derived from univariate models with significance tested using conditional F tests.

Assay	Trait	Effect	Level	Coefficient (SE)	F,con	DF	P
OFT	*Track Length*	sex	Unknown	1.114 (1.244)	0.271	2,44.7	0.764
			Female	1.528 (0.862)			
			Male	1.246 (0.774)			
		Mass		12.387 (6.131)	7.049	1, 111.6	0.009
		Order		0.004 (0.039)	0.009	1, 93.5	0.924
		Replicate		-0.0854 (0.704)	1.470	1, 82.4	0.229
		Time of Day		-0.003 (0.002)	2.453	1, 112.3	0.120
		Set Up	Tank A	1.114 (1.244)	0.068	1, 93.2	0.7944
			Tank B	1.082 (0.126)			
		Sex:Mass	Unknown	1.114 (1.244)	0.058	2, 115.8	0.944
			Female	-1.883 (10.140)			
			Male	1.906(11.608)			
	Area Covered	sex	Unknown	-3.086 (1.273)	0.0717	2, 45.8	0.931
			Female	-1.913 (0.876)			
			Male	-1.870 (0.788)			
		Mass		18.397 (6.232)	4.608	1, 110.4	0.034
		Order		-0.017 (0.040)	0.179	1, 94.9	0.673
		Replicate		0.221(0.072)	9.329	1, 83.6	0.003
		Time of Day		0.002 (0.002)	1.047	1, 113.5	0.308
		Set Up	Tank A	-3.086 (1.273)	15.32	1, 94.8	0.000
			Tank B	-2.581 (0.129)			

		Sex:Mass	Unknown	-3.086 (1.273)	2.073	2, 115	0.130
			Female	-20.171 (19.308)			
			Male	-22.517 (11.844)			
	Wall Distance	sex	Unknown	-0.912 (1.512)	0.251	2, 44.8	0.779
			Female	-0.326 (0.885)			
			Male	-0.907 (0.853)			
		Mass		1.983 (6.303)	0.045	1, 74.9	0.834
		Order		0.0287 (0.051)	0.318	1, 110.4	0.574
		Replicate		-0.220 (0.096)	5.284	1, 88.3	0.024
		Time of Day		0.002 (0.002)	0.906	1, 123	0.343
		Set Up	Tank A	-0.911 (1.512)	9.116	1, 112.5	0.003
			Tank B	-1.404 (0.163)			
		Sex:Mass	Unknown	-0.911 (1.512)	0.437	2, 84.3	0.648
			Female	-10.417 (10.489)			
			Male	-1.422 (13.017)			
	- *(Freezings)*	sex	Unknown	1.586 (1.424)	0.192	2, 46.5	0.826
			Female	2.735 (0.939)			
			Male	2.852 (0.861)			
		Mass		12.195 (6.697)	0.764	1, 101.1	0.384
		Order		0.035 (0.046)	0.574	1, 99.4	0.451
		Replicate		-0.074 (0.0829)	0.803	1, 85.7	0.373
		Time of Day		-0.004 (0.002)	3.112	1, 117.9	0.080
		Set Up	Tank A	1.586 (1.423)	5.044	1, 99.6	0.027
			Tank B	1.915 (0.147)			
		Sex:Mass	Unknown	1.586 (1.424)	1.612	2, 108.1	0.204
			Female	-12.163 (11.088)			
			Male	-33.117 (11.088)			
FST	*Time in Open*	sex	Unknown	-0.161 (1.878)	2.076	2, 49.1	0.136
			Female	-0.718 (0.913)			
			Male	1.306 (0.996)			
		Mass		-0.608 (5.973)	0.081	1, 90.6	0.776

	Order		-0.054 (0.054)	0.980	1, 114.5	0.324
	Replicate		0.051 (0.085)	0.362	1, 87.9	0.549
	Time of Day		0.000 (0.003)	0.000	1, 126.3	0.994
	Set Up	Tank A	-0.161 (1.878)	0.046	1, 114.9	0.830
		Tank B	-0.125 (0.167)			
	Sex:Mass	Unknown	-0.161 (1.878)	1.528	2, 95.6	0.222
		Female	11.61 (10.402)			
		Male	-15.556 (15.261)			
-(Food Latency)	sex	Unknown	-0.827 (1.9136)	1.225	2, 127	0.297
		Female	-2.088 (0.775)			
		Male	0.343 (0.937)			
	Mass		-0.939 (5.300)	0.025	1, 127	0.875
	Order		0.0341 (0.059)	0.329	1, 127	0.567
	Replicate		-0.050 (0.104)	0.228	1, 127	0.634
	Time of Day		-3.086 (1.273)	0.395	1, 127	0.531
	Set Up	Tank A	-0.827 (1.914)	3.805	1, 127	0.053
		Tank B	-1.186 (0.184)			
	Sex:Mass	Unknown	-0.827 (1.914)	2.586	2, 127	0.079
		Female	9.870 (8.915)			
		Male	-24.151 (14.518)			
Track Length	sex	Unknown	-4.143 (1.477)	0.157	2, 49.3	0.855
		Female	-3.449 (0.666)			
		Male	-2.915 (0.756)			
	Mass		5.910 (4.441)	0.267	1, 75.5	0.607
	Time in Arena		0.157 (0.017)	89.060	1, 125.1	0.000
	Order		-0.022 (0.044)	0.2473	1, 122.5	0.620
	Replicate		0.081 (0.072)	1.267	1, 89.4	0.263
	Time of Day		0.004 (0.002)	2.721	1, 124.6	0.102
	Set Up	Tank A	-4.143 (1.477)	0.951	1, 120.9	0.332
		Tank B	-4.010 (0.136)			
	Sex:Mass	Unknown	-4.143 (1.477)	1.465	2, 85.5	0.237
		Female	-11.978 (7.673)			

		Male	22.498 (11.652)			
-						
(Freezings)	sex	Unknown	0.199 (1.251)	0.818	2, 48.8	0.447
		Female	0.187 (0.573)			
		Male	0.028 (0.645)			
	Mass		1.587 (3.804)	0.937	1, 77.4	0.336
	Time in Arena		-0.187 (0.014)	175.700	1, 125.7	0.000
	Order		0.056 (0.037)	2.249	1, 121.1	0.136
	Replicate		0.176 (0.060)	8.657	1, 88.4	0.004
	Time of Day		0.001 (0.002)	0.162	1, 125.4	0.688
	Set Up	Tank A	0.199 (1.251)	3.054	1, 119.4	0.083
		Tank B	-0.001 (0.114)			
	Sex:Mass	Unknown	0.199 (1.251)	0.203	2, 87	0.817
		Female	2.421 (6.591)			
		Male	6.201 (9.926)			

Table S5: Variance-covariance **ID$_{Sex:Mass}$** matrix estimated from the multivariate model with sex:mass included presented in the main text of Chapter 2. Variances and covariances with associated standard errors are presented on the diagonal and lower off diagonal respectively.

Trait	*OFT Track Length*	*OFT Area Covered*	*OFT Wall Distance*	*OFT -(Freezings)*	*FST Time in Open*	*FST -(Food Latency)*	*FST Track Length*	*FST -(Freezings)*
OFT Track Length	0.444 (0.133)	-	-	-	-	-	-	-
OFT Area Covered	0.355 (0.116)	0.425 (0.131)	-	-	-	-	-	-
OFT Wall Distance	-0.171 (0.088)	-0.012 (0.086)	0.188 (0.111)	-	-	-	-	-
OFT -(Freezings)	0.321 (0.111)	0.251 (0.103)	-0.168 (0.090)	0.419 (0.141)	-	-	-	-
FST Time in Open	-0.340 (0.107)	-0.307 (0.103)	0.071 (0.086)	-0.199 (0.101)	0.377 (0.134)	-	-	-
FST -(Food Latency)	-0.097 (0.085)	-0.042 (0.081)	0.070 (0.076)	-0.108 (0.086)	0.095 (0.085)	0.087 (0.106)	-	-
FST Track Length	0.154 (0.077)	0.058 (0.073)	-0.121 (0.067)	0.128 (0.076)	-0.096 (0.078)	0.001 (0.065)	0.170 (0.078)	-
FST -(Freezings)	0.102 (0.064)	0.132 (0.063)	-0.008 (0.054)	0.120 (0.064)	-0.062 (0.065)	0.038 (0.054)	0.095 (0.047)	0.130 (0.055)

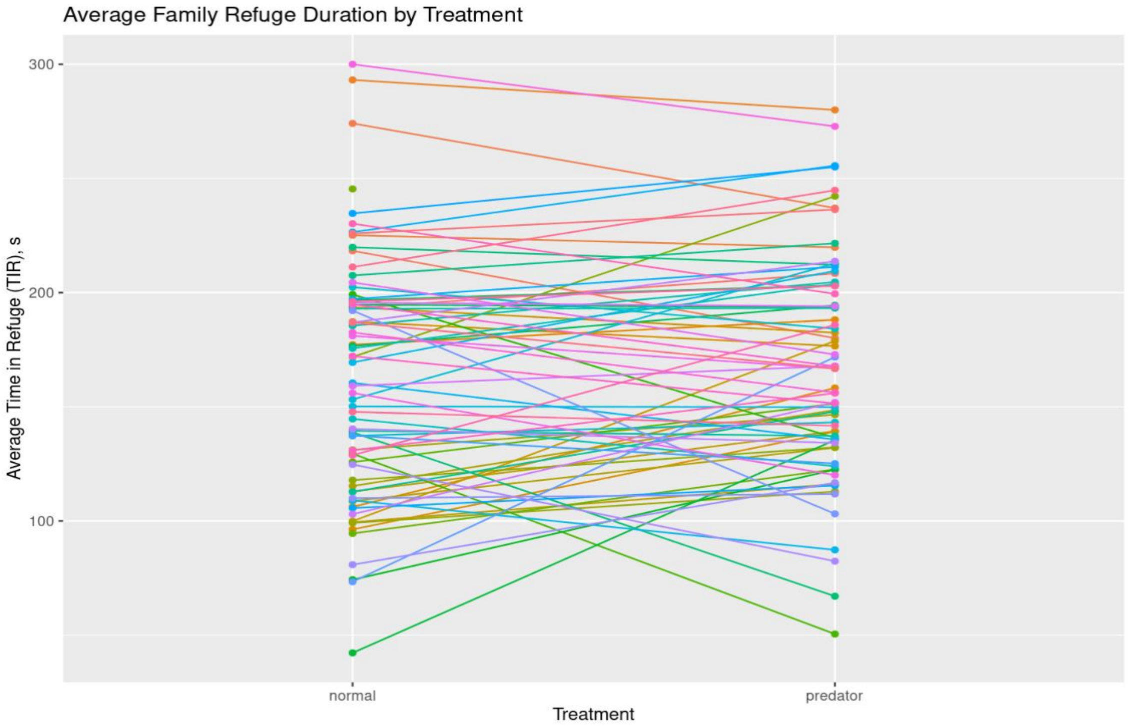


Figure S8: Mean time in the refuge by family across the control and predator treatments described in Chapter 3 presented in reaction norm format.

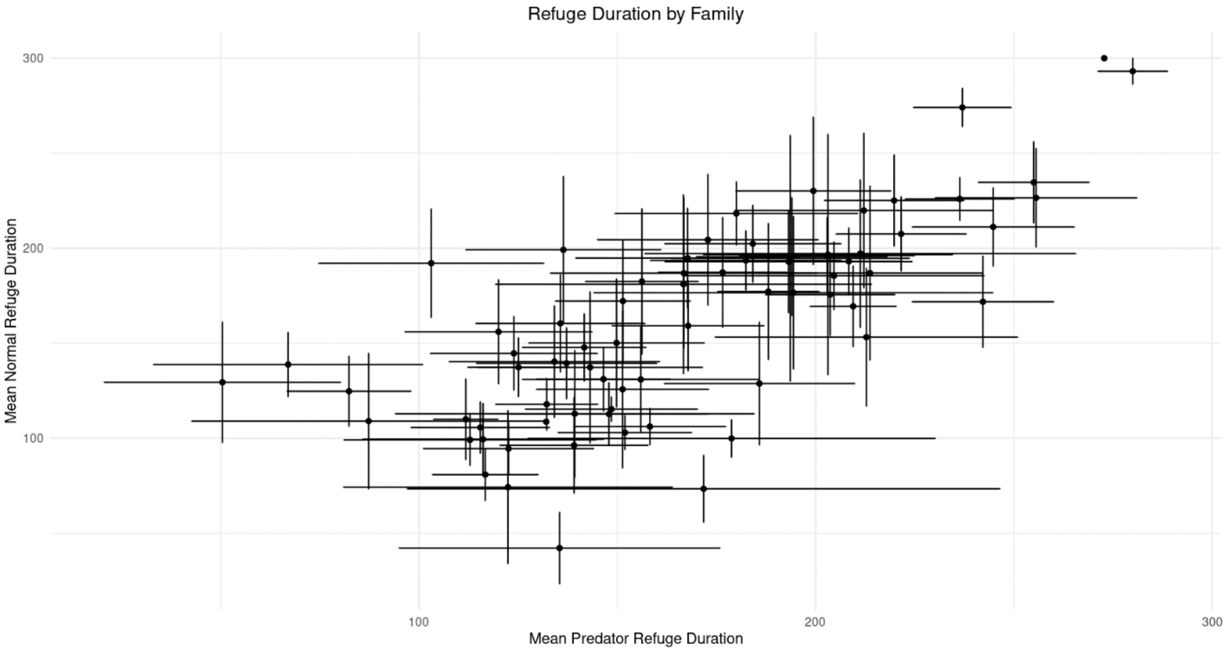


Figure S9: Mean time in refuge by family across the control and predator treatments described in Chapter 3 presented as a scatter plot (with error bars denoting 95% confidence intervals) to illustrate the positive family level correlation.

Bibliography

Ågerstrand, M., Arnold, K., Balshine, S., Brodin, T., Brooks, B.W., Maack, G., McCallum, E.S., Pyle,G., Saaristo, M., & Ford, A.T. (2020). Emerging investigator series: Use of behavioural endpoints in the regulation of chemicals. Environmental Science: Processes & Impacts, 22(1),49–65

Aparicio-Simón, B., Piñón, M., Racotta, R., & Racotta, I. S. (2010). Neuroendocrine and metabolic responses of Pacific white leg shrimp *Litopenaeus vannamei* exposed to acute handling stress. Aquaculture, 298(3–4), 308–314.

Bacqué-Cazenave, J., Berthomieu, M., Cattaert, D., Fossat, P., & Delbecque, J. P. (2019). Do arthropods feel anxious during molts? Journal of Experimental Biology, 222(2), jeb186999.

Baldwin, J. M. (1896). A new factor in evolution. The American Naturalist, 30(354), 441–451.

Bardera, G., Usman, N., Owen, M., Pountney, D., Sloman, K. A., & Alexander, M. E. (2019). The importance of behaviour in improving the production of shrimp in aquaculture. Reviews in Aquaculture, 11(4), 1104–1132.

Barki, A., Jones, C., & Karplus, I. (2010). Chemical communication and aquaculture of decapod crustaceans: needs, problems, and possible solutions. *Chemical communication in crustaceans*, pp.485-506.

Bauer, R.T., & Abdalla, J.H. (2001). Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology*, *107*(3), pp.185-199.

Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1611).

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. Animal Behaviour, 77(4), 771–783.

Bertram, M. G., Martin, J. M., Mccallum, E. S., Alton, L. A., Brand, J. A., Brooks, B. W., Cerveny, D., Fick, J., Ford, A. T., Hellström, G., Michelangeli, M., Nakagawa, S., Polverino, G., Saaristo, M., Sih, A., Tan, H., Tyler, C. R., Wong, B. B. M., & Brodin, T. (2022). Frontiers in quantifying wildlife behavioural responses to chemical pollution. Biological Reviews, 97(4), 1346–1364.

Birch, J., Burn, C., Schnell, A., Browning, H., & Crump, A. (2021). Review of the evidence of sentience in cephalopod molluscs and decapod crustaceans. LSE Consulting. LSE Enterprise Ltd. The London School of Economics and Political Science. https://www.lse.ac.uk/News/News-Assets/PDFs/2021/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf

Biro, P. A., & Sampson, P. (2015). Fishing directly selects on growth rate via behaviour: Implications of growth-selection that is independent of size. Proceedings of the Royal Society B: Biological Sciences, 282(1802), 20142283.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life- history productivity? Trends in Ecology & Evolution, 23(7), 361–368.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology & Evolution, 25(11), 653–659.

Blenderman, J. P. (2020). *Personality in Stomatopod Crustaceans*.

Bondad-Reantaso, M. G., Subasinghe, R. P., Josupeit, H., Cai, J., & Zhou, X. (2012). The role of crustacean fisheries and aquaculture in global food security: Past, present and future. Journal of Invertebrate Pathology, 110(2), 158–165.

Boulton, K., Couto, E., Grimmer, A. J., Earley, R. L., Canario, A. V., Wilson, A. J., & Walling, C. A. (2015). How integrated are behavioral and endocrine stress response traits? A repeated measures approach to testing the stress- coping style model. Ecology and Evolution, 5(3), 618–633.

Boulton, K., Grimmer, A. J., Rosenthal, G. G., Walling, C. A., & Wilson, A. J. (2014). How stable are personalities? A multivariate view of behavioural variation over long and short timescales in the sheeps-head swordtail, *Xiphophorus birchmanni*. Behavioral Ecology and Sociobiology, 68(5), 791–803.

Bouwma, P., & Hazlett, B.A. (2001). Integration of multiple predator cues by the crayfish *Orconectes propinquus*. *Animal Behaviour*, *61*(4), 771-776.

Bridger, D., Bonner, S. J., & Briffa, M. (2015). Individual quality and personality: Bolder males are less fecund in the hermit crab *Pagurus bernhardus*. Proceedings of the Royal Society B: Biological Sciences, 282(1803), 20142492.

Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: Animal personalities in the hermit crab *Pagurus bernhardus*. Proceedings of the Royal Society B: Biological Sciences, 275(1640), 1305–1311.

Briffa, M., Sneddon, L. U., & Wilson, A. J. (2015). *Animal personality as a cause and consequence of contest behaviour*. Biology Letters. 11(3):20141007.

Briffa, M., & Weiss, A. (2010). Animal personality. Current Biology, 20(21), R912–R914.

Brodin, T., & Drotz, M. K. (2014). Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. Current Zoology, 60(3), 410–416.

Brommer, J.E. and Kluen, E. (2012). Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. *Ecology and Evolution*, *2*(12), 3032-3044.

Brown, C., Jones, F., & Braithwaite, V.A. (2007). Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. *Journal of Fish Biology*, *71*(6), pp.1590-1601.

Callander, S., Kahn, A.T., Hunt, J., Backwell, P.R., & Jennions, M.D. (2013). The effect of competitors on calling effort and life span in male field crickets. *Behavioral Ecology*, *24*(5), pp.1251-1259.

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. Oikos, 117(5), 641–653.

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? Biological Reviews, 88(2), 465–475.

Castanheira, M. F., Herrera, M., Costas, B., Conceição, L. E., & Martins, C. I. (2013). Linking cortisol responsiveness and aggressive behaviour in gilthead seabream *Sparus aurata*: Indication of divergent coping styles. Applied Animal Behaviour Science, 143(1), 75–81.

Champagne, D. L., Hoefnagels, C. M., De Kloet, R. E., & Richardson, M. K. (2010). Translating rodent behavioral repertoire to zebrafish (*Danio rerio*): Relevance for stress research. Behavioural Brain Research, 214(2), 332–342.

Chapman, B. B., Hegg, A., & Ljungberg, P. (2013). Sex and the syndrome: Individual and population consistency in behaviour in rock Pool prawn *Palaemon elegans*. PLoS One, 8(3), e59437.

Chapple, D. G., Naimo, A. C., Brand, J. A., Michelangeli, M., Martin, J. M., Goulet, C. T., Brunton, D. H., Sih, A., & Wong, B. B. M. (2022). Biological invasions as a selective filter driving behavioral divergence. Nature Communications, 13(1), 1–11.

Chapple, D. G., Simmonds, S. M., & Wong, B. B. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? Trends in Ecology & Evolution, 27(1), 57–64.

Charmantier, A., Garant, D., & Kruuk, L. E. (2014). Quantitative genetics in the wild. OUP Oxford.

Chow, S., & Sandifer, P. A. (1991). Differences in growth, morphometric traits, and male sexual maturity among Pacific white shrimp, *Penaeus vannamei,* from different commercial hatcheries (Vol. 92, pp. 165–178). Elsevier.

Clutton-Brock, T. H., & Parker, G. A. (1995). Sexual coercion in animal societies. Animal Behaviour, 49(5), 1345–1365.

Cooper Jr, W.E., & Frederick, W.G. (2007). Optimal time to emerge from refuge. *Biological Journal of the Linnean Society*, *91*(3), pp.375-382.

Correa, C., & Thiel, M. (2003). Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. Revista Chilena de Historia Natural, 76(2), 187–203.

Cuzon, G., Lawrence, A., Gaxiola, G., Rosas, C., & Guillaume, J. (2004). Nutrition of *Litopenaeus vannamei* reared in tanks or in ponds. Aquaculture, 235(1–4), 513–551.

Dall, S.R., Houston, A.I., & McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology letters*, *7*(8), 734-739.

Daly, B., Eckert, G. L., & Long, W. C. (2021). Moulding the ideal crab: Implications of phenotypic plasticity for crustacean stock enhancement. ICES Journal of Marine Science, 78(1), 421–434.

Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace- of- life syndromes: A framework for the adaptive integration of behaviour, physiology and life history. Behavioral Ecology and Sociobiology, 72(3), 1–8.

Daniels, J. A., & Kemp, P. S. (2022). Personality-dependent passage behaviour of an aquatic invasive species at a barrier to dispersal. Animal Behaviour, 192, 63–74.

De Silva, K. H. G. M. (1988). Studies on Atyidae (Decapoda, Caridea) of Sri Lanka III. Aspects of the population ecology of *Caridina simoni* Bouvier, 1904. Crustaceana, 54, 85–103.

Dennenmoser, S., & Thiel, M. (2007). Competition for food and mates by dominant and subordinate male rock shrimp, *Rhynchocinetes typus*. Behaviour, 14 4, 33–59.

Dingemanse, N. J., Barber, I., Wright, J., & Brommer, J. (2012). *Quantitative genetics of behavioural reaction norms: genetic correlations* *between personality and behavioural plasticity vary across stickleback populations*. *Journal of Evolutionary Biology*, *25*(3), 485-496.

Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory be -haviour in great tits from the wild. Animal Behaviour, 64(6), 929–938.

Dingemanse, N. J., Drent, P. J., Van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *ANIMAL BEHAVIOUR*, *64*, 929–938.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89.

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1560), 3947–3958.

Dingemanse, N. J., & Wolf, M. (1998). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Piersma & van Gils*.

Dochtermann, N. A., Schwab, T., Anderson Berdal, M., Dalos, J., Royauté, R., & Berdal, A. (2019). The heritability of behavior: A meta-analysis. Journal of Heredity, 110, 403–410.

Dochtermann, N. A., Schwab, T., & Sih, A. (2014). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1798).

Ebert, D., Yampolsky, L., & Stearns, S. C. (1993). Genetics of life history in Daphnia magna. I. Heritabilities at two food levels. *Heredity 1993 70:4*, *70*(4), 335–343.

Eisemann, C.H., Jorgensen, W.K., Merritt, D.J., Rice, M.J., Cribb, B.W., Webb, P.D., & Zalucki, M.P. (1984). Do insects feel pain? A biological view. *Experientia*, *40*(2), pp.164-167.

Elwood, R. W. (2012). Evidence for pain in decapod crustaceans. Animal Welfare, 21(S2), 23–27.

Faimali, M., Gambardella, C., Costa, E., Piazza, V., Morgana, S., Estévez-Calvar, N., & Garaventa, F. (2017). Old model organisms and new behavioral end-points: Swimming alteration as an ecotoxicological response. Marine Environmental Research, 128, 36–45.

Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th Ed.). Pearson.

Ferderer, A., Davis, A. R., & Wong, M. Y. L. (2022). Temperature and body size influence personality and behavioural syndromes in an invasive crayfish. Animal Behaviour, 190, 187–198.

Food and Agricultural Organization of United Nations (FAO). (2014) http://www.fao.org

Food and Agricultural Organization of United Nations (FAO). (2016). The State of World Fisheries and Aquaculture. FAO, Rome. http://www.fao.org

Ford, A. T., Ågerstrand, M., Brooks, B. W., Allen, J., Bertram, M. G., Brodin, T., Dang, Z., Duquesne, S., Sahm, R., Hoffmann, F., Hollert, H., Jacob, S., Klü, N., Lazorchak, J. M., Ledesma, M., Melvin, S. D., Mohr, S., Padilla, S., Pyle, G. G., & Maack, G. (2021). The role of behavioral ecotoxicology in environmental protection. Environmental Science & Technology, 55(9), 5620–5628.

Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 333–339.

Galib, S. M., Sun, J., Twiss, S. D., & Lucas, M. C. (2022). Personality, density and habitat drive the dispersal of invasive crayfish. Scientific Reports, 12(1), 1114.

Garamszegi, L. Z., Eens, M., & Török, J. (2009). Behavioural syndromes and trappability in free- living collared flycatchers, *Ficedula albicollis*. Animal Behaviour, 77(4), 803–812.

Garamszegi, L. Z., Markó, G., & Herczeg, G. (2013). A meta- analysis of correlated behaviors with implications for behavioral syndromes:

Relationships between particular behavioral traits. Behavioral Ecology, 24(5), 1068–1080.

Gherardi, F. (2009). Behavioural indicators of pain in crustacean decapods. Annali dell'Istituto Superiore di Sanità, 45, 432–438.

Gherardi, F., Aquiloni, L., & Tricarico, E. (2012). Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: An imperfect map is better than no map. Current Zoology, 58(4), 567–579.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? Psychological Bulletin, 127(1), 45–86.

Groothuis, T.G., & Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews*, *29*(1), pp.137-150.

Grunst, A. S., Grunst, M. L., Daem, N., Pinxten, R., Bervoets, L., & Eens, M. (2019). An important personality trait varies with blood and plumage metal concentrations in a free- living songbird. Environmental Science & Technology, 53(17), 10487–10496.

Haave-Audet, E., Besson, A. A., Nakagawa, S., & Mathot, K. J. (2022). Differences in resource acquisition, not allocation, mediate the relationship between behaviour and fitness: A systematic review and meta- analysis. Biological Reviews, 97(2), 708–731.

Han, C.S., Jablonski, P.G., & Brooks, R.C. (2015). Intimidating courtship and sex differences in predation risk lead to sex-specific behavioural syndromes. *Animal Behaviour*, *109*, pp.177-185.

Harris, S., Ramnarine, I. W., Smith, H. G., Pettersson, L. B., Harris, S., Smith, H. G., & Pettersson, L. B. (2010). Picking personalities apart: Estimating the influence of predation, sex and body size on bold -ness in the guppy *Poecilia reticulata*. Oikos, 119(11), 1711–1718.

Hauton, C. (2012). The scope of the crustacean immune system for disease control. Journal of Invertebrate Pathology, 110(2), 251–260.

Hazlett, B.A. (1981). The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics*, *12*(1), pp.1-22.

Hazlett, B.A. (1995). Behavioral plasticity in crustacea: why not more? *Journal of Experimental Marine Biology and Ecology*, *193*(1-2), 57-66.

Hazlett, B.A., & Mclay, C. (2005). Responses to predation risk: alternative strategies in the crab *Heterozius rotundifrons*. *Animal Behaviour*, *69*(4), 967-972.

Heerbrandt, T. C., & Lin, J. (2006). Larviculture of red front shrimp, *Caridina gracilirostris* (Atyidae, Decapoda). Journal of the World Aquaculture Socilconety, 37(2), 186–190.

Hill, W. G. (2010). Understanding and using quantitative genetic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1537), 73–85.

Horvath, K., Angeletti, D., Nascetti, G., & Carere, C. (2013). Invertebrate welfare: an overlooked issue. Annali Dell'Istituto Superiore Di Sanità, 49, 9–17.

Houle, D. (1992). *Comparing Evolvability and Variability of Quantitative Traits*. 1;130(1):195-204.

Houslay, T. M., Earley, R. L., White, S. J., Lammers, W., Grimmer, A. J., Travers, L. M., Johnson, E. L., Young, A. J., & Wilson, A. (2022). Genetic integration of behavioural and endocrine components of the stress response. eLife, 11(11), e67126.

Houslay, T. M., Vierbuchen, M., Grimmer, A. J., Young, A. J., & Wilson, A. J. (2018). Testing the stability of behavioural coping style across stress contexts in the Trinidadian guppy. Functional Ecology, 32(2), 424–438.

Hu, X. L., Niu, J. J., Meng, Q., Chai, Y. H., Chu, K. H., & Chan, K. M. (2019). Effects of two juvenile hormone analogue insecticides, fenoxycarb and methoprene, on *Neocaridina davidi*. Environmental Pollution, 253, 89–99.

Ibarra- Zatarain, Z., Fatsini, E., Rey, S., Chereguini, O., Martin, I., Rasines, I., Alcaraz, C., & Duncan, N. (2016). Characterization of stress coping style in Senegalese sole (*Solea senegalensis*) juveniles and breeders for aquaculture. Royal Society Open Science, 3(11), 160495.

Japyassú, H.F., & Malange, J. (2014). Plasticity, stereotypy, intra-individual variability and personality: Handle with care. *Behavioural Processes*, *109*, pp.40-47.

Jensen, P., Buitenhuis, B., Kjaer, J., Zanella, A., Mormède, P., & Pizzari, T. (2008). Genetics and genomics of animal behaviour and welfare-Challenges and possibilities. *Applied Animal Behaviour Science*, *113*(4), pp.383-403.

Jivoff, P., & Hines, A. H. (1998). Female behaviour, sexual competition and mate guarding in the blue crab, Callinectes sapidus. Animal Behaviour, 55(3), 589–603.

Johnson, J.C., & Sih, A. (2007). Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour*, *74*(5), 1131-1138.

Juette, T., Cucherousset, J., & Cote, J. (2014). Animal personality and the ecological impacts of freshwater non- native species. Current Zoology, 60(3), 417–427.

Karavanich, C., & Atema, J. (1998). Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. Behaviour, 135(6), 719–730.

Kasumovic, M.M., Hall, M.D., & Brooks, R.C. (2012). The juvenile social environment introduces variation in the choice and expression of sexually selected traits. *Ecology and Evolution*, *2*(5), pp.1036-1047.

Kellert, S. R. (1993). Values and Perceptions of Invertebrates. *Conservation Biology*, *7*(4), 845–855.

Kim, S.Y. (2016). Fixed behavioural plasticity in response to predation risk in the three-spined stickleback. *Animal Behaviour*, *112*, pp.147-152.

Klotz, W., Miesen, F. W., Hüllen, S., & Herder, F. (2013). Two Asian freshwater shrimp species found in a thermally polluted stream system in North Rhine-Westphalia, Germany. Aquatic Invasions, 8(3), 333–339.

Knolton, N. (1980). Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. Evolution, 34(1), 161–173.

Kralj-Fišer, S., & Schneider, J.M. (2012). Individual behavioural consistency and plasticity in an urban spider. *Animal Behaviour*, *84*(1),197-204.

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: Why bother? Animal Behaviour, 91, 41–52.

Krause, J., Loader, S.P., McDermott, J., & Ruxton, G.D. (1998). Refuge use by fish as a function of body length–related metabolic expenditure and predation risks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1413), pp.2373-2379.

Kruuk, L.E. (2004). Estimating genetic parameters in natural populations using the “animal model.” Philosophical Transactions of the Royal Society of London, Series B. Biological Sciences. 359(1446), 873–890.

Kruuk, L.E., & Hadfield, J.D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of evolutionary biology*, *20*(5), pp.1890-1903.

Kruuk, L. E. B., Slate, J., & Wilson, A. J. (2008). New answers for old questions: The evolutionary quantitative genetics of wild animal populations. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 525–548.

Laine, V.N., & van Oers, K. (2017). The quantitative and molecular genetics of individual differences in animal personality. *Personality in nonhuman animals*. 55-72.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640.

López, P., Hawlena, D., Polo, V., Amo, L., & Martín, J. (2005). Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. Animal Behaviour, 69(1), 1–9.

Luttbeg, B., & Sih, A. (2010). Risk, resources and state- dependent adaptive behavioural syndromes. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1560), 3977–3990.

Lynch M., & Walsh B. (1998). Genetics and analysis of quantitative traits.

MacColl, A.D., & Hatchwell, B.J. (2003). Heritability of parental effort in a passerine bird. *Evolution*, *57*(9), pp.2191-2195.

Macali, A., Ferreti, S., Scozzafava, S., & Carere, C. (2023). Different behavioural profiles between invasive and native nudibranchs: Means for invasion success? bioRxiv. https:// doi. org/ 10. 1101/ 2023. 04. 13. 536773

Mahmoud, H.H., Sastranegara, M.H., & Kusmintarsih, E.S. (2020). The lifecycle of *Neocaridina denticulata* and *N. palmata* in aquariums. Biodiversitas Journal of Biological Diversity.10;21(6).

Malmqvist, B. (2002). Aquatic invertebrates in riverine landscapes. Freshwater Biology, 47(4), 679–694.

Maskrey, D. K., White, S. J., Wilson, A. J., & Houslay, T. M. (2018). Who dares does not always win: Risk- averse rockpool prawns are better at controlling a limited food resource. Animal Behaviour, 140, 187–197.

Mather, J. A., & Logue, D. M. (2013). The bold and the spineless: Invertebrate personalities. In C. Carere & D. Maestripieri (Eds.), Animal personalities: Behavior, physiology, and evolution (pp. 13–35). The University of Chicago Press.

Mathot, K. J., & Frankenhuis, W. E. (2018). Models of pace- of- life syndromes (POLS): A systematic review. Behavioral Ecology and Sociobiology, 72(3), 1–12.

Mathot, K. J., Van den Hout, P. J., Piersma, T., Kempenaers, B., Réale, D., & Dingemanse, N. J. (2011). Disentangling the roles of frequency-vs. state-dependence in generating individual differences in behavioural plasticity. *Ecology Letters*, *14*(12), 1254–1262.

Melvin, S. D., & Wilson, S. P. (2013). The utility of behavioral studies for aquatic toxicology testing: A meta- analysis. Chemosphere, 93(10), 2217–2223.

Merilä, J., & Sheldon, B. C. (2000). Lifetime reproductive success and heritability in nature. *American Naturalist*, *155*(3), 307–310.

Minello, T., & Zimmerman, R. (1991). *The role of estuarine habitats in regulating growth and survival of juvenile penaeid shrimp.* tamug-ir.tdl.org.

Mirera, O. D., & Moksnes, P. O. (2013). Cannibalistic interactions of juvenile mud crabs *Scylla serrata:* The effect of shelter and crab size. African Journal of Marine Science, 35(4), 545–553.

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: A meta-analysis. Ecology Letters, 23(2), 399–408.

Moland, E., Carlson, S. M., Villegas-Ríos, D., Ree Wiig, J., & Moland Olsen, E. (2019). Harvest selection on multiple traits in the wild revealed by aquatic animal telemetry. Ecology and Evolution, 9(11), 6480–6491.

Mulder, H. A., & Bijma, P. (2005). Effects of genotype x environment interaction on genetic gain in breeding programs. *Journal of Animal Science*, *83*(1), 49–61.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America, 105(49), 19052–19059.

Nunn, A. D., Tewson, L. H., & Cowx, I. G. (2011). The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries, 22(2), 377–408.

Nussey, D.H., Wilson, A.J., & Brommer, J. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology. 20*(3), 831–844.

Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. (2005). Evolution: Selection on heritable phenotypic plasticity in a wild bird population. *Science*. *310*(5746), 304–306.

Oh, C.W., Ma, C.W., Hartnoll, R., & Suh, H.L. (2003). Reproduction and population dynamics of the temperate freshwater shrimp, *Neocaridina* *denticulata* (De Haan, 1844), in a Korean stream. *Crustaceana.* 1;76(8):993-1015.

Pantaleão, J. A., Gregati, R. A., Da Costa, R. C., Lopez- Greco, L. S., & Negreiros-Fransozo, M. L. (2017). Post-hatching development of the ornamental “Red Cherry Shrimp” *Neocaridina davidi* (Bouvier,1904) (Crustacea, Caridea, Atyidae) under laboratorial conditions. Aquaculture Research, 48(2), 553–569.

Passantino, A., Elwood, R. W., & Coluccio, P. (2021). Why Protect Decapod Crustaceans Used as Models in Biomedical Research and in Ecotoxicology? Ethical and Legislative Considerations. *Animals 2021, Vol. 11, Page 73*, *11*(1), 73.

Patrick, S. C., & Weimerskirch, H. (2014). Consistency pays: Sex differences and fitness consequences of behavioural specialization in a wide- ranging seabird. Biology Letters, 10(10), 20140630.

Perrot-Minnot, M. J., Banchetry, L., & Cézilly, F. (2017). Anxiety-like behaviour increases safety from fish predation in an amphipod crustacea. Royal Society Open Science, 4(12), 171558.

Petelle, M., Martin, J.G., & Blumstein, D.T. (2015). Heritability and genetic correlations of personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*). Journal of Evolutionary Biology. 1;28(10):1840-8.

Peters, R.H. (1986). *The ecological implications of body size* (Vol. 2). Cambridge university press.

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, *18*(5), pp.228-233.

Pintor, L. M., Sih, A., & Bauer, M. L. (2008). Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos, 117(11), 1629–1636.

Polverino, G., Bierbach, D., Killen, S. S., Uusi- Heikkilä, S., & Arlinghaus, R. (2016). Body length rather than routine metabolic rate and body condition correlates with activity and risk- taking in juvenile zebrafish *Danio rerio*. Journal of Fish Biology, 89(5), 2251–2267.

Polverino, G., Martin, J. M., Bertram, M. G., Soman, V. R., Tan, H., Brand, J. A., Mason, R. T., & Wong, B. B. (2021). Psychoactive pollution suppresses individual differences in fish behaviour. Proceedings of the Royal Society B, 288(1944), 20202294.

Prentice, P. M., Houslay, T. M., & Wilson, A. J. (2022). Exploiting animal personality to reduce chronic stress in captive fish populations. Frontiers in Veterinary Science, 9, 1046205.

Prentice, P. M., Thornton, A., Kolm, N., & Wilson, A.J. (2023). Genetic and context-specific effects on individual inhibitory control performance in the guppy (*Poecilia reticulata*). *Journal of Evolutionary Biology*, *36*(12), pp.1796-1810.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rapkin, J., Archer, C.R., Grant, C.E., Jensen, K., House, C.M., Wilson, A.J., & Hunt, J. (2017). Little evidence for intralocus sexual conflict over the optimal intake of nutrients for life span and reproduction in the black field cricket *Teleogryllus commodus*. *Evolution*, *71*(9), pp.2159-2177.

Razekenari, A. M., Fereidouni, A. E., Movahedinia, A., & Neyshabouri, E. Z. (2023). Impacts of sublethal concentrations of 17 α- ethinylestradiol (EE2) on growth, reproductive performance, and survival in red cherry shrimp *Neocaridina davidi* (Crustacea, Atyidae) during consecutive spawnings. Aquatic Toxicology, 259, 106519.

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010a). Evolutionary and ecological approaches to the study of personality. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1560), 3937–3946.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio,P. O. (2010b). Personality and the emergence of the pace- of- life syndrome concept at the population level. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1560), 4051–4063.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. Biological Reviews of the Cambridge Philosophical Society, 82(2), 291–318.

Rehage, J. S., Cote, J., & Sih, A. (2016). The role of dispersal behaviour and personality in post- establishment spread. In J. S. Weis & D. Sol (Eds.), Biological invasions and animal behaviour (pp. 96–116). Cambridge University Press.

Rickward, R. A., Santostefano, F., & Wilson, A. J. (2024). Among-individual behavioural variation in the ornamental red cherry shrimp, Neocaridina heteropoda. *Ecology and Evolution*, *14*(2), e11049.

Robertson, A. (1959). The Sampling Variance of the Genetic Correlation Coefficient. *Biometrics*. *15*(3), 469.

Roche, D. G., Careau, V., & Binning, S. A. (2016). Demystifying animal "personality" (or not): Why individual variation matters to experimental biologists. *Journal of Experimental Biology*, *219*(24), 3832–3843.

Royauté, R., Buddle, C. M., & Vincent, C. (2015). Under the influence: Sublethal exposure to an insecticide affects personality expression in a jumping spider. Functional Ecology, 29(7), 962–970.

Rudin, F.S., Simmons, L.W., & Tomkins, J.L. (2019). Social cues affect quantitative genetic variation and covariation in animal personality traits. *Evolution*, *73*(3), pp.540-553.

Rudin, F.S., Tomkins, J., & Simmons, L.W. (2018). The effects of the social environment and physical disturbance on personality traits. Animal behaviour. 1;138:109-21.

Salini, J.P., Blaber, S.J.M., & Brewer, D.T. (1990). Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Marine Biology*, *105*(3), pp.363-374.

Sanchez, D. R., Fox, J. M., Lawrence, A. L., Castille, F. L., & Dunsford, B. (2005). A methodology for evaluation of dietary feeding stimulants for the pacific white shrimp, *Litopenaeus vannamei.* Journal of the World Aquaculture Society, 36(1), 14–23.

Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs: A test of the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864).

Sartori, C., Tiezzi, F., Guzzo, N., Mancin, E., Tuliozi, B., & Mantovani, R. (2022). Genotype by Environment Interaction and Selection Response for Milk Yield Traits and Conformation in a Local Cattle Breed Using a Reaction Norm Approach. *Animals*, *12*(7), p.839.

Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky, C., Réale, D., Dochtermann, N. A., Garamszegi, L. Z., & Araya- Ajoy, Y. G. (2020). Robustness of linear mixed- effects models to violations of distributional assumptions. Methods in Ecology and Evolution, 11(9), 1141–1152.

Schoolmann, G., & Arndt, H. (2018). Population dynamics of the invasive freshwater shrimp *Neocaridina davidi* in the thermally polluted Gillbachstream (North Rhine-Westphalia, Germany). Limnologica, 71, 1–7.

Serezli, R., Atalar, M. S., Hamzacebi, S., Kurtoglu, I. Z., & Yandi, I. (2017). To what extent does temperature affect sex ratio in red cherry shrimp, *Neocaridina davidi*? The scenario global warming to off -spring sex ratio. Fresenius Environmental Bulletin, 26, 7575–7579.

Sherwin, C. M. (2001). Can Invertebrates Suffer? or, How Robust is Argument-By-Analogy? *Animal Welfare*, *10*(S1), S103–S118.

Sick, L. V., White, D., & Baptist, G. (1973). The effect of duration of feeding, amount of food, light intensity, and animal size on rate of ingestion of pelleted food by juvenile penaeid shrimp. The Progressive Fish- Culturist, 35(1), 22–26.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology & Evolution, 19(7), 372–378.

Sih, A., Kats, L.B. and Maurer, E.F. (2003). Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, *65*(1), 29-44.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P. O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: A review and guide for empiricists. Trends in Ecology & Evolution, 30(1), 50–60.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. Behavioral Ecology, 19(2), 448–455.

Snell-Rood, E.C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), pp.1004-1011.

Stamps, J., & Groothuis, T.G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, *85*(2), pp.301-325.

Stirling, D. G., Réale, D., & Roff, D. A. (2002). Selection, structure and the heritability of behaviour. Journal of Evolutionary Biology, 15(2), 277–289.

Su, X., Zhu, B., & Wang, F. (2022). Feeding strategy changes boldness and agonistic behaviour in the swimming crab (*Portunus trituberculatus*). *Aquaculture Research*, *53*(2), 419–430.

Sung, H. H., Lin, Y. H., & Hsiao, C. Y. (2011). Differential immune responses of the green neon shrimp (*Neocaridina denticulate*) to dipropyl phthalate. Fish & Shellfish Immunology, 31(3), 511–515.

Taylor, N.G. (2016). *Why are invaders invasive? Development of tools to understand the success and impact of invasive species* (Doctoral dissertation, University of Leeds).

Toghiani, S., Hay, E., Fragomeni, B., Rekaya, R., & Roberts, A. J. (2020). Genotype by environment interaction in response to cold stress in a composite beef cattle breed. *Animal*, *14*(8), 1576–1587.

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A methodological review of personality-related studies in fish: Focus on the shy-bold axis of behavior. International Journal of Comparative Psychology, 23(1), 1–25.

Toscano, B. J., Gatto, J., & Griffen, B. D. (2014). Effect of predation threat on repeatability of individual crab behavior revealed by mark- recapture. Behavioral Ecology and Sociobiology, 68, 519–527.

Tropea, C., Stumpf, L., & Greco, L. S. L. (2015). Effect of Temperature on Biochemical Composition, Growth and Reproduction of the Ornamental Red Cherry Shrimp *Neocaridina heteropoda* heteropoda (Decapoda, Caridea). *PLOS ONE*, *10*(3), e0119468.

Vainikka, A., Rantala, M. J., Niemelä, P., Hirvonen, H., & Kortet, R. (2011). Boldness as a consistent personality trait in the noble crayfish, *Astacus astacus*. Acta Ethologica, 14, 17–25.

Vanden Broecke, B., Sluydts, V., Mariën, J., Sabuni, C. A., Massawe, A. W., Matthysen, E., & Leirs, H. (2021). The effects of personality on survival and trappability in a wild mouse during a population cycle. Oecologia, 195(4), 901–913.

Vazquez, N. D., Delevati-Colpo, K., Sganga, D. E., & López- Greco, L. S. (2017). Density and gender segregation effects in the culture of the caridean ornamental red cherry shrimp *Neocaridina davidi* Bouvier,1904 (Caridea: Atyidae). The Journal of Crustacean Biology, 37(4), 367–373.

Visscher, P. M. (2006). A note on the asymptotic distribution of likelihood ratio tests to test variance components. Twin Research and Human Genetics, 9(4), 490–495.

Wall, D., Paterson, B., & Mohan, R. (2009). Behaviour of juvenile mud crabs Scylla serrata in aquaculture: response to odours of moulting or injured crabs. *Applied Animal Behaviour Science*, *121*(1), pp.63-73.

Weber, S., & Traunspurger, W. (2016). Influence of the ornamental red cherry shrimp *Neocaridina davidi* (Bouvier, 1904) on freshwater meiofaunal assemblages. Limnologica, 59, 155–161.

West-Eberhard, M.J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

White, S. J., Pascall, D. J., & Wilson, A. J. (2020). Towards a comparative approach to the structure of animal personality variation. Behavioral Ecology, 31(2), 340–351.

Wickler, W., & Seibt, U. (1981). Monogamy in Crustacea and man. *Zeitschrift für Tierpsychologie*, *57*(3-4), pp.215-234.

Wilber, D. H. (1989). The influence of sexual selection and predation on the mating and postcopulatory guarding behavior of stone crabs (Xanthidae, Menippe). Behavioral Ecology and Sociobiology, 24, 445–451.

Willis, J., Burt de Perera, T. B., & Thomas, A. L. R. (2019). Review of the organismal biology of Hill stream loaches. Preprints 2019, 2019110322. https://doi.org/10.20944/preprints201911.0322.v1

Wilson, A.J., Reale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A., Kruuk, L.E., & Nussey, D.H. (2010) An ecologist's guide to the animal model. Journal of animal ecology. 1;79(1):13-26.

Wilson, A. J., Pemberton, J. M., Pilkington, J. G., Coltman, D. W., Mifsud, D. V, Clutton-Brock, T. H., & Kruuk, L. E. B. (2006). *Environmental Coupling of Selection and Heritability Limits Evolution*. PLoS biology.1;4(7):e216.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy- bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. Journal of Comparative Psychology, 107(3), 250–260.

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade- offs favour the evolution of animal personalities. Nature, 447(7144), 581–584.

Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(41), 15825–15830.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. Philosophical Transactions of the Royal Society, B: Biological Sciences, 365(1560), 3959–3968.

Yixiong, C. (1996). A revision of the genus Neocaridina (Crustacea: Decapoda: Atyidae). *Dong wu fen lei xue bao= Acta Zootaxonomica Sinica*, *21*(2), pp.129-160.