A behavioural analysis of contest and predation performance in the Australian bronze jumping spider (*Helpis minitabunda)* (Koch, 1880) (Araneae: Salticidae)

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General Abstract

Whole-organism performance encompasses the ability of an individual to perform ecologically significant tasks, including foraging, competition and reproduction. Performance is shaped by environmental influences, physiology, morphology, and behaviour. While there has been a lot of research into individual components of performance, fewer studies have investigated how components of performance might interact. In my thesis, I test whether predation and contest performance interact in the jumping spider *Helpis minitabunda* (Koch, 1880) (Araneae, Salticidae). In Chapter Two, I quantified the contest behaviour of *H. minitabunda*, examining juvenile-juvenile, female-female and male-male contest performance in controlled conditions. I identified patterns in contest escalation and tested how size influences contest outcomes. I found that contests in *H. minitabunda* consist of three escalating phases: the assessment, display and contact phase. I found that juveniles, females and males were equally likely to start the assessment phase. However, males were more likely to escalate into the display phase than females or juveniles, and both females and males were more likely to initiate the contact phase than juveniles. Size differences between opponents did not influence contest outcome. Juvenile assessment strategies most closely match the mutual assessment strategy. However, the assessment strategies of males and females did not match any traditional assessment model. My results suggest that there are differences in agonistic behaviour at different developmental stages in *H. minitabunda*. In Chapter Three, I assessed the predation behaviour of *H. minitabunda* in a standardised model prey assay and a voracity assay to quantify predation performance. I found a correlation between latency for the spider to emerge and prey capture success. However, there was no relationship between latency to first prey capture and the number of prey caught. This suggests that predatory traits are shaped by both personality traits and contextual cues. In

Chapter Four, I tested whether predation and contest performance is correlated in *H. minitabunda*. I assayed predatory behaviour using a voracity assay, and contest behaviour using a mirror assay, both of which can be used as measures of aggression. I found no direct correlation between predation and contest performance. However, body condition strongly influenced voracity, despite controlling recent feeding history. This suggests that predation and contest performance rely on different traits for performance success. My results offer insights into how behaviour, physiology and morphology interact to shape performance in different ecological tasks in the jumping spider *H. minitabunda*.

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Chapter 1:

General Introduction

Animals must complete a multitude of tasks including foraging, competing for resources and reproducing (Lailvaux & Husak, 2014; McGinley et al., 2013). It is important to ascertain how different elements influence individual performance (e.g., speed, endurance, behaviour) as this provides insight into how animals operate and interact in their natural habitat (Lailvaux & Husak, 2014). The ability of an animal to complete key ecological tasks using integrated physiological, morphological and behavioural traits (whole-organism performance) influence the overall fitness of an organism (Lailvaux & Husak, 2014; Matthews, 1998). Life history trade-offs can influence morphology, which can enhance performance (i.e., the effectiveness with which individuals execute fitness related tasks) (Lailvaux & Husak, 2014; Zera & Harshman, 2001). Obtaining and distributing resources during development influences whole-organism performance by prioritising resource allocation towards traits that will increase fitness (Lailvaux & Husak, 2014; Ng'oma et al., 2017; Zera & Harshman, 2001). In addition, immunity, aging, temperature, reproduction and hormones that contribute to physiological phenomena such as growth and hunger can impact performance (Lailvaux & Husak, 2014). Functional traits (e.g., spider body size and hunting mode) are quantifiable characteristics that determine how proficiently a task is performed (Dawson et al., 2021; Sanders et al., 2015).

Factors such as morphology, physiology and personality can interact with animal performance. Body length in *Salmo trutta* (brown trout) (Linnaeus, 1758) (Salmoniformes: Salmonidae) influences locomotive performance (Ojanguren & Brana, 2003). Long individuals with longer paired fins had enhanced endurance were able to withstand swimming in water currents for prolonged durations (Ojanguren & Brana, 2003). Body length also impacted swimming speed (Ojanguren & Brana, 2003). Similarly, body size and mass impacts calling performance in male *Pseudacris crucifer* (spring peeper) (Wied-

Neuwied, 1838) (Anura: Hylidae) frogs during courtship (Zimmitti, 1999). Thus, it can be inferred that body size influences functional traits.

Male *Pseudacris crucifer* demonstrate how physiological factors can shape performance (Zimmitti, 1999). Male *Pseudacris crucifer* exhibit physiological differences in the muscles used during calling, which drive differences in male calling rates (Zimmitti, 1999). Variation in male calling rates within the population is caused by metabolism and body size (Zimmitti, 1999). Comparably, biochemical compounds derived from environmental food sources are linked to physiological modifications, influencing performance in *Dicentrarchus labrax* (seabass) fish (Linnaeus 1758) (Perciformes: Moronidae) (Chatelier et al., 2006). High levels of linoleic and oleic acid in *D. labrax* tissues from their diet increased their critical locomotive swimming speed, aerobic capacity, metabolic rate and peak cardiac and respiratory performance (Chatelier et al., 2006). Thus, physiological modifications can enhance performance, impacting fitness.

In animal behaviour research, personality refers to consistent differences in behaviour between individuals within a population over time (Briffa & Weiss, 2010; Carter et al., 2013; Kralj-Fišer & Schuett, 2014; Sih et al., 2015). Personality can affect how an individual completes fitness related tasks (Careau et al., 2008; Dingemanse & Réale, 2005). For instance, personality affects metabolic rate which determines energetic reserves and can influence foraging and reproductive performance (Careau et al., 2008). Individuals possessing bold personalities catch more prey in *Gasterosteus aculeatus* (three-spined sticklebacks) (Linnaeus, 1758) (Perciformes: Gasterosteidae), enhancing predation success (Ward et al., 2004). Personality can also influence cognitive performance in *Parus major* (great tit) birds (Linnaeus, 1758) (Passeriformes: Paridae) (Titulaer et al., 2012). Females

with a shy personality with a long latency to begin exploring were more adaptable learners than those with a bold personality and short latencies to begin exploring (Titulaer et al., 2012). Conversely, bold males were observed to have greater learning performance than shy males (Titulaer et al., 2012).

1.1 Behavioural syndromes

Animal personality varies between individuals, and personality types across a spectrum can be inferred by behaviour (Sih et al., 2004). Personality encompasses a shy-bold continuum which influences how exploratory, risk-avoidant or risk-taking an individual will be (Wilson et al., 1994; Stamps & Groothuis, 2010). As a result, performance metrics can be influenced by personality traits (Briffa et al., 2015). Bold individuals may exhibit more explorative behaviour and be predisposed to take more risks in confrontations with other animals than shy individuals (Briffa et al., 2015). Enhanced aggression by bold individuals can contribute to successfully securing resources or mates, enhancing biological fitness (Archer, 1988). Conversely, shy individuals may display heightened vigilance and engage in defence mechanisms by seeking refuge to avoid danger (Briffa et al., 2015).

Behavioural syndromes are associated traits that persist across different behavioural contexts (Réale et al., 2007; Sih et al., 2004). Displaying an enhanced level of aggression may be advantageous in some scenarios, such as in contests, yet also disadvantageous in scenarios where vigilance is necessary, such as predator avoidance, resulting in a trade-off (Sih et al., 2004). Behavioural syndromes can constrain flexibility, as an individual should theoretically vary between aggressive and cautious tendencies depending on their objective (Sih et al., 2004). Therefore, behavioural syndromes can impact overall fitness by influencing

how a given task is performed (Sih et al., 2004). Behavioural syndromes may form as a result of environmental factors during development, which can affect correlated behavioural traits later in life (Sih, 2011). Behavioural syndromes could also arise via genetic inheritance (Wisenden et al., 2011) or correlational selection (Bell, 2007). A common behavioural syndrome is the boldness-aggression syndrome, which infers that a bold individual will also display high levels of aggression (Ariyomo et al., 2019; Chapman et al., 2011; Edenbrow & Croft, 2012; Norton et al., 2011). For example, male *Poecilia reticulata* (guppies) (Peters, 1859) (Cyprinodontiformes: Poeciliidae) show an aggression-boldness behavioural syndrome that is absent in females (Ariyomo et al., 2019). The boldness-aggression behavioural syndrome suggests that there may be a link between contest and predation performance. Bold, aggressive individuals that exhibit enhanced risk-taking may be more likely to win contests (Briffa et al., 2015). These bold, aggressive traits may be transferred into foraging contexts, whereby bold individuals will undergo heightened exploration and encounter more prey items, increasing their foraging success (Pereira et al., 2024).

1.2 Contests

Contests are competitive interactions where individuals perform agonistic behaviours to acquire limited resources which can enhance overall fitness (Briffa & Sneddon, 2007). Contest participation is energetically demanding and factors such as levels of stress hormones, neurohormones and androgens can influence success (Briffa & Sneddon, 2007). Body size may also impact contest outcome as larger individuals are capable of enduring longer contests and often win (Palaoro & Briffa, 2017). Contest persistence is facilitated by greater quantities of metabolic reserves (Hahn & Denlinger, 2007; Lindstedt & Boyce, 1985; Schultz & Conover, 1999).

Resource value may determine how much metabolic energy an individual is willing to expend to gain a contested resource (Arnott & Elwood, 2008). The effects of resource value and resource value asymmetries on contest outcomes have been tested in diverse species including *Pagurus longicarpus* (hermit crabs) (Say, 1817) (Decapoda: Paguridae) (Gherardi, 2006), *Notophthalmus viridescens* (red-spotted newts) (Rafinesque, 1820) (Caudata: Salamandridae) (Verrell, 1986), *Acheta domesticus* (male house crickets) (Linnaeus, 1758) (Orthoptera: Gryllidae) (Brown et al., 2007) and *Pomatoschistus minutus* (sand gobies) (Pallas, 1770) (Gobiiformes: Gobiidae) (Lindström, 1992). For example, male *Metellina segmentate* (autumn spiders) (Clerck, 1757) (Araneae: Tetragnathidae) exert more effort when competing for a female with elevated fecundity, as successful copulation will increase male fitness (Hack et al., 1997). Characteristics including body size, body mass, physiological state, previous competitive encounters and combat or defensive traits all contribute to resource holding potential (RHP: an individual's ability to win contested resources) (Allen & Krofel, 2022; Parker, 1974).

Individuals can decide how much energy to invest into a contest by assessing the RHP of their opponent (Arnott & Elwood, 2009; Briffa, 2008; Parker, 1974). There are many different contest assessment strategies including pure self-assessment, cumulative assessment and mutual assessment (Arnott & Elwood, 2009). Pure self-assessment describes a situation where an individual has information of their own RHP but not of their opponent's (Arnott & Elwood, 2009; Tsai et al., 2014). The cumulative assessment model is similar to the pure self-assessment model, but individuals also incorporate costs imposed by their opponent (e.g., injuries, energy consumption), meaning stronger opponents cause individuals to withdraw from a contest faster (Arnott & Elwood, 2009; Lane & Briffa, 2017). The mutual assessment

model describes a situation where individual RHP is compared to their opponent's RHP (Arnott & Elwood, 2009; Schnell et al., 2015). Individuals with similar RHPs will be more likely to initiate a contest than individuals with a large difference in RHP, as individuals with small RHPs may perceive a contested resource to be of higher value than those with high RHP (Gherardi, 2006; Just & Morris, 2003). Different contest assessment models determine whether an individual decides to persist in a contest, affecting contest duration, escalation and outcome (Garcia et al., 2012; López & Martín, 2001; Stuart-Fox, 2006).

There may be strong links between contest and predation performance. Contest performance is an ecologically important task that influences access to resources (Briffa & Hardy, 2013). Similarly, the ability to capture prey is important for foraging success and has downstream effects on fitness (Glen & Dickman, 2014). There are often trade-offs between allocating time to engaging in a contest and investing in predation behaviour (Garland, 2014). These trade-offs become more pronounced when there are environmental selection pressures (Prediger et al., 2014; White, 1978). Predation and foraging success is impacted in environments with low food availability, which increases the likelihood of agonistic contests to acquire limited resources (Luttbeg & Sih, 2010; Prediger et al., 2014; White, 1978).

There is limited research combining animal performance in contests and predation. Morphological traits may enhance both contest and predation performance. For example, large male *Zalophus californianus* (California sea lions) (Lesson, 1828) (Carnivora: Otariidae) are able to dive deeper in the ocean to successfully capture larger prey (Weise et al., 2010). Similarly, larger *Neoscona arabesca* (orb-weaver) (Walckenaer, 1841) (Araneae: Araneidae) spiders are more equipped to invest resources into web improvements, facilitating the capture of large prey items than smaller spiders (Sensenig et al., 2011). Large animals are

151 also more likely to win contests, as in *Hylaeus alcyoneus* (banksia bees) (Erichson, 1842)
152 (Hymenoptera: Colletidae) (Alcock, 1994) and *Phoracantha semipunctata* (Eucalyptus
153 longhorn borer beetle) (Fabricius, 1775) (Coleoptera: Cerambycidae) (Hanks et al., 1996).
154 Thus, it can be inferred that predation and contest performance may be linked through traits
155 like body size.
156
157 Links between contest and predation behaviour can be difficult and time consuming to
158 test and are rarely tested directly. One of the few studies that have considered contest and
159 predation performance found that male *Myrmarachne gisti* (ant-mimicking jumping spiders)
160 (Fox, 1937) (Araneae: Salticidae) with long chelicerae tend to win contests, but prey capture
161 success was not affected as they may compensate for their chelicerae with other traits (Yu et
162 al., 2024). However, there are still many unanswered questions about whether and how
163 contest and predation performance are linked. Jumping spiders are an ideal model organism
164 to test for correlations between contest and predation performance.
165
166 *1.3 Jumping spiders*
167
168 Jumping spiders (Salticidae) are an ideal model system to test ideas about behavioural
169 correlations as they have advanced vision and cognition that contribute to their complex
170 behaviour (Aguilar-Arguello & Nelson, 2021). Jumping spiders perform an array of
171 behaviours which can be assayed such as hunting, defence strategies, exploration activity and
172 courtship (Aguilar-Arguello & Nelson, 2021). Most spiders have rather poor vision
173 (Winsor et al., 2023) and collect information about their environment via chemical cues and
174 vibrations (Fischer, 2019; Wilcox & Jackson, 1998). However, jumping spiders have
175 exceptional vision (Blest & Price, 1984; Tarsitano & Andrew, 1999; Wilcox & Jackson,

1998). Jumping spiders possess eight eyes, consisting of one pair of anterior median eyes and three pairs of secondary eyes (Tarsitano & Andrew, 1999; Wilcox & Jackson, 1998). The large median eyes located at the front of their head have excellent acuity (Blest & Price, 1984; Wilcox & Jackson, 1998) and are also called the 'principle eyes' (Wilcox & Jackson, 1998). When jumping spiders have their cephalothorax in a stationary, fixed position, the anterior median eyes can visually perceive their surroundings in a 30° range from the anterior centre of the head in each direction vertically and horizontally (Tarsitano & Andrew, 1999). Jumping spiders often move their anterior median eyes in vertical and horizontal motions when scouting out their environment (Tarsitano & Andrew, 1999). The field of view is restricted to heighten focus when a stationary item or prey is identified (Tarsitano & Andrew, 1999). Therefore, the direction that the anterior median eyes is facing will be the direction where most of their visual acuity is concentrated – which makes it easier to determine the focus of their attention. The secondary eyes of jumping spiders perceive movement (Tarsitano & Andrew, 1999; Wilcox & Jackson, 1998). This is facilitated by a 360° visual range, beneficial for detecting moving prey (Tarsitano & Andrew, 1999). The excellent vision of jumping spiders is integral to their elaborate contest and courtship displays, and predatory strategies (Wilcox & Jackson, 1998).

Jumping spiders have advanced cognitive abilities for their small brain size (Aguilar-Arguello & Nelson, 2021; Wilcox & Jackson, 1998). Cognition is the processes of perception, acquiring knowledge, storing information, and evaluating ideas (Shettleworth, 2001). The genus *Portia* (Araneae: Salticidae) demonstrate impressive cognition through their elaborate predatory strategies that include stalking, detouring behaviour, and aggressive mimicry of prey or potential mates to lure prey within range of attack (Nelson, 2023; Wilcox

& Jackson, 1998). This technique enables *Portia* to efficiently capture different species of prey, some of which are dangerous predators themselves (Jackson & Wilcox, 1993).

Portia's high intellectual capabilities are demonstrated via their use of deception to catch prey (Jackson, 1992; Jackson, 1995; Wilcox & Jackson, 1998). The jumping spider *P. fimbriata* (Doleschall, 1859) (Araneae: Salticidae) will invade other spider's webs and produce vibrations using their abdomen, legs and palps to mimic prey struggling in the web to lure the resident spider within range of attack (Jackson, 1995; Wilcox & Jackson, 1998). *Portia* will also consume the egg sacs of the resident spider (Jackson, 1995; Wilcox & Jackson, 1998) and any other prey items caught in the web (Wilcox & Jackson, 1998). Enhanced cognitive function is also exhibited through the detours that *Portia* take to capture *Argiope appensa* (Hawaiian garden spider, or banana spider) (Walckenaer, 1841) (Araneae: Araneidae) (Wilcox & Jackson, 1998). Rather than approaching straight through the web and alerting its prey*, P. fimbriata* extend their journey further up the tree and across branches, descend on a silk thread and swing across to seize its prey (Jackson, 1992; Wilcox & Jackson, 1998). This prevents *P. fimbriata* from being propelled off the web by defensive web-pulsing behaviour by *A. appensa* (Jackson, 1992; Wilcox & Jackson, 1998). Thus, *P. fimbriata* possesses the ability to cognitively process scenarios and resolve obstacles, increasing their foraging success (Wilcox & Jackson, 1998).

1.4 The Aussie bronze jumping spider (Helpis minitabunda)

The Aussie bronze jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), is the model organism I use in my thesis to test whether contest and predation performance are correlated. *H. minitabunda* are 4-8mm long, light and dark brown with light brown hairs and

225 a long, oval shaped abdomen with thin long legs (Gardzińska & Żabka, 2010). Males are
226 distinguishable from females by their ornamented front two pairs of legs, which are black in
227 colour decorated with white bands (Hawkeswood, 2003; Fig. 1.1). Females have setae fringes
228 across the femur and patella of their legs and the forelegs of males are longer with more setae
229 compared to females (Gardzińska & Żabka, 2010). Additionally, an ocular fringe can be
230 observed across the head of males (Gardzińska & Żabka, 2010), also described as 'brows'
231 (Żabka & Patoleta, 2014).

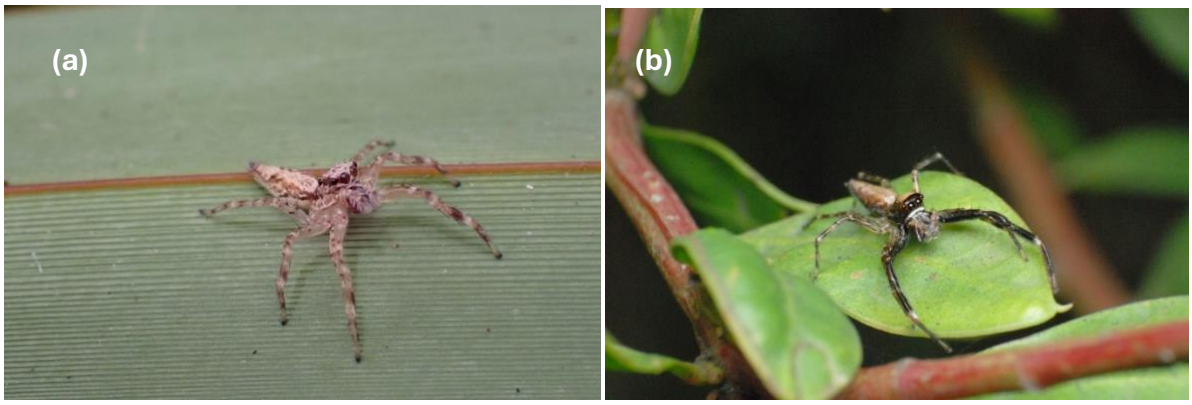

Figure 1.1: (a) Female *H. minitabunda* (Photo credit: A. Wignall), and (b) male *H. minitabunda* (Photo credit: J. Sayers/ iNaturalist (CC BY))

232 *Helpis minitabunda* is a species that inhabits coastal south-western and eastern
233 regions of Australia, typically found in sclerophyll bush and *Eucalyptus* foliage (Gardzińska
234 & Żabka, 2010). More recently, *H. minitabunda* have been introduced to Tasmania, Papua
235 New Guinea, and New Zealand (Żabka & Patoleta, 2014). Although *H. minitabunda* are
236 common spiders, very little is known about their biology and ecology. They may compete
237 with native New Zealand species thus, gleaning any insight into the behaviour of *H.*
238 *minitabunda* would be beneficial. *H. minitabunda* are ideal subjects for my thesis as they are

239 particularly abundant in Auckland, New Zealand. They are easy to maintain in laboratory
240 environments and amenable to experiments testing contest and predation performance.
241
242 *1.5 Thesis outline*
243
244 My thesis tests whether contest performance is correlated to predation performance in the
245 jumping spider *H. minitabunda*. It comprises three data chapters.
246
247 Chapter Two characterises contest behaviour in *H. minitabunda* by characterising the
248 contest performance in juvenile-juvenile, female-female and male-male contests. I distinguish
249 trends in contest escalation and outcome relative to size.
250
251 Chapter Three characterises predation behaviour in *H. minitabunda* by assaying
252 predation performance through standardised prey trials and voracity tests. Additionally, I test
253 the relationship between behaviours associated with bold personalities (i.e., latency to
254 emerge) with predation behaviour.
255
256 Chapter Four tests whether contest and predation performance are correlated in *H.*
257 *minitabunda*. I use mirror assays to quantify contest persistence and voracity tests to quantify
258 predatory behaviour, both of which may be used to measure aggression.
259
260 In chapter Five, I discuss the implications of the results from my three data chapters.
261 Overall, my thesis presents insight into how contest and predation performance in *H.*
262 *minitabunda* is influenced by morphological and physiological traits, and the potential for

263 interactions between behavioural traits. I expand our current understanding of animal
264 personality and highlight the influence of personality on fitness-related traits.

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Chapter 2:

Variation in contest performance in juvenile, female and male jumping spiders (*Helpis minitabunda*) (Koch, 1880) (Araneae: Salticidae)

2.1 Abstract

In intraspecific contests, individuals engage in agonistic behaviours to compete for resources. Contests often consist of multiple phases. As contests progress through these phases, interactions become more intense. An individual's ability to persist through the escalating contest phases is determined by their resource holding potential (RHP). Contests differ across taxa, according to their morphology, physiology and cognitive abilities. While jumping spiders are common models for behavioural research, the contest behaviour of only a few species has been characterised in detail, and usually only describe male-male contests. I describe the contest behaviour of the Aussie bronze jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), including juvenile, female and male contests. I found that contests consisted of three phases (assessment, display and contact phase). Juveniles, females and males were equally likely to start the assessment phase. However, males were more likely to escalate into the display phase than juveniles or females, and female and male contests were more likely to escalate into the contact phase than juvenile contests, with no juveniles escalating into the contact phase. Size, a common proxy for RHP, did not influence contest outcome. Juveniles, females and males appear to use different assessment strategies. My results suggest that *Helpis minitabunda* adjust their competitive behaviour in response to context-specific cues, highlighting the potential costs of engaging in escalated contests.

2.2 Introduction

Contests occur when conspecifics engage in agonistic behaviour to compete for limited resources that enhance their fitness (Briffa & Sneddon, 2007; Green et al., 2022; Roth & Cords, 2016). Animals may engage in contests over mates, territory or food (Arnott &

Elwood, 2019). Individuals who prevail in contests benefit from these limited resources (Briffa & Sneddon, 2007). However, individuals competing in contests incur costs, including the time lost for alternative endeavours, energy consumption, and potential physical damage or death (Arnott & Elwood, 2009; Briffa & Sneddon, 2007; McGinley et al., 2015; Payne, 1998).

Contests can be characterised by displays or tournaments (Smith, 1974). Displays are non-contact events (Smith, 1974), which are typically a series of repetitive motions directed at the opponent, indicative of the individual's physiological condition (Payne & Pagel, 1997). For example, male *Cervus elaphus* (red deer stags) (Linnaeus, 1758) (Artiodactyla: Cervidae) use contest displays including roaring and parallel walking during intrasexual competition throughout the breeding season (Clutton-Brock, 1985; McComb, 1991; Payne & Pagel, 1997). The rate and frequency of roars infers fighting ability and females are also attracted to males who produce a higher roaring rate (McComb, 1991; Payne & Pagel, 1997). Parallel walking is a ritualistic component, often inhibiting the encounter from escalating into physical fighting by allowing individuals to assess their opponent (Jennings et al., 2003). An opponent may decide to retreat at this stage to prevent being overthrown during a tournament (Jennings et al., 2003). Displays in male *Ctenophorus decresii* (tawny dragons) (Duméril & Bibron, 1837) (Squamata: Agamidae) during intraspecific contests include individuals adopting an agonistic posture and performing push-ups (Osborne, 2005; Osborne et al., 2013). The number of push-ups executed represents level of aggression, possibly indicative of motivation to win (Osborne, 2005; Osborne et al., 2013). Many spider species also perform agonistic contest displays. For example, the orb weaving spider *Metabus gravidus* (Keyserling, 1864) (Araneae: Tetragnathidae) generates vibratory signals by web plucking to assert dominance and defend their territory and resources (Buskirk, 1975). Male wolf spiders

Hygrolycosa rubrofasciata (Ohlert, 1865) (Araneae: Lycosidae) drum by tapping their legs on the substrate beneath them as an aggressive display (Randall, 2013). Drumming can resolve a conflict without pairs escalating to a physical fight (Randall, 2013). The individual with the fastest drumming rate wins the contest as drumming rate indicates their contest ability (Randall, 2013). The jumping spider *Plexippus paykulli* (Audouin, 1826) (Araneae: Salticidae) also uses agonistic displays, in which males face their opponent, adjusting their posture by arching their back and standing tall on outstretched legs (Taylor et al., 2001).

In contrast to contest displays, tournaments entail physical contact and possible bodily harm (Smith 1974). In spiders, tournaments often include pedipalp wrestling, grappling and biting (Keil & Watson, 2010). However, for both displays and tournaments the winner is often the individual which performs for the longest duration, outlasting the loser (Parker & Rubenstein, 1981; Smith, 1974; Uehara et al., 2007). Physical injuries may be sustained during contests, possibly resulting in death (McGinley et al., 2015). Thus, deciding on whether to participate in, or escalate a contest is important, considering the potential costs (McGinley & Taylor, 2016).

The term ‘resource holding potential’ (RHP), or ‘resource holding power’, refers to an individual’s endurance and their ability to impose harm on their opponent during a contest (Parker, 1974; Pinto et al., 2019). An individual's RHP determines how much energy an individual can afford to expend (Parker, 1974) and indicates whether they may win or lose a contested resource in a physical tournament (Hardy & Briffa, 2013). RHP can be influenced by internal and external traits (Hardy & Briffa, 2013; Pinto et al., 2019). Internal traits constitute factors that influence the physiological condition of an animal (Colditz & Hine, 2016; Zera & Harshman, 2001). For example, male *Cuterebra austeni* wasps (Sabrosky,

1986) (Diptera: Oestridae) that possess a large quantity of stored energy also maintain a high RHP (Kemp & Alcock, 2003). An external trait pertains to the phenotypic characteristics of an animal (Te Pas et al., 2017). For example, male *Pagurus minutus* crabs (Hess, 1865) (Decapoda: Paguridae) use their chelipeds as weapons during intrasexual contests to defend females (Yasuda & Koga, 2016). Individuals with large chelipeds possess a greater RHP and are expected to win contests (Yasuda & Koga, 2016). Other measures of RHP include weaponry, body size, colour markings or vocalisations indicative of contest proficiency, experience, stamina, ownership of space, energetic condition, and body condition (Kelly, 2008; Kelly & L'Heureux, 2021, Moretz, 2003).

Resource holding value describes the perceived importance of a resource at stake (Hardy & Briffa, 2013). Resource value can affect the outcome of a contest by influencing an individual's motivation to participate as well as their perseverance to win (Arnott & Elwood, 2008; Gherardi, 2006; Gruber et al., 2016; Humphries et al., 2006). Thus, resource value asymmetry can generate a disparity between the two opponents in their valuation of the resource (Parker & Rubenstein, 1981). For example, when *Pagurus longicarpus* (hermit crabs) (Say, 1817) (Decapoda: Paguridae) find a shell compatible with their size then the resource value of the shell increases for the individual (Gherardi, 2006). Individuals who perceive a resource to be of high value will be more inclined to take risks (Enquist & Leimar, 1987). Inferior *Astacus astacus* (crayfish) (Linnaeus, 1758) (Decapoda: Astacidae) within the dominance hierarchy will increase risk-taking behaviour as they have less to lose in agonistic contests (Gruber et al., 2016). Conversely, *A. astacus* that are dominant or possess high reproductive value should exhibit a more cautious behaviour due to having more at stake (Gruber et al., 2016).

Individuals engaged in a contest need to evaluate the potential risks and decide when and if to retreat from their opponent (McGinley et al., 2015). This evaluation process may consist of pure self-assessment, cumulative assessment or mutual assessment (Arnott & Elwood, 2009). The 'energetic war of attrition' (E-WOA) and 'war of attrition without assessment' (WOA-WA) models are recognised as pure self-assessment models (Arnott & Elwood, 2009). Within the self-assessment strategy, an individual's own capabilities (i.e., RHP) will dictate their decision to terminate or continue a contest, without reference to their opponent's RHP (McGinley et al., 2015). For example, male *Hipposideros armiger* (great Himalayan leaf-nosed bats) (Hodgson, 1835) (Chiroptera: Hipposideridae) use self-assessment energetic war of attrition strategies resulting in a positive correlation between the contest loser's body mass and contest duration, but no relationship between the winner's body mass and contest duration (Sun et al., 2019). Similarly, there is a positive correlation between the loser's body mass and contest duration in male *Gammarus pulex* (Linnaeus, 1758) (Amphipoda: Gammaridae) contests and no correlation between contest duration and the body mass of contest winners (Prenter et al., 2006). Thus, both male great Himalayan leaf-nosed bats and amphipods use pure self-assessment of their own RHP when deciding whether to continue in a contest, with contest duration determined by the loser's physiological condition (Prenter et al., 2006; Sun et al., 2019).

The cumulative assessment model (CAM) relies on an individual's own RHP, but also incorporates costs incurred from an opponent during the contest (Arnott & Elwood, 2009). Thus, the cumulative assessment model falls under the umbrella of self-assessment, incurring costs from personal activity (Arnott & Elwood, 2009). However, the cumulative assessment model is distinguished by incorporating harm caused by their opponent (McGinley et al., 2015). Within the cumulative assessment model, the intensity of agonistic behaviour

increases within phases. Additionally, de-escalation can occur in non-contact phases of the contest (Briffa & Hardy, 2013). For example, male *Hemideina crassidens* (Wellington tree wētā) (Blanchard, 1851) (Orthoptera: Anostostomatidae) use the cumulative assessment model when engaging in intrasexual contests (Kelly, 2006). Males can injure their opponent using their mandibles, resulting in intraphase escalation and conflict resolution is determined by self-assessment of the loser's RHP (Kelly, 2006). Withdrawing when the individual reaches a RHP threshold reduces the accumulation of costs (Kelly, 2006).

Individuals using a mutual-assessment model assess an opponent's capabilities relative to their own capabilities (McGinley et al., 2015). Mutual assessment embodies the 'sequential assessment model' (SAM) and the 'asymmetric war of attrition model' of animal conflict (AWOA) (Arnott & Elwood, 2009). According to the sequential assessment model, each individual gains insight into the RHP of their opponent as a contest escalates (Briffa & Hardy, 2013). As the contest progresses, intensity and aggression escalate in each phase, increasing the risk (Briffa & Hardy, 2013). In the sequential assessment model, the degree of agonistic behaviour is consistent within each phase and only shifts between phases (Briffa & Hardy, 2013). The asymmetric war of attrition model infers that within a contest, the individual who outperforms their opponent secures possession of the resource at stake (Hammerstein & Parker, 1982). The individual must prevail before the cost outweighs the benefit of the reward (Hammerstein & Parker, 1982). When there are disparities between opponents, such as the possession of resources, age, size or sex, it is deemed an asymmetric contest (Kim, 1993). For example, male *Sepia apama* (giant Australian cuttlefish) (Gray, 1849) (Sepiida: Sepiidae) employ the mutual assessment strategy in intrasexual contests (Schnell et al., 2015). The decision to persist in a contest is influenced by the difference in RHP (i.e., body size) between the opponents, as opposed to one's own RHP (Schnell et al.,

2015). When faced with an opponent larger than themselves, individuals attempt to retreat, but when presented with an opponent smaller than themselves, individuals respond with agonistic behaviour (Schnell et al., 2015).

There has been a lot of debate about the predominant assessment strategies implemented by individuals in contests (Elias et al., 2008). Different spider species approach contests differently. For example, the jumping spider *Phidippus clarus* (Keyserling, 1885) (Araneae: Salticidae) primarily uses the self-assessment model, although mutual assessment plays a role in gauging the risk of entering into combat with an opponent (Elias et al., 2008). Male *Lyssomanes viridis* (Walckenaer, 1837) (Araneae: Salticidae) jumping spiders use mutual assessment strategies, with size difference influencing contest escalation (Tedore & Johnsen, 2015). The contest behaviour of male *Servaea incana* (Karsch, 1878) (Araneae: Salticidae) jumping spiders best correlate with the self-assessment strategy, as contest continuation is dependent on individual resource holding capacity (based on body size) (McGinley et al., 2015). For opponents of different sizes, the likelihood of contest escalation was determined by the size of the smallest individual, rather than the size difference between the opponents (McGinley et al., 2015). Moreover, escalation to physical contact was more frequent in similarly sized, large opponents (McGinley et al., 2015).

Jumping spiders are excellent models for contest experiments. Jumping spiders have large anterior median eyes and excellent visual perception (Forster, 1977; Blest & Price, 1984; Zurek et al., 2010). The excellent visual acuity of jumping spiders enables them to perform complex stalking behaviours (Nentwig, 2012), that are also often used in conspecific contests (Elias et al., 2010). Jumping spider contests are often characterised by visual displays between opponents (McGinley & Taylor, 2016). Visual displays may entail

individuals orienting towards the conspecific, hunching their body, and elevating it above the substrate (Elias et al., 2008). Additionally, vertical flaring motions of the forelegs are often conducted in contests, consisting of individuals holding their forelegs in an outstretched position (Tedore & Johnsen, 2012). Display behaviours are usually performed during the precontact contest phase (Elias et al., 2008). If the precontact contest phase escalates into the contact phase, 'leg fencing' may be performed, where individuals physically push their opponent with their forelegs (Elias et al., 2008). An individual may also employ 'grappling' techniques by securing their chelicerae against that of their opponent's (Elias et al., 2008). Repetitive physical impacts may occur where the opponents ram their chelicerae against each other (Tedore & Johnsen, 2012). The objective is to prompt the opponent to surrender (Briffa & Sneddon, 2007).

Here, I describe and characterise the contest assessment strategies of *Helpis minitabunda* (Aussie bronze jumping spider) (Koch, 1880) (Araneae: Salticidae). *H. minitabunda* are native to eastern Australia and occupy eastern coastal environments in Papua New Guinea, Tasmania and New Zealand (Żabka & Patoleta, 2014). Despite their abundance (Żabka & Patoleta, 2014), there is little is known about their contest behaviour. I compared the contest behaviour of juveniles, adult females and adult males in conspecific contests. I predicted that body size influences contest outcome, whereby large individuals will be more likely to win contests than small individuals. I also predicted that juveniles use a self-assessment strategy as juvenile size varies greatly, therefore, determining contest trajectory based on its own RHP, rather than an opponents would be beneficial to reduce potential contest costs. I predicted that females may similarly use a self-assessment strategy and may be less likely to escalate contests than males. Moreover, I predicted that males may employ a

mutual assessment strategy, willing to take greater risks due to the high potential for increasing reproductive success.

2.3 Methods

2.3.1 Study Species

I collected 160 *Helpis minitabunda* spiders (64 adult females, 36 adult males and 60 juveniles). Spiders were collected from native vegetation (*Phormium tenax,* flax) in Albany (Auckland, New Zealand), from December 2023 to February 2024. Spiders were maintained in individual, transparent vials (120mL) in the laboratory at Massey University, Albany. Each spider was provided water *ad libitum* via moistened paper towel placed in a small white vial lid. A stick was provided in the vial for environmental enrichment (Carducci & Jakob, 2000). The lab was maintained on a 12 : 12 hr day : night cycle with a one hour ramp up and ramp down period to simulate dawn and dusk. Lab temperature was 19.5°C $\pm$ 0.5°C and relative humidity 60%. The spiders were not fed for the duration (three days) that they were in the laboratory. Spiders are opportunistic feeders that can go long periods of time without feeding. Spiders acclimatised to the laboratory for two days before the contest trials. Following the experiment, spiders were placed back into their maintenance vial where they were held till the end of the third day when they were released back into the field.

2.3.2 Experimental Procedure

Juvenile-juvenile (n = 30), female-female (n = 32) and male-male (n = 18) contests were conducted between 9am and 5pm during their most active time of day (D. Cox, personal

observation). Individuals were only assayed once, and had no previous contest experience within the laboratory to reduce prior contest experience influencing experimental contest outcomes. However, I cannot exclude the possibility that spiders may have had previous contest experience from the field.

Contest trials were performed inside a transparent Perspex container (150mm × 150mm × 150mm). As jumping spiders have excellent vision (Forster, 1982), the experimental arena was placed inside a white photography tent (1m × 1m × 1m) to limit external visual distractions. All contests were recorded with a camcorder (Canon XA11 or Canon XA20) mounted on a tripod placed at the open side of the photography tent. A removable opaque divider was used to separate the two halves of the experimental arena to act as a visual and physical barrier at the beginning of each trial during the acclimation period to separate the contest opponents.

To begin a contest trial, two spiders of the same age and/or sex were selected at random and placed on opposite sides of the barrier inside the experimental arena. The barrier remained in place during the five minute acclimation period. At the end of the acclimation period, the barrier was removed, allowing the opponents to interact with one another. A transparent Perspex square lid (150mm × 150mm) was placed on top of the arena to contain the spiders within the experimental arena. Spiders were given ten minutes to interact. I recorded whether a contest occurred (yes/no) and latency to begin a contest (measured from the instant the arena barrier was removed until one individual began the assessment phase, signalling the initiation of a contest). I also recorded the identity of the contest winner and loser, which was tracked visually. An individual was deemed to have lost the contest when they retreated from their opponent. The contest trial ended as soon as an individual lost a

contest. If a contest exceeded the 10 minute maximum duration allocated then the trial ended at the ten minute mark. The experimental arena, lid and acclimation barrier were cleaned with 70% ethanol between each contest. After the contest trial, individuals were photographed (Canon 700D camera) under a microscope (Motic SMZ 168) and weighed to the nearest 0.01mg (Ohaus EX125D semi-micro balance). The photographs were then imported into the software ImageJ (Schneider et al., 2012) to measure the cephalothorax width of the spiders.

2.3.3 Statistical Analyses

The statistical analyses were conducted in R version 4.4.1 (R Core Team, 2024). To test whether there were differences between juveniles, females, and males in the likelihood of initiating each contest phase (assessment, display and contact phases), I used the *base* R package and the 'fisher.test()' function to perform Fisher's exact tests.

To test whether spider size influences contest escalation, I used the 'glm()' function in the *lme4* package (Bates et al., 2015) to fit a generalised linear mixed model (GLM). My model included spider size difference as a fixed effect with a binomial family and a 'link = "logit"' function. Juveniles, females and males were tested separately. To test whether the size difference between contestants influences contest outcome, I fit another GLM using the 'glm()' function with a binomial family and a 'link = "logit"' function, including size difference as a fixed effect.

To explore contest assessment hypotheses, I ran a series of linear regression analyses (Taylor and Elwood 2003). Size was used as a proxy for individual RHP and contest duration was used as a proxy for contest cost. For each of the juvenile, female and male contests, I ran

a regression for absolute loser RHP (a regression between contest loser size and contest duration), absolute winner RHP (a regression between contest winner size and contest duration) and relative RHP difference (a regression between the relative size of opponents and contest duration). As my sample sizes were relatively small, I also calculated the effect sizes using the methods of Nakagawa and Cuthill (2007). All plots were created using *ggplot2* (Wickham, 2016).

2.4 Results

2.4.1 Contest Phases

Helpis minitabunda contests are divided into three phases: the assessment phase, the display phase and the contact phase. The assessment phase begins when each individual orients towards their opponent. Orientation is defined as an individual directing its cephalothorax toward the opponent and then remaining stationary (McGinley & Taylor, 2016). Some individuals instantly retreated during the assessment phase, signalling the end of the contest (Elias et al., 2010), whilst other contest pairs escalated to the display contest phase.

The display phase is characterised by active behaviours exhibited by an individual towards their opponent. Active behaviours consist of stalking or displaying. When an individual stalks their opponent, they steadily approach the other individual then pounce to capture the opponent (Bear & Hasson, 1997). Individuals that perform physical displays toward their opponent sometimes start doing so prior to their opponent orienting their body towards them. Spiders may flare their first pair of legs dorso-ventrally, or hold their legs stretched out laterally above the substrate, whilst approaching their opponent (Taylor &

300 Jackson, 2003; Wells, 1988). Spiders may also hover, stepping from side to side (Taylor &
301 Jackson, 2003). Moreover, displaying spiders may run towards their opponent in a diagonal,
302 back and forth pattern, lifting the side of their opisthosoma in the direction which they are
303 travelling (Taylor & Jackson, 2003; Wells, 1988).
304
305 The final contest phase is the contact phase which entails physical grappling. In
306 grappling, the opponents orient toward each other, with the first two pairs of legs held
307 laterally out from their body (Whitehouse, 1997). The individuals pulse their bodies, moving
308 antero-posteriorly at a high frequency, knocking their chelicerae together (Whitehouse,
309 1997). This may escalate into wrestling which entails handling their opponent with their two
310 first pairs of legs and using their chelicerae to bite their rival (Whitehouse, 1997).
311 Alternatively, the contact phase can be initiated by one individual jumping at their opponent,
312 using their forelegs to tackle and push them (Taylor & Jackson, 2003; Whitehouse, 1997).
313 The contact phase continues until one individual retreats from their opponent, indicating
314 defeat.
315
316 *2.4.2 Contest Behaviour*
317
318 There was no difference between juveniles, females and males in their likelihood of starting
319 the assessment contest phase (Fisher's exact test: *P*-value = 0.15; Fig. 2.1a). There was a
320 difference between juveniles, females and males in their likelihood of starting the display
321 contest phase, with males more likely to escalate into the display phase than juveniles or
322 females (Fisher's exact test: *P*-value = 0.02; Fig. 2.1b). There was also a difference between
323 juveniles, females and males in their likelihood of starting the contact phase (Fisher's exact
324 test: *P*-value < 0.01; Fig. 2.1c).

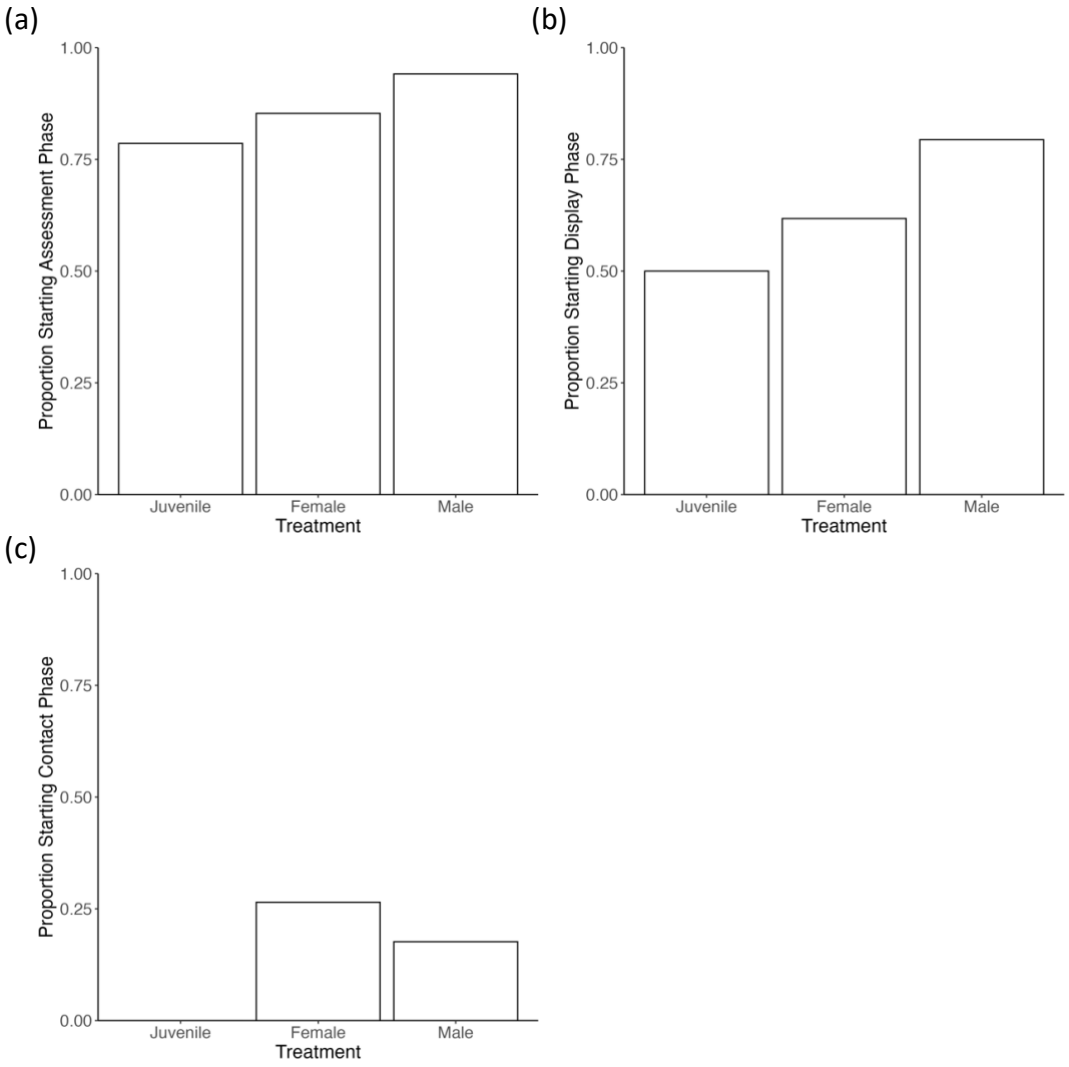

Figure 2.1: Proportion of juvenile (n = 60), female (n = 64) and male (n = 36) *H. minitabunda* starting the (a) assessment, (b) display, and (c) contact contest phases.

Spider size difference did not influence whether juveniles (GLM: Z = 0.86; *P*-value = 0.39), females (GLM: Z = 1.37; *P*-value = 0.17) or males (GLM: Z = 0.73; *P*-value = 0.46) started the assessment contest phase (Table 2.1). Size difference influenced contest escalation in juveniles into the display phase (GLM: Z = 2.13; *P*-value = 0.03; Table 2.1). However, size difference did not influence contest escalation into the display please in females (GLM: Z = -0.41; *P*-value = 0.68; Table 2.1) or males (GLM: Z = -0.71; *P*-value = 0.48; Table 2.1). No juveniles escalated into the contact phase. Size did not influence contest escalation into the

contact phase in females (GLM: Z = -1.23; *P*-value = 0.22; Table 2.1), or males (GLM: Z = -0.65; *P*-value = 0.52; Table 2.1). Females and males were more likely to start the contact phase than juveniles (Fig. 2.1c). Size differences between opponents did not influence contest outcome in juveniles (GLM: Z = 1.43, *P*-value = 0.15; Fig. 2.2b; Table 2.2), females (GLM: Z = 1.72, *P*-value = 0.09; Fig. 2.2a; Table 2.2), or males (GLM: Z = 1.53, *P*-value = 0.13; Fig. 2.2c; Table 2.2).

Table 2.1: GLM for *H. minitabunda* testing whether size influences contest escalation into the assessment, display and contact phases in (a) juveniles, (b) females and (c) males.

(a) Juveniles				
Start assessment phase	Estimate	SE	z	*P*
Intercept	1.27	0.47	2.71	**0.01**
Size difference	2.70	3.14	0.86	0.39
Escalation to display phase	Estimate	SE	z	*P*
Intercept	0.00	0.43	0.00	1.00
Size difference	0.93	3.26	2.13	**0.03**
Escalation to contact phase	Estimate	SE	z	*P*
Intercept	-25.57	41570.00	-0.00	1.00
Size difference	-0.00	253400.00	0.00	1.00
(b) Females				
Start assessment phase	Estimate	SE	z	*P*
Intercept	1.39	0.85	1.64	0.10
Size difference	8.97	6.54	1.37	0.17
Escalation to display phase	Estimate	SE	z	*P*
Intercept	0.79	0.69	1.14	0.25
Size difference	-1.34	3.29	-0.41	0.68
Escalation to contact phase	Estimate	SE	z	*P*
Intercept	-1.61	0.86	-1.87	0.06
Size difference	4.78	3.90	-1.23	0.22
(c) Males				
Start assessment phase	Estimate	SE	z	*P*
Intercept	3.18	1.56	2.04	**0.04**
Size difference	6.92	8.59	0.73	0.46
Escalation to display phase	Estimate	SE	z	*P*
Intercept	0.62	0.56	1.10	0.27
Size difference	-2.97	4.16	-0.71	0.48
Escalation to contact phase	Estimate	SE	z	*P*
Intercept	-2.09	0.91	-2.30	**0.02**
Size difference	-3.66	5.66	-0.65	0.52

$P < 0.05$ indicated in bold

Table 2.2: GLM testing whether opponent size differences influence contest outcome in (a) juvenile, (b) female and (c) male *H. minitabunda*.

(a) Juveniles				
	Estimate	SE	z	*P*
Intercept	2.62	1.47	1.79	0.07
Size difference	20.39	14.24	1.43	0.15
(b) Females				
	Estimate	SE	z	*P*
Intercept	-0.12	0.58	-0.22	0.83
Size difference	6.94	4.03	1.72	0.09
(c) Males				
	Estimate	SE	z	*P*
Intercept	-0.41	1.12	-1.26	0.21
Size difference	15.98	10.44	1.53	0.13

$P < 0.05$ indicated in bold

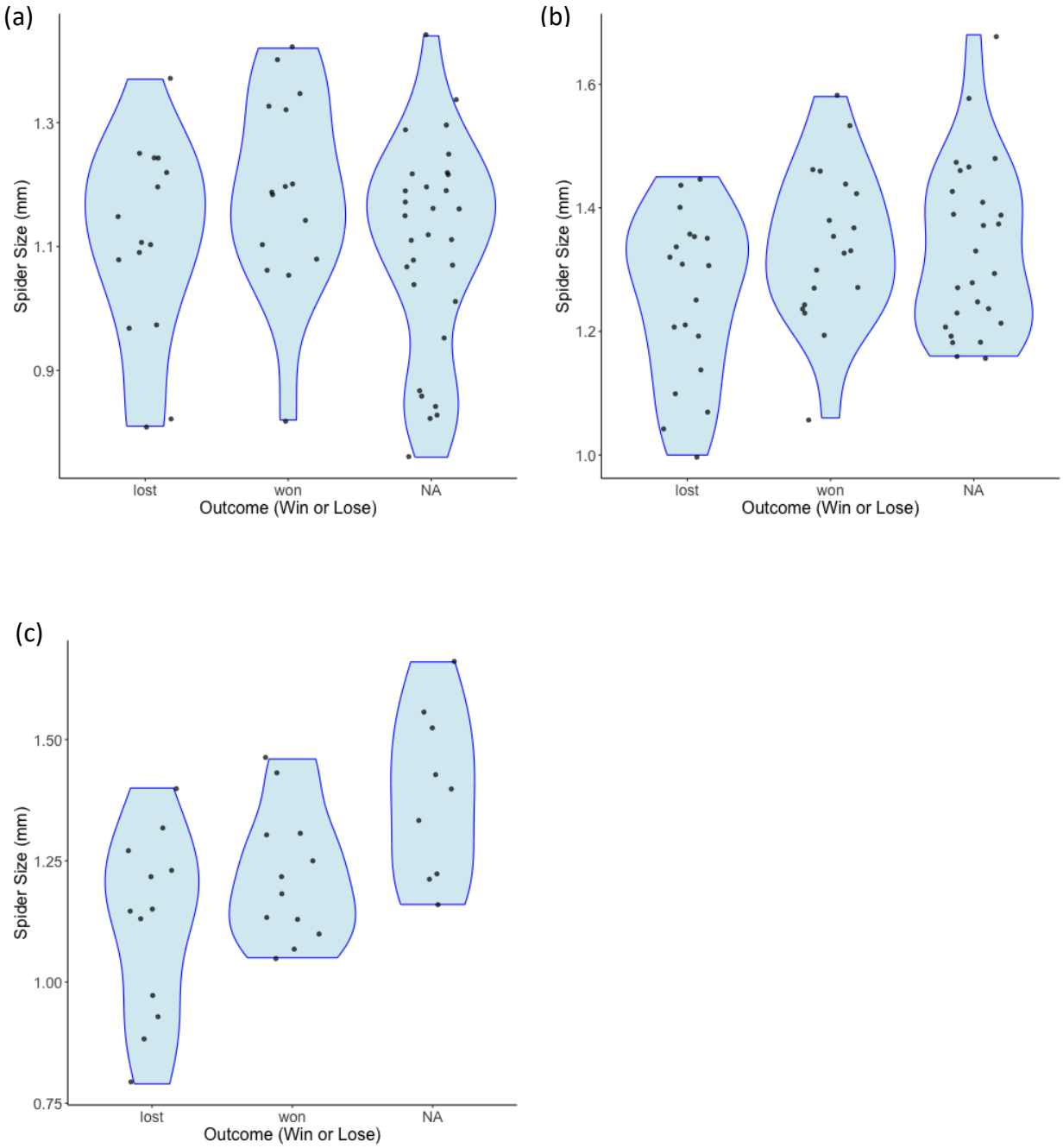

Figure 2.2: Spider size (mm) of *H. minitabunda* by contest outcome (win, lose or no contest) for (a) juveniles, (b) females, and (c) males.

2.4.3 Assessment Strategies

2.4.3.1 Juveniles

In juveniles, there was no relationship between absolute size and contest duration in losers (*P-value* = 0.91; Effect size = -0.03; Fig. 2.3a; Table 2.3) or winners (*P-value* = 0.15; Effect size = -0.39; Fig. 2.3a; Table 2.3). However, there was a negative correlation between relative size and contest duration in juveniles (*P-value* = 0.02; Effect size = -0.63; Fig. 2.3b; Table 2.3). These results are most consistent with a mutual assessment strategy.

2.4.3.2 Females

In females, there was no relationship between absolute size and contest duration in losers (*P-value* = 0.10; Effect size = -0.38; Fig. 2.3c; Table 2.3) or winners (*P-value* = 0.78; Effect size = -0.07; Fig. 2.3c; Table 2.3). Additionally, there was no relationship between relative size and contest duration in females (*P-value* = 0.17; Effect size = 0.33; Fig. 2.3d; Table 2.3). These results do not match any of the traditional assessment models.

2.4.3.3 Males

In males, there was no relationship between absolute size and contest duration in losers (*P-value* = 0.44; Effect size = 0.25; Fig. 2.3e; Table 2.3) or winners (*P-value* = 0.66; Effect size = 0.14; Fig. 2.3e; Table 2.3). There was also no relationship between relative size and contest

361 duration in males (*P-value* = 0.31; Effect size = -0.33; Fig. 2.3f; Table 2.3). These results do
362 not match any of the traditional assessment models.

Table 2.3: Pearson correlations for *H. minitabunda* between absolute size of losers and contest duration, absolute size of winners and contest duration, and relative size and contest duration in (a) juveniles, (b) females and (c) males.

(a) Juveniles				
	t	df	*P*	r
Winners	-1.53	13	0.15	-0.39
Losers	-0.11	13	0.91	-0.03
Relative size	-2.81	12	**0.02**	-0.63
(b) Females				
	t	df	*P*	r
Winners	-0.28	17	0.78	-0.07
Losers	-1.71	17	0.10	-0.38
Relative size	1.42	17	0.17	0.33
(c) Males				
	t	df	*P*	r
Winners	0.45	10	0.66	0.14
Losers	0.81	10	0.44	0.25
Relative size	-1.07	9	0.31	-0.33

$P < 0.05$ indicated in bold

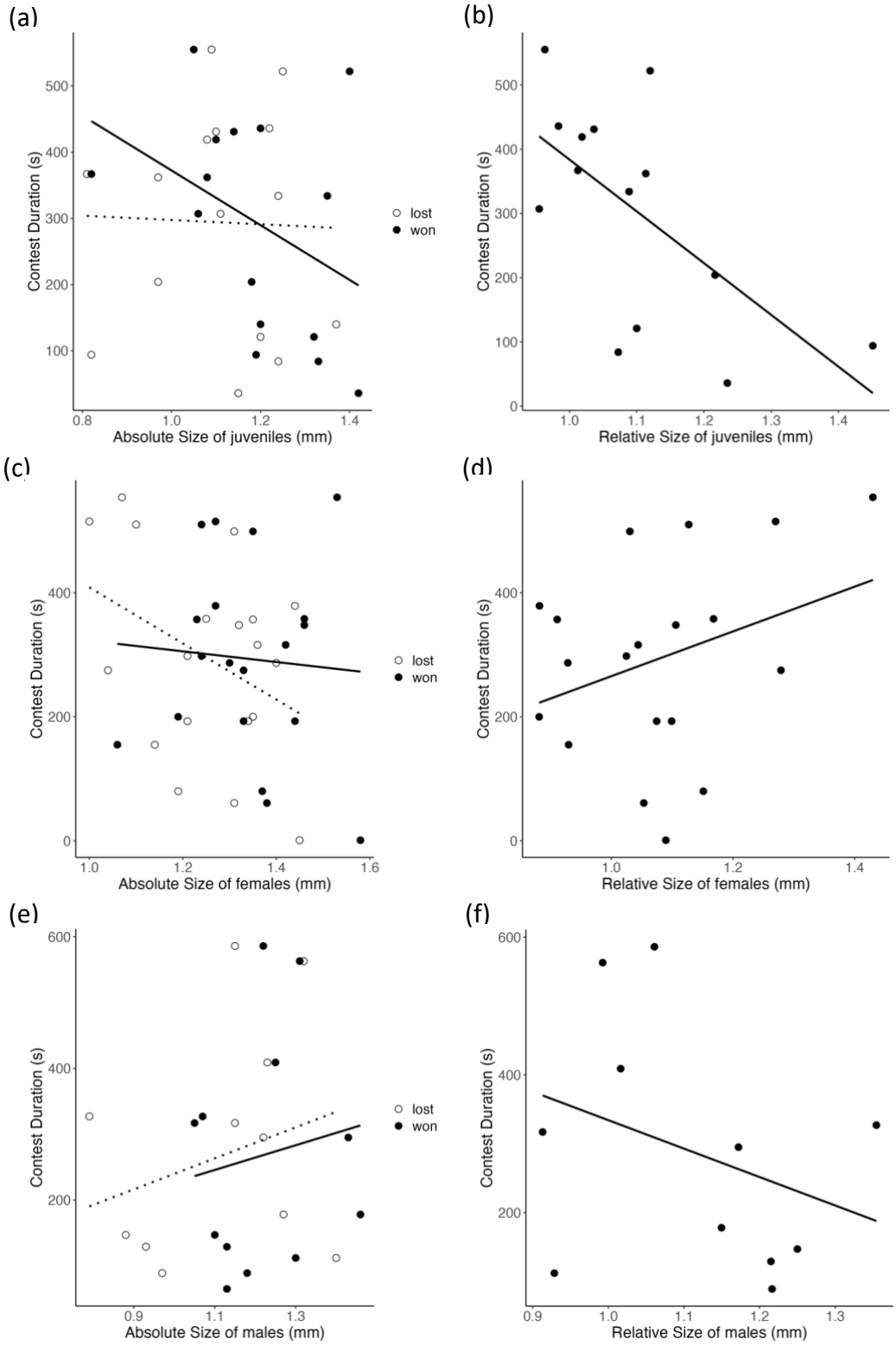

Figure 2.3: Correlations between contest duration in *H. minitabunda* and: (a) absolute size of juvenile losers and winners; (b) relative size of juveniles; (c) absolute size of female losers and winners; (d) relative size of females; (e) absolute size of male losers and winners; and (f) relative size of males.

2.5 Discussion

I found that the contests of *Helpis minitabunda* jumping spiders consist of three escalating phases. Spiders first go through an initial assessment phase, which may then escalate into the display phase and then the contact phase. There was no difference between juveniles, females or males in whether they initiated the assessment contest phase. However, male contests had a greater likelihood of escalating to the display phase than juvenile or female contests, and both female and male contests had a greater likelihood of escalating to the contact phase than juvenile contests. Surprisingly, contest outcome was not influenced by size differences between opponents in juvenile, female or male contests, although it did influence contest escalation in juveniles. Juvenile assessment strategies most closely resemble mutual assessment models, but neither female or male assessment strategies appear to match traditional assessment models.

I found that there was no difference between juveniles, females and males in whether they initiated the assessment contest phase. This suggests that the underlying motivation for entering into a contest is similar across age and sex. However, male contests were more likely to escalate into the display phase compared to female or juvenile contests (i.e., 75% of males entered the display phase compared to 32.8% of females and 46.7% of juveniles). This may be due to adaptive differences in male reproductive behaviour, as performing contest displays demonstrate their quality to prospective mates and increase their chances of reproductive success (Weiss & Dubin, 2018). It is often advantageous for males to perform displays to signal their competitive ability to rival males and deter them from competing for a potential mate (Clutton-Brock & Huchard, 2013). Therefore, males may be more inclined to perform

physical displays to secure access to a mate (Fusani et al., 2014). Further, differences in hormone levels between sexes may influence progression through contest phases (Briffa & Sneddon, 2007).

Males and females were more likely than juveniles to escalate contest to the contact phase, consisting of physical agonistic interactions. The adults in my experiments reached maturity in the field and may have been mated. Contest persistence may be higher in mature individuals that have already acquired reproductive success, and thus be more inclined to take risks in dangerous physical contests than unmated individuals with more future reproductive potential (Jennings & Gammell, 2013).

Surprisingly, I found little evidence that body size, a common measure of RHP, influences contest escalation or contest outcome, although I did find that size influences contest escalation in juveniles from the assessment to display phase. This suggests that factors other than body size must have contributed to contest outcome in *H. minitabunda* in my experiments. These factors may include prior contest experience or motivational state.

Prior contest experience can influence contest performance (Oyegbile & Marler, 2005). For example, *Peromyscus californicus* (California mice) (Gambel, 1848) (Rodentia: Cricetidae) that win three agonistic interactions are more likely to continue winning future contests (the 'winner effect'; Oyegbile & Marler, 2005). Testosterone levels increased following contest success, contributing to subsequent wins (Oyegbile & Marler, 2005). Contest outcome in *Teleogryllus commodus* (black field crickets) (Walker, 1869) (Orthoptera: Gryllidae) is dependent on prior fighting experience rather than body size in contests that end before the contact phase (Reaney et al., 2011). However, contest outcomes in contests that

escalate to the contact phase are based on opponent body size (Reaney et al., 2011). *Junco hyemalis oreganus* (dark-eyed juncos) (J. K. Townsend, 1837) (Passeriformes: Passerellidae), that initiate contests also have a greater likelihood of winning (Jackson, 1991).

My contest experiments with *H. minitabunda* consisted of dyads with no resources in the arena. This experiment may have different results if the spiders had a resource to fight over (Enquist & Leimar, 1987). Resource value can shift an individual's motivational state, determining how much effort is exerted into the contest (Enquist & Leimar, 1987). When a resource has increased value, willingness to engage in risky activity is heightened (Enquist & Leimar, 1987). Resource value varies between individuals depending on their physiological state and how much benefit they would receive from acquiring ownership of it (Enquist & Leimar, 1987). The opponent that has the greatest RHP tend to win in contests, however, if there is minimal difference in RHP between opponents then the individual that perceives the contested resource to be of the highest value tends to win (Humphries et al., 2006). For instance, queen *Polistes dominula* (paper wasps) (Christ, 1791) (Hymenoptera: Vespidae) exhibit more vigilant and aggressive behaviour when competing over large nests than small nests (Injaian & Tibbetts, 2015). Similarly, male *Euophrys parvula* (Bryant, 1935) (Araneae: Salticidae) jumping spiders escalated contests more often when a deceased female model was also present in the arena, illustrating how motivational state can alter agonistic behaviour in contests (Wells, 1988). This suggests that if a resource was present in the arena during *H. minitabunda* contests, aggression may have been increased resulting in different contest outcomes.

I found that juvenile contest assessment strategies most closely resemble a mutual assessment model (Arnott & Elwood, 2009), although the supporting evidence is not strong

and requires further testing. In mutual assessment models, contests are resolved faster when a greater asymmetry exists between contestants and when the loser is large in size (Arnott & Elwood, 2009). Body size can be indicative of the RHP of an individual (Elias et al., 2008). When the difference between RHP between opponents is pronounced, the loser is able to identify that they are at a disadvantage and retreat (Elias et al., 2008). Juvenile body size varies greatly with their stage of development. Therefore, small juveniles are more likely to withdraw from a contest when paired with a larger opponent (Hsu et al., 2008). Conversely, if there is minimal difference in the RHP between opponents, they will engage in a longer contest (Elias et al., 2008).

I did not find evidence to support use of any of the traditional assessment strategy models by females or males. This indicates that, similar to juvenile contests, other factors played a role in contest duration and outcome in adult jumping spiders. Aggression may influence contest duration. For example, contest duration increases with gill bailer beating, an agonistic behaviour in *Necora puber* (velvet crabs) (Linnaeus, 1767) (Decapoda: Polybiidae) (Briffa & Sneddon, 2007). In female *Sceloporus jarrovi* (mountain spiny lizards) (Cope, 1875) (Squamata: Phrynosomatidae), aggression levels are linked to hormone levels (Woodley & Moore, 1999).

Contest duration may also be linked to resource value. Individuals will persist for longer in contests when resource value is high (Arnott & Elwood, 2008). In my experiment, contests were set up in an experimental arena with no immediate resources for opponents to fight over. This lack of resources may have influenced contest behaviour, reducing links between RHP, contest duration and outcomes. Chemical cues from unmated female wolf spiders generate heightened aggression in male contests, and visual cues from females

462 escalate male contests even further (Rypstra et al., 2009). Providing resources (e.g., cues
463 from a potential mate, or food) in future contest experiments with *H. minitabunda* may reveal
464 stronger links between RHP and contest outcomes than my current results.
465
466 Stamina may also influence contest duration (Mowles et al., 2009). Stamina is
467 indicative of an individual's RHP (Taylor et al., 2001) and individuals with stamina possess
468 large endurance capacities to persist in a contest despite sustaining costs as agonistic activity
469 continues (Mowles et al., 2009). Contests with a correlation between contest duration and
470 stamina align with the cumulative assessment strategy (Mowles et al., 2009). The efficiency
471 of agonistic behavioural sequences can influence an individual's contest endurance (Briffa &
472 Lane, 2017). If locomotive movements are executed effectively, this can reduce the energetic
473 costs from the interaction, and facilitate greater endurance (Briffa & Lane, 2017). Therefore,
474 individuals with limited energy reserves are generally the first to withdraw from a contest
475 (Kelly & L'Heureux, 2021). Male *Calopteryx maculata* (damselflies) (Palisot de Beauvois,
476 1807) (Odonata: Calopterygidae) with high fat reserves are more likely to win contests than
477 damselflies with lower fat reserves (Marden & Waage, 1990). When an individual's fat
478 reserves decline past a threshold, it may signal to the animal to withdraw from a contest
479 (Briffa, 2014; Marden & Waage, 1990).
480
481 Environmental conditions such as food availability can also influence contest
482 performance. If an individual perceives a resource to be of high value to them, it can increase
483 their motivation to compete for the resource. For example, when food availability is scarce,
484 the resource value of a prey item may increase. Resource value also increases if a prey item
485 contains a high nutrient content or is larger in size (Chancellor & Isbell, 2008). The

progression of contests in *H. minitabunda* in the presence of prey of different values would be interesting to test.

Resident effects occur when one individual possesses a resource which is contested by an intruder, creating resource value asymmetry (Papaj & Messing, 1998). The resource is perceived to be of greater value to the resident in a contest as they have more to lose (Mesterton-Gibbons & Sherratt, 2016). Thus, when a resident of a resource is faced with an intruder, the resident often exhibits a greater motivation to win in contest and is more likely to win the contest (Mesterton-Gibbons & Sherratt, 2016). In my experiment, resident effects were removed, as no resources were provided to the spiders in the experiment and I controlled contest interactions to remove the potential for resource value asymmetry by providing opponents with the same acclimatisation time. It would be interesting to test whether providing a resource or adjusting acclimatisation times would create resident effects in *H. minitabunda*.

2.5.1 Conclusion

My experiments suggest that agonistic behaviour varies with developmental stage and sex in *H. minitabunda*. Size may not play a strong role in contest outcome in *H. minitabunda* when there are no resources present. However, the influence of size on contest outcome requires further testing by providing resources such as potential mates or prey during contest trials. Other physiological parameters, such as stamina and endurance, motivation, or environmental conditions may also influence contest performance.

509 *2.6 References*

510

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Chapter 3:

Predatory performance in a jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), is influenced by personality traits

3.1 Abstract

Predatory behaviour can be shaped by a multitude of factors including personality, body condition, and environmental factors. Understanding how these factors can modify behaviour will shed light on predator-prey dynamics. However, predator-prey research often focuses on the behaviour of prey, rather than the predator. Here, I investigate predatory performance in the Aussie bronze jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), using two assays that quantify predator responses to a model prey, and quantify voracity. I found that latency to emerge into the predation arena was correlated with both latency to capture prey and prey capture success. However, there was no relationship between latency to first prey capture and total number of prey caught. Further, there was no relationship between latency to catch first prey in the model prey assay and latency to catch first prey in the voracity assay. My results indicate that predatory behaviour is sensitive to environmental contexts, and that personality traits associated with boldness (i.e., latency to emerge) influence prey capture in jumping spiders.

3.2 Introduction

Predators employ a variety of tactics to maximise foraging success. For example, predators that cruise enhance their foraging success by travelling across extended distances to increase the likelihood of encountering potential prey (Greene, 1986). Predators that cruise include harbour seals (Linnaeus, 1758) (Carnivora: Phocidae) (Bowen et al., 2002), Atlantic cod (Linnaeus, 1758) (Gadiformes: Gadidae) (Laurel & Brown, 2006), and leatherback sea turtles (Vandelli, 1761) (Testudines: Dermochelyidae) (Fossette et al., 2012). Predators that ambush

remain stationary, observe prey and wait for the perfect time to strike and detain it (Greene, 1986). Large prey items tend to be targeted by ambush (Greene, 1986), perhaps due to the greater risk to the predator. Ambush predators include mantis shrimp (Linnaeus, 1758) (Stomatopoda) (DeVries et al., 2012), midges (Insecta) (Spitze, 1985*),* diamond pythons (Lacépède, 1804) (Squamata: Pythonidae) (Slip & Shine, 1988), crab spiders (Clerck, 1757) (Araneae: Thomisidae) and ambush bugs (Melin, 1930 (Hemiptera: Reduviidae) (Kevan & Greco, 2001). Other common predatory tactics include stalking (Bartos, 2007), pursuit and aggressive mimicry (Jackson, 1992). Predatory tactics are typically comprised of both innate and learned responses (Gibbons et al., 2005).

Optimal foraging theory predicts that animals will employ the most efficient strategy to acquire food, maximising their energetic reserves (Pyke & Starr, 2021). Optimal foraging infers that predators should target high quality prey when available (King & Marshall, 2022). When prey availability fluctuates due to seasonality or resource scarcity, it may be necessary for predators to adapt their foraging tactics to maximise prey capture success (Heithaus et al., 2004). Adopting different predatory tactics to enhance predation performance can facilitate the capture of larger prey items (Griffiths, 1980). Further, body condition can influence predatory behaviour. For example, brown pelicans (*Pelecanus occidentalis*) (Linnaeus, 1766) (Pelecaniformes: Pelecanidae) in poor body condition travel further to acquire food, demonstrating how body condition can alter predatory behaviour (Walter et al., 2014). Similarly, mouthbrooding cichlids, *Simochromis pleurospilus* (Pellegrin, 1927) (Cichliformes: Cichlidae), that are in poor body condition are more inclined to feed in risky conditions (Segers & Taborsky, 2011).

Latency to emerge from shelter can provide information about both personality traits and the body condition of a predator. A fast latency to emerge from shelter is often indicative of a bold, risk taking personality (Vainikka et al., 2011). Individuals with poor body condition are often reactive and express traits associated with boldness, disregarding potential risks (Schmitz, 2017). Conversely, individuals in good body condition have a propensity to exhibit shy or cautious behaviour, as they have greater future reproductive potential and investing resources into reproduction should have greater fitness benefit than performing risky behaviours (Clermont et al., 2023). As a result, individual personality plays a role in determining fitness (Chang et al., 2017). A bold personality infers that an individual acts in an aggressive, risk-taking manner and actively explores their environment (de Azevedo & Young, 2021). Boldness leads to a trade-off between greater predation risk due to increased proximity and recognition by predators, and greater access to resources (de Azevedo & Young, 2021). On the contrary, individuals that possess a shy personality are more vigilant than bold individuals and refrain from high risk situations (Kortet et al., 2010). Thus, I predict that individual personalities differ within a population as each individual will be positioned along a shy-bold continuum (Wilson et al., 1994).

Personality traits can influence predator prey dynamics (Blake et al., 2018). Personality can impact the longevity and fitness of an individual (Belgrad & Griffen, 2016) and can be a selection pressure, affecting predation risk (Belgrad & Griffen, 2016; Blake et al., 2018). For example, shy roach fish (*Rutilus rutilus*) (Linnaeus, 1758) (Cypriniformes: Leuciscidae) are at greater risk of predation from pike fish (*Esox lucius*) (Linnaeus, 1758) (Salmoniformes: Esocidae) than bold roach fish (Blake et al., 2018).

Jumping spiders have diverse predatory tactics which make them ideal models for predation research. Predatory tactics in jumping spiders include stalking, camouflage (Bear & Hasson, 1997), ambush (Heiling et al., 2005), web invasion, aggressive mimicry, trial and error strategies, and detouring (Jackson & Pollard, 1996). For example, *Plexippus paykulli* (Audouin, 1826) (Araneae: Salticidae) jumping spiders camouflage themselves and stalk their prey before attacking (Bear & Hasson, 1997). *Myrmarachne* (MacLeay, 1839) (Araneae: Salticidae) jumping spiders mimic the behaviour and morphology of ants to capture their ant prey (Hashimoto et al., 2020; Shamble et al., 2017). *Myrmarachne* also invade other spider's nests to prey upon their eggs (Hashimoto et al., 2020; Jackson, 1986; Jackson & Willey, 1994). Jumping spiders have excellent vision which contributes to their ability to stalk and pounce on prey (Richman & Jackson, 1992).

The Aussie bronze jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), is introduced to New Zealand (Żabka & Patoleta, 2014). Although common, very little is known about its predatory behaviour. In this chapter, I quantify the predatory behaviour of *H. minitabunda* using model prey and voracity assays. I predicted that spiders with a short latency to emerge and begin hunting would have higher voracity, capturing more prey than spiders with a long latency to emerge.

3.3 Methods

3.3.1 Study Species

I collected 28 adult female spiders from native vegetation (flax, *Phormium tenax*) in Albany (Auckland, New Zealand). Spiders were kept in separate, transparent vials (120mL) in the

laboratory at Massey University, Albany. Water was supplied *ad libitum* via moistened paper towel placed in a small, white lid inside the spider's vial. A stick was provided in each vial for environmental enrichment (Carducci & Jakob, 2000). The lab remained on a 12 : 12 hr day : night cycle with a one hour ramp up and ramp down period to simulate dawn and dusk. Lab temperature was 19.5°C $\pm$ 0.5°C and relative humidity maintained at 60%. Spiders were photographed under a microscope (Motic SMZ 168) and weighed (Ohaus EX125D semi-micro balance). Cephalothorax width was measured from photographs using ImageJ (Schneider et al., 2012).

3.3.2 Experimental Procedure

All experiments were conducted between 9am and 5pm. Each spider completed two assays – a model prey assay and a voracity assay. All spiders completed the model prey assay first, then the voracity assay so that I could standardise their satiation levels. Spiders were weighed and photographed immediately after collection, then maintained in individual vials for three days to acclimatise to the laboratory environment. Spiders were weighed again before the model prey assay. In the model prey assay, one spider was placed inside a small, transparent, plastic, cylindrical vial with a lid (30ml). This small vial was placed inside a larger, transparent, plastic, cylindrical container (500ml), inside a photography tent (1m × 1m × 1m). The photography tent helped to reduce visual distractions during the assay. The spider was given a five minute acclimation period. After acclimation, I removed the lid of the small vial allowing the spider to emerge into the large container, and introduced one *Drosophila melanogaster* fly to the large container. *Drosophila melanogaster* were selected as a representative, standardised, safe prey item that was similar to prey items that spiders would encounter in the field. Assays were filmed using a camcorder (Canon XA11 or Canon XA20).

I recorded the latency for the spider to emerge from the small acclimation vial (defined by the complete emergence of the spider's body), and latency to orient towards the prey once it was outside of the acclimation vial (determined by the whole body turning towards the prey item). The anterior median eyes have the greatest acuity of all jumping spider eyes, but have a small visual field (Zurek et al., 2010). Therefore, the object that the jumping spider is oriented towards is the object that it is visually focussed on (Zurek et al., 2010). I also recorded latency to capture the fly (measured from the end of the five minute acclimation period to the time the spider captured the fly with its legs or mouth). I also recorded if the spider successfully captured the fly (yes/no). Spiders were given one hour to capture the prey. After one hour, the spiders were placed back into their maintenance vials. The cylindrical containers and vials were cleaned with 70% ethanol solution between assays.

After the model prey assay, all spiders were fed four drosophila each (sufficient for satiation). Spiders were then not fed for seven days to standardise satiation levels for the voracity assays. On the day of the voracity assay, each spider was weighed again to obtain a baseline weight for the experiment. Ten *D. melanogaster* were placed within a petri dish (diameter: 90mm), and one spider was introduced. Assays were conducted within a photography tent (1m × 1m × 1m) and recorded with a camcorder (Canon XA11 or Canon XA20) mounted on a tripod directly above the experiment. Spiders were given one hour to catch prey. I recorded the latency to orient towards the first prey, latency to first prey capture and the number of prey caught after one hour. Spiders were weighed again at the end of their voracity assay and returned to their maintenance vials where they were held until they were released back into the field after the voracity experiment.

3.3.3 Statistical analyses

All statistical analyses were conducted using R version 4.4.1 (R Core Development Team). For the model prey assay, I calculated spider condition by regressing spider weight with cephalothorax width using the 'lm()' function and extracting the residuals. These residuals denote how far an individual's weight deviates from the expected value for their size and were used as a metric of spider condition in subsequent analyses (Heimerl et al., 2022; Jakob et al, 1996; Wilder & Rypstra, 2008; Wilder et al., 2016). To assess whether latency to emerge or spider condition influenced latency to capture the model prey, I used the glm() function from the lme4 package (Bates et al., 2015) to fit a generalized linear model (GLM) with a 'gaussian' family. I included latency to emerge and spider condition as fixed effects. *P*-values were calculated using the *lmerTest* package (Kuznetsova et al., 2017). To test whether prey capture success was influenced by latency to emerge from the acclimation vial or spider condition I used the 'glm' function to fit a GLM with a binomial family. Latency to emerge and spider condition were included as fixed effects. To calculate condition before the voracity assay, I again extracted the residuals from a correlation between spider weight and cephalothorax width prior to the voracity assay. To test whether latency to catch the first prey item or condition influenced the total number of flies caught in the voracity assay, I ran a GLM using the 'glm' function with a Poisson family, including latency to catch the first prey item and spider condition as fixed effects. There was no evidence of overdispersion in my models. I assessed if latency to catch prey in model prey assays correlated with latency to first prey capture in voracity assays using a Pearson correlation using the 'cor()' function.

173 *3.4 Results*

174

175 Spider size and spider weight were positively correlated in the model prey assay (t = 4.64, *P*-
176 value = <0.01; Table 3.1). I found that there was a significant, positive correlation between
177 the latency to emerge from the acclimation vial and the latency to capture the model prey (t =
178 5.15, *P*-value = 0.01; Fig. 3.1; Table 3.2). However, body condition did not influence latency
179 to capture prey (t = 1.21, *P*-value = 0.24; Fig. 3.1; Table 3.2). I found that latency to emerge
180 from the acclimation vial influenced prey capture success (t = -2.17, *P*-value = 0.03; Fig. 3.2;
181 Table 3.3), but body condition did not (t = 0.62, *P*-value = 0.54; Table 3.3).

Table 3.1: Linear model between *H. minitabunda* spider size and weight in the model prey assay.

Coefficients	**Estimate**	**SE**	**t**	***P***
(Intercept)	-0.01	0.01	-1.73	0.10
Size_mm	0.03	0.01	4.64	**< 0.01**

P < 0.05 are indicated in bold

Table 3.2: GLM showing the relationship between latency to emerge and body condition on latency to capture prey in the model prey assay for *H. minitabunda.*

Coefficients	**Estimate**	**SE**	**t**	***P***
(Intercept)	359.90	134.50	2.68	**0.01**
Latency to emerge	0.97	0.19	5.15	**< 0.01**
Condition	29230.00	24110.00	1.21	0.24

P < 0.05 are indicated in bold

Table 3.3: Effects of latency to emerge from acclimation vial on prey capture success in model prey assay for *H. minitabunda.*

Coefficients	Estimate	SE	z	*P*
(Intercept)	2.79	0.83	3.36	**< 0.01**
Latency to emerge	-0.00	0.00	-2.17	**0.03**
Condition	66.88	108.40	0.62	0.54

$P < 0.05$ are indicated in bold

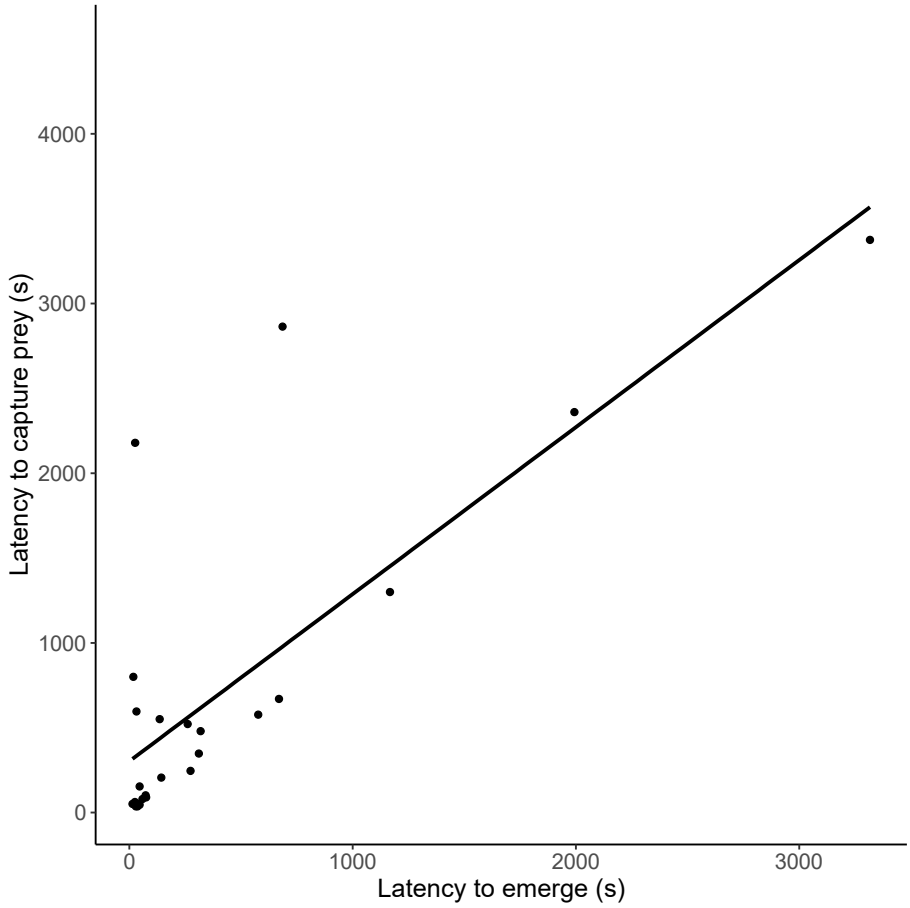

Figure 3.1: Correlation between latency to emerge and latency to capture prey in the model prey assay for *H. minitabunda.*

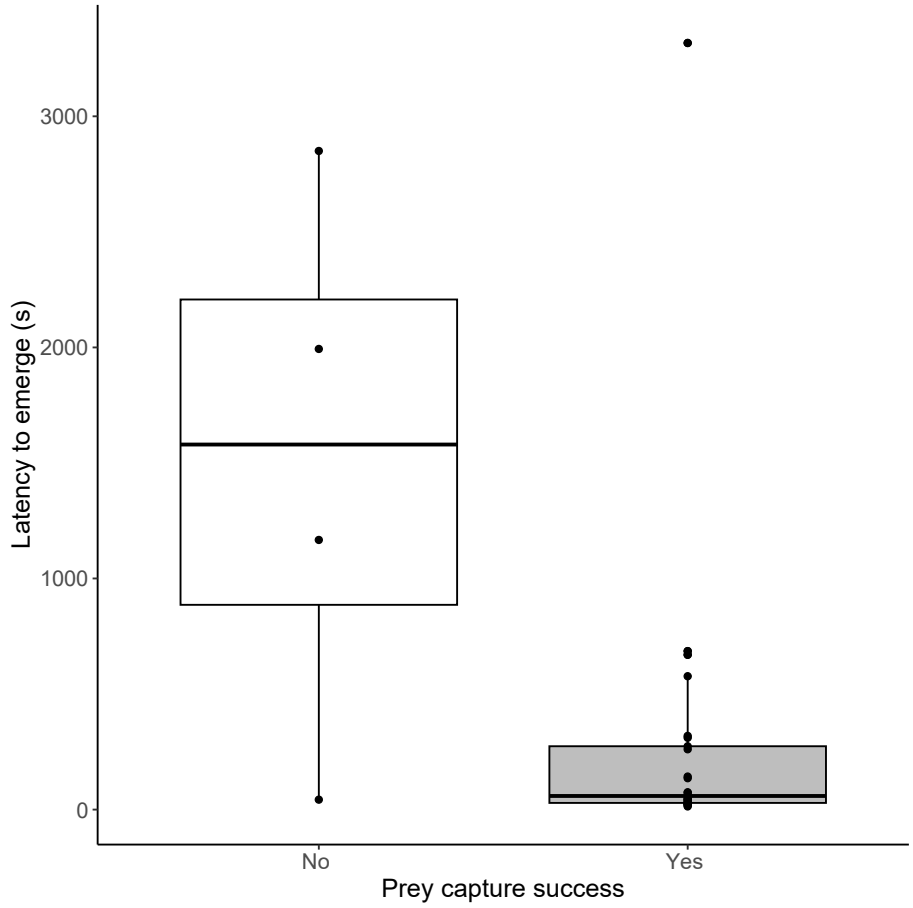

Figure 3.2: Boxplot depicting the relationship between latency of *H. minitabunda* to emerge from the acclimation vial and prey capture success in the model prey assay. The boxes represent the 25% and 75% quartiles, and the line within each box represents the median. The whiskers represent the spread of the data within 1.5 times the interquartile range from the first and third quartiles. Outliers are situated beyond the whiskers.

In the voracity assay, latency to catch the first prey item did not influence the total number of flies caught (z = -0.79, *P*-value = 0.43; Fig. 3.3; Table 3.4). Additionally, body condition of the spider did not influence the total number of flies caught (z = 1.01, *P*-value = 0.31; Table 3.4). There was no correlation between latency to catch prey in model prey assay

186 and latency to capture first prey in the voracity assay (t = 0.32, df = 23, *P*-value = 0.75, r =

187 0.07; Fig. 3.4).

Table 3.4: GLM testing the effect of latency to catch the first prey item and condition on the total number of flies caught in the voracity assay by *H. minitabunda.*

Coefficients	Estimate	SE	z	*P*
(Intercept)	1.43	0.13	10.91	**< 0.01**
Latency to first prey capture	-0.00	0.00	-0.79	0.43
Condition	22.67	22.44	1.01	0.31

P < 0.05 are indicated in bold

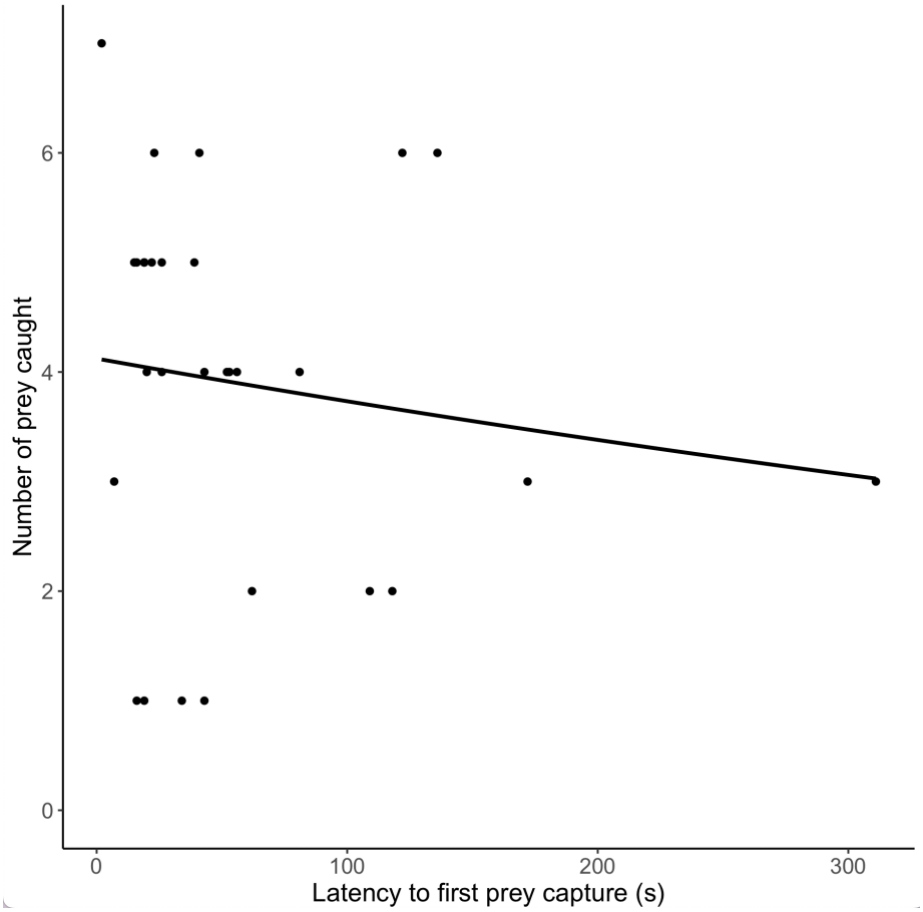

Figure 3.3: Relationship between latency to catch the first prey item and total number of prey caught in the voracity assay by *H. minitabunda.*

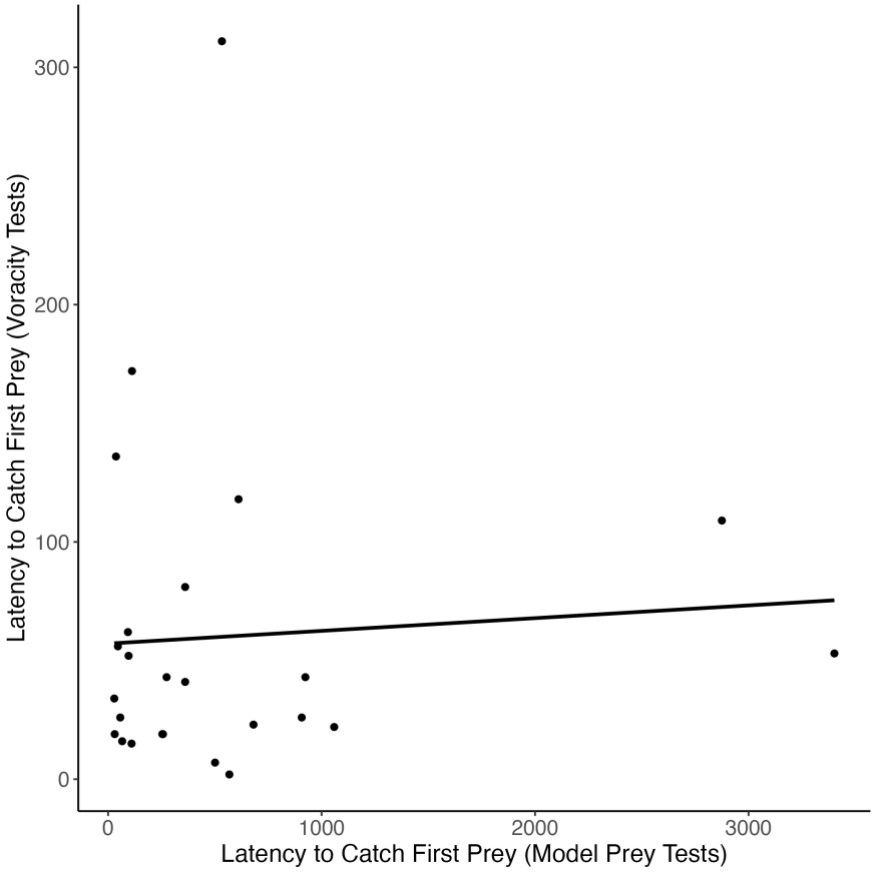

Figure 3.4: Correlation between the latency to catch first prey in the model prey assay and the latency to catch first prey in the voracity assay for *H. minitabunda.*

188 *3.5 Discussion*

189

190 I found that latency to emerge correlated with both latency to capture prey and prey capture
191 success in the jumping spider, *H. minitabunda*. Spiders that emerged faster were more likely
192 to capture the prey in the model prey assay. This suggests that boldness (characterised by
193 latency to emerge) may enhance predation performance in *H. minitabunda*. However, neither
194 body condition or latency to first prey capture predicted the total number of prey items caught
195 in the voracity assay. Further, I found no correlation between latency to catch prey in the

model prey and voracity assays. This suggests that jumping spiders may be sensitive to contextual or environmental cues when hunting.

3.5.1 Model prey assay

The latency for the spider to emerge from the acclimation vial correlated with latency to capture prey in the model prey assay. Latency to emerge is a trait that is often associated with boldness (Carter et al., 2013). Individuals that possess bold personalities display explorative, risk-taking behaviours, which in turn may facilitate efficient prey capture (Garamszegi et al., 2012; Guenther et al., 2014; Hall et al., 2015). Thus, bold individuals are more likely to leave a refuge sooner than shy individuals (Brown et al., 2007b) and exhibit shorter latencies to feed (Ward et al., 2004). Latency to emerge and latency to capture prey may both be associated with an individual's degree of caution as those that are less vigilant against risk of predation may also be faster to emerge and commence foraging. Time to emerge from a refuge influences the time available for other behaviours that can increase fitness (Cooper & Frederick, 2007).

Latency to emerge from the acclimation vial was also correlated with prey capture success in the model prey assay. Individuals that have a short latency to emerge from the acclimation vial were more successful at capturing prey than spiders who had a longer latency to emerge from the acclimation vial. Prey capture success is also correlated with latency to resume behaviour after a simulated predator attack in the red-veined darter dragonfly (*Sympetrum fonscolombii*) (Selys, 1840) (Odonata: Libellulidae) (Everling & Johansson, 2022). Personality traits influence predatory-prey interactions (Chang et al., 2017). Shy, submissive *Portia labiata* (Thorell, 1887) (Araneae: Salticidae) jumping spiders

needed more attempts to capture predictable prey than bold, aggressive *P. labiata* (Chang et al., 2017). Conversely, bold, aggressive *P. labiata* could capture unpredictable prey and needed fewer attempts than shy, submissive *P. labiata* (Chang et al., 2017). This suggests that predation performance is shaped by an interaction between predator personality and prey predictability (Chang et al., 2017). The locomotor crossover hypothesis suggests that shy predators with low activity rates tend to target shy prey with low activity rates (Chang et al., 2017; Toscano et al., 2016). Moreover, bold predators with high rates of activity tend to target bold prey with high rates of activity (Chang et al., 2017; Toscano et al., 2016). Together, these results and mine suggest that traits associated with boldness can have a strong influence on foraging success.

In my experiment, *H. minitabunda* were presented with a safe prey type (small flies). However, many predators adapt their predatory tactics to prey type, particularly if prey are dangerous (Bowen et al., 2002; Formanowicz Jr & Bradley, 1987; Michalko & Pekár, 2016; Mukherjee & Heithaus, 2013). Shifts in predatory behaviour are exhibited in *Portia* jumping spiders which perform cryptic stalking to creep up on prey when hunting other spiders, holding its palps in close to its chelicerae and remaining stationary when their prey orient towards them (Harland & Jackson, 2000; Jackson, 1985), but regular stalking when hunting safer prey with poor vision (Harland & Jackson, 2000). Personality traits may influence risk-taking behaviour and tendency to hunt dangerous prey. Bold individuals may be more inclined to hunt dangerous prey (Mukherjee & Heithaus, 2013), as bold individuals are more willing to take risks (Hulthén et al., 2017). Further, physical traits may impact tendencies to engage with dangerous prey. Larger individuals may be more likely to successfully capture dangerous prey as small individuals may be more prone to injury (Mukherjee & Heithaus,

2013). It would be interesting to compare the behaviour of *H. minitabunda* when hunting safe and dangerous prey types.

Body condition had no influence on the predatory performance of *H. minitabunda* in my experiments. This is not surprising, as I standardised satiation prior to testing. Further, body condition may be more likely to influence risk-taking behaviours such as when hunting dangerous prey (Bachman, 1993; Jablonszky et al., 2018; Mohring et al., 2022). I predict that spiders in poor body condition would be more likely to target dangerous prey as they have more need for food than spiders in good body condition (Gillette et al., 2000; Wignall & Taylor, 2009). I would also predict that spiders in good body condition would be more cautious than spiders in poor body condition as they have greater potential fitness to protect (Schmitz, 2017). Future experiments may test the effects of body condition on predatory performance in different contexts.

An individual's position on the bold-shy continuum can be influenced by sex (Brown et al., 2007a). For example, bold individuals with a fast latency to emerge from a refuge were disproportionately male in *Brachyrhaphis episcopi* fish (Steindachner, 1878) (Teleostei: Poeciliidae) (Brown et al., 2007b). Differences in bold traits may be attributed to differences in hormone levels and sex (Brown et al., 2007a; Oswald et al., 2012). For example, female zebrafish (*Danio rerio*) (Hamilton, 1822) (Cypriniformes: Cyprinidae) were bolder and produced less cortisol than males (Oswald et al., 2012). I only used adult female spiders as test subjects in my experiments as adult males tend to display lower predatory drive than females. It would be interesting to test how sexual dimorphism may influence both predatory and personality traits in *H. minitabunda*.

3.5.2 Voracity tests

There was no relationship between latency to capture the first prey item and total number of prey caught in my voracity tests. Latency to capture prey can be used as a measure of aggressiveness and boldness (Lichtenstein et al., 2017b). The lack of correlation is surprising as boldness can predict the quantity of prey items consumed, whereby individuals that are bold and daring tend to capture and consume more prey than shy individuals (Ioannou et al., 2008). The lack of correlation between latency to first prey capture (boldness) and the number of prey caught indicates that the predation strategy used by *H. minitabunda* in the voracity test does not rely on being bold. During the voracity tests, I observed that *H. minitabunda* would sit and wait, then rapidly pounce on their focal prey. This sit and wait style of predation is also a type of ambush tactic (Zoroa et al., 2011). Ambush tactics enhance predation efficiency and success by the predator remaining stationary until active prey enter their immediate vicinity before striking (Pembury Smith & Ruxton, 2020). Thus, to prevent startling potential prey, cautious behaviour is required for ambush tactics to be effective (Nilsson et al., 2010).

The lack of correlation between latency to catch the first prey item in the model prey assay and latency to catch the first prey in the voracity assay may be due to differences in experimental context. The voracity test may have tested hunger as motivation for prey capture (Sternson et al., 2013). *H. minitabunda* were starved for seven days prior to participating in the voracity assay, which may have generated strong motivation to capture prey faster than the motivation generated prior in the model prey assay. Moreover, the voracity assay provides insight into predation tactics employed when prey are abundant (Parsons et al., 2022). Conversely, the model prey assay tested how predators respond to just

one prey item. Therefore, the voracity assay may test motivation in an environment abundant with prey. The presence of multiple prey items may have triggered enhanced foraging motivation and increased arousal, leading to more rapid or opportunistic capture behaviour than when only a single prey item is present. This highlights the need to be cautious when interpreting the results of apparently similar assays.

3.5.3 Conclusion

I found that latency to emerge was correlated with both latency to capture prey and prey capture success. This suggests that individuals that are risk-adverse may also have reduced prey capture success. Conversely, bold individuals that are risk-takers may have greater prey capture success. I found no correlation between latency to capture the first prey item and the number of prey caught in the voracity assay. This was surprising, as I predicted that bold individuals that emerge quickly and capture their first prey item quickly would capture more prey than shy individuals. Altogether, my results suggest that personality traits in spiders influence predatory traits, but that they are also sensitive to contextual cues. Future experiments may extend this work by assessing the influence of personality traits when hunting dangerous prey types, the effects of hormones and sex differences on predatory behaviour and the effects of body condition on predatory behaviour.

314 *3.6 References*

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Chapter 4:

From combat to consumption: assaying contest and predation performance in *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae)

4.1 Abstract

Performance in fitness-related tasks like foraging and competing may be correlated due to physiological, morphological or personality traits. Both predation and contest performance may be linked to individual aggression. However, predation and contest performance are typically studied independently of one another. In this chapter, I test whether predation and contest performance are correlated in adult female jumping spiders, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), using voracity and mirror assays. I found that the number of prey consumed in the voracity tests was not correlated with contest display duration in the mirror tests. Moreover, I found no relationship between weight change after the voracity tests and display time in the mirror tests. However, I did find that spiders with lower body condition scores consumed more prey than spiders with higher body condition scores, despite controlling satiation levels. My results suggest that predation and contest performance may be sensitive to environmental conditions, rather than intrinsic levels of aggression.

4.2 Introduction

Predation and contests for resources are key ecological interactions that shape intra- and interspecific dynamics (Briffa & Sneddon, 2007). Predation is the process of individuals hunting and killing other individuals for consumption (Errington, 1963). Contests are interactive, aggressive events between individuals to attain resources for reproduction, food or territory (Crump, 2020). Predation and contest ability both contribute to whole organism performance, which constitutes how successful an individual is in traits of ecological importance (Lailvaux & Husak, 2014). Whole organism performance is a measure of how

well an animal thrives and interacts with their environment (Lailvaux & Husak, 2014). This can include behavioural and physiological responses (Irschick et al., 2008). Whole organism performance can be influenced by factors such as personality, with an individual's position on the shy-bold spectrum affecting their behaviour and fitness (Wilson et al., 1994).

Bold individuals are more inclined to display aggressive behaviour (de Azevedo & Young, 2021). Aggression is a key trait that is expected to be selected for in contests as it is often coupled with winning a contest (Smith & Harper, 1988). Further, individuals with bold traits are more likely to initiate and win a contest (Garnham et al., 2019). Bolder individuals have a tendency to take greater risks than shyer individuals, which has implications for increasing contest success (Briffa et al., 2015). Aggression is also deemed beneficial for predators in prey capture (Chang et al., 2017). Aggression varies in populations due to natural selection, with trade-offs between the costs and benefits of aggressive behaviour (Archer, 2009; Smith, 1974). For instance, individuals that are bold and aggressive are more likely to target profitable but dangerous prey which may enhance their risk of injury (Mukherjee & Heithaus, 2013). Hence, it can be advantageous or disadvantageous to express aggression across different contexts (Wolf et al., 2007).

An individual's personality encompasses sustained behaviour and analytical perception (Gosling, 2001). Animals who exhibit boldness and risk-taking behaviours during predation activities may also exhibit these behaviours when interacting with conspecifics (Sih & Bell, 2008). Behavioural syndromes occur when individuals display similar behaviours across different contexts (Sih & Bell, 2008). For instance, there is a behavioural syndrome in crickets whereby individuals who win conspecific contests also have shorter latencies to emerge in a new environment (Kortet & Hedrick, 2007). Bold personalities with greater

tendencies to explore may increase predation risk (Kortet & Hedrick, 2007). While links between ecologically-relevant tasks are expected, they are rarely tested directly in behavioural studies. However, there is evidence of strong links between predatory behaviour and other behaviours. For example, in *Anelosimus studiosus* (Hentz, 1850) (Araneae: Theridiidae) (comb-footed spiders), social individuals display heightened aggression, were faster to react and capture prey, were more exploratory and expressed increased aggression to predators, compared to asocial individuals (Pruitt et al., 2008). We do not know whether links between predation and contest performance exist in other spider taxa.

In this chapter, I test whether predation and contest performance is correlated in the Aussie bronze jumping spider (*Helpis minitabunda*) (Koch, 1880) (Araneae: Salticidae). I predicted that there will be a positive correlation in prey capture rates and contest display duration in adult female jumping spiders.

4.3 Methods

4.3.1 Study Species

I collected 28 adult female *Helpis minitabunda* spiders from native vegetation (flax, *Phormium tenax*) in Albany (Auckland, New Zealand). Each spider was kept in separate transparent vials (120mL) in the laboratory at Massey University, Albany. Spiders were provided with water *ad libitum* with moistened paper towel placed in a small vial lid and a stick for environmental enrichment (Carducci & Jakob, 2000). The lab was maintained on a 12 : 12 hr day : night cycle with a one hour ramp up and ramp down period to simulate dawn and dusk. Lab temperature was 19.5°C $\pm$ 0.5°C and relative humidity 60%. Spiders were

photographed (Canon 700D camera) under a microscope (Motic SMZ 168) and weighed to the nearest 0.01mg (Ohaus EX125D semi-micro balance) on the day of capture. Cephalothorax width was measured using the software ImageJ v1.54 (Schneider et al., 2012).

4.3.2 Experimental procedure

I used a voracity assay to quantify predation behaviour, and a mirror assay to quantify contest behaviour. Each spider was tested once in each of the voracity and mirror assays. Voracity assays were conducted first, followed by the mirror test so that satiation levels could be standardised for each test. Spiders were not fed for seven days prior to the voracity assay (spiders are opportunistic feeders that can go long periods of time without feeding). Spiders were rested overnight after the voracity assay, then completed the mirror assay the next day. All assays were conducted inside a photography tent (1m × 1m × 1m) to minimise visual distractions during the trials. After the mirror assay, spiders were transferred back into their holding vial before being released back into the field.

4.3.2.1 Voracity assay

I conducted voracity assays to quantify aggression within a predatory context. On the day of the experiment, ten live *Drosophila melanogaster* (Meigen, 1830) (Diptera: Drosophilidae), commonly known as vinegar flies, were placed in a petri dish. The spider was then introduced into the petri dish. I counted the number of flies consumed after one hour. The spider was then weighed again to record its post-assay weight.

4.3.2.2 Mirror assay

I conducted mirror assays to quantify aggression within a contest context (Chang et al., 2019). I placed a transparent Perspex container (150mm × 150mm × 150mm) into the photography tent (1m × 1m × 1m). The open side of the container was placed up against a mirror (300mm × 300mm). Trials were recorded with a camcorder (Canon XA11 or Canon XA20) mounted on a tripod. An opaque barrier was inserted between the arena and the mirror during a five minute acclimation period. The spider was introduced using a small paint bush to guide it out of a small holding vial. After the five minute acclimation period, the opaque barrier was removed and the spider was given 20 minutes to interact with its reflection. I began recording on the camcorder as soon as the opaque barrier was removed. Aggressive behaviour was defined by the spider hunching their opisthosoma (characterised by moving their opisthosoma dorsally or ventrally), flaring their first pair of legs (moving legs laterally above the substrate), or facing their reflection whilst walking side to side (Fig. 4.1). I recorded the duration (seconds) of display behaviour. The display ceased when the spider retreated from their reflection in the mirror, at which point I stopped the camcorder. If the spider did not display to their reflection or did not retreat from their reflection, the trial was terminated after 20 minutes. After the trial, spiders were placed back into vials before being released at the end of the day. After each trial, the arena, opaque barrier and mirror were cleaned with 70% ethanol solution and dried.

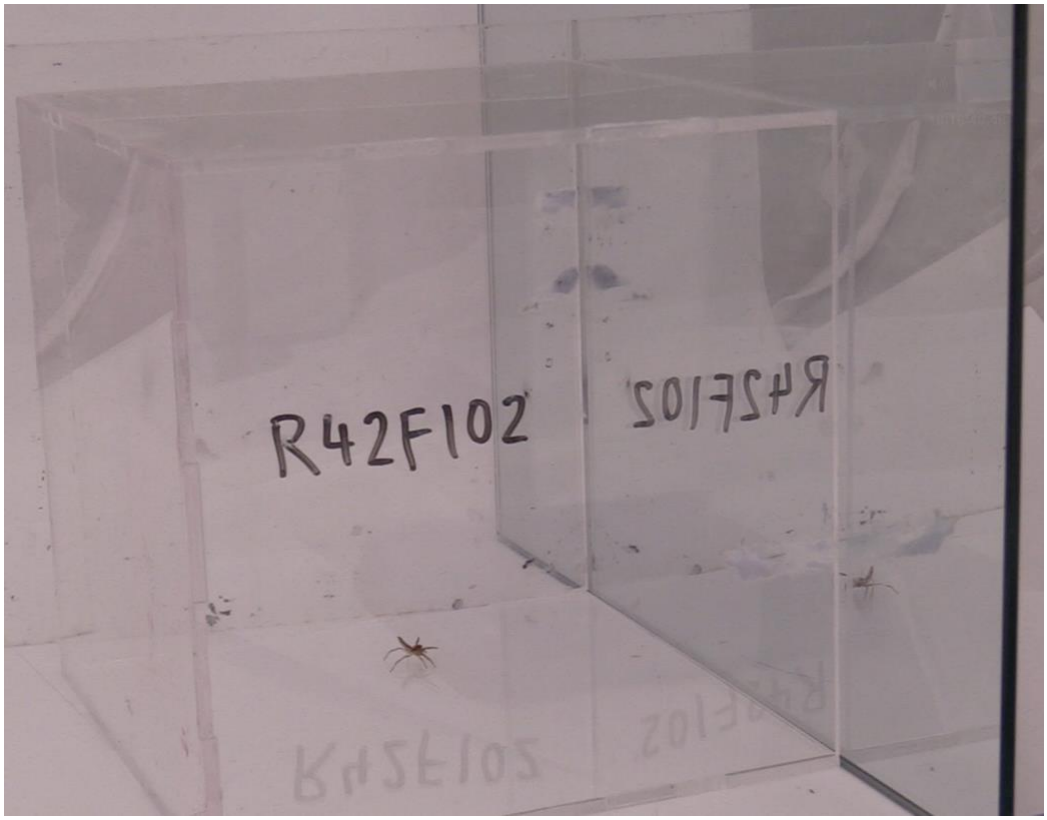

Figure 4.1: Adult female *H. minitabunda* in the mirror assay performing agonistic displays, hunching it's opisthosoma and flaring first pair of legs while facing the mirror. (Photo: D. Cox).

120 *4.3.3 Statistical Analyses*

121

122 All statistical analyses were conducted using R version 4.4.1 (R Core Development Team). I
123 calculated the body condition of spiders at the start of the voracity tests by calculating the
124 residuals from a regression between body size (cephalothorax width) and weight using linear
125 regression (Heimerl et al., 2022; Jakob et al., 1996; Wilder & Rypstra, 2008; Wilder et al.,
126 2016). I then tested whether condition influenced the number of prey eaten in the voracity
127 assay using a generalised linear model (GLM) with a Poisson distribution in the *lme4*
128 package (Bates et al., 2015). I also tested whether weight before the voracity assay or size
129 influenced number of prey eaten using a linear model (LM), and whether there was a

correlation between number of prey eaten and weight change after the voracity assay using a Pearson correlation. I tested whether condition influenced display time in the mirror test using a LM. I also tested whether size and weight influenced display time in a separate LM. To assess whether there is a relationship between predation and contest performance in the voracity and mirror assays, I used the 'cor()' function to calculate the Pearson correlation between the number of prey eaten in the voracity test and display duration. Figures were built using the '*ggplot2*' package (Wickham, 2016).

4.4 Results

There was a significant, positive correlation between spider weight and size (t = 5.62, *P*-value < 0.01; Fig. 4.2; Table 4.1). Spider condition had a strong influence on the number of prey eaten in the voracity assay (GLM: Z = -3.67, *P*-value < 0.01; Fig. 4.3; Table 4.2). However, neither weight before the test (t = -1.27, *P*-value = 0.21; Table 4.3) or size (t = 0.67, *P*-value = 0.51; Table 4.3) influenced the number of prey eaten in the voracity test. Further, there was no correlation between weight change and number of prey eaten in the voracity assay (Pearson's correlation: r = 0.05, t = 0.28, *P*-value = 0.78).

Table 4.1: Linear model testing correlation between *H. minitabunda* spider weight taken before voracity and size

Coefficients	**Estimate**	**SE**	**t**	***P***
(Intercept)	-0.03	-3.12	-3.12	**< 0.01**
Size (mm)	0.04	5.62	5.62	**< 0.01**

P < 0.05 indicated in bold

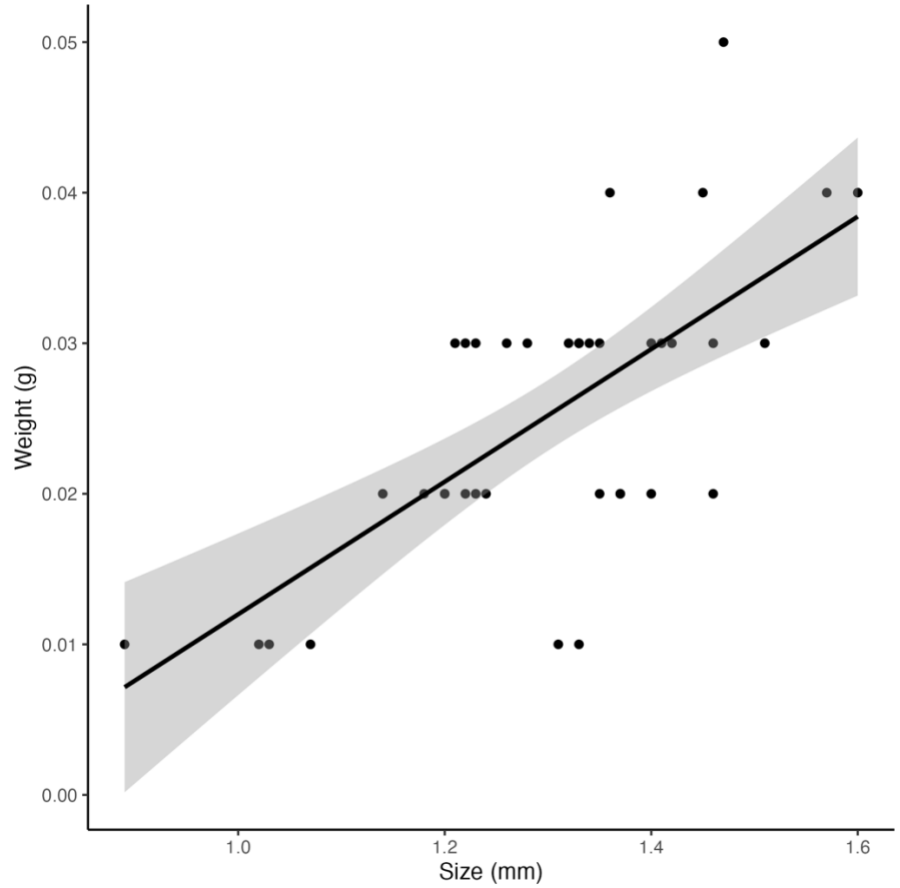

Figure 4.2: Relationship between *H. minitabunda* spider body size and weight before the voracity assay.

Table 4.2: Generalised linear model testing whether the body condition of *H. minitabunda* influences the number of prey eaten in the voracity assay.

Coefficients	Estimate	SE	z	*P*
(Intercept)	1.13	0.09	11.93	**< 0.01**
Condition	-44.99	12.25	-3.67	**< 0.01**

P < 0.05 indicated in bold

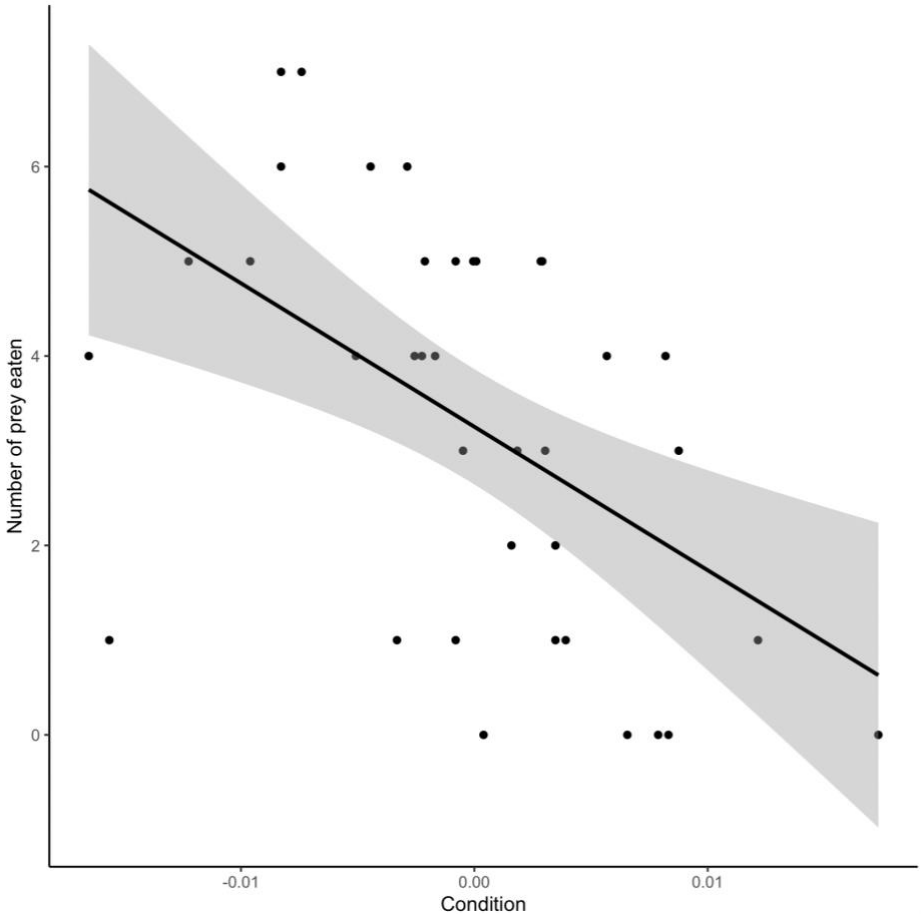

Figure 4.3: Relationship between body condition of *H. minitabunda* spiders and the number of prey eaten in the voracity assay.

Table 4.3: Linear model testing whether spider weight before the voracity test or size influenced the number of prey eaten in the voracity test for *H. minitabunda.*

Coefficients	Estimate	SE	t	*P*
(Intercept)	1.89	3.17	0.60	0.56
Weight before voracity test (g)	-32.88	25.85	-1.27	0.21
Size (mm)	1.75	2.62	0.67	0.51

$P < 0.05$ indicated in bold

147 There was no relationship between condition and display time in the mirror assay
148 (LM: t = 0.13, *P*-value = 0.90; Table 4.4). There was also no relationship between size (LM: t
149 = 0.52, *P*-value = 0.61; Table 4.5) or weight (LM: t = 0.52, *P*-value = 0.61; Table 4.5) and

display time in the mirror assay. There was no correlation between display time in the mirror assay and the number of prey eaten in the voracity assay (Pearson's correlation, r = -0.10, t = -0.54, *P*-value = 0.60; Fig. 4.4).

Table 4.4: Linear model testing whether body condition of *H. minitabunda* influences display time in the mirror assay.

Coefficients	Estimate	SE	z	*P*
(Intercept)	179.18	35.92	4.99	**< 0.01**
Condition	582.21	4605.07	0.13	0.90

P < 0.05 indicated in bold

Table 4.5: Linear model testing whether the weight or size of *H. minitabunda* spiders influenced display time in the mirror assay.

Coefficients	Estimate	SE	t	*P*
(Intercept)	-9.39	305.05	-0.03	0.98
Weight (g)	888.51	1709.12	0.52	0.61
Size (mm)	124.07	240.00	0.52	0.61

P < 0.05 indicated in bold

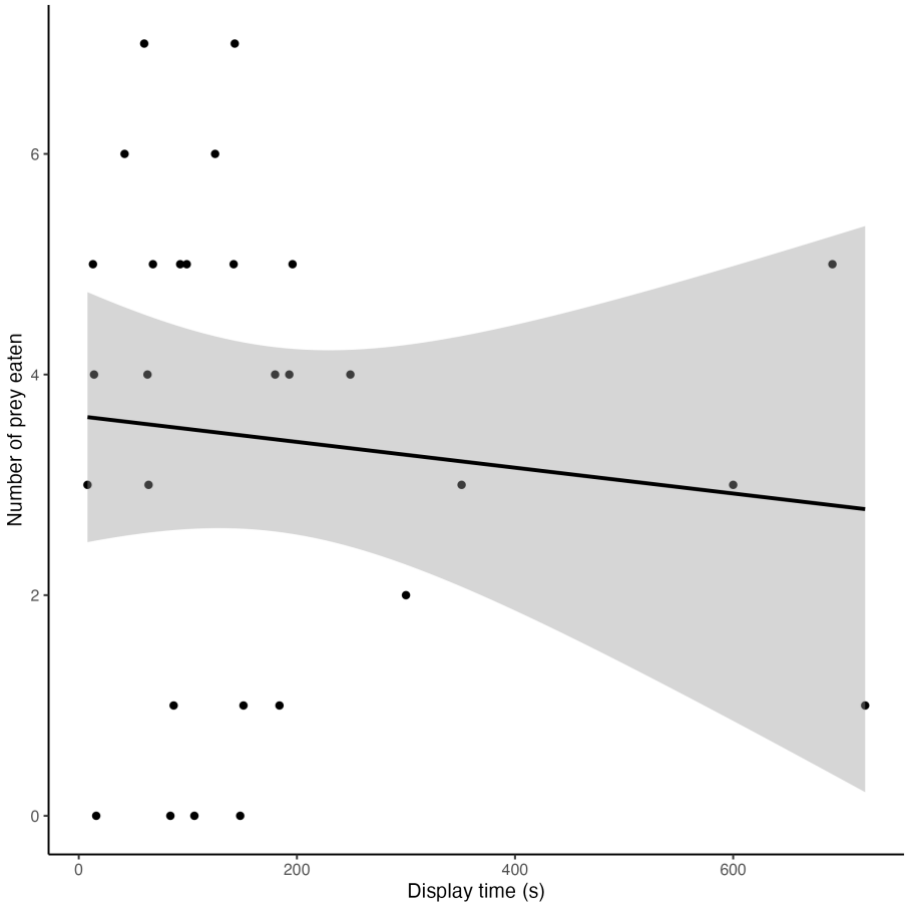

Figure 4.4: Relationship between display time (s) in the mirror assay and number of prey eaten by *H. minitabunda* in the voracity assay.

153 *4.5 Discussion*

154

155 I found no evidence of a direct relationship between predation and contest performance in *H.*
156 *minitabunda*. I found that spiders in poor condition consumed more prey in the voracity test
157 than spiders in good condition, despite controlling satiation in my experimental design. There
158 was no relationship between condition and display time in the mirror assays. My results are
159 in contrast with my prediction that individual performance in predation and contest contexts
160 are correlated in jumping spiders. Instead, my results suggest that predation and contest

161 behaviour are not directly related in *H. minitabunda*, and may be influenced by different
162 selection pressures.
163
164 *4.5.1 Body condition and predatory drive*
165
166 I found that voracity is strongly influenced by body condition, with individuals in poor body
167 condition consuming a larger number of prey than individuals in good body condition. These
168 findings are somewhat surprising as prior to the spiders participating in the voracity test, I
169 standardised their feeding regime by starving them for a period of seven days. One possible
170 explanation for this result is that my measure of body condition was not influenced by recent
171 feeding history. There has been some debate over the use of body condition indices in
172 invertebrates (Wilder et al., 2016). In my experiment, individual body condition prior to the
173 experimental starvation period may have influenced both their responses to the starvation
174 period and their behaviour in the assay.
175
176 When prey is scarce within the environment, predators may be more inclined to
177 behave aggressively to increase predation success (Pintor et al., 2008). In my study, the
178 starvation period prior to the voracity assay may have caused *H. minitabunda* in poor
179 condition to perceive their environment as one with scarce prey. This may have then
180 motivated spiders in poor condition to consume more prey items than spiders in good
181 condition. Clubionid spiders (Araneae: Clubionidae) that are starved for a period of 14 days
182 may consume up to 18 *Helicoverpa armigera* (Hübner, 1808) (Lepidoptera: Noctuidae) eggs
183 in a day, which is a significant increase in food consumption compared to eight eggs a day
184 under normal feeding conditions (Pearce et al., 2004). Therefore, starved individuals may be

consuming more to compensate for the lack of nutrients received over a prolonged period in the voracity assays.

4.5.2 The relationship between predation and contest performance

The lack of correlation between predation and contest performance may be the result of different selection pressures acting on these behaviours. For example, voracity may be most strongly influenced by physiological factors such as metabolic rate or hunger level. Although spiders can go long periods without eating, short periods of starvation can have strong effects on their predation behaviour. Another jumping spider, *Servaea vestita* (Karsch, 1878) (Araneae: Salticidae) was more likely to orient towards prey after a seven day starvation period than when they were recently fed (Zurek et al., 2010). Zurek et al. (2010) used the same starvation period I used in my voracity assay with *H. minitabunda.* Moreover, female *S. vestita* were more inclined to stalk prey after the starvation period (Zurek et al., 2010). Similarly, there is a correlation between hunger level and predation performance in the jumping spider *Phidippus coccineus* (Peckham & Peckham, 1901) (Araneae: Salticidae) (Gardner, 1966). Additionally, *Nesticodes rufipes* (Lucas, 1846) (Araneae: Theridiidae) spiders exhibit faster attack rates following a starvation period of 20 days compared to spiders which were only starved for five days (Rossi et al., 2006). Given the strong potential effects of starvation on predation behaviour, assessing voracity under a non-restricted food regime may alter individual performance rankings in *H. minitabunda*.

An alternative explanation for why I did not find a correlation between predation and contest performance in my experiment is that I only tested female spiders. My experiment was conducted near the end of the breeding season when females were abundant, with fewer

males and juveniles available for collection. Females are often highly predatory as they increase their energy reserves for reproduction (Anderson, 1978; Austad & Thornhill, 1986; Wen et al., 2020). For instance, females require enhanced nutrition for their eggs whereby the fecundity of female *Pardosa pseudoannulata* (Bösenberg & Strand, 1906) (Araneae: Lycosidae), also known as wolf spiders, increases on a high lipid diet (Feng et al., 2022). In terms of consumption quantity, female *Phidippus audax* (Hentz, 1845) (Araneae: Salticidae) jumping spiders consume high numbers of prey until oviposition compared to males who consume fewer prey (Givens, 1978). Moreover, females favour medium sized prey items, whilst males favoured small prey items (Givens, 1978). Females may not be under strong selection for contest performance, whereas male spiders are typically under strong selection for intrasexual competition (Austad, 1983; Keil & Watson, 2010; Whitehouse, 1997). Thus, predation and contest performance in *H. minitabunda* may be more influenced by sex specific selection on ecological traits, than by personality traits such as boldness and aggression.

During the voracity assay trials, some prey were not entirely consumed. This may be because the spider had ingested the nutritional contents that are easily obtained from the prey item (Givens, 1978). Some parts of prey may require excessive energy to extract the nutrients from, which may cause an individual to proceed with other predation attempts instead (Givens, 1978). Pursuing new prey items in this way may be an optimal foraging strategy with individuals searching for and consuming food in the most efficient way possible, to receive the maximum amount of energy (Pyke & Starr, 2021; Schoener, 1987). Predators favour prey items that are of high nutritious value (Zumpe et al., 2001). Thus, in my experiment *H. minitabunda* may have shifted their priority to extracting easily obtainable nutrients from other prey that were available if doing so required less energy expenditure, inflating their prey capture rates.

Another possible explanation for the lack of correlation between predation and contest performance is that females may have recognised themselves in the mirror assay, affecting display duration. If spiders recognised their reflection in the mirror, this would mean the mirror test is not an accurate assay of contest (and aggression) performance. The purpose of the mirror test is to assay how an individual responds when confronted with a conspecific with identical morphology. Mirror self-recognition studies have mostly been conducted on great apes who show evidence of self-recognition (Anderson, & Gallup, 2015). Bottlenose dolphins (*Tursiops truncatus*) (Montagu, 1821) (Cetacea: Delphinidae) (Reiss & Marino, 2001) and Asian elephants (*Elephas maximus*) (Linnaeus, 1758) (Proboscidea: Elephantidae) also demonstrate mirror self-recognition (Plotnik et al., 2006). Self-recognition tends to occur in large-brained mammals however, there is evidence of self-recognition in *Ocypode quadrata*, known as ghost crabs (Fabricius, 1787) (Decapoda: Ocypodidae) (Robinson, 2023). Although mirror self-recognition is not accepted in many species, the exceptional cognitive abilities of many species of jumping spiders (Cross et al., 2020; Wilcox & Jackson, 1998; Wilcox & Jackson, 2002) could provide an explanation for the lack of correlation I recorded between predation and contest performance in *H. minitabunda*.

4.5.3 Conclusion

I found no evidence that predation and contest performance is correlated in the jumping spider *H. minitabunda*. I suggest that the most likely explanation for the lack of correlation in performance is that predation and contest tasks depend on different traits. Female predation performance may be strongly dependent on building reserves for reproduction, with few resources allocated to contest performance. It may be that females are balancing trade-offs

between engaging in prolonged contests and increasing their energy reserves for investment in reproductive efforts. For future research, it would be interesting to test male *H. minitabunda* to see if their performance in the predation and contest assays differs to females. Moreover, further investigation into self-perception in jumping spiders would determine whether self-recognition is possible in *H. minitabunda*, giving insight into whether mirror assays measure aggression in competitive contexts.

266 *4.6 References*

267

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Chapter 5:

General Discussion

My thesis describes the contest and predation behaviour of the Aussie bronze jumping spider, *Helpis minitabunda* (Koch, 1880) (Araneae: Salticidae), and tests whether there are links in performance between these two traits. I found that contests in *H. minitabunda* are characterised by three, escalating phases (assessment, display and contact; Chapter Two). Juveniles, females and males were equally likely to start the contests at the assessment phase, however adults were more likely to escalate contests. Males were more likely to escalate into the display phase compared to females or juveniles, and both females and males were more likely to initiate the contact phase than juveniles. Interestingly, size did not influence contest outcomes. Juvenile contest assessment strategies most closely match the mutual assessment strategy, however evidence for female and male assessment strategies does not currently fit traditional assessment models. I found that latency for the spider to emerge correlated with prey capture behaviour (Chapter Three). However, there was no evidence of correlations in predatory behaviour between model prey assays and voracity assays, suggesting that predation performance is sensitive to environmental context. I found no correlation between individual predation and contest performance (Chapter Four). However, body condition appears to influence voracity. Together, my results suggest that while there are some links between boldness and aggression, behaviour in jumping spiders is sensitive to context, with performance across different ecological tasks influenced by distinct underlying mechanisms.

In behavioural ecology, aggression involves performing violent displays or actions to gain ownership of resources or for social hierarchy purposes (Briffa & Hardy, 2013; Natarajan et al., 2009). Many behaviours are influenced by levels of aggression, including contests and predation behaviour. In contests, individuals may compete for food, territory and mates (Eibl-Eibesfeldt, 1961). Contests involve aggressive signalling behaviours which may consist of displays of morphological weapons to rivals, and locomotive display sequences

(van Staaden et al., 2011). Fighting encompasses agonistic behaviour with a risk of incurring or receiving injuries (Arnott & Elwood, 2009; Eibl-Eibesfeldt, 1961). Predation is also considered an aggressive behaviour, as predators pursue potential prey, capture and kill it (Estes & Goddard, 1967). In addition, many species give aggressive vocalisations to defend territories (Kirchhof et al., 2001) or to alert conspecifics of predators (Cunningham & Magrath, 2017). While many behaviours may be considered aggressive, we do not always understand the links between those behaviours.

I did not find any evidence of a correlation between predation and contest performance in *H. minitabunda* (Chapter Four). This was surprising, as both predation and contest behaviours are regarded as aggressive traits. Individuals with high levels of aggression are expected to be more likely to both escalate contests and catch more prey than individuals with low levels of aggression (Pintor et al., 2009; Sih et al., 2012). For instance, when there are lots of *Pacifastacus leniusculus* (Dana, 1852) (Decapoda: Astacidae) crayfish within a vicinity they exhibit heightened agonistic behaviour between conspecifics in addition to spending more time foraging (Pintor et al., 2009). However, few studies have experimentally tested these links. My results to date suggest that in jumping spiders, predation and contest performance is determined by factors other than direct levels of aggression.

Aggressive behaviour may be influenced by genetics, hormones and physical ability. For example, aggression in male chickens appears to be influenced by multiple genes (Craig et al., 1965). Serotonin levels in male *Gryllus bimaculatus* (De Geer, 1773) (Orthoptera: Gryllidae) crickets influence the level of aggression they express (Rillich & Stevenson, 2018). Predation and contest performance may also be linked by physical strength, as

strength is often required to resolve physical conflicts by overpowering their opponent (Arnott & Elwood, 2009), in addition to catching and killing prey (Griffiths, 1980).

Predation and contest performance may not have been correlated in *Helpis minitabunda* due to the role of hormones on behaviour. I found that display time in the mirror assay did not correlate with voracity, indicating that these tasks rely on different factors. A study on *Manduca sexta* (Linnaeus, 1763) (Lepidoptera: Sphingidae), also known as the tabacco hornworm caterpillar, found elevated concentrations of the neuropeptide F1 (NPF1) in its midgut following starvation, a hormone responsible for controlling hunger cues (Kaur et al., 2024). This suggests that in the voracity tests, predatory behaviour of *H. mintabunda* may have been driven by hormonal stimulants to acquire food. Conversely, behaviour in the mirror tests may have been driven by different hormones, such as testosterone which contributes to aggression in *Gallus gallus* (Linnaeus, 1758) (Galliformes: Phasianidae) birds, a species also recognised as the red jungle fowl (Johnsen & Zuk, 1995). Thus, different hormones may contribute to contest and predation activity in *H. minitabunda*.

Another potential explanation for why I did not find a correlation between predation and contest performance is my experimental design. My experimental assays may have been testing traits that are not related to aggression. This is supported by my finding no correlation between performance in the model prey and voracity assays in Chapter Three. The voracity assay may have tested how *H. minitabunda* perform in high prey density environments (Parsons et al., 2022). Performance in high prey density environments may be quite different to performance in low prey density environments, such as in the model prey assay. Further, spiders were starved for seven days prior to the voracity assays. Therefore, hunger level may have stimulated faster prey capture to ensure acquisition of a food source whilst it was

available to them (Parsons et al., 2022). This context (high hunger – high prey availability) is also quite different to the context presented to spiders in the mirror assay, which may have driven differences in performance. Alternatively, my contest assays may not have been accurate measures of aggression, as contests were set up in scenarios where there was no resource to contest (e.g., a potential mate, nest or prey) (Arnott & Elwood, 2019; Briffa & Sneddon, 2007; Enquist & Leimar, 1987; Murray & Gerrard, 1985). Assessing aggression in a low-stakes contest may not result in an accurate measure of aggression.

Another potential explanation for the lack of correlation between predation and contest performance is that performance in these tasks is under different selection pressures. Traits responsible for contest success may include body size, signalling, stamina or strength (Briffa & Lane, 2017). However, predation success may be attributed to traits such as reaction speed (Domenici, 2002), visual acuity (Thery & Gomez, 2010), stealth (Chevallay et al., 2024) and composure (Clark, 2016). This indicates that different traits contribute to an individual's predation and contest performance. Further research into how different morphological, physiological and cognitive traits contribute to performance and interact in jumping spiders is needed.

Cognitive ability may influence contest and predation activity. Cognition can influence contest performance by adapting behaviour based on prior contest experiences (Reichert et al., 2017). Learned experiences can improve predation performance (Shettleworth, 2001). Cognition enables an individual to assay resource value, determining how much effort they are willing to exert into fighting for a contested resource (Reichert et al., 2017). Individuals that adopt mutual assessment strategies in contests require heightened cognition, which could result in variation within a species in individual performance

(Reichert et al., 2017). For example, it takes adequate mental aptitude for an individual to calculate opponent body size and use this information to evaluate its physiological capacity and resource holding potential (Reichert et al., 2017). I found evidence to suggest that juveniles adopt mutual assessment strategies in contests (Chapter Two), which in turn suggests strong cognitive capacity in *H. minitabunda.* In addition, cognitive ability influences how individuals process and store information about prey densities and travel times, affecting their foraging decisions and potentially influencing foraging success (Shettleworth, 2001). It would be interesting to test how cognitive ability influences predation and contest performance in *H. minitabunda*, particularly as jumping spiders are known for having complex cognitive abilities such as detouring behaviours and trial-and-error strategies (Cross et al, 2020; Jackson et al., 2001; Wilcox, & Jackson, 1998).

I found that body size did not influence contest outcome in juvenile, female or male *H. minitabunda* (Chapter Two), indicating that personality traits may play a stronger role in contest behaviour than size. Other studies have found that large individuals may also be strong and therefore more inclined to engage in aggressive behaviour due to a higher likelihood of winning (Wright et al., 2019). Conversely, small individuals may have a higher likelihood of incurring more costs in contest, eliciting a retreating response (Hardy & Briffa, 2013). Body size influences contest outcomes in many species including *Ctenophorus decresii* (Duméril & Bibron, 1837) (Squamata: Agamidae), the tawny dragon (Umbers et al., 2012); *Teleogryllus commodus* (Walker, 1869) (Orthoptera: Gryllidae), the black field cricket (Reaney et al., 2011); male *Metellina segmentata* (Clerck, 1757) (Araneae: Tetragnathidae), the Autumn spider (Hack et al., 1997); *Misumenoides formosipes* (Walckenaer, 1837) (Araneae: Thomisidae), male crab spiders (Dodson & Schwaab, 2001) and *Xiphophorus helleri* (Heckel, 1848) (Cyprinodontiformes: Poeciliidae), swordtail fish (Prenter et al., 2008).

However, in my study contests were set up without a resource to compete over. Individuals engage in contests to settle ownership disputes over nests, territory, mates, food and shelter (Briffa & Hardy, 2013). As a result, spiders in my contest assays had no incentive to exert themselves in contests (Enquist & Leimar, 1987; Arnott & Elwood, 2008), and thus their performance in my contest assays may not be an accurate representation of the influence of body size on contest outcome.

I found that adults were more likely to escalate contests than juveniles. Contest escalation in adults may be predicted as adults have more to gain from winning contests (i.e., reproductive success) than juveniles. Males may engage in escalated contests over females to gain copulations, as observed in *Euophrys parvula* (Bryant, 1935) (Araneae: Salticidae) jumping spiders (Wells, 1988). Juveniles may engage in play fights which have lower costs and are less likely to escalate as they are simply engaging in practicing events (Cenni & Fawcett, 2018). Further, in my experiments adult *H. minitabunda* may have possessed previous fighting experience from agonistic encounters in the field. This may have affected contest escalation in my experiments as experience influences contest behaviour (Hsu et al., 2006).

I found a correlation between latency for *H. minitabunda* to emerge from the acclimation vial in the model prey assay and prey capture success (Chapter Three). Latency to emerge into a new environment is a common measure of boldness (DiRienzo et al., 2013; Herde & Eccard, 2013; Niemelä et al., 2012; White et al., 2013). Personality traits like boldness can influence foraging behaviour by shaping decision-making during foraging activity, and even fostering specialisation in foraging (Toscano et al., 2016). Bold individuals are predicted to make faster decisions, consume more prey and pursue different types of prey

than shy individuals (DiRienzo et al., 2013; Ioannou et al., 2008). For example, bold *Callithrix jacchus* (Linnaeus, 1758) (Primates: Callitrichidae), referred to as common marmosets, make faster decisions to approach an unfamiliar food source than shy individuals (Šlipogor et al., 2016). Bold *Parus major* (great tits) also make faster decisions to relocate to new food patches compared to shy individuals *(*Arvidsson & Matthysen, 2016). Bold *Tenebrio molitor* (Linnaeus, 1758) (Coleoptera: Tenebrionidae), or mealworm beetles have greater metabolic rates than shy individuals (Krams et al., 2013). This may drive bold personalities to invest more effort into foraging to fulfil metabolic requirements (Troxell-Smith & Mella, 2017). Food consumption patterns therefore vary between individuals due to personality type (Toscano et al., 2016).

5.1 Future Research

Future research may test how body size shapes contest outcome in *H. minitabunda* when a resource is included in the experimental arena. I predict that body size would have a stronger influence on contest outcome in the presence of limited resources than in my experiments that were conducted without the presence of resources. I also suggest testing whether predation and contest performance is correlated in adult males, as my research only explored links in performance in adult females. It is possible that hormone levels may drive differences in female and male performance, which may affect links between predation and contest performance. My research to date suggests that different selection pressures drive predation and contest performance. Identifying the factors that influence performance across ecological tasks would provide further insight into whole organism performance.

5.2 Conclusions

Overall, in my thesis I found evidence that predation and contest performance is influenced by different traits in *H. minitabunda*. Contests are characterised by three escalating phases, with adults more likely to escalate than juveniles. Interestingly, body size had little influence on contest outcomes, but this may be due to assaying contest behaviour without a contestable resource such as a potential mate or food in the experiment. Predation behaviour in *H. minitabunda* appears to be shaped by a combination of personality traits (i.e., boldness) and contextual cues. My findings provide insight into understanding whole organism performance and how behaviour, physiology and morphology interact to shape performance across different ecological tasks.

186 *5.3 References*

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