# Does exploratory behaviour predict predatory behaviour in the Aussie bronze jumping spider (*Helpis minitabunda*)?

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# GENERAL ABSTRACT

Individual variation in behaviour, also known as animal personality, has been described in diverse taxa for hundreds of years. However, it is only recently that information about the influence of personality traits on populations and ecosystem dynamics has started to emerge. Predator-prey interactions are important drivers of evolutionary processes, shaping communities and altering trophic cascades. Most studies to date that have investigated the links between personality and predation have focussed on the effects of personality traits of prey on predator-prey interactions. It is becoming increasingly evident that the personality traits of predators and the interactions between predator and prey personalities also influence predatory interactions. Personality assays are usually performed in the laboratory where researchers have greater control over environmental variables than in field assays. However, the controlled environment of the laboratory may change animal behaviour leading to results that are not ecologically relevant.

In my thesis, I first investigated whether individual performance in emergence and exploration assays is correlated between laboratory and field environments in the Aussie bronze hopper (*Helpis minitabunda*; Araneae, Salicidae) (Chapter Two). Then, using what I learned in Chapter Two about the design of exploration assays, I investigated whether exploration behaviour in *H. minitabunda* is correlated with predatory behaviour (Chapter Three). While I found no correlation in emergence behaviour between my laboratory-based and field-based assays, there was a strong correlation in exploration behaviour. I also found no correlations between exploration behaviour and predatory behaviour. This suggests that laboratory-based exploration assays, but not emergence assays, are likely to generate ecologically relevant results in the jumping spider *H. minitabunda*. However, exploration behaviour may not be a good predictor of predatory behaviour in jumping spiders. Further testing with more complex arenas and different types of prey may be more likely to show a relationship between exploration and predation behaviour. The results of my research support the use of laboratory assays to test personality traits but also highlight the importance of comparative tests to check that laboratory assays reflect behaviour in more natural environments. My results will hopefully encourage further research investigating personality traits and their influence on predator-prey interactions.

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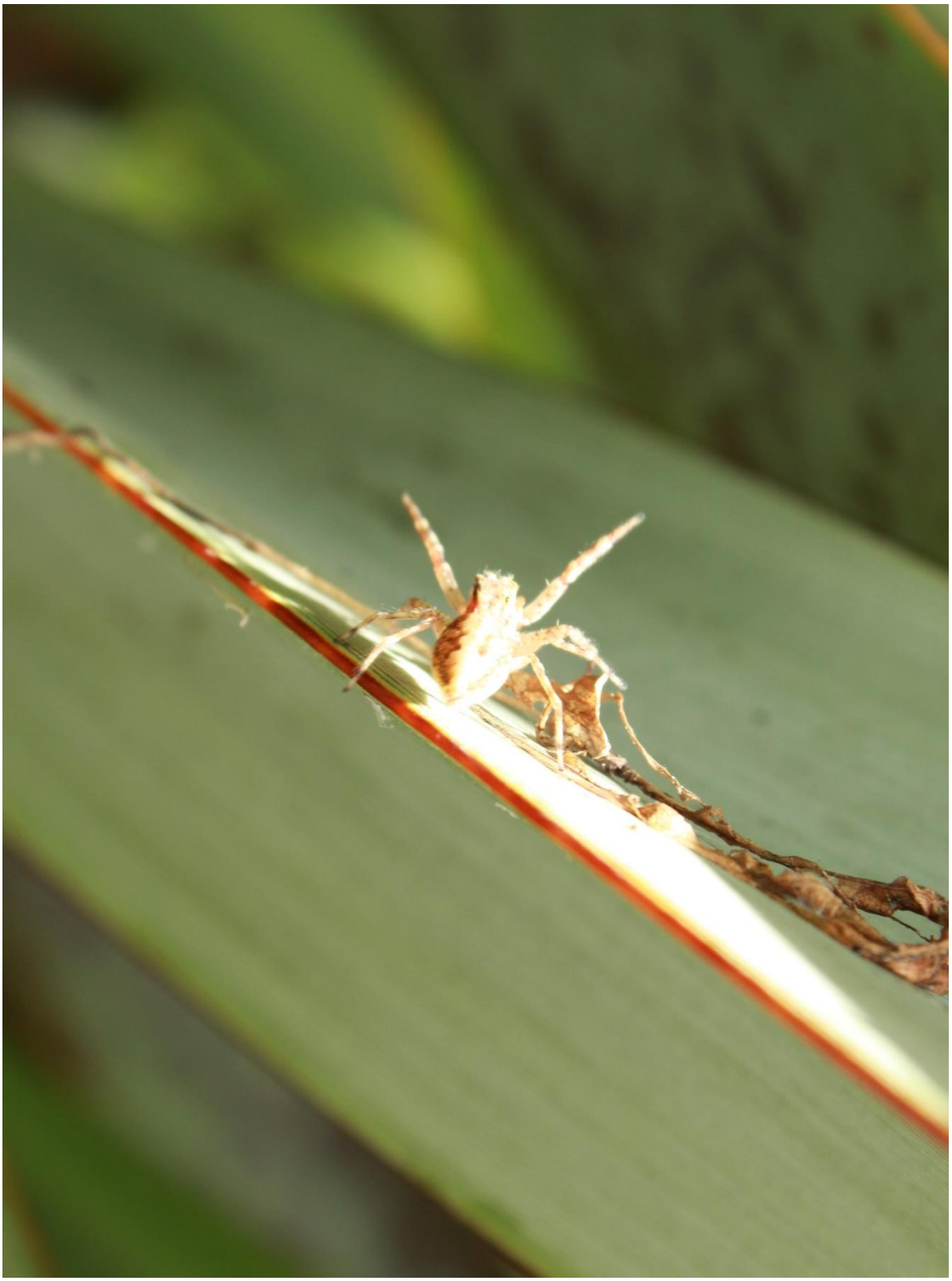
CHAPTER ONE

# GENERAL INTRODUCTION



Predators play a pivotal role in controlling prey population numbers, shaping communities, promoting evolutionary processes, maintaining variation within populations and overall balance within ecosystems (Hofbauer & Sigmund, 1989; Bruno & Cardinale, 2008; Dingemanse et al. 2009; Belgrad & Griffen, 2016; Start & Gilbert, 2017; Szopa-Comley et al. 2020; Freestone et al. 2021). Therefore, understanding predator behaviour is essential to understanding predator-prey interactions and the ecological processes that they mediate. However, while research into prey behaviour has been carried out rather extensively (Belgrad & Griffen, 2016), until recently the role of predator behaviour in predator-prey interactions has tended not to be recognised (Lima, 2002; Szopa-Comley et al. 2020).

## 1.1. VARIATION IN PREDATOR BEHAVIOUR

Research is now starting to shed light on variation in predator behaviour and how it affects predator-prey interactions. Most of these studies have been either theoretical (e.g., Chesson 1978; Okuyama 2008; Okuyama, 2017) or examined the ability of predators to learn about aposematic prey (e.g., Endler & Mappes, 2004; Skelhorn et al. 2016). Theoretical studies have tended to focus on prey selection. Predators often consume multiple types of prey and models of prey selection have demonstrated that prey choice is often frequency dependent (e.g., Sherratt & Harvey, 1993; Aditya et al. 2005; Hoy et al. 2021; Sheldon et al. 2023). Advancements in modern technology have begun to quantify predator behaviour through observation and surveying techniques. This includes the use of GPS tracking, aerial surveys, following spoors and examining prey remains (Ordiz et al. 2020; Hoy et al. 2021), scat collections and spotlight surveys (Sheldon et al. 2023), identifying nests in use and examining these for prey remains (Götmark & Post, 1996), mounted video cameras (Bowen et al. 2002), video surveillance cameras (Clark et al. 2012) and even through the use of online gaming (Fraser Franco et al. 2022). More recently, there has been growing interest in trying to assess interindividual variation in predator behaviour (i.e., animal personality).

Predator personality can impact prey survival (Exnerova et al. 2010). Personality traits can influence the type of prey that predators encounter and successfully capture (Chang et al. 2017). A predator's personality can also influence the type of prey a predator is willing to hunt depending on the level of risk that they are willing to take on (Mukherjee & Heithaus, 2013). As personality can also influence activity and dispersal behaviour (e.g., Dingemanse et al. 2003; Kurvers et al. 2009; Cote et al. 2010; Menzies & Timonin, 2013; Schirmer et al. 2019), it is also likely that predator personality can influence prey behaviour via non-consumptive effects (Wirsing et al. 2021). Non-consumptive effects of predators are the results of prey modifying their behaviour or physiological traits to aid predator avoidance (Russell et al. 2022). So far, most studies of personality in predator-prey theory still focus on prey behaviour, observing how prey vary in their reaction to predators and how the predator may adjust to variation in prey behaviour (Belgrad & Griffen,

2016). Few studies have focussed on predator behaviour and even fewer have directly tested the effects of variation in predator personality in a controlled environment (Pettorelli et al. 2015).

## 1.2. WHAT IS KNOWN ADOUT ANIMAL PERSONALITY?

Individuals vary in their behaviour (Dall et al. 2012; Laskowski et al. 2022). 'Animal personality' is defined as behavioural differences between individuals that remain constant across time and context (Réale et al. 2007; Kaiser & Müller, 2021). Many statistical techniques have been introduced to estimate consistency in personality traits, one of the most popular being the intraclass correlation coefficient (i.e., repeatability; Bell et al. 2009). Behavioural differences between individuals can also be referred to as behavioural types or animal personalities (Spiegel et al. 2015). Behavioural syndromes are correlated suites of behavioural traits (Sih et al. 2004; Carter et al. 2013). Exploration, boldness, aggressiveness, sociability, and activity are the five most commonly measured traits in personality studies (Dall et al. 2004). Although differences in personality traits have been noticed across multiple taxa since Darwin and Aristotle's time (Dall et al. 2012), the role of differences in individual behaviour was given little consideration in ecology until recently (Laskowski et al. 2022). Personality research has been gaining ground since 2010 and studies are now demonstrating how influential and important these differences between individuals are (Dall et al. 2012; Wolf & Weissing, 2012).

Personality traits can influence how animals interact with their environment and affect the outcome of competition, cooperation, predation, parasitism, and mate choice events (Réale et al, 2007; Roche et al, 2016). Personality itself is often influenced by environmental stimuli via feedback between an individual's behaviour and their state (MacGregor et al. 2021). However, there is still much controversy around how personality traits influence individual fitness. There is evidence that some personality traits can affect reproductive success (Cote et al. 2008; Smith & Blumstein, 2008; Patrick & Weimerskirch 2014; Yoshida et al. 2016), foraging success (Carter et al. 2010; Patrick & Weimerskirch 2014), growth (Adriaenssens & Johnsson 2011; Wilson et al. 2014), mortality (Smith & Blumstein, 2008; Belgrad & Griffen, 2016), and survival (Dingemanse et al. 2004; Cote et al. 2008; Yoshida et al. 2016). However, there are also studies revealing contradicting results. Betini & Norris (2012) found that personality did not predict reproductive success in female tree swallows, and the fitness benefits of aggressiveness in males was context dependent. Exploratory behaviour was not correlated with survival in red knots (Bijleveld et al. 2014); and a meta-analysis by Moiron et al. (2020) revealed that 'riskier' behaviours were not linked to mortality. It's clear we still have much to discover about the effects of behavioural variation at both the individual level as well as at larger ecological scales.

## 1.3. ARE WE TESTING PERSONALITY CORRECTLY?

Most assays of personality traits are performed in a laboratory environment as this allows experimenters to control many variables such as temperature, weather, and food availability (Campbell et al. 2009). However, there are some potential downfalls of using laboratory-based studies to conduct behavioural research. Behaviour in the laboratory could change as a result of the clinical laboratory environment itself, artefacts from captivity or breeding in the laboratory, or the absence of natural environmental stimuli (Calisi & Bentley, 2009; Herborn et al. 2010; Wiggins et al. 2018). All these factors should be taken into consideration when conducting animal studies in a laboratory environment.

One way to check whether behaviour tested in the laboratory reflects behaviour in the field is to directly compare individual responses between the two environments. Interestingly, repeatability of behaviour tends to be higher in the field compared to the laboratory (Bell et al. 2009). There have been studies that have compared lab and field results and found correlations in individual performance. For example, exploratory tendency and neophobia of blue tits in the lab predicted personality traits in the wild (Herborn et al. 2010). Learning ability in the great tit is correlated between the lab and field (Cauchoix et al. 2017). Further, initial dispersal of brown trout was correlated between the lab and field, but activity and growth in the two environments was not correlated and survival in the wild was not predicted by laboratory activity (Závorka et al. 2015). Other studies have also found discrepancies between the two environments. The results of a lab-field study of brown trout suggested that laboratory conditions may overestimate the fitness advantages of aggressive behaviour (Höjesjö et al. 2002). Meza-Hernandez & Díaz-Fleischer (2006) found that Mexican fruit flies bred in the lab performed better in the lab than in the field, while wild caught flies have reduced sexual performance in the laboratory. A meta-analysis of field and lab experiments revealed numerous differences in the results between lab and field environments (Calisi & Bentley 2009). It is clear that while laboratory research is essential for forming a more complete understanding of the behavioural traits being studied, there is still a lot of controversy around how much we can trust laboratory results and infer their ecological relevance.

## 1.4. PREY PERSONALITY AND PREDATOR-PREY INTERACTIONS

Predator-prey interactions are important components of community structure and function (Belgrad & Griffen, 2016; Schmitz 2017). The behaviour of prey is more frequently studied than the behaviour of predators and as a result is better understood. For example, many studies have investigated the behavioural responses of prey to predators or predatory cues (e.g., Lima & Dill, 1990; Ferrari et al. 2010; Paterson et al. 2013; Cremona et al. 2014; Wagner & Moore, 2022). There is a considerable amount of evidence now that personality traits in prey are linked to prey's ability to evade predators and survive predation events (Blake

& Gabor, 2014; Toscano, 2017), their predation risk from different species of predator and their mode of hunting (Blake et al. 2018; Sweeney et al. 2013; Belgrad & Griffen, 2016), and the mediation of trophic cascades (Sommer & Schmitz, 2020).

Predators and prey play equal parts in predator-prey interactions, wherein the behaviour of one influences the behaviour of the other and both can determine the outcome of an interaction. It is vital to understand the influence of personality traits in predators and prey separately so that we can get a more complete understanding of predator-prey interactions. In addition, the personality traits of predators and prey may interact. For example, a study of predator-prey interactions between the cannibalistic white-moustached jumping spider and its prey, the shiny jumping spider, showed that aggressive predators excelled at capturing unpredictable prey, while docile predators were better at capturing predictable prey (Chang et al. 2017). This highlights the importance of studying the combined effects of behavioural variation in predators and prey on the predator-prey dynamic.

## 1.5. STUDY ORGANISM – *HELPIS MINITABUNDA*

For this study, I used female Aussie bronze jumping spiders (*Helpis minitabunda*, Koch; Araneae, Salticidae) as my model predator. Invertebrates are ideal models to examine personality traits as they are easier to access, maintain and handle than many vertebrates (Kralj-Fišer & Schuett, 2014). Spiders in particular make excellent study models across many disciplines due to their versatility and accessibility (Hesselberg & Gálvez, 2023). Jumping spiders (Araneae: Salticidae) are highly active hunters who venture out and search for prey rather than using webs. This makes them ideal candidates for exploration, boldness, and hunting assays.

Aussie bronze jumping spiders are found in tropical and sub-tropical regions of Australia (Kempraj et al. 2020). They were introduced to New Zealand in the 1970's and are now a common sight around the North Island of New Zealand and considered naturalised (Sirvid et al. 2012). They are excellent dispersers and may also come to New Zealand from Australia via ballooning, a form of air dispersal used by spiders who produce a silk thread which can be caught up by air currents (Zabka et al. 2002). They are diurnal and are usually found in New Zealand on foliage in moist areas where they build nests or 'retreats' out of silk, typically along the midrib of leaves (Kempraj et al. 2020). Males are usually larger than females and both sexes are easily distinguished from one another (M. Caffell, personal observations). They hunt small insects and capture them using a 'stalk and pounce' method, often from distances that far exceed their body length (M. Caffell, personal observations). *Helpis minitabunda* are common and easily accessed around the Massey University, Auckland campus.

Figure 1.1: Study species *Helpis minitabunda*. Male on the left, female on the right. Photo credit: M. Caffell.

## 1.6. THESIS AIMS

The aims of my study were twofold. Firstly, I test whether the behaviours I obtained in laboratory exploration assays are correlated with behaviours expressed in a field exploration assay in the jumping spider *H. mintabunda*. This experiment created a logical foundation for using the laboratory exploration assay as a representation of exploration behaviour in more natural ecological settings. Secondly, I used the laboratory exploration assay to test whether exploration behaviour in predators correlates with their ability to hunt prey.

The results from my research will add to our understanding of predator behaviour. I hope to shed a little light on how variation in a personality trait impacts not only individual predators, but the predator-prey interactions that mediate the communities that they live in.

## 1.7. THESIS OUTLINE

Firstly, in Chapter Two, I tested using *H. minitabunda* whether the behaviour of spiders in exploration assays under strictly controlled laboratory conditions are correlated with their behaviour in exploration assays under field conditions. As well as changing the environment, I also tested whether the arena type influences spider behaviour. I compared the performance of spiders in an arena made from an unnatural substrate (Perspex) with their performance in an arena made of a familiar, natural plant material (agapanthus).

Secondly in Chapter Three, I tested whether exploration behaviour is correlated with predatory behaviour in *H. minitabunda*. I assessed exploration behaviour using the laboratory exploration assay developed in Chapter Two. I quantified predatory behaviour in a hunting assay, measuring emergence time, the amount of time it took spiders to capture the prey, whether they were successful at capturing prey and how many failed attempts to capture prey occurred. I then looked for correlations between exploration behaviour and predatory behaviour.

Finally in Chapter Four, I combine everything I have learned from these two studies. I discuss how personality experiments can help further our understanding of predator behaviour, how it is tested, and how it may influence predator-prey interactions and community dynamics. I also propose directions for future research.

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CHAPTER 2

# LABORATORY-BASED EXPLORATION ASSAYS PROVIDE A ROBUST METHOD TO ASSESS EXPLORATION BEHAVIOUR, BUT NOT EMERGENCE, IN *HELPIS MINITABUNDA* (ARANEAE: SALTICIDAE).

## 2.1 ABSTRACT

Assays that quantify individual variation usually test animals in the laboratory. However, few studies have tested whether individual performance in lab-based assays correlates with performance in the field. I investigated whether individual performance in exploration assays in the Aussie bronze hopper (*Helpis minitabunda*) was correlated between laboratory and field environments. Each spider received three different tests: two tests in a lab environment (one in an arena made from natural materials and another in an arena made from Perspex), and one test in the field (in an arena made from natural materials). Spiders were run through each test three times to quantify repeatability. I compared latency to emerge and exploration behaviour across the three tests. Latency to emerge was measured by how long it took spiders to enter the arena and exploration was measured by how many turns spiders took in the Perspex arena or how many sticks they explored in the natural arena. My results partially supported my prediction that performance in exploration assays is highly correlated between the lab and field. Spiders were more likely to emerge in the field environment than the laboratory environment. This suggests that the emergence behaviours that we observe in laboratory assays may not reflect behaviour in the field. However, the arena type (natural vs Perspex) did not influence emergence behaviour. I did, however, find that the exploration behaviour of spiders was similar across all three assay types. This suggests that exploration assays in a laboratory setting reflect exploration behaviour in natural environments. My results have implications for how individual variation assays are conducted in the laboratory and how well laboratory studies reflect exploration behaviour in the field.

## 2.2 INTRODUCTION

Individual variation in populations has been recognised since Darwin (1859). More recently, biologists have started studying the significance of individual variation in behaviour, especially in an ecological context (Dall et al. 2012; Wolf & Weissing, 2012). Consistent differences in an individual's behaviour across time and contexts (i.e., animal personality) have gained particular attention (Réale et al, 2007; Liedtke et al, 2015; Noer et al, 2016; Philip et al, 2022). Behavioural traits that exhibit repeatable and heritable among-individual variation include exploration, aggression, sociability, activity, reactivity, and boldness, many of which may be correlated forming 'behavioural syndromes' (Dall et al, 2004; Sih et al, 2004; Réale et al, 2007; Roche et al, 2016).

Individual variation has consequences for how animals interact with their environment and affect the outcome of competition, cooperation, predation, parasitism, and mate choice events (Réale et al, 2007; Roche et al, 2016). Wolf and Weissing (2012) proposed 14 implications of individual variation for evolutionary and ecological processes which include life history, demography, population density,

population stability and resilience, dispersal and colonization. It is important to consider individual variation even if not directly testing it. For example, sampling bias can occur when breeding animals in the laboratory as this can select for lab-based traits (Roche et al, 2016). Similarly, researching wild-caught animals may lead to a sample of individuals with traits associated with being more easily captured (Roche et al, 2016). Therefore, the traits we measure may not always reflect the full range of variation within a population.

Most assays of individual variation are performed in a laboratory environment. There are numerous pros and cons associated with this, most notably experiments in the laboratory allow control over many variables such as temperature, weather, and food availability (Campbell et al, 2009). As a result, laboratory assays allow us to investigate the effects of specific manipulations and collect relatively 'clean' data (Calisi & Bentley, 2009). However, removing an animal from its natural environment where they are exposed to a wide array of environmental and social stimuli and placing it in a highly controlled artificial situation may deprive researchers of results that are ecologically relevant (Fusani et al. 2005; Calisi & Bentley, 2009; Biro, 2012; Wiggins et al, 2018). Also, animals who spend an extended amount of time in captivity may adjust or acclimatize to captive conditions and change their behaviour to suit (Herborn et al, 2010). Furthermore, some behavioural traits vary in how long individuals take to acclimatize (Herborn et al, 2010). There are numerous examples of discrepancies between laboratory experiments and field experiments (Calisi & Bentley, 2008). However, there are very few studies that use the same individual to investigate whether behaviour is correlated between the lab and the field (Herborn et al, 2010).

Exploration, boldness, aggressiveness, sociability, and activity assays can be used to measure personality (Massen et al, 2013). Invertebrates are often ideal models to examine the development, function and maintenance of personality traits as they are easier to access and study than many vertebrates (Kralj-Fišer & Schuett, 2014). Spiders, in particular, have served as profitable models for animal behaviour research (Hesselberg & Gálvez, 2023). Jumping spiders (Araneae, Salticidae) are active predators with well-developed eyes (Forster, 1977; Forster, 1979). Jumping spiders do not use webs to capture their food - instead they venture out into the environment to hunt down their prey. This makes them ideal candidates for comparing performance in exploration assays between the laboratory and field.

I investigated whether exploration behaviour is correlated between a laboratory and field environment in the Aussie bronze jumping spider (*Helpis minitabunda*, Koch) using a common emergence and exploration assay paradigm. As personality is defined as consistent behaviour over time and contexts, I predicted that the behaviour of individuals in a lab environment would be correlated with their behaviour in a field environment. This experiment will both gain insight into the presence of among-individual variation in a jumping spider, and test whether individual performance in laboratory-based exploration assays reflects performance in field-based assays.

## 2.3 METHODS

Thirty-two female *Helpis minitabunda* were collected from flax | harakeke (*Phormium tenax*, Forst. & Forst.) and *Agapanthus praecox* (Willd.) plants located on Massey University Ōtehā Rohe campus in Auckland, New Zealand. The collection and assays took place between August and October 2019 over a period of seven weeks. Spiders were collected in small groups of up to five individuals each week, two days before beginning assays to allow time for acclimatization to the lab. Spiders were maintained in the lab in 120ml plastic sample containers with screw caps. The centre of these caps was cut away and replaced with a piece of gauze to allow air to pass through. Pieces of paper towel were placed in a small vial lid at the bottom of the containers and regularly soaked with water to prevent spiders from becoming dehydrated. A stick was also placed in each container to provide stimulation (Carducci & Jakob, 2000). Spiders were not fed during their one-week testing period as they remained alert, well and active during this period of time while also motivated to explore. They received three assays each day, one of each type, for three days, one with an unnatural arena in the lab (UNL), one with a natural arena in the lab (NL) and one with a natural arena in the field (NF), so that each spider received a total of nine assays.

Spiders were weighed to the nearest mg using a Ohaus EX125D digital balance scale and photographed under a Motic SMZ 168 microscope with a ruler for scale on the same day as their capture. The Java-based image processing program ImageJ v1.53t (Rasband, W.S, 2018) was used to measure cephalothorax width behind the anterior lateral eyes and tibia - patella length of the first right leg. Once all the assays where complete, spiders were released in a different area to the collection points to avoid recapture.

### 2.3.1 Unnatural arena in the lab (UNL) assay.

Unnatural arena in the lab assays were performed in a lab environment (temperature 22°C, relative humidity 50-60%). A plastic hexagon-shaped maze was used to assay exploration behaviour (Figure 2.1a). At the centre, a vial (30 mL) was attached with Blu-Tack (Bostik, Colombes, France) below the surface. The maze was placed in a pop-up photography tent (1m x 1m x 1m) to minimize visual distractions during the test with a Canon XA20 camcorder (Tokyo, Japan) set up on a tripod overhead (Figure 2.1c). Spiders were placed in the vial which was then covered for two minutes to allow spiders to acclimate after being handled. The cover was then removed, and a large clear sheet of plastic was placed over the entire maze to prevent spiders escaping during assays. Spiders were given three minutes to emerge and explore the maze. I measured latency to emerge (s) from the vial (i.e., when the spider's entire cephalothorax had passed over the rim of the vial) and the number of turns taken within the maze (i.e., when a spider's cephalothorax had passed ¾ of the way across the side of a 'Y' within the maze). Assays were spiders did not emerge and

explore were noted and given a turn number of 0 as survival analysis (details below) accounts for censored data. The maze and vial were cleaned with 70% ethanol between each test and dried.

### 2.3.2 Natural arena in the lab (NL) assay.

The experimental procedure for the natural arena in the lab assay was very similar to that used for the unnatural arena in the lab assay. The plastic, unnatural arenas were replaced with a natural arena made from dried *Agapanthus* stalks cut to craft a cylindrical holding area (3cm high x 3cm diameter) analogous to the vial used in the unnatural arena. Eight sticks (10cm long) were then hot glued evenly around the edge of the holding area (Figure 2.1b). Spiders were placed in the holding area and covered for two minutes to allow spiders to acclimate. After two minutes the cover was removed, and the spider given three minutes to emerge and explore the sticks. I collected latency to emerge as described in the unnatural arena in the lab test. Exploration behaviour was quantified by counting the number of sticks explored (i.e., the entire cephalothorax crossed out onto the stick). Spiders that did not emerge and explore were noted and given an exploration score of 0.

### 2.3.3 Natural arena in the field (NF) assay.

The experimental procedure for the natural arena in the field assay was very similar to that used for the natural arena in the lab assay. However, assays were performed outdoors in the field under the shade of a tree. The natural arenas were temporarily attached to the top of a retort stand (60cm) using Blu-Tack with a Canon XA20 camcorder above on a tripod to record. A black blanket was place on the ground under the arena to help the arena and spider stand out on screen during recording (Figure 2.1d). This assay design mimics an exploration task in the natural environment, while also standardising the exploration arena in a way that allows comparison between individuals.

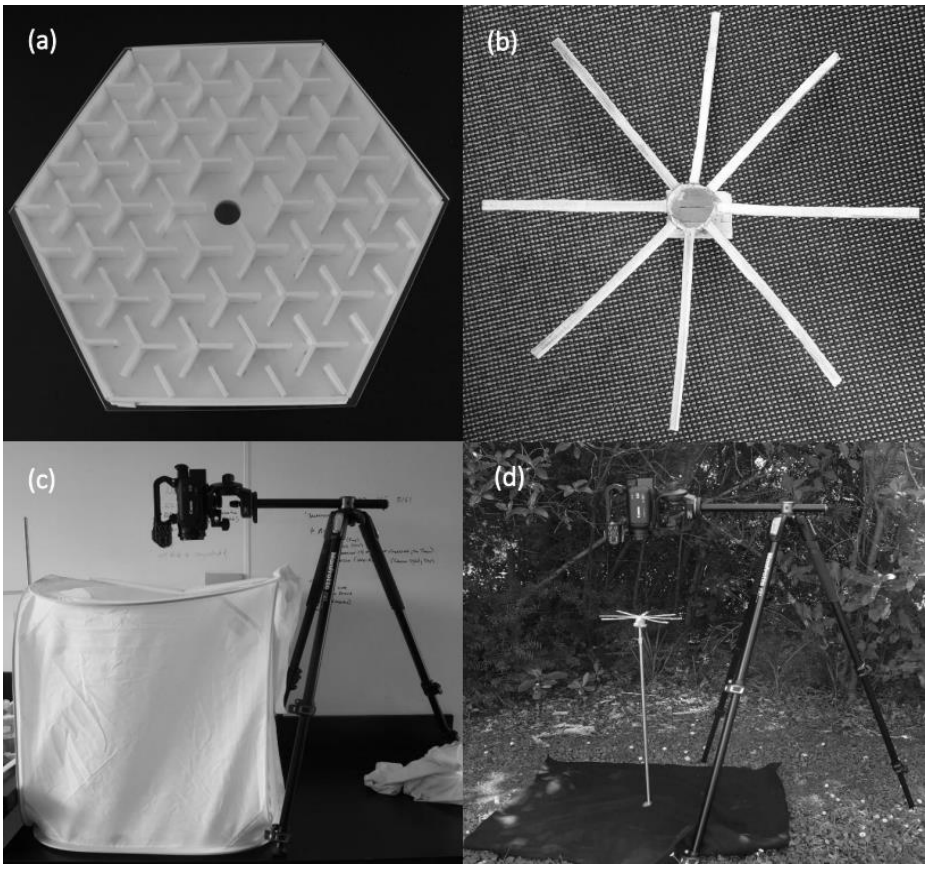


**Figure 2.1.** Unnatural plastic maze with a hole for a holding cylinder in the middle (a) and a natural maze made from *Agapanthus* stems with eight sticks attached to a holding cylinder (b) used in the exploration and emergence assays. Experimental set-up in the laboratory showing the pop-up tent with maze placed inside (c) and in the field with the natural maze on a retort stand (d).

123 2.3.4 Data analysis

124 Data analyses were performed in R Studio v2022.07.1 (RStudio Team 2020).

125

126 2.3.4.1 Latency to Emerge

127 I used survival analysis to compare latency to emerge during the three assays using the 'coxph' function and
128 the "survival" (Therneau, 2015), "survminer" (Kassambara & Kosinski, 2018) and "dplyr" (Wickham et al,
129 2018) packages. Data was right censored if spiders did not emerge within 180 seconds. A cox proportional
130 hazard model was used to test for significant differences in latency to emerge between the three assay
131 types. Assay type and test order were set as fixed effects and spider ID was included as a frailty term to
132 account for repeated testing of individuals. A generalised linear mixed model (GLMM) with a binomial
133 distribution was used to test whether there was a difference in the probability of spiders to emerge in the
134 field and lab assays. Treatment was set as a fixed effect and spider ID was included as a random effect.

Repeatability of emergence behaviour (emerged/did not emerge) was assessed using the 'rptBinary' function in the "rptR" package (Stoffel et al, 2017).

#### 2.3.4.2 Exploration

A generalized linear mixed model (GLMM) with a negative binomial distribution was used to test for significant differences in exploration behaviour between the three different assay types. The negative binomial distribution was used due to overinflation caused by multiple zero data entries. I used the 'glmmTMB function in the "glmmTMB" package (Brooks et al. 2017). To test for zero inflated data, I used the 'testZeroInflation' function in the "DHARMa" package (Hartig, 2022). Assay type, cephalothorax length and test order where set as fixed effects with spider ID included as a random affect. Repeatability of exploration behaviour was assessed using the 'rpt' function in the "rptR" package.

## 2.4 RESULTS

### 2.4.1 Latency to Emerge

There was a significant difference in the latency for *H. minitabunda* to emerge from the maze between the three assay types (NF, NL & UNL; Table 2.1; Figure 2.2). Spiders emerged faster during the field assay (NF) compared to the two laboratory assays (NL, UNL) (Table 2.1; Figure 2.2). Further, spiders were more likely to emerge in the field assay than the two lab assays (NF-NL GLMM, $z = -2.47$, $p = 0.01$; NF – UNL GLMM, $1 = -3.58$, $p < 0.01$). There was no significant difference in latency to emerge between the unnatural arena in the lab (UNL) and natural arena in the lab assays (NL; Table 2.1; Figure 2.2). There was no effect of test order on emergence behaviour (Table 2.1). Emergence behaviour was moderately repeatable in the natural arena in the field (NF: $R = 0.23$, $p = 0.03$) and unnatural arena in the lab assays (UNL: $R = 0.27$, $p = 0.02$), but not in the natural arena in the lab assay (NL: $R = 0.06$, $p = 0.25$).

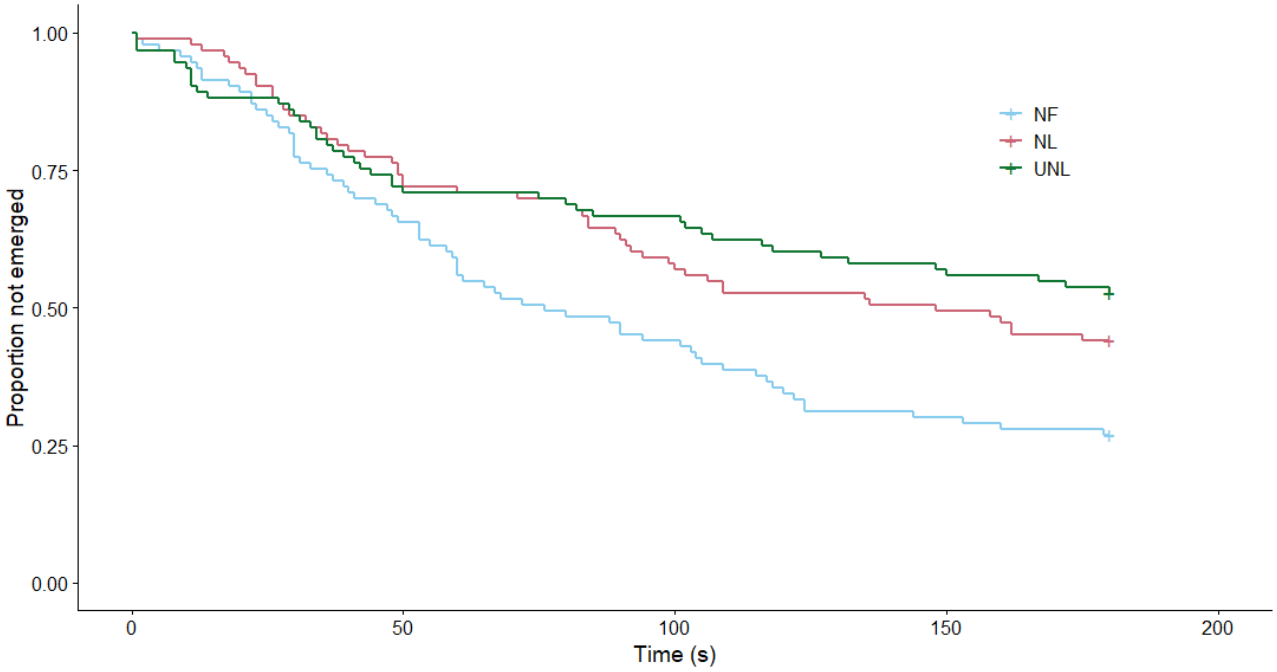


**Figure 2.2.** Kaplan-Meier curves of emergence during field-based assays using a natural maze (NF – Blue line), laboratory-based assays with a natural maze (NL – Red line) and laboratory-based assays with an unnatural maze (UNL – Green line).

**Table 2.1.** Generalised linear mixed model results comparing latency to emerge during the three assays. Effects show pairwise comparisons between assays.

| *Effect* | *Hazard Ratio* | *95% Confidence Interval* | *Z Value* | *P Value* |
|---|---|---|---|---|
| *NF – NL* | 0.63 | 0.44 – 0.90 | 2.54 | **0.01** |
| *NF – UNL* | 0.51 | 0.35 – 0.75 | 3.44 | **<0.001** |
| *UNL – NL* | 1.22 | 0.98 – 0.33 | 0.97 | 0.33 |
| *Order* | 1.01 | 0.95 – 1.07 | 0.18 | 0.86 |

*P*-values <0.05 are in bold.

158 2.4.2. Exploration

159 There was no significant difference in the exploration behaviour of spiders between the three assays (NL, NF
160 & UNL; Table 2.2; Figure 2.3). There was no effect of test order on exploration behaviour (Table 2.2; Figure
161 2.4). Exploration behaviour was moderately repeatable in the natural arena in the field assay (R = 0.27, p =
162 0.01), but there was borderline moderate repeatability in the unnatural arena in the lab assay (R = 0.26, p =
163 0.06) and low repeatability in the natural arena in the lab assay (R = 0.18, p = 0.12).

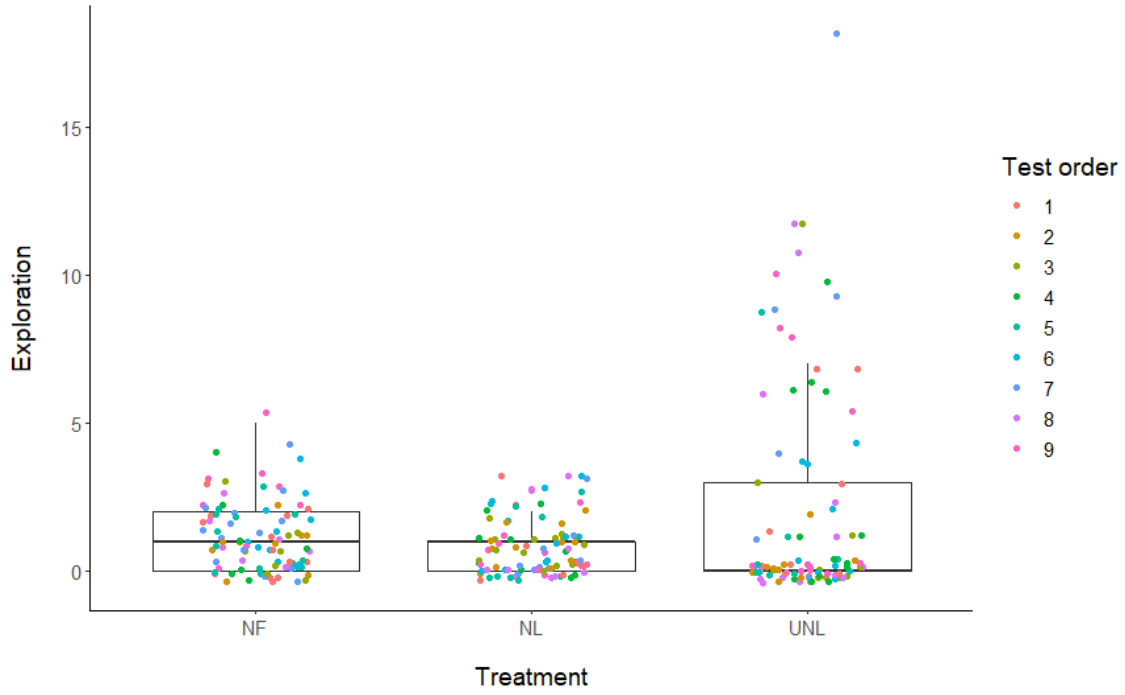


**Figure 2.3.** Boxplot comparing exploration behaviour (number of sticks or number of turns) during each of the three assays (NF, NL and UNL). Data points are colour-coded according to test order.

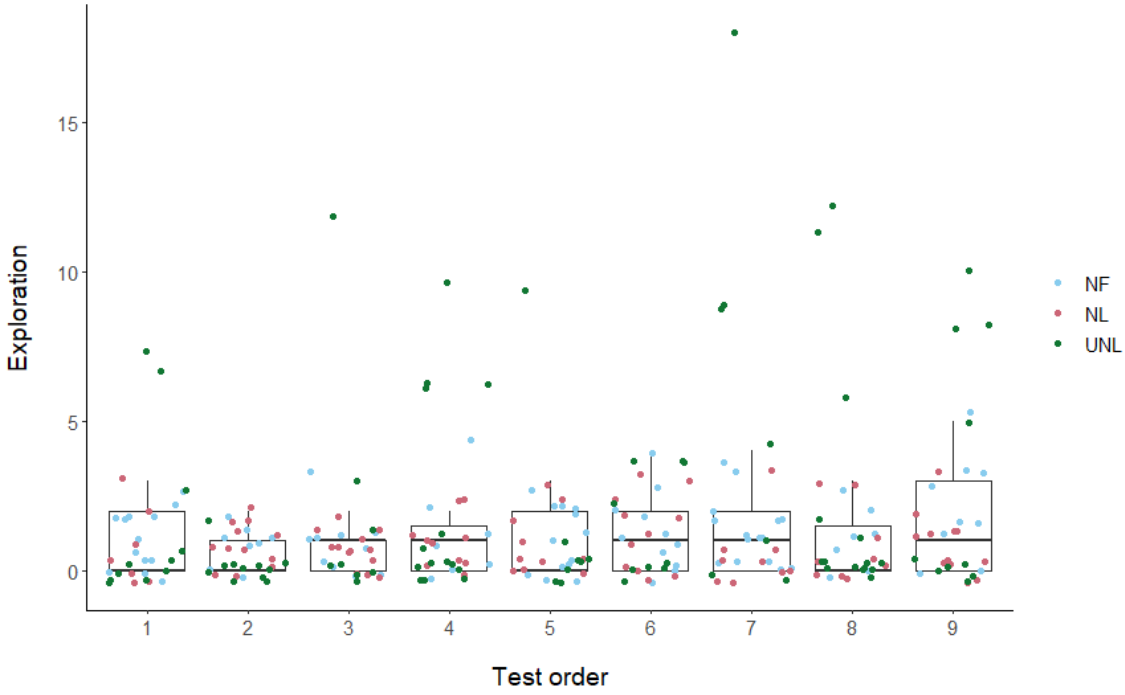


**Figure 2.4.** Boxplot comparing exploration behaviour (number of sticks or number of turns) over the nine assays. Data points are colour-coded via according to assay type (NF, NL or UNL).

**Table 2.2.** Generalised linear mixed model results comparing exploration behaviour in the three assays. Exploration behaviour in the natural arena in the field (NF) assay was used as a reference against which to compare exploration behaviour in the natural arena in the lab (NL) and unnatural arena in the lab (UNL) assays.

| *Effect* | *Estimate* | *Standard Error* | *Z-Value* | *P-Value* |
|---|---|---|---|---|
| *Intercept* | -0.62 | 0.59 | -1.06 | 0.29 |
| *NL* | 0.20 | 0.49 | 0.41 | 0.68 |
| *UNL* | 0.04 | 0.46 | 0.10 | 0.92 |
| *Cephalothorax length* | 0.10 | 0.13 | 0.80 | 0.43 |
| *Order* | 0.07 | 0.06 | 1.21 | 0.23 |

*P*-values <0.05 are in bold.

## 2.5 DISCUSSION

I found that there is evidence to partially support the hypothesis that the performance of spiders in exploration assays in lab environments is correlated with performance in assays in field environments. There was no difference in the exploration behaviour of spiders between the three assay types. This suggests that exploration assays in a laboratory setting reflect exploration behaviour in natural environments. However, there was a significant difference in emergence behaviour between the two lab-based assays and the field-based assay. *Helpis minitabunda* were more likely to emerge in the field assay than in the two lab assays. This was contrary to my prediction and suggests that there may be some variation in how emergence behaviours are expressed between the laboratory and the field. My experiment supports the use of exploration assays in the laboratory to reflect exploration in the field, but not the use of emergence assays.

*Helpis minitabunda* were more likely to emerge in the field environment in comparison to the laboratory environment. However, arena type did not seem to influence emergence behaviour. This suggests that the emergence behaviours that we observe in the lab may not reflect behaviour in the field. *Helpis minitabunda*, like most jumping spiders, are highly exploratory, with excellent vision compared to most other spider species, and are active hunters (Forster, 1977; Forster, 1979; Taylor, 1998). Rather than relying on a web, they move about the environment to hunt prey (Forster, 1977; Forster, 1979). Jumping spiders collect information about their surroundings using vision, touch, vibration, and taste (Ganske & Uhl, 2018). In my assays, unnatural mazes were cleaned between each trial, or a new natural arena used for each trial. Further, the plastic structure of the unnatural maze itself is different from the vegetative substrate they are used to. The reduction in environmental cues could have resulted in a lack of initial

arousal and hence lower emergence values in the laboratory assay. Environmental cues have been shown to affect animal behaviour. For example, temperature changes affect boldness in coral reef fish (Biro et al. 2010). Short-term environmental fluctuations alter components of behavioural consistency in European green lizards (Horváth, 2017). Daan (1981) discovered that time of day, water temperature and airflow influence emergence behaviour in the chironomid midge. Moving highly exploratory animals like jumping spiders into an artificial laboratory environment lacking many of the elements that usually provide stimulation could influence their behaviour (Kralj-Fišer & Gregorič, 2019; Liedtke et al. 2015). There have been reports of animals, specifically spiders, becoming less responsive in captivity when reared in environments with little stimulation (Carducci & Jakob. 2000). Several studies have demonstrated a positive link between complex environments, cognition and personality, especially during development (Kazlauckas et al. 2011; Liedtke et al. 2015). Although sticks were provided in the holding containers during the week-long period of my experiment to help mediate this (Carducci & Jakob, 2000), much of the environmental information that they usually receive (e.g., fluctuating temperature, absence of sound, humidity, hetero- and con-specific cues) was absent and may have affected spider behaviour. To assess whether emergence behaviours in the lab are influenced by environmental cues, I suggest systematically introducing ecologically relevant stimuli such as prey, vibratory or visual cues to the assays and comparing spider emergence behaviour.

Spiders in my experiments may have suffered a degree of 'shock' when suddenly exposed to the assay environments. Behavioural assays typically include an acclimatisation period to allow animals to become used to their environment or settle after being handled so that they may resume their normal behaviour during testing (Biro, 2012). Further, acclimatisation rate is a behavioural trait itself, with individuals differing dramatically in the time it takes for them to acclimatise to a new environment and resume normal behaviour (Biro, 2012). Spiders in my experiment were caught and held in the lab for two days before testing began and given a three-minute acclimatisation period before testing commenced to allow for settling. In a preliminary study using the same experimental procedures, I used spiders that were freshly caught and hence new to the laboratory environment. I found similar results between the preliminary and the present study which suggests that differences in the laboratory and field emergence rates were not the result of differences in acclimation behaviour.

I found that the exploration behaviour of spiders was similar across the three assays suggesting that exploration in a lab setting reflects exploration behaviour in a natural environment. Similarly, exploration behaviour in rufous-collared sparrows is correlated between the lab and field (van Dongen et al. 2010). My study helps to support the relevance of lab based behavioural assays to quantify behaviour in natural environments, however much more evidence is needed. Different behavioural traits and different taxa are likely to respond differently in laboratory and field environments.

There appeared to be greater variation in exploration behaviour in the unnatural arena in the lab assays than the two natural arena assays. This is likely due to differences in the two arena designs. The natural arenas required spiders to jump to move to a new stick, requiring a certain amount of risk assessment and distance calculation as they moved around the arena. Further, once the spider had explored to the end of an stick, there was nowhere else for them to go other than back the way they had come as the distance between sticks at the ends was too great to jump. However, in the plastic maze spiders were only required to choose which way to go and rarely came across dead ends. This makes the unnatural maze arena potentially quicker to navigate and less risky than the natural arenas. Despite this difference in design, I found that the exploration performance of individuals across all three assays was similar which indicates that the laboratory assays are ecologically relevant.

In conclusion, my results suggest that laboratory-based exploration assays provide a robust method to assess exploration behaviours. However, the performance of spiders in the laboratory emergence assays does not reflect performance in assays in a field environment. One possible explanation for the difference in emergence behaviour could be a reduction in environmental cues, such as sound or hetero- and con-specific cues, to initiate spider emergence in the lab assays. Further studies could investigate the role of environmental cues on emergence behaviours. More research on how to test different personality traits in the lab in ecologically relevant ways is needed. My results have implications for our interpretation of how assays in the laboratory reflect behaviour in the field.

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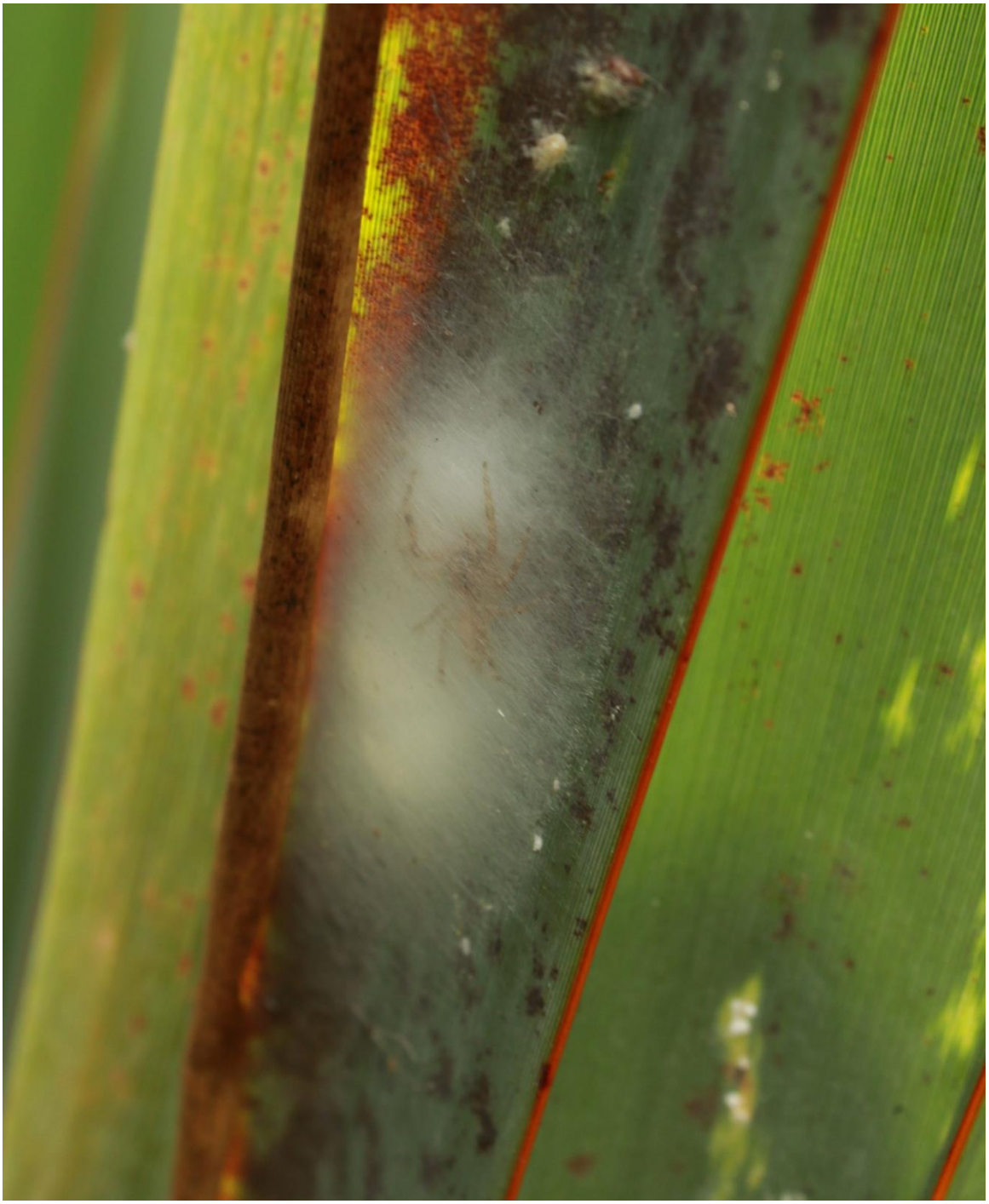
CHAPTER THREE

# EXPLORATION BEHAVIOUR DOES NOT CORRELATE WITH PREDATORY BEHAVIOUR IN THE AUSSIE BRONZE JUMPING SPIDER (*HELPIS MINITABUNDA*)



## 3.1 ABSTRACT

Individual variation or 'personality' has been noted in many animal taxa. However, it is only in the last twenty years that scientists have begun to test how individual variation in behaviour can impact population and ecosystem dynamics. Predation plays a pivotal role in evolutionary processes, shaping communities, and maintaining variation within populations. While there have been quite a few studies exploring how individual variation impacts different prey species in the predator-prey dynamic, there are far fewer exploring the influence of variation on predators and predator behaviour. In this study, I examined how variation in exploration behaviour correlates with predation behaviour in the Aussie bronze jumping spider (*Helpis minitabunda*). I compared the exploration behaviour of spiders in a maze with predatory behaviour when hunting a house fly (*Musca domestica*). Exploration behaviour is often included in a behavioural syndrome with aggression and boldness, each of which are often related to risky behaviours and high activity levels. I therefore predicted that spiders with high exploration rates would be more successful at capturing prey than spiders with low exploration rates. My results, however, showed no correlation between exploration behaviour and predatory behaviour. I found no correlation between exploration behaviour and latency for spiders to emerge to hunt, hunt duration or the number of failed attempts to capture prey. These results are surprising and while there was little variation in predatory behaviour in my experiment, there is evidence that variation affects other aspects of predator-prey dynamics. I suggest further testing to see whether larger or riskier prey might generate variation in predatory behaviour in jumping spiders.

## 3.2 INTRODUCTION

The different ways that individual animals behave has been recognised since antiquity (Dall et al. 2012). But until relatively recently, individual behavioural variation, often termed 'animal personality' or 'temperament', was traditionally ignored in ecology (Laskowski et al. 2022). Animal personality is characterised by repeatable individual differences in behaviour across time and context (Réale et al. 2007; Hertel et al. 2020), and personality traits have been quantified in diverse taxa (Bergmüller et al. 2010). Traits that have been demonstrated to show repeatable individual differences include exploration behaviour (Jones & Godin, 2010), boldness (Sprau & Dingemanse, 2017), and aggression (Modlmeier & Foitzik, 2011). Personality traits are often influenced by environmental stimuli via feedback between an individual's behaviour and their state (MacGregor et al. 2021). Personality traits also often correlate with each other, forming behavioural syndromes (Sih et al. 2004; Sih et al. 2012). Over the last twenty years, there has been growing appreciation for how individual variation in behaviour can influence population and ecosystem dynamics (Laskowski et al. 2022). However, there is still much controversy and little experimental evidence

demonstrating the effects of individual variation in behaviour on individual fitness or at larger ecological scales.

The growing research interest in individual behavioural variation is due to the realisation that it might be the product rather than simply the raw material of natural selection (Laskowski et al. 2022). Several hypotheses have been developed seeking to explain the generation and maintenance of individual behavioural variation in populations such as niche expansion, dispersal, or social organisation (Laskowski et al. 2022; Réale et al. 2007). Behavioural variation could have consequences for ecological processes at many levels. For example, it may influence individual fitness, an individual's role in a group, or an individual's interactions with conspecifics and heterospecifics (Laskowski et al. 2022; Réale et al. 2007). A study investigating foraging and collective behaviour in wild birds found that wild great tits exhibit collective behaviours, but its expression varied with personality (Aplin et al. 2014). Bolder individuals may be more likely to encounter sources of infection, and once infected, they may also facilitate the spread by acting as 'super-spreaders' (Ezenwa et al. 2016). Bolder and more aggressive male zebrafish fertilise more eggs, and aggressive sticklebacks are more likely to survive a predatory challenge than less aggressive sticklebacks (Ariyomo & Watt, 2012; Bell & Sih, 2007).

Boldness and activity are often used to assess individual predation risk (Szopa-Comley et al. 2020). However, variation in the behaviour of predators has rarely been tested experimentally. Numerus studies have examined the effect of predator presence on prey behaviour, but predators are often seen as varying in behaviour relatively little compared to prey (Szopa-Comley et al. 2020; Lima 2002). Predation plays a pivotal role in evolutionary processes, including shaping communities, altering trophic cascades, and maintaining variation within prey populations (Dingemanse et al. 2009; Szopa-Comley et al. 2020; Start & Gilbert, 2017). So, understanding individual variation in predatory behaviour will provide useful insights into ecological dynamics.

In this study, I investigated whether variation in hunting success is correlated with variation in exploration behaviour in the Aussie bronze jumping spider (*Helpis minitabunda*, Koch). Invertebrates are ideal models to study individual variation as they are easier to access and work with than many vertebrates (Kralj-Fišer & Schuett, 2014). Spiders are versatile, found in almost all terrestrial ecosystems, and have served as profitable models in many subdisciplines including behavioural research (Hesselberg & Gálvez, 2023). Jumping spiders (Araneae, Salticidae) are active, cursorial spiders with well-developed eyes (Forster, 1977; Forster, 1979) that venture out from their nest to hunt their prey. This makes them ideal candidates for exploration and predation assays. To test whether exploration behaviour correlates with predation behaviour, I first quantified individual exploration behaviour using a common emergence and exploration assay paradigm. This paradigm was used in Chapter Two and I found that the exploration behaviour of

spiders in the lab assay reflected behaviour in a field-based exploration assay. I then quantified individual predatory behaviour in a predation assay in which spiders were allowed to hunt a prey item in a controlled arena. The aim of my study is to generate insights into whether exploration behaviour correlates with predation behaviour and how individual variation in predation behaviour may influence predator-prey dynamics.

## 3.3 METHODS

Over a period of three months beginning mid-December of 2019, 50 female *Helpis minitabunda* were collected from harakeke | New Zealand swamp flax (*Phormium tenax*, Forst. & Forst.) and agapanthus (*Agapanthus praecox*, Willd.) plants located on the Oteha Rohe campus of Massey University (Auckland, New Zealand). Spiders were collected and held in the lab 48 hours before any testing commenced. Spiders were maintained in 120ml plastic sample containers with screw caps and were fasted to increase their motivation to hunt. The lids of these containers were pierced with tiny holes to allow continuous, passive air flow. Pieces of damp paper towel were placed inside the containers to prevent spiders from becoming desiccated. A short stick was also placed inside to provide stimulation (Carducci & Jakob, 2000).

Each spider received two assays in total (hunting and exploration), tested on separate days. The assay order was randomly selected using the number generating app 'Random UX' (UXAPPS Ltd, 2016). The hunting assay exposed spiders to a small live prey, in which I recorded emergence time and hunting behaviour (details below). Exploration assays were performed in a maze (described below), in which I recorded emergence time and exploration behaviour (number of turns). Between the two testing days was a rest day where no assays were performed for 24hrs. Once both assays were completed, spiders were weighed (mg) using a Ohaus EX125D digital scale and photographed under a Motic SMZ 168 microscope with a ruler for scale. The Java-based image processing program 'ImageJ' (National Institutes of Health, 1997) was used to determine size (mm) by measuring the cephalothorax width behind the anterior lateral eyes; and the leg length was gained by measuring the tibia - patella of the first right leg. Laboratory temperature was maintained at 22°C throughout the experiment.

### 3.3.1 Hunting assays

Individual spiders were first placed in a clean 120ml vial and given at least three minutes to acclimate. The vial was then placed within a clear plastic cube (15 × 15 × 15cm) in which one panel was missing which was placed face down to the substrate. A house fly (*Musca domestica*, Linnaeus) was placed in the fridge for two minutes to slow it down to enable it to be released in the hunting arena without escaping, then also placed

in the cube. The spider was left in the vial with the lid on for another minute, providing time for the fly to warm up and become active before the lid was removed allowing the spider to leave and explore the cube of its own accord. The assay was performed inside a white, pop-up photography tent (80 × 80 × 80cm) to minimize visual distractions (Figure 3.1). A Canon XA20 camcorder on a tripod filmed each trial from above. Spiders were given one hour to emerge from the vial and hunt the fly. I recorded latency to emerge (the time from lid removal for the cephalothorax to cross the vial rim), hunting success (prey caught or not caught) and the time it took the spider to capture the fly. Once the hour was up or as soon as the spider successfully captured the fly, the test ended. The fly, if caught, was immediately taken away from the spider to prevent consumption and maintain motivation for the second assay.

Figure 3.1. Laboratory assay set up. Assays were set up within mazes placed in a pop-up tent and recorded from above.


### 3.3.2 Exploration assays

Exploration assays took place inside the plastic, hexagon-shaped maze used in Chapter Two. At the centre of the maze below the surface a 60ml vial cut in half was attached using Blu-Tack (Bostik). A spider was placed inside the halved vial at the centre of the maze and the entrance to the maze was covered for two minutes to allow the spider to acclimate. The maze was placed inside a pop-up photography tent (80 × 80 × 80cm) to minimize visual distractions during the trial, and a Canon XA20 camcorder was set up on a tripod to film

from above (Figure 3.1). Once the acclimation period was over the cover on the vial was removed and a transparent cover was placed over the entire maze to prevent the spider leaving the arena. Spiders were given three minutes to emerge and explore the maze. Spiders were given three minutes as it has been shown in preliminary assays that if a spider is going to emerge, it will usually occur within this time period. I recorded latency to emerge, and the number of turns taken. A spider was considered to have emerged when its cephalothorax passed over the rim of the vial. A turn was only counted when the cephalothorax passed ¾ of the way along one side of the Y shapes within the maze (Figure 3.2). Spiders who did not emerge and explore were noted and given an emergence time of 180 seconds (censored data) and a turn number of 0.

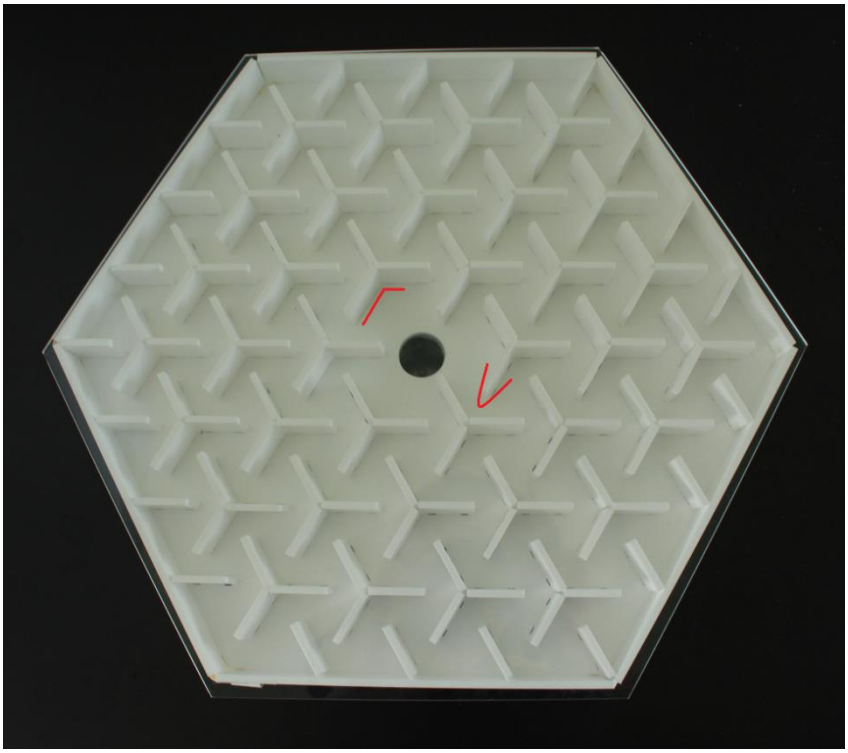


Figure 3.2. Maze arena used during exploration assays. Red lines indicate the path spiders could take to complete a turn.

### 3.3.3 Data analysis

I used generalized linear models to test whether exploration behaviour (number of maze turns) is correlated with emergence (emerged/did not emerge) in the hunting assay, latency to emerge in the hunting assay, how long it took to catch prey, hunting success, and the number of failures to capture prey using the packages “lme4” (Bates et al. 2015) and “lmertest” (Kuznetsova et al. 2017). Emergence and hunting success were tested using binomial distributions. Latencies to emerge and catch prey were tested using gaussian distributions. Number of failures to capture prey was tested using a Poisson distribution.

Cephalothorax width was included as a fixed effect for all analyses. I used a Kendall's correlation using the 'cor.test' function to test whether there was a correlation between latency to emerge in the exploration and hunting assays.

I used "ggplot2" (Wickham, 2016) to plot the results using the 'ggplot' function and the 'ggarrange' function in the "gridextra" package (Baptiste, 2015) to arrange the plots. Data analysis was performed using R v4.3.0 (R Core Development Team) in RStudio v2023.03.0 (RStudio Team 2020).

## 3.4 RESULTS

I found no correlation between exploration behaviour and the probability of spiders to emerge during the hunting assay (Table 3.1; Figure 3.3a), the latency to emerge during the hunting assay (Table 3.1; Figure 3.3b), hunting success (Table 3.1; Figure 3.3c), the latency to catch prey (Table 3.1; Figure 3.3d) or the number of failures to capture prey (Table 3.1; Figure 3.3e). Spider size did not influence predatory behaviour (Table 3.1). Additionally, there was no correlation between the latency for spiders to emerge during the exploration assay and latency to emerge during the hunting assay ($z = -0.29$, $P$-value = 0.77; Figure 3.3f).

Table 3.1. Results of generalised linear models comparing the emergence probability (A); latency to emerge (B); hunting success (C); latency to capture prey (D); and number of failures to capture prey (E), with the exploration behaviour (number of maze turns) of spiders.

| | *Coefficient estimate* | *Standard error* | *z value* | *P-value* |
|---|---|---|---|---|
| (A) *Probability of emerging to hunt vs exploration behaviour* | | | | |
| *(Intercept)* | -2.1917 | 3.6710 | -0.597 | 0.550 |
| *Maze turns* | -0.1193 | 0.1029 | -1.158 | 0.247 |
| *Cephalothorax width* | 1.0440 | 0.8242 | 1.267 | 0.205 |
| (B) *Latency to emerge to hunt vs exploration behaviour* | | | | |
| *(Intercept)* | -182.335 | 228.463 | -0.798 | 0.429 |
| *Maze turns* | -5.437 | 6.891 | -0.789 | 0.435 |
| *Cephalothorax width* | 70.433 | 44.371 | 1.587 | 0.120 |
| (C) *Hunting success vs exploration behaviour* | | | | |
| *(Intercept)* | 1.72312 | 2.54583 | 0.677 | 0.499 |
| *Maze turns* | 0.12767 | 0.11288 | 1.131 | 0.258 |
| *Cephalothorax width* | -0.08355 | 0.49584 | -0.168 | 0.866 |
| (D) *Latency to capture prey vs exploration behaviour* | | | | |
| *(Intercept)* | 1490.57 | 1186.35 | 1.256 | 0.216 |
| *Maze turns* | -43.75 | 36.37 | -1.203 | 0.236 |
| *Cephalothorax width* | -23.51 | 231.83 | -0.101 | 0.920 |
| (E) *Number of fails to capture prey vs exploration behaviour* | | | | |
| *(Intercept)* | -0.56133 | 1.81746 | -0.309 | 0.757 |
| *Maze turns* | 0.02428 | 0.05080 | 0.478 | 0.633 |
| *Cephalothorax width* | -0.15199 | 0.36018 | -0.422 | 0.673 |

*P*-values $\leq$ 0.05 are in bold.

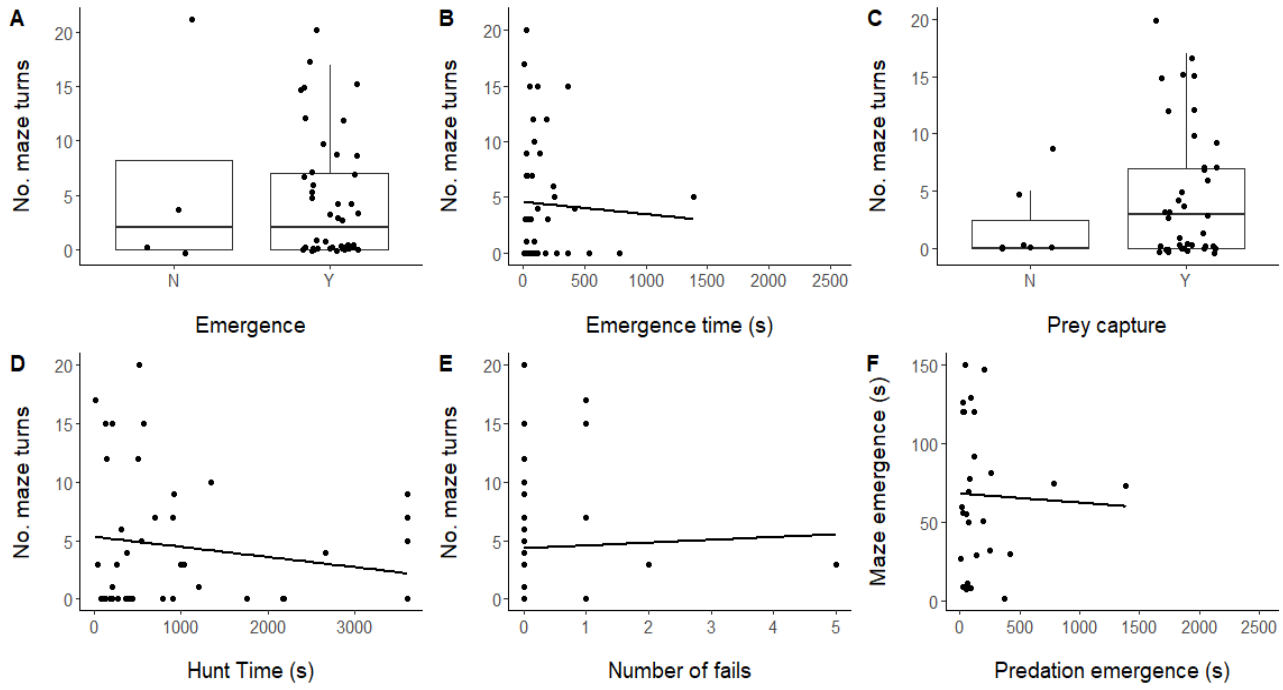



Figure 3.3. Box plot comparing emergence (a) against exploration behaviour (number of turns). Scatterplot with trend line comparing emergence latency (b). Box plot comparing successful prey capture against exploration behaviour (c). Scatterplots with trend lines comparing hunt time (d), and failed capture attempts (e) against exploration behaviour. Scatterplot with regression line comparing latency for spiders to emerge in the exploration and the hunting assays (f). Boxes show median and inter-quartile ranges.

## 3.5 DISCUSSION

I found that there was no evidence that exploration behaviour is correlated with predatory behaviour in the jumping spider *H. minitabunda.* Exploration behaviour (quantified as number of turns in the maze) was not correlated with prey capture success. Further, there was no correlation between exploration behaviour and latency for spiders to emerge during the hunting assay, the time it took to capture prey or the number of failed capture attempts. It is not necessarily surprising that emergence latency between the exploration and hunting assays was not correlated as the results from my first chapter did not indicate that emergence in the exploration assay was a good measurement of emergence behaviours in the field. However, the lack of relationship between exploration and predatory behaviours overall was surprising.

Several studies on animal personality and behavioural syndromes have found links between behaviour types and fitness-related traits (Cote et al. 2008; Carter et al. 2010; Sih et al. 2012; Patrick & Weimerskirch 2014). Behavioural syndromes are suites of correlated behaviours across situations. For example, boldness and aggression, or boldness and exploration behaviours often correlate with each other in individuals and are considered to represent behavioural syndromes (Sih et al. 2004; Scales et al. 2011; Martins & Bhat, 2014; Mazué et al. 2015; Kudo et al. 2021). These personality traits have been shown to

affect fitness-related traits such as growth rate, survival, and reproductive success (Smith et al. 2008; Cote et al. 2008; Carter et al. 2010; Adriaenssens & Johnsson, 2011; Patrick & Weimerskirch 2014). It is therefore reasonable to predict that exploration behaviour, which is linked to aggressiveness and boldness in other taxa, would also correlate with predatory behaviour. For example, individuals that explore more are expected to take more risks during hunts which should in turn influence prey capture success (Sih et al. 2012). One potential reason why I did not find any correlation between exploration and predatory behaviour could be because the experimental set up was small and simple compared to the spider's natural environment. This significantly reduced the 'challenge' presented during a hunt that is usually experienced in a natural environment. The arenas also allowed spiders to make multiple strike attempts before capture, as the prey could not escape the arena as they would in a natural environment. However, there was also no correlation between the number of failed strikes and exploration behaviour in my experiment.

Alternatively, the house flies used as prey in my experiments were safe prey, and predatory drive is ubiquitous. The flies are active and fast, but do not react aggressively and they lack physical defence systems that could pose a threat to a spider. Flies are, therefore, a relatively safe prey that all individuals were willing to hunt. It would be interesting to test whether other prey types that are larger, or that are dangerous and pose some risk to the predator would generate more variation in predatory behaviour (Mukherjee & Heithaus, 2013). There is also evidence that hunting experience over time can also play a role in prey capture success (Morse, 2000; Morse, 2000). Other ways in which individual variation could affect predatory behaviour include when an individual will hunt (e.g. at certain times of day or limited to certain weather conditions), how far an individual is willing to travel to find prey or an individual's willingness to hunt under environmental stressors (e.g., during climate events, starvation, or while another predator is present). Each of these traits may correlate with exploration behaviour.

Individual variation could have consequences for ecological processes at many levels from population dispersal and potential niche expansion to an individual's role within a group and how it interacts with others inside and outside of its group (Laskowski et al. 2022; Réale et al. 2007). For instance, there is evidence that behaviours such as aggression and boldness affect reproductive success, survival during predatory events, foraging behaviour, and pathogen dispersal (Bell & Sih, 2007; Ariyomo & Watt's, 2012; Aplin et al. 2014; Ezenwa et al. 2016). These ecological processes, among others, play a pivotal role in not only an individual's fitness, but how a population evolves over time. Predation plays an important role in evolutionary processes, the shaping of communities, altering trophic cascades and maintaining variation within prey populations (Dingemanse et al. 2009; Start & Gilbert, 2017; Szopa-Comley et al. 2020;). Further investigation of how individual variation affects not only prey behaviour but also the behaviour of the predator, could lead to some interesting discoveries, and help us further our understanding of ecosystem dynamics.

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CHAPTER FOUR

# GENERAL DISCUSSION

My aim for this study was to determine whether personality traits are correlated with predatory behaviour in the jumping spider *Helpis minitabunda*. I first tested whether individual performance in emergence and exploration assays was correlated between the laboratory and field environment. In this experiment I used two different arena types, one constructed out of natural material and the other constructed from plastic, to assess whether the substrate material used in personality tests could also influence spider behaviour. Then, using what I learned from the design of exploration assays in Chapter Two, I tested whether exploration behaviour was correlated with predatory behaviour.

My results comparing lab and field exploration assays showed no difference in exploration behaviour between the lab and field assays. However, there was a significant difference in emergence behaviour. *Helpis minitabunda* were more likely to emerge in the field assay than in the laboratory assays. This difference suggests that emergence behaviour is affected by the laboratory environment and therefore the results from lab studies should be interpreted with this in mind where field studies are not possible. The arena type (natural/unnatural) did not seem to influence emergence, although there did appear to be more variation in exploration behaviour in the unnatural arena than the natural arena. Despite this, the exploration behaviour of individuals between the two arena types was similar. My results suggest that exploration assays performed in the laboratory using unnatural arenas reflect exploration behaviour in the field and support the use of laboratory assays to quantify exploration behaviour.

There is no evidence from my experiments that exploration behaviour and predation behaviour are correlated in *H. minitabunda*. There was no correlation between exploration behaviour and the spider's ability to capture prey. Indeed, there was very little variation in predatory behaviour between individuals in the hunting assay as most spiders successfully captured their prey before the hunting assay ended. I also found that there was no correlation between exploration behaviour and any other measure of predatory behaviour, including time taken to capture prey, number of failed capture attempts and how long it took spiders to emerge to begin hunting. While I was not surprised that there was no relationship between emergence in the exploration and hunting assays due to there being no association between emergence in the lab and field assays of Chapter Two, I was surprised that there was no correlation between exploration and any other predatory behaviour that I measured. Overall, my results suggest that exploration behaviour does not correlate with predatory behaviour in *H. minitabunda.*

## 4.1. ASSAYING BEHAVIOUR IN THE LABORATORY VS. THE FIELD

My results in Chapter Two indicated that emergence behaviour in lab and field assays is not correlated. Spiders were more likely to emerge in the field assay in comparison to the laboratory assay. This suggests that assays that test emergence behaviour in the laboratory may not always produce results that reflect

emergence behaviour in the natural environment. *Helpis minitabunda,* like most jumping spiders, have excellent vision and are active hunters (Forster, 1977; Forster, 1979; Richman & Jackson, 1992). Jumping spiders collect information about their surroundings using vision, touch, vibration, and taste (Ganske & Uhl, 2018). Moving highly exploratory animals like jumping spiders into an artificial laboratory environment lacking many of the elements that usually provide sensory stimulation could influence their behaviour (Liedtke et al, 2015; Kralj-Fišer & Gregorič, 2019). The lack of environmental cues in the laboratory may have reduced arousal in the spiders, causing a longer latency to emerge in the two lab assays in comparison to the field assay. My field assay design did not completely replicate a natural environment as there was still a level of control, human disturbance and use of unnatural objects. This was necessary in order to maintain standardisation between trials. Spiders also did not get the option to emerge from their own silken retreats or chosen safe space as they usually would in the wild. However, my field assays did include natural stimuli such as wind, natural light, scents, and sounds which should have elicited more natural behaviours during assays. Changing laboratory environments to simulate salient components of the natural environment may result in emergence behaviour that more closely reflects behaviour in the field.

I found that exploration behaviour in *Helpis minitabunda* was similar between the laboratory and field assays, suggesting that exploration assays performed in a laboratory reflect the expression of exploration behaviour in more natural settings. Other studies that have also compared exploration behaviour between the lab and field have found correlations in behaviour. For example, the exploration behaviour of rufous-collard sparrows was correlated between lab and field environments (van Dongen et al. 2010). Further, the exploratory tendency and neophobia of blue tits in the lab predicted their exploration behaviour and neophobia in the wild (Herborn et al. 2010). The exploration behaviour of adult greats tits in the lab was also correlated with the dispersal distance of their offspring in the wild (Dingemanse et al. 2003). My results support the use of laboratory-based exploration assays to reflect the behaviour of animals in their natural environments.

Arena type did not seem to influence emergence behaviour. However, there appeared to be more variation in exploration behaviour in the unnatural arenas than in the natural arenas. This may be due to the design rather than the type of material used to construct the arenas. The natural arena created slightly more risk to navigate compared to the unnatural arena as spiders either needed to jump between sticks, or backtrack towards the centre to move onto the adjacent stick. The natural arena also presented less area for spiders to explore in comparison to the unnatural arena. Spiders take time to scan, assess potential routes and risks, and make decisions before finally moving to their desired location, particularly if this involves jumping (Tarsitano, 2006; Aguilar-Argüello et al. 2020; Aguilar-Argüello et al. 2021). There is also evidence that different species of salticid spiders exhibit different cognitive abilities which can affect the ability and rate of their decision making (Aguilar-Argüello et al. 2019). At this time, though there are

cognitive studies that demonstrate that salticid spiders have a diverse array of behaviours (Aguilar-Argüello & Nelson, 2021), there are no studies that have investigated the specific cognitive ability of *Helpis minitabunda* so their decision-making behaviours have not yet been described. Despite apparent differences in how the spiders used the two types of arenas, exploration behaviour was still correlated across all three assays. This suggests that the use of unnatural materials to construct behavioural arenas to test exploration behaviour can provide ecologically relevant results.

## 4.2. EXPLORATION AND PREDATION

Exploration is often included in behavioural syndromes with activity, aggression, and boldness traits (Bourne & Sammons, 2008; Sih et al. 2012; Sih & Del Giudice, 2012; Mazué et al. 2015; Hertel et al. 2019). I predicted that exploration behaviour would be correlated with predatory behaviour as other studies have found correlations between exploration and boldness (Patrick et al. 2017) or aggression (Santostefano et al. 2016). This suggested that more exploratory individuals would be more likely to take risks during hunts which would in turn influence performance in the hunting assay (Chapter Three). However, I did not find any evidence to support a relationship between exploration behaviour and predatory behaviour.

There are a few potential reasons why I failed to find a correlation between exploration and predatory behaviour. Firstly, the experimental arenas for the hunting assay were quite small and simple, which may have made the hunt too easy for the spiders to show variation in predation behaviour. The prey was also trapped in the arena with the spiders for the duration of the hunting assay, allowing the spiders to make multiple strike attempts to capture the prey if they missed the first time. However, I did not see any correlation between the number of strikes it took to capture prey and exploration behaviour. Alternatively, the prey themselves may have been too 'safe'. Houseflies, while active and fast, do not react aggressively and lack any physical defence systems that could pose a threat to a jumping spider and are, therefore, a relatively safe prey item that all individuals in my assay were willing to hunt. There is evidence that predators will avoid more dangerous prey when possible, and their willingness to go after dangerous prey can be linked to sex, size, age, experience, and reproductive class (Mukherjee & Heithaus, 2013).

Personality type can affect the type of prey that spiders target. More aggressive spiders are more likely to choose and are better at hunting unpredictable prey than more docile spiders that prefer predictable prey (Chang et al. 2017). Spider personality can also influence whether they use venom or silk to capture prey (Beydizada & Pekar 2023). Further, highly active jumping spiders consume more low-activity prey, while less active spiders consume fewer but more active prey (Sweeney et al. 2013). In the black widow spider, bolder individuals consume bolder prey and shyer spiders consume shyer prey (DiRienzo et al. 2013). Potentially, the role of personality in predator-prey interactions may only become apparent when

there is a range of prey and some risks involved in predation. Lastly, it could be that for *H. minitabunda* exploration behaviour is part of a different behavioural syndrome that does not correlate with predatory behaviour. Predation may be more closely linked to other personality traits such as aggression or boldness, as seen in several other species (Webster et al. 2012; Toscano et al. 2016; Chang et al. 2017; Beydizada & Pekar, 2023). While exploration behaviour is often linked to aggression, exploration has also been linked to activity or neophobia (Exnerova et al. 2010; Herborn et al. 2010; Andersson et al. 2014; Toscano et al. 2016; Hammond et al. 2021). There are multiple behavioural syndrome types and often how they present is species, or perhaps context, dependent.

Predator-prey interactions are important drivers of evolutionary processes, including the shaping of communities, altering trophic cascades, and maintaining variation within prey populations (Dingemanse et al. 2009; Start & Gilbert, 2017). To date, the effects of personality traits of prey in predator-prey interactions have been more intensely studied than the effects of personality traits in the predator. There is plenty of evidence showing that prey species adjust their behaviour in response to predatory cues (e.g., Lima & Dill, 1990; Ferrari et al. 2010; Paterson et al. 2013; Cremona et al. 2014; Wagner & Moore, 2022) and there is also evidence that personality traits are linked to these behavioural adjustments and the prey's ability to survive predatory interactions (Blake & Gabor, 2014; Toscano, 2017). Several studies have explored predator behaviour (e.g., Chesson 1978; Sherratt & Harvey, 1993; Endler & Mappes, 2004; Ordiz et al. 2020; Sheldon et al. 2023), however there is still much to learn before we understand the behaviour of predators. As more is revealed about predator behaviour, it is apparent that both predators and prey play equal parts in predator-prey interactions and that the personality traits of predators and prey interact and each influence the outcome of predatory events (Sweeney et al. 2013; DiRienzo et al. 2013; Chang et al. 2017). It is important to examine the roles of personality traits in both predators and prey so that we can get a more complete understanding of predatory-prey interactions as a whole.

### 4.3. PERSONALITY AND FITNESS

There is considerable evidence that personality traits can influence fitness related traits, although the evidence is somewhat controversial. Personality traits have been linked to reproductive success (Cote et al. 2008; Smith et al. 2008; Patrick & Weimerskirch 2014; Yoshida et al. 2016), foraging success (Carter et al. 2010; Patrick & Weimerskirch 2014), growth (Adriaenssens & Johnsson 2011; May et al. 2016), and survival (Dingemanse et al. 2004; Cote et al. 2008; Yoshida et al. 2016; May et al. 2016; Germano et al. 2017; Allard et al 2019). However, the links are inconsistent between studies. For example, Both et al. (2005) and Dingemanse et al. (2004) found a correlation between exploration behaviour and survival in great tits, Réale & Festa-Bianchet (2003) and Bremner-Harrison et al. (2004) found a correlation between boldness and

survival in Bighorn ewes and swift foxes, however Dutra et al. (2016) found no correlations at all in saffron finches. I suggest that while personality traits can influence or predict fitness related traits, species, sex, age, experience, and the environment can also affect the degree and form of those relationships. It's clear we still have much to discover about the effects of individual behavioural variation on both individual fitness as well as at larger ecological scales.

### 4.4. WHERE CAN WE GO FROM HERE?

There are numerous pros and cons associated with using laboratory-based assays to investigate animal behaviour. The pros include the ability to control variables that generate confounding effects on behaviour in the field, such as temperature fluctuations, weather changes and interference from other animals. The ability to control and manipulate both the environment and the test subject allows for better precision in testing and hopefully provides cleaner data (Calisi & Bentley, 2009). But this very advantage could also be a disadvantage, as taking an animal out of its natural environment and placing it in a highly controlled, almost clinical, environment may change the animal's behavioural responses, depriving researchers of ecologically relevant data (Fusani et al. 2005; Calisi & Bentley, 2009; Biro, 2012; Wiggins et al, 2018). Long-term captivity can also influence behaviour (Herborn et al, 2010). Laboratory based assays are a great way to test specific hypotheses that were first gathered in the field, and help scientists gain more precise understanding of the behaviours of interest. However, I argue that it should be more commonplace to also make sure that the results gained in the laboratory are correlated with behaviours observed in field-based assays.

In addition to normalising comparative tests between the laboratory and field, I would like to assess the effects of environmental stimuli on behaviour by systematically re-introducing ecologically relevant stimuli into laboratory based behavioural assays. Jumping spiders are highly visual and collect information about their surroundings using vision, touch, vibration, and taste (Ganske & Uhl, 2018). In the hunting assay, I saw that spiders were more reactive to prey that were moving. At times, the flies remained still for several minutes, and spiders often would stay put, not emerging into the arena or would emerge but remain relatively inactive, seemingly unaware of the fly until it moved. Therefore, I suggest testing whether introducing physical cues that are present in the natural environment (such as substrate vibrations, airflow, or variable lighting) to emergence assays in the laboratory would lead to a correlation between emergence behaviour in the laboratory and field. Introducing controlled environmental stimuli to laboratory assays could provide test animals with a more natural and complex test environment that is closer to what they would experience naturally and hence hopefully induce more natural behaviours.

## 4.5. CONCLUSION

The results of my thesis suggests that laboratory exploration assays provide a robust method to assess exploration behaviour in jumping spiders and supports the small number of other studies that have also investigated correlations in exploration behaviour in both the laboratory and field (Dingemanse et al. 2003; van Dongen et al. 2010; Herborn et al. 2010; Adriaenssens & Johnsson 2011). However, performance in laboratory-based emergence assays do not reflect performance in field-based assays. My results highlight the importance of comparative testing between the laboratory and field to ensure the results from behavioural studies are ecologically relevant. My results also show that exploration behaviour is not correlated with predation behaviour in *H. minitabunda.* Exploration behaviour may not be a good predictor of predatory behaviour, at least in this species. To understand the influence of personality traits on predator-prey interactions we need more studies that explore individual variation in predator behaviour. We also need more studies that examine the interactions between predator and prey personality.

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