Locomotory mimicry in ant-like jumping spiders (Salticidae)

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Zoology at the University of Canterbury

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2012

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Acknowledgements

I would like to thank my supervisors, Ximena Nelson for her incredible ability to quickly review documents and send critical feedback, which was of vital importance to my work, and Robert Jackson for being there for questions and for his hospitality in letting a 1st year undergraduate student help look after his collection of tropical jumping spiders. I would also like to thank Aynsley Macnab for teaching me how to look after the spiders once I had the opportunity. This all helped increase my interest and understanding of these fascinating animals.

Abstract

The jumping spider genus *Myrmarachne* (Salticidae) contains many different morphological ant mimics that resemble a wide variety of ant species. This mimicry enables *Myrmarachne* to evade ant-averse predators that confuse the spiders with ants. A conspicuous trait of *Myrmarachne,* which is frequently mentioned in the literature but has been overlooked experimentally, is locomotory mimicry. In this thesis, I quantified, for the first time, the locomotory pattern of non-ant-like salticids, *Myrmarachne,* and their presumed models. Indeed, I found that the locomotion of the mimics resembles that of ants, but not of other salticids. I then attempted to identify whether this behavioural mimicry enhances the morphological component of the mimicry signal. The locomotion component was tested by modelling a 3D computer animation based on the morphology of *Myrmarachne*, and then applying either non-ant-like salticid motion characteristics or ant-like locomotion to the models. These animations were presented to ant-eating salticid predators, which are known to have acute vision, in order to identify any differences in how the predators reacted to each virtual prey type based solely on differences in locomotory behaviour. No significant effect was identified for enhancing the deception, but there was a non-significant trend that hinted at an enhancement of the mimicry signal, suggesting that a more robust finding would be found with a larger sample size. Additionally, ant mimics are unusual in their relationship to their model organism, as the ant models are also potential predators of the mimic. Predation by visual ant species may exert selection pressure on *Myrmarachne* across some aspects of morphological or behavioural mimicry. In turn, this may select for traits that improve *Myrmarachne'*s survival in close proximity to their highly aggressive models. Consequently, I investigated whether ant-like locomotion is salient to a visual ant species, *Oecophylla smaragdina*. I found that the locomotion typical of ants and *Myrmarachne* is more attractive to ants than non-ant-like salticid locomotion. This suggests that the trade-off of increased resemblance to ants is not just towards being categorised as prey by ant-eating species, but also by being more attractive to ant species. This may place them at greater risk of predation by the model. As a whole, these results suggest that there is selection pressure on *Myrmarachne* for increased resemblance to a model by locomotory mimicry, despite associated costs when faced with ant-eating predators and when living in proximity to models that are both aggressive and visual.

Chapter 1: Introduction

Henry Walter Bates first proposed his theory for mimicry among insects in 1862 (Bates 1862). From observations of sympatric butterflies in the family Heliconidae and others, Bates proposed that resemblances in external appearance, shape, and colour can occur between widely distinct families, suggesting that the effect is like imagining "a Pigeon to exist with the general figure and plumage of a Hawk." He noticed that some butterflies, which apparently mimicked the Heliconidae, flew in the same parts of the forest and generally alongside their model. Bates did not restrict his idea to the Lepidoptera, extending it to certain families within most other insect orders. Since this discovery, mimicry has been found or hypothesised in many different invertebrate taxa in addition to butterflies (Srygley 1994, 1999; Srygley & Ellington 1999), including beetles (Taniguchi et al. 2005), hemipterans (Ceccarelli 2009), flies (Golding et al. 2001; Golding & Edmunds 2000) ants (Ito et al. 2004), and spiders (Cushing 2012, 1997).

Fisher (1958) described the theory of mimicry as the greatest post-Darwinian application of natural selection. Fisher (1958) explained that one aspect of the environment, such as predation, can affect a set of characters in an organism, such as coloration, pattern, and behaviour. He pointed out that the theory of mimicry enables us to precisely define cause and effect and to identify the adaptive significance of these characters. Having all of these factors explained under one umbrella of mimicry theory is a rarity for students of the natural world (Fisher 1958). However, well over a century after its first description (Bates 1862), experimental data on this phenomenon is still generally lacking. A significant fraction of proposed Batesian mimics are yet to receive rigorous experiments required to demonstrate that resemblance functions as a signal to deceive predators, thereby reducing predation on the mimic.

The mimicry signal deceives species that receive the signal into accepting that the identity of the mimic is the same as that of its model because it possesses identical traits

to the model. The most often cited examples in the literature are Müllerian and Batesian mimicry representing two ends of a mimicry continuum (Speed 1999). At one end lies Müllerian mimicry, where several noxious species share the same aposematic, or warning, signal (Ruxton et al. 2004). Aposematic species, which are frequent Batesian and Müllerian models, benefit from being common as otherwise the noxious signal would not be recognised by predators (Joron & Mallet 1998; Edmunds 2000; Ruxton et al. 2004). Because this signal is strengthened when displayed by many individuals, the signalling species will benefit if other noxious species share the same signal. Thus, noxious species are expected to be monomorphic (Joron & Mallet 1998) and often gregarious (Mappes & Alatalo 1997; Gamberale & Tullberg 1998). The noxious signal can then cross the species boundary, resulting in Müllerian mimicry. In the case of Müllerian mimicry, both model and mimic benefit from the mimicry signal (Macdougall & Stamp Dawkins 1998). The idea that Müllerian mimicry is truthful has been criticised, as a benefit to all species within a Müllerian mimicry ring will only occur if they are all equally noxious (Fisher 1958). It is now widely recognised that the honesty of the signal varies across the mimicry continuum. If one species is slightly less noxious (less honest), it will have a negative effect on the other, more noxious (more honest), species within the mimicry ring. This means these lesser-noxious species slide down the continuum towards Batesian mimicry.

As a deceptive signal where a palatable or harmless species mimics the model's noxious signal, Batesian mimicry differs from Müllerian mimicry because only the mimic benefits, while the model suffers because predators that experience the non-noxious mimic may target the model species (Edmunds 1974, 2000; Joron & Mallet 1998). In Batesian mimicry, it is suggested that the mimic should exist at a lower density and abundance than the noxious or dangerous model species (Edmunds 1974; Joron & Mallet 1998). This is because the palatable or safe mimic hides among noxious or dangerous species that can 'validate' their harmful characteristics (Ruxton et al. 2004). Alternatively, if the mimics were to become too common, predators would learn to ignore the deceptive signal (Edmunds 1974; Joron & Mallet 1998). Subsequently, diversifying frequency-dependent selection would be expected favouring rare mimetic morphs (Joron & Mallet 1998). These morphs could lead to stable polymorphisms (different models being mimicked by one species) (Joron & Mallet 1998), as found in the jumping spider (Salticidae) genus *Myrmarachne* (Salticidae) (Borges et al. 2007).

Batesian mimics are often regarded as either 'general' (also known as 'non-specific', 'poor' or 'imperfect') or 'specific' (also known as 'good' or 'perfect') mimics of their model (Edmunds 2000, 2006; Nelson 2010). General mimics only share a few characteristics of their model taxa, such as movement and colour, and do not show precise resemblance, at least to the human eye. For example, general ant-mimicking spiders often lack the ant-like constriction between the cephalothorax and abdomen (Edmunds 2006; Pekár & Jarab 2011). Where this has been investigated, the perception of general mimicry as being somewhat imprecise seems also to hold with their predators (Nelson 2012). A general morphological mimic may benefit from copying movement more than morphology (Pinheiro 1996), as at speed a general mimic may appear as a specific mimic (Pekár et al. 2011; Pekár & Jarab 2011). Batesian mimicry will be covered in more detail in Chapters 2 and 3 of this thesis.

Aside from the Müllerian - Batesian continuum, there are several other recognised forms of mimicry such as mimicry to deceive the model itself. If the species mimics traits of its model to prey on its model, the mimicry is regarded as aggressive. Examples of aggressive mimicry include araneophagic spiders of the genus *Portia* (Salticidae), which can mimic a struggling insect by plucking on the silk of a spider's web in order to attack the resident spider (Jackson & Blest 1982; Jackson & Hallas 1986), or may mimic the courtship display of other spider species in order to lure them towards *Portia* for attack (Jackson & Wilcox 1990).

Mimicry to deceive the model also occurs in taxa that live in close proximity to ants (myrmecophilous species). Myrmecophiles can utilise a range of tactics to live alongside their aggressive neighbours. These include behavioural avoidance, chemical defence, or chemical or tactile mimicry (For reviews see: Hölldobler & Wilson 1990; Dettner & Liepert 1994). Additionally, if the species mimics traits of the model that allow it to live with its model, the mimicry is referred to as Wasmannian mimicry. This was described by Rettenmeyer (1970) as "resemblances that facilitate a mimic's living with its host. The host species is the selective agent and is usually exploited by the mimic, but the relationship between the two species may be mutualistic or beneficial to both". Wasmannian mimicry will be covered in further detail in Chapter 4 of this thesis.

Ants (Formicidae) can be the most numerous insect in an ecosystem (Hölldobler & Wilson 1990). They can also be the leading predator of other invertebrates, possessing a diverse range of offensive and defensive techniques. The vast majority of ants live in social organisations and are able to mob animals with their powerful jaws and/or a fierce sting, sometimes even possessing an acid spray which can be deployed in defence (Edmunds 1974; Hölldobler & Wilson 1990). Because of these characteristics, ants provide a worthy model for Batesian mimicry. They can also provide a personal army if an animal was able to live in proximity to them (myrmecophily). Ants themselves are also abundant and a nest contains a high density of nutritious larvae. If defences can be overcome, ants present an abundant food source (myrmecophagy). Consequently, ants have influenced the evolution of many species by providing an exploitable resource, by symbiosis, and by acting as models for numerous mimetic organisms (Edmunds 1974; Hölldobler & Wilson 1990).

Batesian mimics often share visible traits of the model as the selection pressure is driven by the deception of model-averse, visual predators (Ruxton et al. 2004), although the finding that mimicry is often in the visual modality may simply be an artefact of our own highly visual perception of the world. In the case of aposematic species, mimics share the aposematic signal. In the case of ant-mimics, the mimics often resemble ants in morphology and behaviour (Cushing 1997, 2012) and are known as myrmecomorphic (ant-like) species. Among the Hymenoptera, it is the behaviour of some ants and wasps that is their most striking feature (Rettenmeyer 1970). Certainly, given that most ant species are often drab in colour, they seem unlikely candidates as aposematic species based on striking warning colouration (Jackson & Nelson 2012).

Most myrmecomorphic spiders appear to be Batesian mimics as the spiders lack stings and have weak-biting chelicerae (Rettenmeyer 1970; Cushing 1997, 2012). The potent stings and/or strong mandibles of their models may not threaten the mimic because in most situations there appear to be few interactions between mimic and model, and when they do encounter each other, mimics often exhibit avoidance behaviour (Reiskind 1977; Ceccarelli 2007). If myrmecomorphic spiders did possess methods to deceive their models in addition to visual predators, the most likely form of deception would be chemical, because ants mainly communicate through olfaction and generally have poor eyesight, with even slight changes to worker ant surface-odour triggering attack by her

sisters despite no change in her appearance (Hölldobler & Wilson 1990). To fool an ant, the mimic would therefore need to acquire cuticular hydrocarbons from the specific ant colony, as found in the iridescent non-ant-like salticid *Cosmophasis bitaeniata*, which is known to frequently invade ant's nests undetected in order to feed on ant larvae (Allan & Elgar 2001; Allan et al. 2002). Indeed, there are a large number of myrmecophiles fully integrated into the host ant's colony that do not resemble their host morphologically (Hölldobler & Wilson 1990).

All species in the salticid genus *Myrmarachne* are myrmecomorphic, or mimics that look like ants (Wanless 1978; Cushing 1997; Nelson et al. 2006). The ant-like appearance of *Myrmarachne* is due to a narrow, constricted abdomen and cephalothorax, which creates the illusion of a more hymenopteran body, possessing three body parts (head, thorax and abdomen) rather than two (cephalothorax and abdomen), as found in spiders. The genus *Myrmarachne* is also characterised by possessing slender legs, having antennal mimicry based on the raising of one pair of legs, and potentially a more ant-like and erratic locomotion than that of other salticids (Cushing 1997, 2012; Edmunds 2006; Ceccarelli 2008). *Myrmarachne* contains a large number of closely related species that mimic many different ant species (Wanless 1978; Jackson 1986; Edmunds 2006; Ceccarelli & Crozier 2007). Here, myrmecomorphy is a Batesian method of deceptive communication aimed at visual predators, such as spider-eating salticids and mantids (Nelson et al. 2006; Nelson & Jackson 2006; Nelson 2012; Huang et al. 2011). This deception causes ant-averse predators to confuse *Myrmarachne* with ants and therefore *Myrmarachne* evades predation from these visual predators (Nelson et al. 2006; Nelson & Jackson 2006).

As suggested by Rettenmeyer (1970), ants possess highly conspicuous behaviour likely to be mimicked. Ants generally move with continual, and often rapid, forward movement with a very limited number of stops, making frequent changes in direction while in motion (Chapter 2). Salticids also have characteristic movement patterns, which differ strikingly from those of ants. Salticid motion is generally composed of short bursts of movement with frequent stops of over one second and changes in direction are often carried out while stationary (Chapter 2). If a given mimic looked like its model but did not behave like it, predators may quickly learn to differentiate mimic and model. Consequently, mimicry should also extend to behaviour, such as

locomotion, in order to complete the charade. Locomotory mimicry is the similarity in swimming, walking, or flying of distantly related animals (Srygley 1994) and is the subject of Chapters 2 and 3 of this thesis. The motion and appearance of *Myrmarachne* may also provide an additional method of co-habitation with ants (Nelson et al. 2005).

Here I investigate the walking behaviour of *Myrmarachne* in order to ascertain whether *Myrmarachne* is a locomotory ant mimic. Because this thesis is written as a series of three stand-alone papers, there is inevitably some repetition of information in the introductions and reference sections of the respective chapters. In Chapter 2, I compare the locomotion of several species of *Myrmarachne* to their ant models to determine the similarity of their walking patterns, and also compare the locomotion of *Myrmarachne* with that of non-ant-like salticids. In Chapter 3, I investigate whether locomotory mimicry deceives visual animals by testing if ant-eating predators can distinguish mimic from model based solely on motion. In Chapter 4, I investigate the idea that morphological and locomotory mimicry may in some instances aid *Myrmarachne* living in sympatry with an ant species that is highly aggressive and likely to be unusually visual, *Oecophylla smaragdina* (Wheeler et al. 1922; Hölldobler 1983; Hölldobler & Wilson 1990) and which is often a model species for *Myrmarachne* (Cushing 1997; Edmunds 2006). Finally, in the discussion I coalesce my findings and consider the implications of my results in light of the rather scant current knowledge in the area of motion mimicry (Thery & Casas 2009).

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Chapter 2: The locomotory mimicry of *Myrmarachne*

Abstract

Species in the large ant-mimicking jumping spider genus *Myrmarachne* (Salticidae) have long been suspected of moving more like ants than their spider relatives. For these active spiders, locomotion that is more ant-like than spider-like may provide additional deceptive signals to complement their morphology, which has been shown to offer protection from ant-averse, visual predators. Through the use of video recordings, locomotory mimicry was investigated by comparing the movement patterns of several species of *Myrmarachne*, their putative model ants, as well as species of ordinary salticids. Support was found for locomotory mimicry of ants. However, there was no support for species-specific locomotory mimicry, suggesting that general ant-like movements are sufficiently deceptive to ant-averse predators.

Introduction

Batesian mimicry is a form of deceptive communication whereby a palatable species avoids predation by mimicking characteristics of a harmful model (Edmunds 2000). This type of mimicry is names after Henry Bates, who in 1862 recognised that the English bee hawkmoth (*Hemaris*) appeared to have the same size, form, and flight behaviour as a bee (Bates 1862). Behavioural mimicry has been frequently noted in the literature but has generally received little attention, with the vast majority of studies on Batesian mimicry investigating solely the morphological cues of the mimic. As defined in Srygley (1994), locomotory mimicry is the similarity in swimming, walking, or flying of distantly related animals. Of the empirical studies available on behavioural mimicry, wing motion of four species of *Heliconius* butterflies was more similar to the butterflies' co-mimics than to their sister taxa (Srygley 1999b). This form of

behavioural deception has been experimentally supported in the honeybee mimicking drone flies (Diptera) in the genus *Eristalis,* whose time spent on flowers and flying between flowers was more similar to honeybees (Hymentoptera) than to either other hymenopterans or other dipterans (Golding et al. 2001; Golding & Edmunds 2000).

The jumping spider genus *Myrmarachne* (Salticidae) contains over 200 species of ant-like, or myrmecomorphic, spiders (Wanless 1978; Edmunds 2006; Jackson 1986a). Studies suggest that *Myrmarachne*'s ant-like morphology is due to selection for Batesian mimicry against spider-eating predators like mantids and araneophagic salticids (Nelson et al. 2006a; Nelson & Jackson 2006; Nelson 2012; Huang et al. 2011; but see Nelson & Jackson 2009), but studies of behavioural mimicry of locomotion are sorely lacking, despite the fact that behavioural mimicry (including motion mimicry) is commonly acknowledged for *Myrmarachne* (McIver & Stonedahl 1993; Cushing 1997, 2012). As a whole, the focus of studies investigating ant mimicry has been on their appearance. However, myrmecomorphic spiders like *Myrmarachne* might be at risk of being distinguished from their model if their locomotory pattern, as well as their morphology, did not resemble that of the model.

When prey are at high densities, selection against odd individuals is expected to increase, a phenomenon known as anti-apostatic selection (Srygley 1999a). Although often used to explain similarity in morphology within a group (Srygley 1999a), anti-apostatic selection can also explain behavioural similarity. Experiments on the larvae of the blowfly *Calliphora* have demonstrated that, when the larvae are at high densities, faster larval movement increases predation on odd-appearing individuals (Wilson et al. 1990). Behavioural convergence may amplify the mimicry signal, as each signal conveyed to a receiver may enhance the learning of an additional signal (Wickler 1968; Rowe 1999), leading to a stronger receiver response than might occur if only one component of communication (modality) was used (Rowe 1999). In order to be lost in a crowd of harmful models, Batesian mimics should benefit by being rare relative to the model (Joron & Mallet 1998) and so we might anticipate that anti-apostatic selection should also select for locomotory mimicry among morphological mimics that rely heavily on locomotion.

Jumping spiders rarely run, instead usually moving with a 'choppy' movement pattern with frequent changes of direction, and often walking for only a few millimetres before pausing. This has been referred to as a 'stop-and-go' fashion of locomotion (Jackson 1990, 1986b). Ants, on the other hand, walk with a more continual pattern of forward motion and appear to run most of the time (pers. obs.), in significant contrast with the movement pattern of jumping spiders. The conspicuous manner in which ants move (Rettenmeyer 1970) has for a long time led authors to suggest that myrmecomorphic spiders move in a more ant-like and erratic fashion than ordinary spiders (Pocock 1908; Reiskind 1977; Wing 1983; Fowler 1984; Jackson 1986a; Oliveira 1988; Nelson et al. 2004). For example, the myrmecomorphic species *Myrmarachne lupata* moves rapidly across substratum and, despite pauses (cessation of stepping) being present in the locomotory pattern, it usually moves in a continual stepping motion for several minutes (Jackson 1986a). This is similar to the continual movement pattern observed in ants.

Ant-like spiders also hold their front pair of legs in the air, as if to mimic antennae (Pocock 1908; Reiskind 1977; Wing 1983; Jackson 1986a; Oliveira 1988; Lighton & Gillespie 1989). Antennal mimicry by *Myrmarachne* has recently been empirically supported (Ceccarelli 2008). However, ant-like locomotion, despite being acknowledged for *Myrmarachne* (Reiskind 1977; Jackson 1986a), has not been investigated. Locomotory mimicry may offer equally significant protection from predators as morphological mimicry and could be an important reason why some myrmecomorphic spiders are avoided by spider-eating predators (Pekár et al. 2011; Pekár & Jarab 2011).

The aim of this study was to determine whether the locomotion of the salticid genus *Myrmarachne* is closely matched to its ant models and to identify examples of species-specific locomotory mimicry within the genus. The most distinguishable locomotory behaviour belonged to the ant genus *Opisthopsis*, which moves with rapid and 'jerking' bouts of movement (Wheeler 1918), giving the genus the common name of strobe ant. This genus is the most probable model for *M. rubra* (Ceccarelli 2010) and the locomotion of these two species was examined in further detail.

Methods

With the exception of the non-ant-like salticid *Servaea vestita*, which was collected from Sydney, in New South Wales, I collected ants, non-ant-mimicking salticids (ordinary salticids) and ant-mimicking *Myrmarachne* salticids (Table 1) from three localities in Queensland, Australia (Cairns, Townsville, and Brisbane).

In northern Queensland, *M. lupata, M. rubra,* and *M. smaragdina* were found on palm fronds and other large leafed plants in close proximity to their models. The spiders were often caught running over the leaves (Fig. 1) or within their silken retreats (usually located on the underside of leaves over the leaf rachis). In Brisbane, *M. aurea* was collected running on the trunks of eucalypt trees. After testing, all animals were released where they were found.

Figure 1. Examples of where *Myrmarachne*, ordinary salticids, and ants were collected. A) *M. lupata* walking over a wide leaf. B) *Polyrhachis australis* (prospective model of *M. lupata*) walking over palm frond. C) Leaf type (*Licuala ramsayi*) where *Myrmarachne* and ants were often found.

Salticids were housed in individual plastic containers (40 mm diameter x 50 mm) containing a single small leaf and were fed vinegar flies (*Drosophila sp.*) and other small dipterans once each week. Salticids were fed with four or five small dipterans at one time. A piece of damp cotton wool was placed in the container to provide humidity.

Table 1. Species collected for locomotion tests. Ordinary salticids: species that do not resemble ants. Myrmecomorphic salticids: species that resemble ants in morphology. Ants: prospective models (Formicidae) of the myrmecomorphic salticids.

Species collected	Category	N
Myrmarachne aurea (Ceccarelli, 2010)	Myrmecomorphic salticid	7
Myrmarachne lupata (Koch, 1879)	Myrmecomorphic salticid	20
Myrmarachne rubra (Ceccarelli, 2010)	Myrmecomorphic salticid	20
Myrmarachne smaragdina (Ceccarelli, 2010)	Myrmecomorphic salticid	4
Oecophylla smaragdina (Fabricius, 1775)	Ant	17
Opisthopsis haddoni (Emery, 1893)	Ant	15
Polyrhachis ammon (Fabricius, 1775)	Ant	7
Polyrhachis australis (Mayr, 1870)	Ant	20
Polyrhachis daemeli (Mayr, 1876)	Ant	12
Cosmophasis micans (Koch, 1880)	Ordinary salticid	6
Cytaea sp. (Thorell, 1881)	Ordinary salticid	17
Hypoblemum sp. (Keyserling, 1883)	Ordinary salticid	19
Opisthoncus sp. (Koch, 1880)	Ordinary salticid	5
Servaea vestita (Koch, 1879)	Ordinary salticid	14

The experimental setup (Fig. 2) to record locomotion of the collected species consisted of a piece of white card (135 x 125 mm) with two perforated holes (5 mm from the top corners), which was hung vertically with two pieces of cotton threaded through both holes (hereafter referred to as 'card'). The card was hung within a topless white cardboard box (610 mm x 450 mm x 450 mm) 100 mm from the box floor. The distance between the hanging card and the closest side of the cardboard box (narrow side) was 50 mm. An individual ant, *Myrmarachne* or ordinary salticid (Table 1) was placed on the bottom right corner of the open side (side facing the video camera) of the hanging card. The test individual was then left on the card for 30 s to habituate, so that they were not recorded demonstrating escape behaviour.
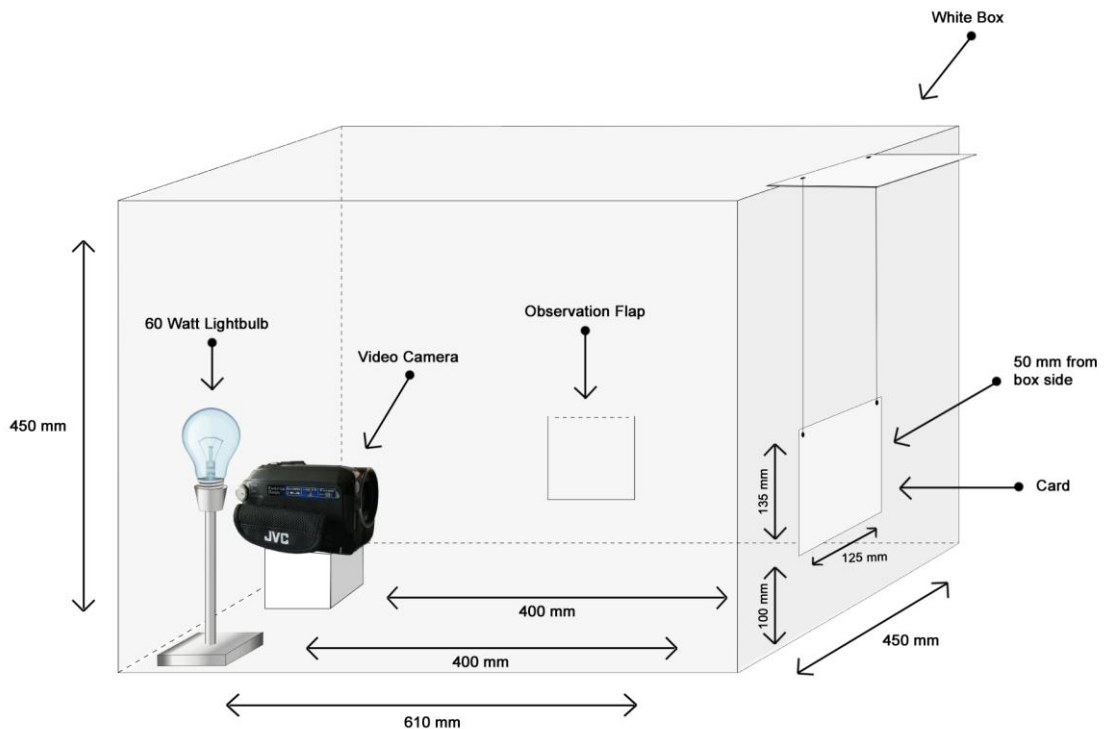

Figure 2. Experimental setup for recording locomotory behaviour of *Myrmarachne*, ordinary salticids, and ants.

A JVC Everio Hybrid hard disk video camera (model GZ-MG575AA) was placed opposite the card at a distance of 400 mm, and behaviour of the test individuals was recorded (at 25 frames per second) to capture 30 s of movement. When 30 s of movement was recorded, or when recording was stopped due to inactivity for 15 mins,

the test individual was removed and placed back in its individual housing container. The card was gently wiped with 90% ethanol to remove any chemical deposits and draglines from the test individual and was left to evaporate for 10 mins before testing resumed with another test individual. Recording was carried out between 8:00 and 16:00 h. Lighting was provided by a 60-watt lamp placed inside the box at a distance of 400 mm from the card.

Video analysis was conducted using the multi-platform video editing software Avidemux 2.5, Iconico Inc. Screen Callipers (version 4) and Screen Protractor (version 4). A 10 mm line drawn down the middle of the card was used for calibration of the computer callipers. The test individual was then tracked on the video for 30 s of movement. During this period, I measured the distance of each bout of movement (mm) as well as the number of frames that each bout lasted. The number of frames were subsequently converted into seconds to obtain bout duration. A bout of movement was defined by movement uninterrupted by a stop, time off screen, or stationary turns of over five consecutive frames. Turns were defined as a rotation (while either stationary or moving) of over 45° and the angle of each turn was measured using Screen Protractor. The time, in frames, to complete each turn was also recorded and converted into seconds. Rotations were not recorded within a 5 mm perimeter of the card edge.

Generalised linear models (GLM) with a quasi-poisson distribution to account for overdispersion of the data were used for the movement analysis. Data analysed were the number of movement bouts per 10 mm, the number of movement bouts per 10 s, speed per s and the distance travelled per bout of movement. Grouping variables were 'ants', '*Myrmarachne*' and 'ordinary salticids'. All analyses were performed using R version 2.15.0 (R core development team 2012). Pairwise analyses were done using Tukey HSD tests with Bonferroni corrections run using the 'multcomp' and 'nlme' packages.

The average rotation angle and turn duration for each of the three groups was also analysed. These data were obtained using three species of *Myrmarachne* (*M. lupata*, n = 18; *M. rubra*, n = 12; *M. aurea*, n = 5; N = 35), five ant species (*P. australis,* n = 8; *O. smaragdina*, n = 10; *O. haddoni,* n = 9; *P. daemeli*, n = 3; *P. ammon*, n = 5; N = 35) and three species of ordinary salticids (*Cytaea* sp., n = 9; *Hypoblemum* sp., n = 6; *Servaea vestita,* n = 3; N = 18). Data for rotation angle was normally distributed and was

analysed using ANOVA with Tukeys pairwise comparisons for each of the three groups (ants, ordinary salticids and *Myrmarachne*). Data for turn duration were not normally distributed and were analysed using Kruskal-Wallis tests, using Dunn's multiple comparisons for pairwise analyses.

Additionally, whether rotations were made by animals while moving (classed as 1) or while stationary (classed as 2) was investigated. The average value for each type of rotation per individual tested within the 30 s of analysis was used. These data were also obtained using three species of *Myrmarachne* (*M. lupata*, n = 20; *M. rubra*, n = 12; *M. aurea*, n = 5; N=37), five ant species (*P. australis,* n = 8; *O. smaragdina*, n = 10; *O. haddoni,* n = 9; *P. daemeli*, n = 3; *P. ammon*, n = 5; N = 35) and three species of ordinary salticids (*Cytaea* sp., n = 9; *Hypoblemum* sp., n = 6; *Servaea vestita,* n = 3; N = 18). Because these data were not normally distributed they were analysed using Kruskal-Wallis tests for each of the three groups (ants, ordinary salticids and *Myrmarachne*), using Dunn's multiple comparisons for pairwise analyses.

Results

There was a significant effect of grouping on the duration of movement per bout (F_2 = 34.866; $P < 0.0001$; Fig. 3A, Fig. 4, Table 2). Ordinary (non-ant-like) jumping spiders moved for significantly shorter periods of time during individual bouts of movement than did either ants or *Myrmarachne*, which did not differ significantly from each other.

Table 2. Coefficient results table for GLM conducted on the duration (s) of each bout of movement.

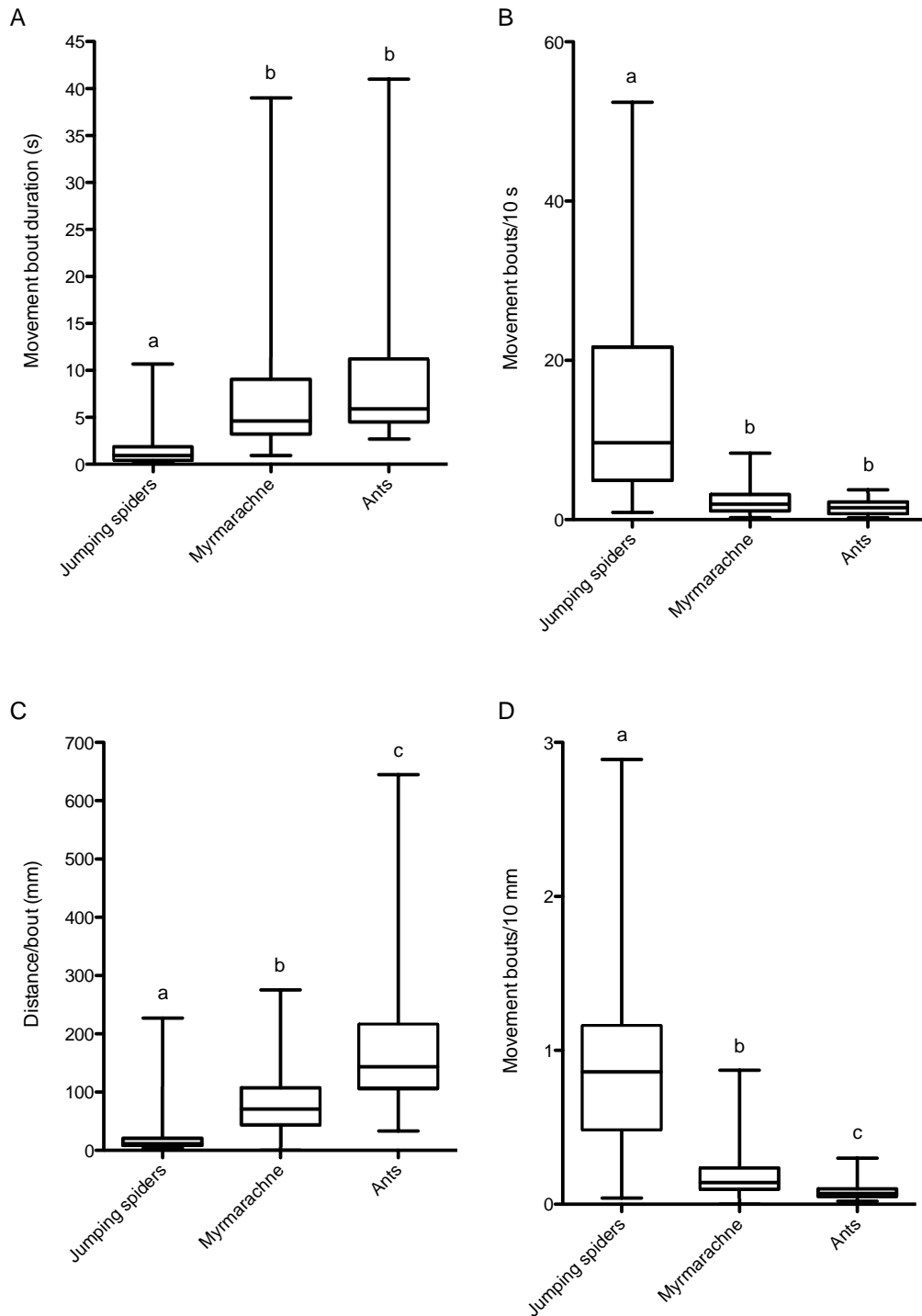| Grouping	Estimate	SE	t value	P
Intercept	2.3010	0.0949	24.235	<0.0001
Salticid	-1.8015	0.2644	-6.814	<0.0001
Myrmarachne	-0.2932	0.1566	-1.873	0.0628

Figure 3. Movement characteristics (median and 1st and 3rd quartiles; whiskers represent range) for ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. A) Duration of movement bouts. B) Number of bouts of movement in 10 s. C) Distance travelled per bout of movement. D) Number of movement bouts per 10 mm travelled. Letters denote significant differences using Tukeys pairwise comparisons (all P < 0.0001).
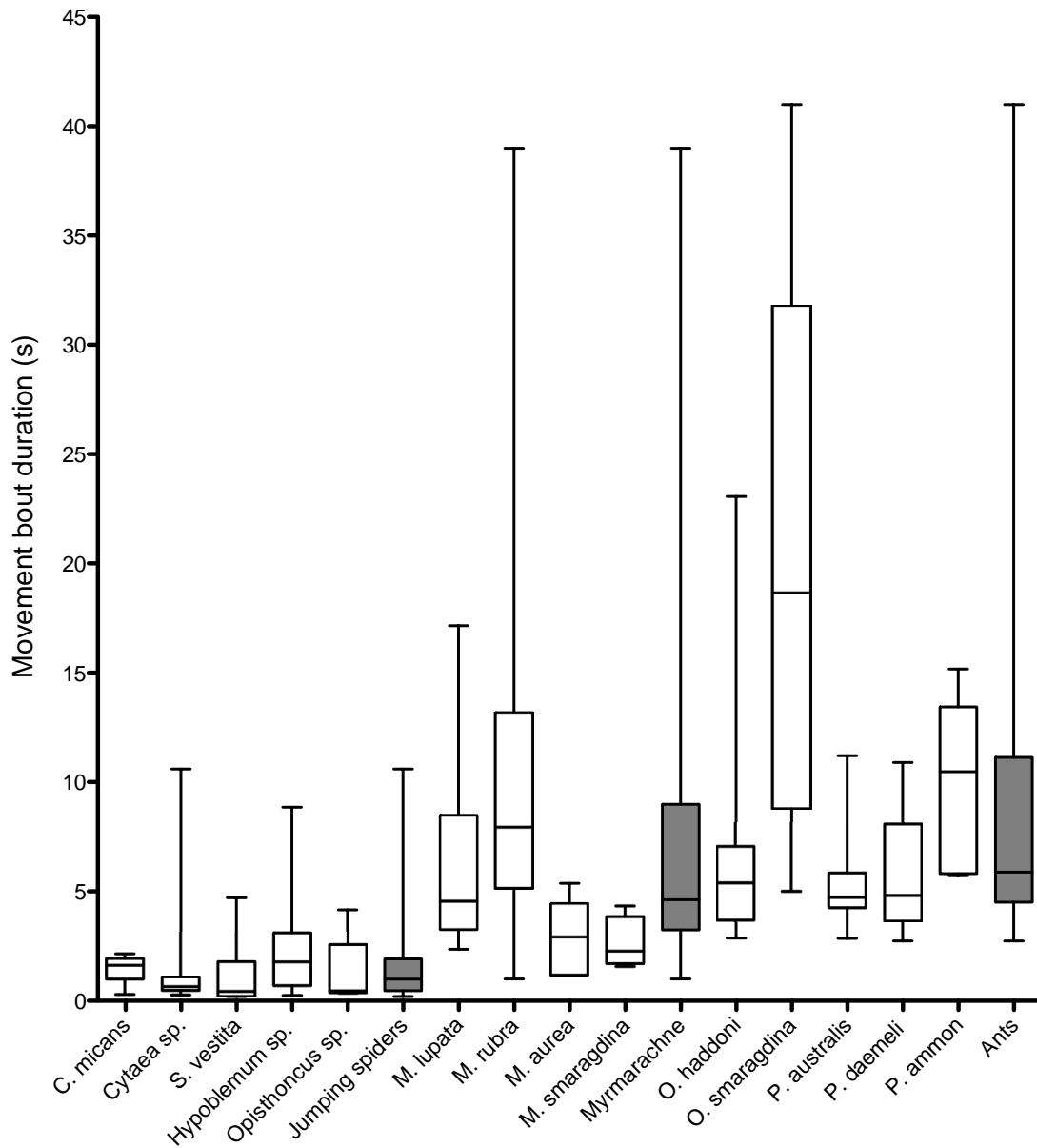
Figure 4. Duration of movement bouts (median and 1st and 3rd quartiles; whiskers represent range) for each tested species of ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. Grey boxes represent pooled data for each group.

There was a significant effect of grouping on the number of bouts in a 10 s period ($F_2 = 114.46$; $P < 0.0001$; Fig. 3B, Fig. 5, Table 3). Ordinary (non-ant-like) jumping spiders had significantly more bouts of movement in a 10 s time period than did either ants or *Myrmarachne*, which did not differ significantly from each other.

Table 3. Coefficient results table for GLM conducted on bouts of movement per 10 s.

Grouping	Estimate	SE	t value	P
Intercept	0.4915	0.2005	2.451	0.0152
Salticid	2.2524	0.2129	10.582	<0.0001
Myrmarachne	0.3621	0.2788	1.299	0.1957

There was also a significant effect of grouping on the on distance travelled per bout of movement ($F_2 = 89.624$; $P < 0.0001$; Fig. 3C, Fig. 6, Table 4). Ordinary (non-ant-like) jumping spiders travelled significantly shorter distances than did *Myrmarachne*, which in turn travelled significantly shorter distances than did ants.

Table 4. Coefficient results table for GLM conducted on distance travelled per bout of movement.

Grouping	Estimate	SE	t value	P
Intercept	5.2255	0.0673	77.619	<0.0001
Salticid	-2.297	0.2325	-9.881	<0.0001
Myrmarachne	-0.817	0.1323	0.1323	<0.0001

Finally, there was a significant effect of grouping on the on the number of bouts of movement per 10 mm travelled ($F_2 = 204.8$; $P < 0.0001$; Fig. 3D, Fig. 7, Table 5). Ordinary (non-ant-like) jumping spiders performed significantly more bouts of movement than did *Myrmarachne*, which in turn performed significantly more bouts of movement than did ants as a whole.

Table 5. Coefficient results table for GLM conducted on bouts of movement per 10 mm.

Grouping	Estimate	SE	t value	P
Intercept	-2.5014	0.1571	-15.921	<0.0001
Salticid	2.3711	0.1654	14.333	<0.0001
Myrmarachne	0.8366	0.1982	4.221	<0.0001

We found no evidence in any of the above movement characteristics that suggested that *M. rubra* moved more like its model (*Opisthopsis haddoni*) than other ants (Figs. 4-7).
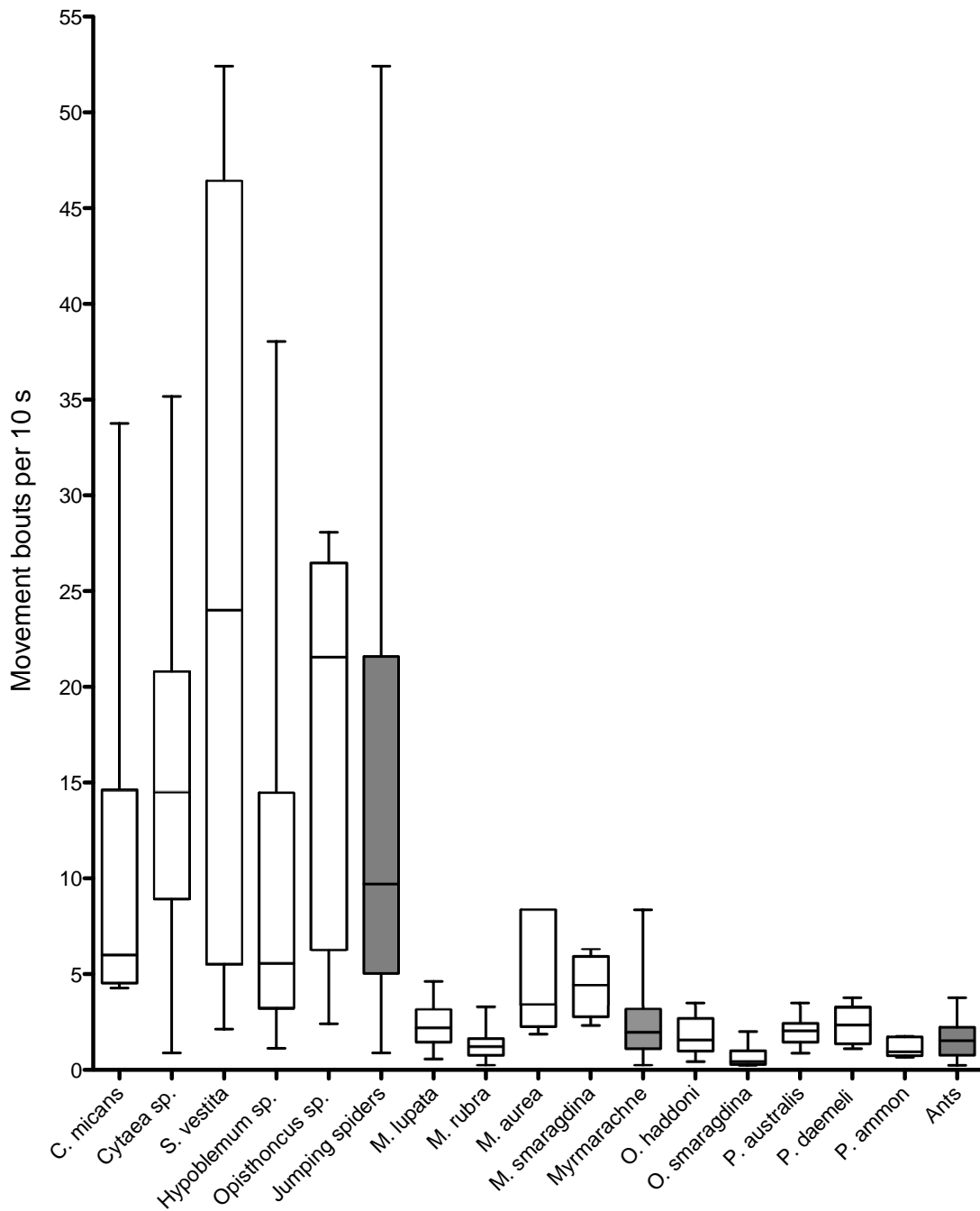
Figure 5. Number of bouts of movement in 10 s (median and 1st and 3rd quartiles; whiskers represent range) for each tested species of ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. Grey boxes represent pooled data for each group.

Figure 6. Distance travelled per bout of movement (median and 1st and 3rd quartiles; whiskers represent range) for each tested species of ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. Grey boxes represent pooled data for each group.

Figure 7. Number of movement bouts per 10 mm travelled (median and 1st and 3rd quartiles; whiskers represent range) for each tested species of ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. Grey boxes represent pooled data for each group.
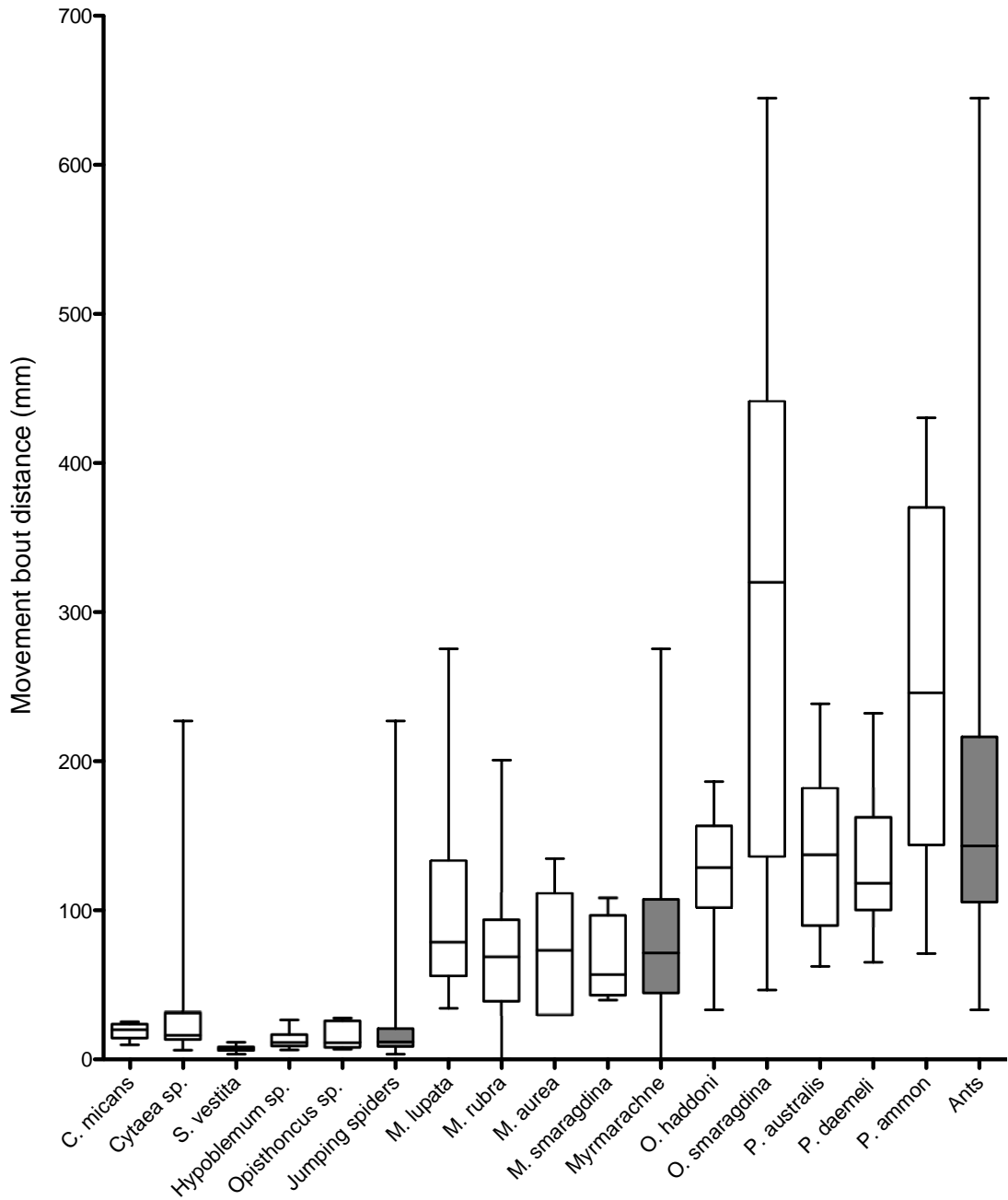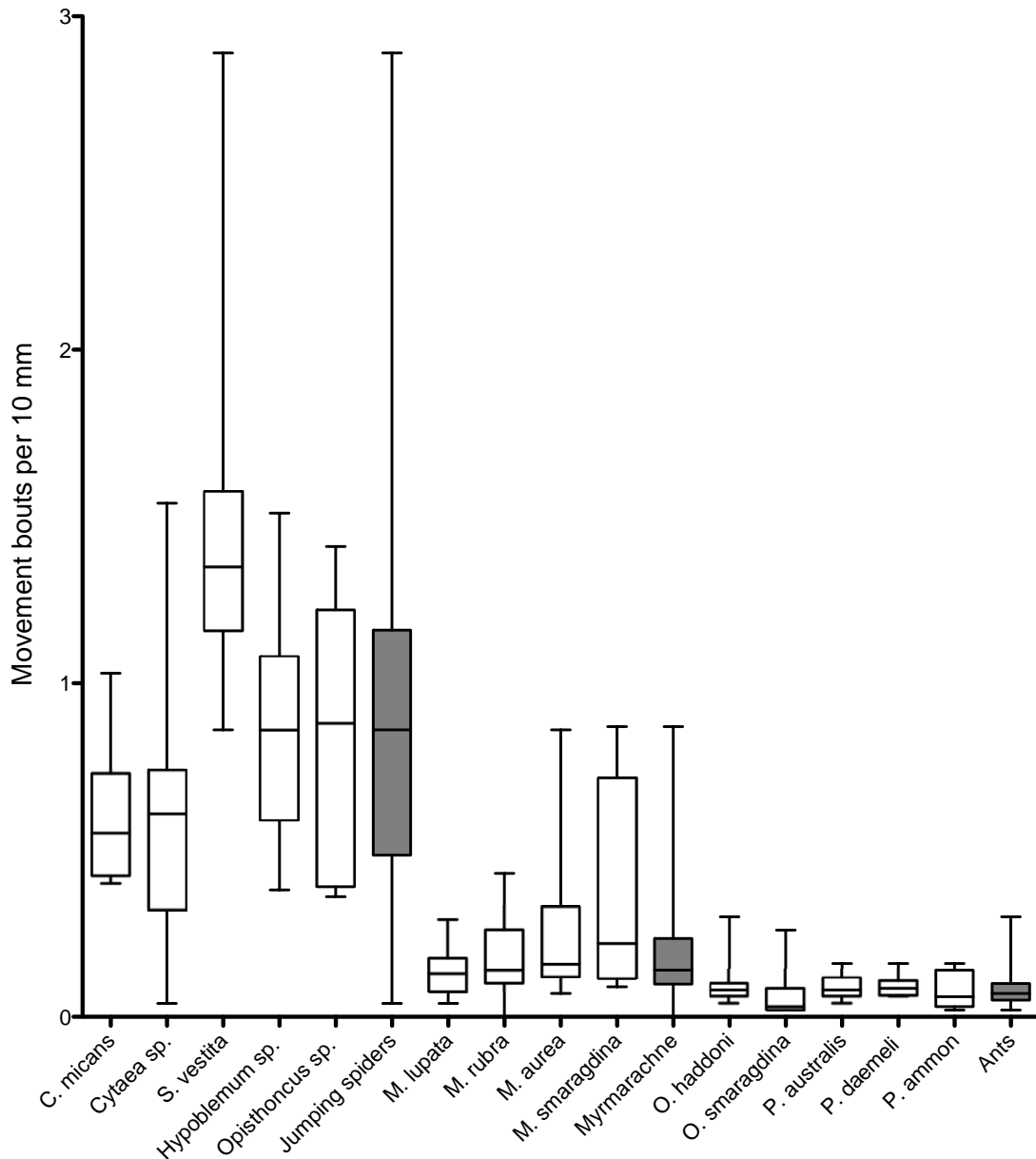
There was an overall difference in average turn angle depending on whether the arthropods were ants, *Myrmarachne* or ordinary salticids ($F_2 = 5.692$, $P = 0.005$). Pairwise comparisons revealed no differences between *Myrmarachne* and ants, but significant differences between these two groups and ordinary salticids (Fig. 8A). There was also an overall difference in median turn duration depending on grouping ($H_2 = 19.16$, $P < 0.0001$). Pairwise comparisons revealed no differences between

Myrmarachne and ants, but significant differences between these two groups and ordinary salticids (Fig. 8B).
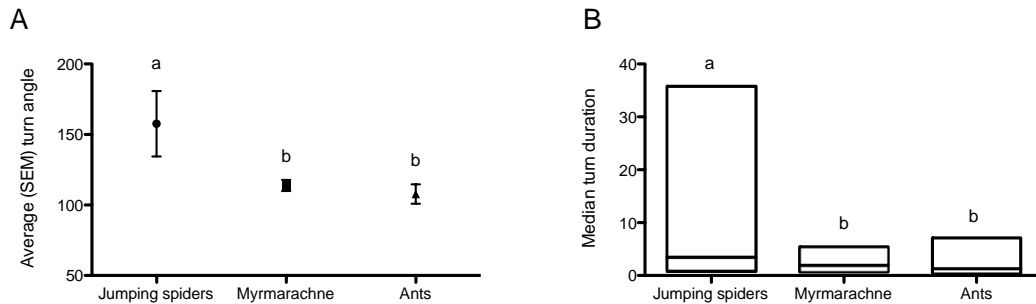

Figure 8. Turn characteristics for ordinary jumping spiders, ant-like jumping spiders (*Myrmarachne*) and ants. A) Average rotation angle. B) Median (1st and 3rd quartiles) duration of turns. Letters denote significant differences using pairwise comparisons.

There was also a significant difference in whether turns were performed while stationary or while moving depending on the grouping variable ($H_2 = 50.30$, $P < 0.0001$). While there was no difference between how turns were performed between *Myrmarachne* and ants (both median = 1.0, 1st and 3rd quartiles also = 1.0), with both tending to rotate while moving, there were significant differences between both *Myrmarachne* and ants (both $P < 0.0001$) and ordinary salticids (median = 2.0, 1st quartile = 1.5, 3rd quartile = 2.0), which tended to rotate while stationary.

Discussion

This is the first investigation of locomotory mimicry in *Myrmarachne*, a large genus of ant-like salticids that has been extensively investigated in terms of morphological similarity to ants in relation to Batesian mimicry (Nelson & Jackson 2006; Nelson et al. 2006a; Nelson et al. 2006c; Huang et al. 2011; Nelson 2012). These results suggest that *Myrmarachne* are locomotory mimics of ants. This complements previous research that *Myrmarachne* species mimic ant morphology (Nelson et al. 2006a; Nelson & Jackson 2006) and antennal waving behaviour (Ceccarelli 2008), and adds support to the assumption, commonly found in the literature, of ant-like locomotion among *Myrmarachne* (Cushing 1997). Locomotory mimicry of ants by *Myrmarachne* was

found across several different components of motion: distance of a bout of movement, the number of bouts per unit of time, distance travelled per unit of time, number of movement bouts per unit of time, and turning behaviour.

Locomotory mimicry may exert some costs to the mimic in terms of physiological and biomechanical constraints. Previous research indicates that for maximum efficiency, spiders are expected to move faster than insects of the same size (Lighton & Gillespie 1989). This implies that *Myrmarachne* would have to exert more energy by mimicking the models' speed than if they were to move faster than the model, and myrmecomorphic salticids do outrun their models when necessary (Pekár & Jarab 2011). Although the graph for distance covered per bout (Fig. 3c) shows that ordinary salticids covered less distance per bout of movement, these bouts of movement were considerably shorter than for either *Myrmarachne* or ants (Fig. 5) and do not correlate with speed. A limitation of locomotory mimicry may be selection to maintain the ability to escape if detected, as found in some butterflies (Srygley & Chai 1990; Srygley 1994). On the other hand, a potential cost of the mimicry may be that mimics living in sympatry with visual predators are selected for accurate morphological mimicry at the expense of reduced escape ability.

Myrmecomorphic salticids avoid predation by ant-averse salticid predators (Nelson et al. 2006a; Nelson & Jackson 2006). However, myrmecomorphic spiders will be at risk from ant-eating species, as these choose ants and ant-like salticids significantly more often than ordinary salticids as prey (Nelson et al. 2006c). This may be an important threat for myrmecomorphic mimics, as a significant fraction of spiders and predatory insects have evolved specialisations for feeding on ants (Jackson et al. 1998; Jackson & Li 2001; Huseynov et al. 2005; Pekar et al. 2008), although the significance of this trade-off is poorly understood. Nevertheless, the accuracy of ant mimicry by spiders may be due to the respective balance of selection pressure from both ant-eating predators and ant-averse predators (Pekár et al. (2011).

Some species of *Myrmarachne* are regarded as 'specific' or 'accurate' mimics, whereby the mimic has a close morphological resemblance to a specific model (Edmunds 1978, 2000, 2006). This differs from 'general' or 'inaccurate' mimics, whereby mimics only show partial resemblance, such as only mimicking colour or locomotion. For example,

general ant-mimicking spiders often lack a constricted section between the cephalothorax and abdomen, which is used by accurate mimics to resemble the three body parts (head, thorax and abdomen) characteristic of insects (Edmunds 2000; Pekár & Jarab 2011). Specific resemblance offers *Myrmarachne* protection from ant-averse predators (Nelson et al. 2006a; Nelson & Jackson 2006; Nelson 2012), but can be maladaptive when faced with ant-eating predators (Nelson et al. 2006c). On the few occasions when *Myrmarachne* encounters an ant-eating predator, the spiders may resort to honest communication and display to the predator, communicating that they are not ants (Nelson et al. 2006b). In addition to fooling ant-averse predators with morphological mimicry (Nelson et al. 2006a; Nelson & Jackson 2006), *Myrmarachne*'s locomotory similarity, found in this study, suggests there is also selection pressure to move like an ant. Combined with specific morphological mimicry, this may make it harder for ant-eating predators to distinguish *Myrmarachne* from ants, but should also make it harder for spider-eating predators, the selecting agent for the morphological mimicry (Nelson et al. 2006a; Nelson & Jackson 2006), to target *Myrmarachne*. Pekár et al. (2011) suggest that a possible explanation for specific and general ant mimicry by spiders is to optimise mimicry dependent on the ratio of ant-eating and spider-eating species living in sympatry. If the selection pressure from ant-eating species and spider-eating species is equal, it may favour general ant-mimics. General ant mimics may avoid predation from ant-eating species because they do not resemble ants precisely, while avoiding predation from spider-eating predators by mimicking ant locomotion (Pekár et al. 2011). Recently, research was carried out on three myrmecomorphic species of spider, *Liophrurillus flavitarsis*, *Phrurolithus festivus* (both Corinnidae), and *Micaria sociabilis* (Gnaphosidae), which were regarded as inaccurate mimics as resemblance is due to coloration and not gross morphological characteristics (Pekár & Jarab 2011). The results of this study suggest that morphological mimicry is not necessary for deceiving spider-eating predators, as long as locomotion is mimicked (Pekár & Jarab 2011; Pekár et al. 2011). However, we do not know how predators classify these species based solely on morphology. Nevertheless, evidence does suggest that certain invertebrate predators share our classification system of a mimic's accuracy (Nelson 2012). Interestingly, despite locomotory mimicry being found in the previous study, this was based solely on speed, with other motion variables lacking similarity (Pekár & Jarab 2011). In contrast, the results of this study on *Myrmarachne*, which are far more accurate mimics, show similarities not only in speed, but in turn characteristics, distance moved per bout of

movement, and bout duration.

Behavioural mimicry has been suggested to be the first mimicry component to evolve (Pocock 1908). If this is correct and morphological mimicry evolved later, it may render the locomotory component redundant. Given its potential physiological cost (Lighton & Gillespie 1989), locomotory mimicry should be lost once morphological mimicry is acquired. As the results of this study suggest that *Myrmarachne* is a locomotory mimic despite research demonstrating morphological mimicry alone is sufficient to avoid predation by visual predators (Nelson & Jackson 2006; Nelson et al. 2006a; Nelson 2012), there may be an additional benefit for having locomotory mimicry. Morphological ant mimics achieve protection from spider-eating predators when static (Nelson et al. 2006a; Nelson & Jackson 2006) and this may be optimum for species that generally remain stationary, such as the pod-sucking hemipteran *Riptortus serripes* (Alydidae) that mimics the weaver ant *Oecophylla smaragdina* (Ceccarelli 2009). As *O. smaragdina* is an active ant species, it may seem as if *R. serripes* and the many other hemipteran species that mimic ants (Kumar 1966; Jackson & Drummond 1974; Oliveira 1985) will stand out to predators by being stationary. However, like other hemipterans, *R. serripes* feeds from young shoots and new growth of plants (pers. obs.) in the same manner as the wide diversity of hemipterans frequently tended by *O. smaragdina* for honeydew, which provides a crucial food source for weaver ants (Bluthgen & Fiedler 2002). These localities are often occupied by ants, which tend hemipterans and are often stationary while guarding the bugs for the carbohydrate-rich honeydew that the ants readily consume and store (trophobiosis) (Dorow & Maschwitz 1990; Hölldobler & Wilson 1990; Delabie 2001; Bluthgen & Fiedler 2002). As weaver ants will be frequently seen static around groups of hemipterans, *R. serripes* may avoid weaver ant-averse predators by mimicking ants waiting for honeydew and therefore may not stand out, despite being stationary. From time to time, juvenile alydids will be in motion while walking between host plants (Tabuchi et al. 2007), but even then they are suspected to adopt a more ant-like pattern of locomotion (Oliveira 1985). Generally, however, the bugs remain static while feeding from plant fluids. Conversely, *Myrmarachne* is an active predatory spider, frequently seen running over leaves in the same habitat as ants, and *Myrmarachne* would break the deception if it did not mimic ants in both morphology and locomotion.

There may be a dynamic hierarchy of cues used by predators to identify potential prey (e.g. Nelson & Jackson 2012). For example, when prey are static, morphology may be the dominant cue, while when prey are in motion their locomotory pattern may be the dominant cue. The high degree of morphological and behavioural mimicry in *Myrmarachne* (Edmunds 2000, 2006; Ceccarelli 2008) implies that there is strong selection pressure for both morphological and behavioural mimicry components. If selection pressure for mimic accuracy in myrmecomorphic species is mainly due to the ratio of ant-eating and spider-eating predators (Pekár et al. 2011), there may be more spider-eating predators in the environments where you find specific *Myrmarachne* mimics.

The major predators of spiders are thought to be birds (Gunnarsson 2007), however, the effect of invertebrate predators is potentially underemphasised. Invertebrates are frequently observed feeding on spiders and some are specialist spider predators (Li & Jackson 1996; Nelson et al. 2004; Cross & Jackson 2006; Jackson et al. 2008; Wignall & Taylor 2010). Some staphylinid beetles are Batesian mimics of ants (Taniguchi et al. 2005) and beetles that mimic the roaming army ants of Central and South America (Kistner 1982) may gain a survival advantage by fooling birds that specialise in following ant swarms through the forest (Hölldobler 1971). Myrmecomorphy in staphylinids has been shown to provide a survival advantage with other vertebrate predators, such as frogs (Taniguchi et al. 2005). The birds rarely eat the ants themselves, but instead prey on the high number of invertebrates running from the army ant swarm (Willis 1969; Willis & Oniki 1978; Wrege et al. 2005; Rettenmeyer et al. 2011). The few ants consumed by the birds are probably attached to the non-ant prey item targeted by the birds (Rettenmeyer et al. 2011). The Batesian staphylinid therefore deceives the birds when it runs alongside the ants. Potentially, if other birds are averse to certain ants in the same manner because they are harmful or because they lack nutritional benefit, Batesian mimicry may also provide *Myrmarachne* with a survival advantage from some bird predators.

As well as occurring at high local densities, ants are particularly harmful and carry formidable weapons (Hölldobler & Wilson 1990). Ants are important predators of salticids and other invertebrates (Hölldobler & Wilson 1990; Nelson et al. 2004). Many invertebrates, including salticids, will be under high selection pressure to identify ants,

as failure to do so may often result in death. Considering that failure to identify an ant can be so detrimental to survival, species that mimic ants may benefit with only a general similarity to trigger avoidance behaviour in ant-averse animals. This is congruent with theories to explain general mimicry (Edmunds 2000). A flaw in this theory is that the same model often has mimics with differing degrees of accuracy (Edmunds 2000), perhaps because the selecting agents (with different cognitive and sensory ability) for each mimic may be different. An additional explanation for this phenomenon is that phylogeny constrains a mimic's ability to evolve close behavioural or morphological similarity with its model (Golding et al. 2001). However, a recent study of the phylogeny of *Myrmarachne* (Ceccarelli & Crozier 2007) appears to show strong selection pressure to evolve close similarity to different ants living in sympatry. This study also suggests that general mimics may represent phenotypic stages where selection can act more strongly maintaining the high amount of polymorphism within the genus (Ceccarelli & Crozier 2007). A factor for the high degree of morphological and behavioural mimicry in *Myrmarachne* (Edmunds 2006; Ceccarelli 2008) could be the cognitive ability of the selecting agents (Kikuchi & Pfennig 2010). This assumes that mimics will be under higher pressure to evolve beyond the predator's cognitive capacity than are the predators to distinguish mimic from model, according to the life-dinner principle (Dawkins & Krebs 1979). Some spider-eating predators can have a high cognitive capacity (Jackson et al. 2001) and require a high degree of mimic accuracy in order to confuse mimic with model (Nelson 2012).

The myrmecomorphic salticid genus *Myrmarachne* shares the same general locomotory behaviour as ants and can therefore be classed as locomotory mimics. However, further research is required to ascertain if the locomotory pattern of the precise mimic *M. rubra* is more similar to its model *Opisthopsis* than it is to other ants. It may be that because of the highly aggressive nature of ants (Hölldobler & Wilson 1990), and the danger they pose for spider-eating predators (Nelson et al. 2004), species-specific locomotory mimicry is not required to gain a survival advantage (Edmunds 2000).

In previous studies (Nelson & Jackson 2006; Nelson et al. 2006a), the morphological mimicry of *Myrmarachne* provided a survival advantage when faced with visual spider-eating predators. Despite locomotory mimicry being defined as similarity in motion to an unrelated organism (Srygley 1999a), to accurately identify its adaptive significance

as a component of Batesian mimicry, the locomotion of *Myrmarachne* needs to be judged by predators. Future directions for research would be to test locomotory mimicry with visual predators sharing habitat with *Myrmarachne,* such as salticids, skinks, geckos, mantids, and birds.

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Chapter 3: Are Visual Predators Deceived By Locomotory Mimicry?

Abstract

Ant mimicking species are known to deceive ant-averse predators through their morphological similarity to ants. Throughout the literature, not only is their resemblance to ants in body-form mentioned but also their more ant-like walking pattern. Despite this, unlike morphological mimicry, the similarity in walking behaviour has not been experimentally supported with visual predators and so its significance as a mimicry component is not known. The effect of locomotory mimicry of ants on visual predators was tested using 3D animations to tease effect of locomotion from the effect of morphology. No significant effect of locomotory behaviour was found. However, the results did show a non-significant trend towards visual deception by locomotion. The results were attributed to a potential hierarchy of cues used by some predators to distinguish prey.

Introduction

Batesian mimicry is a common phenomenon whereby a harmless and palatable species mimics a noxious species. By using deceptive signals, the mimic dupes potential predators regarding its identity and palatability, and consequently avoids predation (Srygley 1999; Edmunds 2000). The study of Batesian mimicry has a well-established history, being used as a model system with which to explore evolutionary questions and selection since its first description (Bates 1862). However, throughout the literature the terms *mimic* and *model* are often ascribed with little supporting data and are judged by the human eye. To effectively apply these terms, experiments designed to test whether the model species is unpalatable to predators and whether potential predators are deceived by the mimic are required (Whittington 1994). Because the selecting agents

for the mimicry will have different cognitive and sensory ability to humans and our perception can be different to other animals (Dittrich et al. 1993), these are fundamental questions that need to be addressed in any mimicry system.

In invertebrates, Batesian mimicry is particularly common (Srygley 1994; Cushing 1997; Golding et al. 2001; Ito et al. 2004; Ceccarelli 2009), and among these, it appears that mimicry of ants (myrmecomorphy) is especially prevalent (McIver & Stonedahl 1993; Cushing 1997). It is among spiders that ant mimicry, or myrmecomorphy, is often found, perhaps because of the similar body size of ants and many spiders, and because they are often found in the same habitat (Edmunds 2006; Pekár & Jarab 2011). There are especially many myrmecomorphic species from the family Salticidae (Cushing 1997) and there is considerable evidence that ant-averse mantises and ant-averse salticids respond to the myrmecomorphic salticids as though they were ants (Wanless 1978; Cutler 1991; Edmunds 1993; Nelson et al. 2006a; Nelson et al. 2006c; Nelson & Jackson 2006b; Huang et al. 2011). These findings are evidence that these myrmecomorphic spiders are Batesian mimics of ants. Among the Salticidae, *Myrmarachne,* containing over 200 species, is a large genus consisting entirely of morphological ant mimics (Wanless 1978; Cushing 1997, 2012; Proszynski 2007).

In general, salticids are significant predators of insects and spiders (Harland & Jackson 2000) but are generally averse to close proximity with ants (Nelson & Jackson 2006b), usually preying on other insects (Jackson & Pollard 1996). Salticids are frequent prey of ants (Nelson et al. 2004), and with their formidable weapons and high numbers (Hölldobler & Wilson 1990), the best defence salticids have is to spot an ant at a distance in order to escape (Nelson et al. 2004). This they are able to do because unlike most spiders (Land 1985; Land & Nilsson 2002), salticids possess exceptional vision and visual acuity almost as high as primates (Harland & Jackson 2004). Indeed, salticids can distinguish between objects of similar size and structure from as far as 40 body lengths away (Harland et al. 1999).

Their acute vision has enabled some salticids to become predatory specialists. Some of these species have a predatory preference for other spiders (Li et al. 1997), but a small fraction of salticids specialise in eating ants (Jackson et al. 1998; Jackson & Li 2001; Huseynov et al. 2005). Nelson et al. (2006c) found that ant-eating salticid species from

nine different genera (*Aelurillus, Chalcotropis, Chrysilla, Corythalia, Habrocestum, Natta, Siler, Xenocytaea*, and *Zenodorus*) choose ants and ant-like salticids more than they choose other prey types. Given that ant-eating spiders choose ants and ant-like salticids over ordinary salticids, the simplest explanation is that the ant-eating salticids confuse myrmecomorphic salticids with ants. The predators would therefore be confusing cues from the ant-like salticid with cues received from ants. The experiments described by Nelson et al. (2006c) used static lures made from dead arthropods mounted in a life-like posture. Consequently, the cues available to test spiders would have been morphological rather than behavioural.

Recently, there have been calls to investigate the role of behaviour in mimicry (Thery & Casas 2009). For example, it has been shown that dronefly mimics of bees resemble their models' behaviour when foraging (Golding & Edmunds 2000) and in flight (Golding et al. 2001). Salticids generally move in short bursts of movement and make stationary turns (they rotate only when they are standing still rather than in forward motion). In contrast, ants use a more continual movement pattern with longer bursts of locomotion and generally turn while in forward motion. Behavioural mimicry of ants by *Myrmarachne*, which includes this so called 'erratic' locomotion, as well as raising the anterior-most (usually) pair of legs in semblance of ant antennae, is often mentioned (Cushing 1997), but apart from the work described in Chapter 2, there has been little empirical work done on the subject. Nevertheless, it is clear that *Myrmarachne* are behavioural mimics of ants (Chapter 2). Consequently, if ant-eating predators use behavioural assessments to make judgements regarding the identity of their prey, *Myrmarachne*'s behaviour may be detrimental. Although salticids can distinguish between different kinds of static prey (Jackson et al. 2005), locomotion and behaviour are nevertheless important for salticids when making acute distinctions (Nelson et al. 2006b; Pekár & Jarab 2011). Due to the conspicuous locomotory pattern of ants, ant-eating predators may use this as a cue to distinguish ants. Indeed, locomotory mimicry of running speed has been hypothesised as a primary reason why some ant mimicking spiders are attacked by myrmecophagic predators and are avoided by spider-eating species (Pekár et al. 2011). In fact, if ant-eating predators use *Myrmarachne*'s behaviour as a cue to elicit predatory sequences, we can be confident that this is behavioural mimicry, as assessed by a potential predator.

We can disassociate behaviour from morphology using 'virtual' prey. Previous research on prey-choice behaviour demonstrates that salticids successfully react to computer animated virtual prey (Harland & Jackson 2002; Nelson & Jackson 2006a, 2012). The use of virtual stimuli has many advantages over the use of living prey, as confounding variables, such as odour and interactions between predator and prey, can be controlled. Animations can also have some advantageous over the use of lures, as motion, which can be important for prey identification (Pekár & Jarab 2011), can be incorporated into the experimental design. For example, jacky dragons shown animations of the death adder caudal luring signal were able to determine that this signal mimics certain aspects of the movement characteristics of the jacky dragon's invertebrate prey (Nelson et al. 2010). Here, my aim was to investigate, through the use of animations, locomotory mimicry in *Myrmarachne*. In particular, my hypothesis was to consider whether ant-eating salticids would approach an animation depicting a morphological ant-like salticid more when its movement pattern resembled that typical of ants than when its movement resembled that typical of non-ant-like salticids.

Methods

The predators used as test spiders were two species of salticids that eat ants. *Cytaea* sp. was observed feeding exclusively on ants in the wild (see Appendix Table 1) and *Servaea vestita* has often been found hunting and eating ants (Ximena Nelson, personal communication). *Cytaea* sp. was collected in the vicinity of Cairns in northern Queensland, Australia, and was found in the same habitat as *Myrmarachne lupata*, the species on which the morphology of the animations was based (see below). *Servaea vestita* was collected in Sydney, in New South Wales, Australia. This species is also often found living in the vicinity of both *Myrmarachne* spp. and ants. The average body length of *Servaea vestita* was 8.9 mm, while the average body length of *Cytaea* sp. was 7.8 mm. Salticids were housed in individual containers (cylinder of 40 mm diameter x 50 mm) and fed approximately five vinegar flies (*Drosophila* sp.) and other small dipterans once each week. All predators used were females, as adult male salticids are known to be less responsive to prey (Li & Jackson 1996; Jackson & Pollard 1997; Zurek et al. 2010).

Two animations that resembled *Myrmarachne* in morphology were created in the 3D modelling and rendering software 3Ds Max. One animation was made to move with *Myrmarachne*/ant-like locomotion (*Myrmarachne* model; Fig.1a) and the other to move with jumping-spider-like locomotion (salticid model; Fig.1b). Models of the stimulus were based on photographs of *Myrmarachne lupata* that were placed in the modelling software and traced to create the 3D outline of the model. Colouration was then applied to match the photographs of *M. lupata* and the model was animated. The *Myrmarachne* model was animated to walk in a pattern observed for *M. lupata* on a piece of card. The pattern used was recreated from a recording of an *M. lupata* moving from the bottom left corner of the card to the top right corner of the card. This span made the most use of the area available. Hence, in recreation, the virtual model was visible for the longest amount of time.

The speed of movement for the animation was 17.5 mm/sec (the average speed for 20 collected *Myrmarachne lupata*). The salticid model was identical to the *Myrmarachne* model except in its movement pattern, which, while having the same speed of motion as the *Myrmarachne* model, was characterised by having the stop-start locomotion typical of non-ant-like salticids (Chapter 2). The stop-start behaviour of the animation consisted of a pause of one second after every two seconds of movement, which was the average pause for cessation of stepping for the salticids studied in Chapter 2. Both the *Myrmarachne* model and salticid model were programmed to make two six s display behaviours towards the observing predator: one after 80 mm of 'walking', and another after 120 mm of 'walking'. Both model animations then disappeared off screen for 8 s, as if crawling under the piece of card. The animation was looped, creating the overall impression of the model walking back across the card out of sight of the predator before beginning its walk back down the piece of card.

Animations were displayed using an Apple iPod Touch with a retina display, which has high resolution and to which salticids respond using naturalistic behaviours (pers. obs.). The model was displayed at an actual size of 4.2 mm. The experimental setup (Fig.2) consisted of the iPod being placed at the top of a wooden ramp (dimensions 170 x 60 mm, at an angle of 30°). The ramp and iPod were placed inside a white box which used as a testing arena (450 mm x 450 mm x 610 mm) to minimise disturbance to spiders during testing. For each test, one of the predators (either *Servaea vestita* or *Cytaea* sp.)

was chosen randomly, placed at the base of the ramp (by allowing the spider to descend on a silken line) approximately 50 mm from the iPod, during the phase in the animation when the model was off screen. Test spiders were positioned facing the iPod. Tests lasted for 15 min or until the predator had touched the screen. Lighting was provided by a lamp placed inside the white box at a distance of 200 mm from the ramp. The ramp and iPod were cleaned with 90% ethanol to remove any chemical odours and residues from the salticids, which may have confounded results.
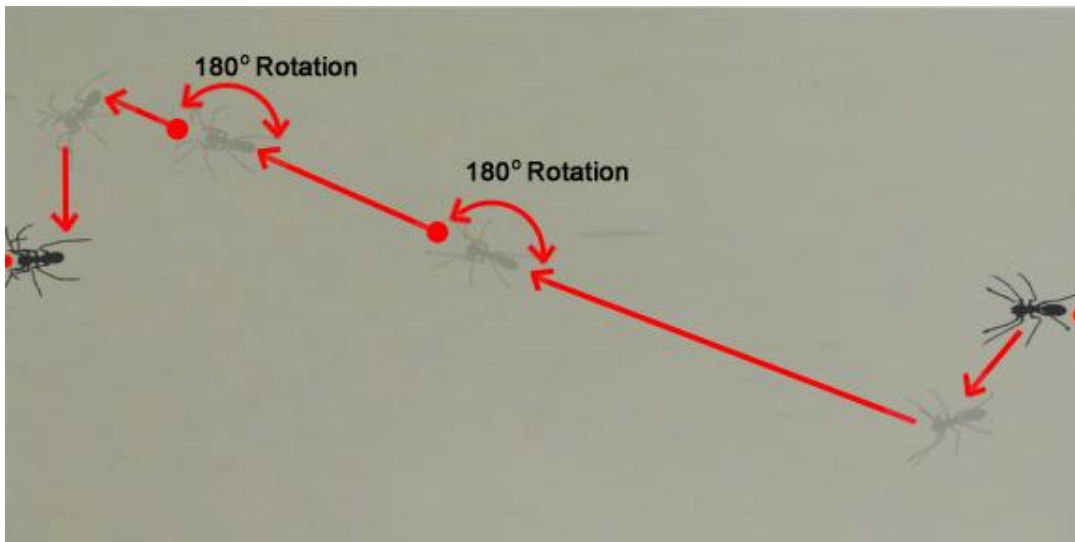

Figure 1a. Pattern of movement for the animated model with *Myrmarachne*/ant-like locomotion (*Myrmarachne* model). The red dots indicate where the model was stationary.
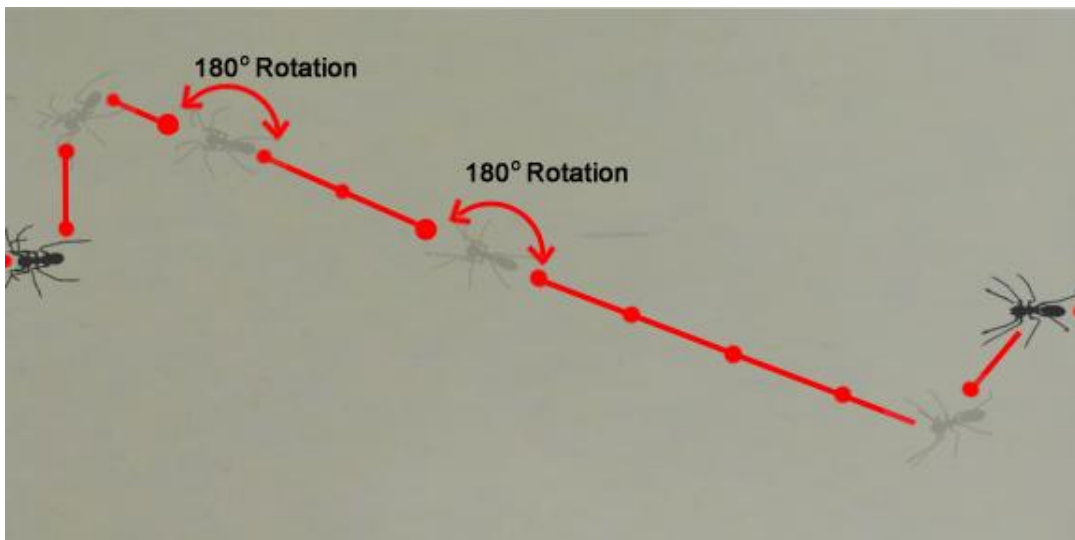

Figure 1b. Pattern of movement for the animated model with salticid-like locomotion (Salticid model). The red dots indicate where the model stopped.
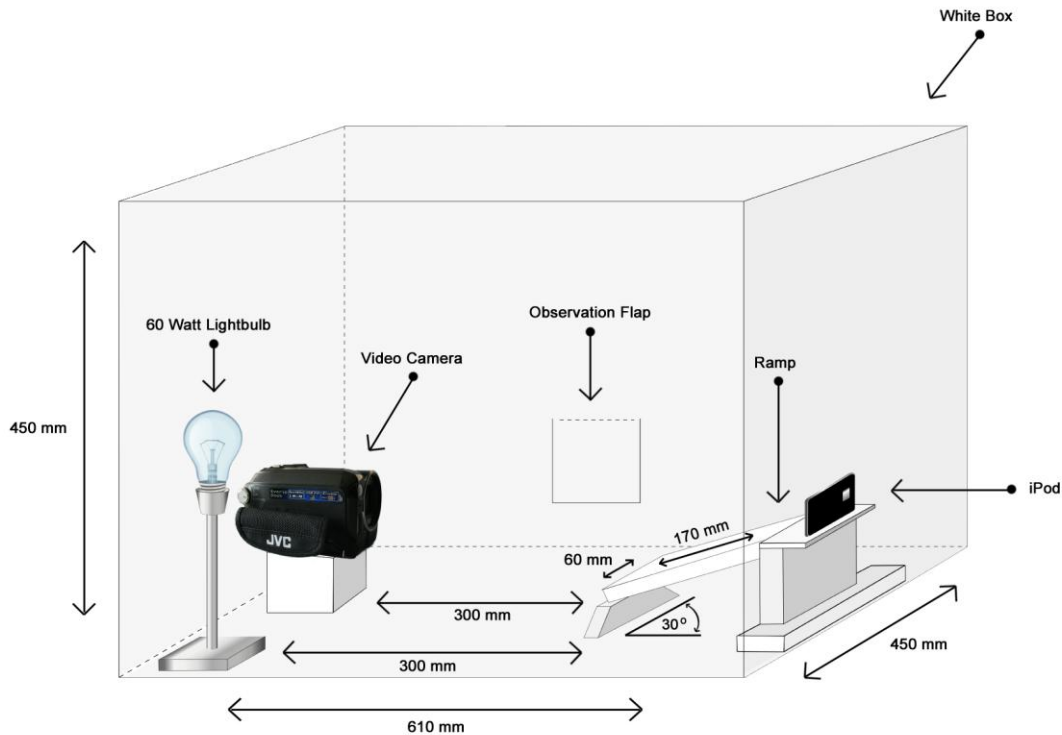
Figure 2. Experimental setup to record salticid responses to animations of either a *Myrmarachne* model with salticid motion or jumping spider motion.

Paired tests were carried out, with each spider tested with both animations in random order. The second test was always carried out 24 h after the first test. Spiders had last been fed four days prior to the first test. For scoring the behavioural response of test spiders, I measured the number of approaches to each animation and the number of tests in which the spider did not approach either animation (essentially ignoring the stimuli). An approach was defined as the predator orienting towards the animation, maintaining orientation, and approaching the iPod. Results were analysed using Wilcoxon matched-pairs signed rank tests and binomial tests to determine if there was any difference in response to the *Myrmarachne* model and the salticid model.

Results

Roughly half of the tested *Cytaea* sp. did not respond at all to the animations, and this proportion was considerably higher in *Servaea vestita*. *Cytaea* sp. did not behave toward the *Myrmarachne* model differently to how it behaved with the salticid model

(W = -13.00, P = 0.594, N = 19; Fig. 3), and this was also true of *Servaea vestita* (W = -9.00, P = 0.233, N = 13; Fig. 3). However, when the approach data were pooled, there was a non-significant trend to choose animations based on the motion pattern of ants (2-tailed binomial tests, P = 0.097, N = 32; Fig. 3).
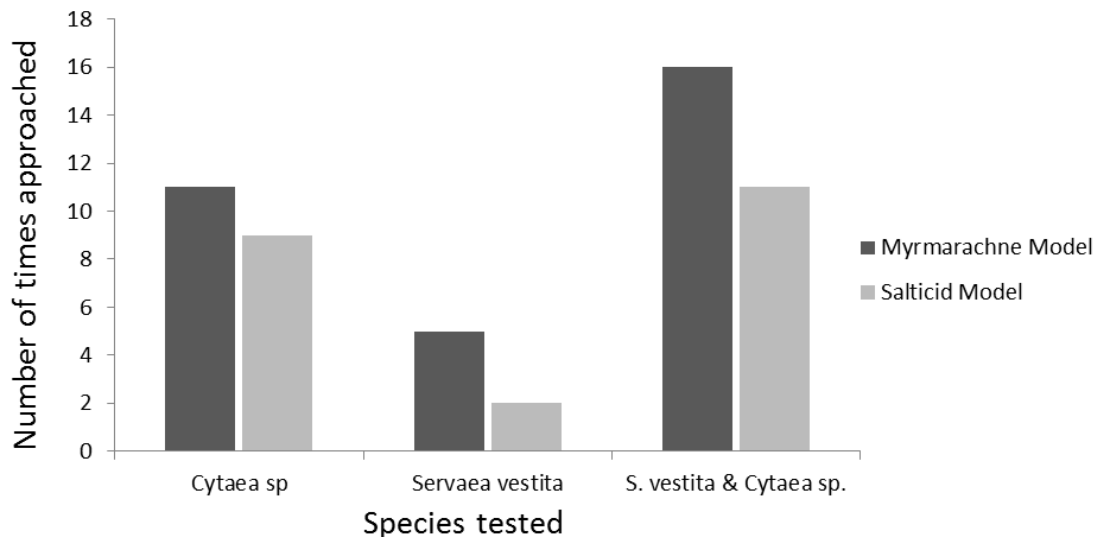

Figure 3. Number of times *Cytaea* sp. or *Servaea vestita* approached an animation of *Myrmarachne* with either salticid motion (salticid model) or *Myrmarachne* motion (*Myrmarachne* model).

Discussion

Species in the salticid genus *Myrmarachne* are morphological mimics of ants (Wanless 1978; Nelson et al. 2006a; Nelson et al. 2006c; Nelson & Jackson 2006b), as has been attested by numerous experiments using visual predators, such as mantids and spider-eating salticids (Nelson et al. 2006a; Nelson & Jackson 2006b; Huang et al. 2011). Other components of the mimicry of these species include antennating behaviour, typically using the spider's anterior-most pair of legs, which seems to mimic the motion of the antennae of ants (Ceccarelli 2008). Locomotory mimicry by *Myrmarachne* may be another component of the deceptive signal (Cushing 1997; Thery & Casas 2009) and my work (Chapter 2) suggests that *Myrmarachne* locomotion does resemble that of ants. However, in order to fully explore whether this is mimicry the response of potential predators needs to be investigated. Here, I found that the effect of locomotion pattern on the decision to attack prey by ant-eating salticids was inconclusive.

The lack of a significant difference for ant-eating predators distinguishing non-antlike salticids from ant-like salticids based on locomotion may be attributed to small sample size. Of the spiders tested, only 27 responses to either of the two animations were recorded. It is possible that in general these predators may not have responded to the animations due to factors such as slight inaccuracies in model morphology. Salticids use a range of characteristics to identify prey, including shape, size and position of eyes, the number and characteristics of legs, and other body features (Harland & Jackson 2000; Harland & Jackson 2002, 2004; Nelson 2010). If the predator does not rely heavily on motion characteristics and instead relies mainly on morphology, there was nothing to pick from in these tests. Nevertheless, the non-significant trend to approach the animation with ant-like characteristics found in this study is suggestive that with further testing a more robust finding might be obtained. Corroborating this, I found that test spiders often did approach and stalk (a characteristic behaviour in salticids whereby the spider lowers its body as it approaches prey) the animation, and two spiders even leapt on and attempted to 'eat' the animation, suggesting that, for these spiders at least, the animation was recognised as prey. Although inconclusive, these results do suggest that motion characteristics are attended to by potential predators.

Since the predators used were wild caught spiders, nothing was known of their experience and other salticid species are known to make some predatory decisions based on experience (Jackson et al. 2001; Jakob et al. 2007; Vandersal & Hebets 2007; Jackson & Nelson 2011). However, nine species of ant-eating salticids tested using static lures of ants, *Myrmarachne*, and non-ant-like salticids indicate that myrmecomorphic salticids are targeted by ant specialists more than ordinary salticids (Nelson et al. 2006c). These results were obtained using salticids with no prior experience of ants or other salticids and held regardless of whether the ant-eating salticid occurred in sympatry with the predator (Nelson et al. 2006c), suggesting that the role of experience is an unlikely explanation for my findings.

For a Batesian mimic, if certain signal components trigger aversive behaviour, while other components trigger predation behaviour, this may lead to confusion and hesitation by the predator, giving the mimic time to escape. This has been suggested as an explanation for general mimicry (Howse & Allen 1994), also known as 'inaccurate' or 'poor' mimicry, whereby mimics do not resemble their models precisely (Edmunds

2000). General ant mimics resemble the model in some characteristics, such as gross morphology, movement, or colour, but they often lack the ant-like constriction between the cephalothorax and abdomen (Edmunds 2000, 2006; Pekár & Jarab 2011). In this study, confusion may also have accounted for the results. Being based on salticids (even ant-like salticids), these animations would have components of both ants and spiders, and this would be especially true of the model that moved like a salticid. These spiders may only rarely feed on other spiders, and so the potential cues from both spiders and ants may have led to confusion.

Research on general mimics suggests that different predators may select the level of mimicry specificity through their different, and sometimes conflicting, predatory preferences and cognitive abilities (Kikuchi & Pfennig 2010; Pekár et al. 2011; Pekár & Jarab 2011). General ant mimics may evade predation by spider-eating predators by mimicking locomotion while evading predation by ant-eating predators by not mimicking ants precisely (Pekár et al. 2011; Pekár & Jarab 2011). Predator cognition is implicated under the "sensory limitation hypothesis," because, if the general mimic exploits cognitive limitations of the predator there will be no selective force for more specific mimicry (Chittka & Osorio 2007; Kikuchi & Pfennig 2010). A study on the mimicry of the deadly coral snake (*Micrurus fulvius*) by the non-venomous king snake (*Lampropeltis elapsoides*) revealed that despite the colour of the ring body pattern being mimicked, there was no pressure to mimic the precise ordering of the coloured rings, implying that, while not accurate, the mimicry was sufficient to fool the cognitive ability of the predators (Kikuchi & Pfennig 2010). Within the Salticidae, there is considerable variation in visual and cognitive ability (Harland et al. 1999; Jackson & Nelson 2011). The results of this study may be explained if the predators in these tests are deceived by morphology alone and lack the cognitive capacity to distinguish between prey based on locomotion. However, the similarity in walking behaviour found in Chapter 2 suggests that there may be an adaptive significance of locomotory mimicry, as otherwise it should be lost due to potential physiological costs (Lighton & Gillespie 1989). Combined with the non-significant trend of this study, this is suggestive that locomotory mimicry may function to deceive predators by adding to the deceptive signal.

The cues that predators use to decide what to attack is an important consideration in predator-prey interactions and for research on mimicry because each predator most likely has different cognitive and sensory capacity and may rely on different cues to identify prey. The high degree of mimic specificity in animals like *Myrmarachne* could be caused by a suite of predators. Some species may distinguish prey by a hierarchy of different characteristics. If a suite of predators had a different hierarchy of cues to identify prey, it would place selection pressure on different aspects of mimicry, such as morphology and locomotion. This implies that some components of the mimicry may be redundant with certain predators, while adaptively significant to others. In the context of this study, morphology may be a dominant cue and locomotion a subordinate cue for these predators. Locomotion has been hypothesised as the main reason why some mimics are selected by ant-eating predators (Pekár et al. 2011). However, Pekár & Jarab's (2011) study tested inaccurate or general mimics, which to human eyes did not match the model species accurately in morphology. As predators may not have been able to distinguish prey clearly based on morphology, they may have relied more on locomotion. The species of *Myrmarachne* used as the basis for animations in the current study, on the other hand, is regarded as a specific or accurate morphological mimic.

The results of this study may imply that predators may use a hierarchy of cues differing in importance. This approach is adopted by another spider within the Salticidae, the mosquito-eating species *Evarcha culicivora* (Nelson & Jackson 2012). This species has a preference for blood-fed female mosquitoes (Jackson et al. 2005; Nelson & Jackson 2006a) and uses cues from the abdomen, head, and thorax to distinguish prey (Nelson & Jackson 2012). Nelson & Jackson (2012) raise the idea that representations of prey are created by category-specific, spatiotemporal features shared by various prey-like stimuli. This prey representation is from simultaneous processing of multiple prey characteristics, such as movement (Edwards & Jackson 1994; Ewert 2004; Kral & Prete 2004) and morphological characteristics (Harland & Jackson 2000; Nelson & Jackson 2012). The importance of each characteristic can change depending on experience (Edwards & Jackson 1994; Vandersal & Hebets 2007), but the importance of key characteristics can be innate (Nelson et al. 2006c). If *Evarcha* has identified the abdomen as belonging to a blood-fed female, no other cue is required. However, if *Evarcha* fails to identify the abdomen as belonging to a blood-fed female, it switches to aspects of the head and thorax, most notably the antennae, choosing prey with more

female-like characteristics (Nelson & Jackson 2012). This tactic was hypothesised to occur when the spider encounters unreliable 'noisy' stimuli such as a mosquito with an obscured abdomen (Nelson & Jackson 2012). The 'noisy' stimuli in the current study would be an animation with ant-like morphology and salticid-like locomotion. This hypothesis leads to the conclusion that here morphology is regarded as the most reliable cue to determine prey.

One of the predators used (*Servaea vestita*) may not have been exposed to the model ant species in its natural environment, and in the case of this experiment, it may not have regarded the *Myrmarachne* model as prey. If so, this mirrors some of the suggested constraints of Batesian mimicry. The notion is that if mimics occur outside their model's range they will not benefit from the mimicry because both model and mimic should occur in sympatry (Prudic & Oliver 2008). Research on butterflies suggests that when the mimic and model move from sympatry to allopatry, the species divert from each other in appearance (Pfennig et al. 2001; Pfennig & Mullen 2010). This is consistent with the idea that the selection pressure has been released due to the absence of the noxious model, with the mimic reverting to a non-mimetic form (Rettenmeyer 1970; Azmeh et al. 1998). If the species was at one time a specific mimic, it would pass through some intermediate stage of mimicry evolution showing only partial resemblance. This has been hypothesised as an additional explanation for the existence of general mimicry (Azmeh et al. 1998). However, research suggests that ant-averse salticids seem to be 'taken in' by myrmecomorphic salticids irrespective of whether they co-occur with either model or mimic (Nelson 2011). Evidently, this hypothesis is one which needs to be explored in further detail.

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Chapter 4: Trade-offs of mimicry for myrmecomorphic spiders that live in proximity to dangerous models

Abstract

Batesian mimics are expected to live in close proximity to their models in order to maintain the deception of their potential predators. An important, but often overlooked, distinguishing difference between ant mimicry and other Batesian mimicry systems is that ants can be highly aggressive predators of the mimics themselves. Another potential cost for the mimic is that it may fall prey to specialist ant-eating predators. For this particular problem, ant mimicking salticids resort to behavioural displays communicating to the predator that they are not ants. Nevertheless, given their high numbers and aggressive nature, predation by ants is potentially a more significant threat than predation by ant-eating predators. This raises the question of what behavioural or morphological characteristics ant mimicking salticids possess to reduce the probability of falling prey to their models. In this study, I tested whether morphological or locomotory mimicry confers a survival advantage to ant-like salticids that live with their highly aggressive models, using the models themselves as a potential selection factor. I investigated whether small groups of Australian green weaver ant workers, *Oecophylla smaragdina,* were differentially attracted to non-ant-like salticids, conspecific weaver ants and to *Myrmarachne*. To tease the effect of behaviour, I also tested ants with animations of *Myrmarachne* and animations of *Myrmarachne* which moved using the locomotion pattern typical of non-ant-like salticids. No significant difference was found for attraction to live *Myrmarachne*, a conspecific, or a large salticid. However, experiments using the animated models suggest ant-like movement is more attractive to weaver ants than salticid movement, which may mean *Myrmarachne* is *more* at risk of predation by its models adding to the trade-off of being more at risk of predation from ant-eating predators.

Introduction

Batesian mimicry is a type of deceptive communication whereby a palatable signalling species (the mimic) shares signals from a noxious species (the model) and so avoids being eaten by model-averse predators receiving the signal (Edmunds 2000). Ants (Formicidae) are very likely the most common models for Batesian mimics. This is due in part to their numerousness and geographically widespread habitat, but also because of their powerful defences and often aggressive nature (Hölldobler & Wilson 1990; Cushing 1997). One widely studied ant-like, or myrmecomorphic, spider genus is *Myrmarachne* (Salticidae), which contains a large number of morphologically diverse species (Nelson 2010; Wanless 1978). All *Myrmarachne* species are myrmecomorphic Batesian mimics (Wanless 1978; Edmunds 2006; Cushing 2012), although in *Myrmarachne melanotarsa* it has been found that, in addition to being Batesian mimics (Nelson & Jackson 2009b), the spiders also use their resemblance to ants to obtain (spider) prey (Nelson & Jackson 2009a).

Myrmecomorphy provides a survival advantage when faced with spider-eating predators, such as mantises and other spiders (Nelson et al. 2006a; Nelson & Jackson 2006b). However, the similarity to ants is maladaptive when faced with ant-eating predators (Nelson et al. 2006c). This may be a significant trade-off for the mimic, as many invertebrates are ant-eating specialists (Jackson et al. 1998; Jackson & Li 2001; Huseynov et al. 2005; Pekar et al. 2008). To counter this problem, it appears that *Myrmarachne* adopts honest signalling displays to communicate to ant-eating predators that they are not ants, thereby reducing the probability of predation by predators that specifically target ants (Nelson et al. 2006b).

Batesian mimics should live among the noxious and harmful models that can validate their deceptive signal (Joron & Mallet 1998). Specific *Myrmarachne* mimics that closely resemble a particular model ant are usually closely associated with a particular model (Edmunds 1978, 2006). However, this presents an unusual problem for *Myrmarachne,* as ants are known to prey on salticids (Nelson et al. 2004; Nelson et al. 2005) and in defence of the colony ants readily attack anything nearby (Hölldobler & Wilson 1990). Therefore, species of *Myrmarachne* 'walk a tightrope' of avoiding spider-eating predators averse to ants (Nelson et al. 2006a; Nelson & Jackson 2006b)

and avoiding potentially lethal encounters with their aggressive models (Nelson et al. 2005). It is even possible that the threat of being eaten by their models is more significant than the threat posed by ant-eating predators, due to the social nature and higher local density of ants in any given area.

Edmunds (1974) suggested that in addition to Batesian mimicry, *Myrmarachne* may utilise aspects of mimicry to deceive the model species, but this has not been tested. The salticid's resemblance to ants is often mentioned as having little or no significance to the ants themselves (Jackson 1986) and empirical evidence supports the notion that species of *Myrmarachne* are primarily, if not exclusively, Batesian, not aggressive, mimics (Nelson et al. 2006a; Nelson & Jackson 2006b; Nelson 2011). The idea that myrmecomorphy is a mechanism to deceive ants (Eisner et al. 1978; Kistner 1982) is often criticised because ants mainly rely on chemical cues, not visual cues, to interpret their world (Hölldobler & Wilson 1990), and to date there has been no empirical support for aggressive mimicry of ants among *Myrmarachne*. Chemical mimicry of ants, notably by *Cosmophasis bitiaenta* (Allan & Elgar 2001; Allan et al. 2002), occurs among the Salticidae, but here there is no visual resemblance to its model, the Australian green weaver ant, *Oecophylla smaragdina*. In this case, *C. bitiaenta* is an aggressive mimic of ants, successfully invading their colonies to steal and eat ant larvae due to their chemical resemblance to the ants. There is some evidence to suggest that one species of *Myrmarachne* (*M. formicaria*) acquires cuticular hydrocarbons and deceives their morphological model, *Formica rufibarbis* (Pekár & Jiros 2011), which is likely also the case for *Cosmophasis bitiaenta*. However, fooling ants in order to obtain prey (aggressive mimicry) may not be the only driving force behind this ability among myrmecomorphic spiders. For *M. formicaria* chemical mimicry is suggested as a mechanism whereby the spider reduces ant aggression to itself (Pekár & Jiros 2011). In a similar manner, it is possible that visual resemblance may also reduce ant aggression toward the spider, especially if the ant model is a species that relies substantially on vision.

Although ants in general rely on chemical cues to interpret their surroundings (Hölldobler & Wilson 1990), recent research on navigation has demonstrated that certain species also have well developed visual capability (Ehmer 1999; Collett et al. 2001; Bisch-Knaden & Wehner 2003; Narendra 2007; Riabinina et al. 2011) and when

navigating their environment can switch from chemical cues to more efficient visual cues once experienced with the route (Aron et al. 2001). Increased spatial acuity in insects is achieved by increasing the number of facets in the compound eye, often leading to increased eye size (Barlow 1952; Land 1997; Gonzalez-Bellido et al. 2011). In ants, eyes range considerably in size: West African army ants (*Aenictus* sp.) completely lack eyes (Campione et al. 1983) and rely on chemical cues, while the exceptionally large eyes of *Gigantiops destructor* enable it to accurately navigate its visually complicated rainforest habitat using landmarks (Macquart & Beugnon 2004; Beugnon et al. 2005; Macquart et al. 2006). There is also evidence that a reduction in eye size may not necessarily limit all aspects of vision, as experiments on *Cataglyphis bicolor* desert ants reveal the size of the visual field can be maintained despite reductions in head and eye size (Zollikofer et al. 1995).

Green weaver ants (*Oecophylla smaragdina*) are a highly aggressive territorial ant species found in northern Queensland, Australia (Hölldobler 1983; Hölldobler & Wilson 1990). There are two species in this genus (*O. smaragdina* and, in Africa, *O. longinoda*) and both are dominant ants in their habitats across tropical Asia, Australia, and a large part of tropical Africa (Vanderplank 1960; Lokkers 1986). This is also the range shared by almost all species of *Myrmarachne* (Jackson & Willey 1994). As well as being highly aggressive, *O. smaragdina* possess large compound eyes (Wheeler et al. 1922), which may correlate with well-developed visual ability. Possibly due to its aggressive character, *O. smaragdina* is a common model for Batesian mimicry, and there are many accurate weaver ant mimics within the genus *Myrmarachne*. These include *M. ramosa* and *M. plataleoides* in South-East Asia and India (Edmunds 2006; Borges et al. 2007*), M. assimilis* in the Philippines (Nelson et al. 2006a; Nelson & Jackson 2007) and *M. smaragdina* in Australia (Ceccarelli 2010). These mimic species may gain a higher degree of protection than mimics of other ant species due to the aggression of their model ant. However, this means that living in close proximity to the model ants, as predicted by mimicry theory and corroborated by fieldwork (Edmunds 2006), may pose a particularly difficult challenge for *Myrmarachne* (Nelson et al. 2005).

Myrmarachne generally avoids contact with ants (Ceccarelli 2007) but when contact does occur certain characteristics enable ant-mimicking salticids to have higher survival

rates than ordinary salticids (Nelson et al. 2004; Nelson et al. 2005). When tested with small groups of its model, *O. smaragdina*, the accurate mimic *M. assimilis* had a higher proportion of survivors than did other myrmecomorphic salticids from the same genus (Nelson et al. 2005). Interestingly, the number of surviving *M. assimilis* did not differ significantly from other myrmecomorphic salticids when using a variety of ant species (Nelson et al. 2004). As the tested *M. assimilis* were raised from cultures, there was no opportunity to acquire cuticular hydrocarbons, as found in *M. formicaria* (Nelson et al. 2005; Pekár & Jiros 2011). Therefore, evidence suggests that certain non-chemical characteristics of *M. assimilis* led to increased survival with their model ant species.

O. smaragdina may habituate visually to conspecifics moving within their territory and are likely to only investigate conspecifics if they come in close proximity. At a distance, it is likely that *O. smaragdina* will react less to an object that moves and looks like a conspecific than a contrasting species that looks and moves differently. At a distance, therefore, the morphological and behavioural mimicry of *Myrmarachne* may offer some benefit for animals living in sympatry with their highly aggressive and visual models. Given the considerably higher visual acuity of salticids over insects (Land 1997; Harland & Jackson 2000; Harland & Jackson 2002, 2004), *Myrmarachne* will be able to detect ants before ants are aware of *Myrmarachne,* and research shows that salticids can detect objects of similar size as far as 40 body lengths away (Harland et al. 1999). Weaver ant mimicking *Myrmarachne* should, therefore, be able to see the ants and maintain a safe distance. However, being arboreal, weaver ants live in a visually cluttered canopy habitat (Hölldobler 1983), often making discrimination from a distance difficult. Additionally, the canopy, unlike the ground, requires a flightless animal to keep to a maze of branches and leaves, limiting possible escape routes (although *Myrmarachne* are able to drop on draglines from their perch). This canopy environment can be dominated by a very high number of weaver ant workers (Vanderplank 1960). Overall, this means *Myrmarachne* will inevitably venture close to weaver ants and very likely walk within range of the ants' view. If *O. smaragdina* workers are visually habituated to nearby conspecifics and the morphology and movement pattern of *Myrmarachne* is sufficient to fool their visual system, the mimic may be able to gain a survival advantage by being able to move in closer proximity to weaver ants without being detected, unless near contact is made, whereby the ant can make a chemical

assessment of the spider. This would offer a significant survival advantage for *Myrmarachne*.

Using live *O. smaragdina,* its accurate *Myrmarachne* mimic and a non-ant-like salticid species in the absence of odour cues, I tested whether visual assessment by *O. smaragdina* led to different responses toward these stimuli. In these experiments movement and morphology co-varied, so I carried out another test using 3D animation. Here, I tested the hypothesis that movement is an important recognition cue used by *O. smaragdina* to detect conspecifics. I predicted that *O. smaragdina* would respond less aggressively toward the visual stimulus of a morphological ant mimic moving in its characteristic ant-like manner then it would to that of a morphological ant mimic moving like a non-ant-like salticid.

Methods

Oecophylla smaragdina and its accurate mimic, *Myrmarachne smaragdina,* were collected from Townsville, in Queensland, Australia. All *M. smaragdina* were found in proximity to weaver ant nests. The non-ant-like salticids (*Cytaea* sp.) were collected from Cairns (Queensland, Australia). Salticids were housed in individual containers (cylinder of 40 mm diameter x 50 mm) and fed vinegar flies (*Drosophila sp.*) and other small dipterans once each week. Salticids were fed with four or five small dipterans at one time. A piece of damp cotton wool was placed in the container to provide humidity and fluid along with a single small leaf. Ants were tested immediately after collection. In addition to live ants and spiders, a virtual *Myrmarachne* was created to walk with two patterns of locomotion. One animation was made to move with *Myrmarachne*/ant-like locomotion (*Myrmarachne* model) and the other to move with jumping-spider-like locomotion (salticid model) (see Chapter 3 for details). The animated model was in motion for 60 s of the total 84 s of playback (71.4% of the time).

The experimental setup consisted of a glass formicarium (300 mm x 150 mm x 300 mm) and a rectangular transparent container (120 mm x 70 mm x 30 mm) placed in the corner against the side of the formicarium (Fig.1). The inside of the formicarium was lined with white paper. The paper was changed after each trial and the inside of the formicarium wiped down with 90% ethanol between trials to remove any chemical

deposits. A square (150 mm x 60 mm) was drawn on the paper around where the container was located (test area). The formicarium was then placed inside a large cardboard white-box (610 mm x 450 mm x 450 mm) to minimise disturbances to the ants. Lighting was provided by a 60-watt lamp placed inside the white-box, 200 mm from the formicarium.
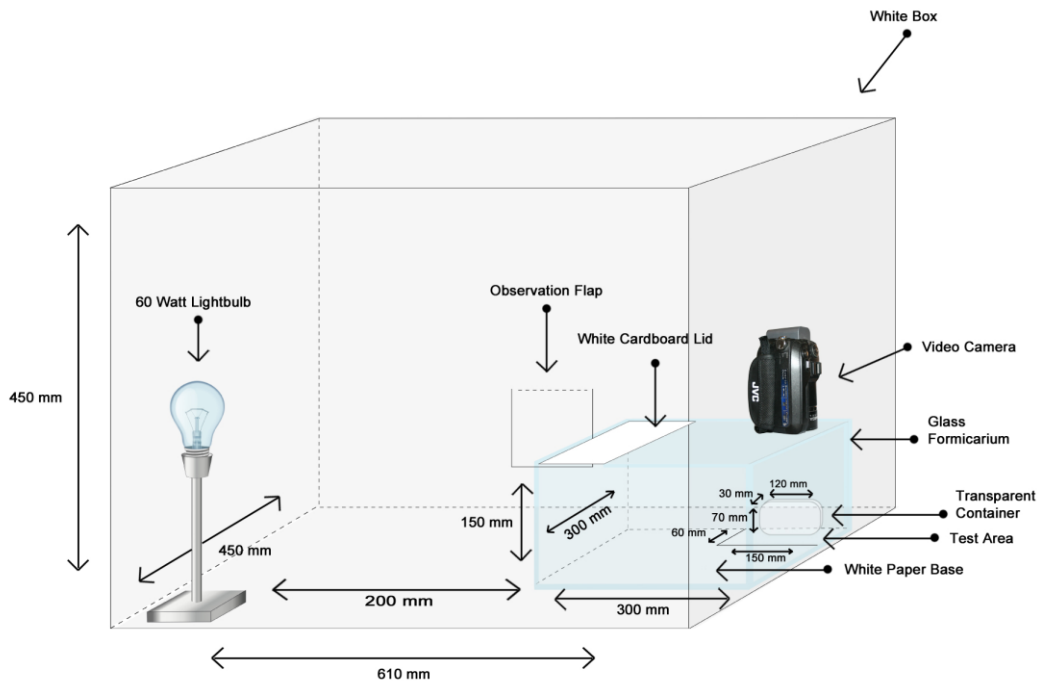

Figure 1. Experimental setup for recording the response of *Oecophylla smaragdina* workers toward either a conspecific, a jumping spider, *Myrmarachne smaragdina*, a *Myrmarachne* model with jumping spider motion, or a *Myrmarachne* model with ant motion.

Two types of experiments were conducted, these being live tests and animation tests. The live tests used a single living *O. smaragdina,* its accurate mimic *Myrmarachne smaragdina* or a non-ant-like salticid species, *Cytaea* sp., as stimuli to be presented to the group of ants in the absence of odour cues. However, while this is realistic, both movement and morphology co-varied in live tests, so other tests were carried out using 3D animation. Here, the movement pattern (ant-like or salticid-like, see Chapter 2) was the only variable, with both stimuli being based on the morphology of *Myrmarachne*.

The conditions were: 1. a single *O. smaragdina*; 2. a single *M. smaragdina*; 3. a single non-ant-like salticid, *Cytaea* sp. 4. the salticid-motion animation; 5. the *Myrmarachne-*

motion-animation. The first three conditions were for the live tests and the second two conditions were for the animation tests. Body size of stimuli for all five conditions was c. 9 mm. Each condition was tested five times using a different set of five ants from the same colony, with a minimum of 30 minutes between tests. This was repeated across three separate colonies of ants.

Tests were carried out between 8:00 and 16:00 h. For tests, five *O. smaragdina* workers, collected from the same colony, were initially placed inside the formicarium for 15 min to habituate. Five ants were used because, being social, this would reduce the chance of the ants behaving erratically due to being tested in isolation. While the ants were habituating to the environment, a white paper flap covered the section where the container was (Fig. 1), so ants were not disturbed while one of the five (randomly chosen) different conditions were added to the container. For the iPod conditions, the transparent container was replaced with an iPod showing either the salticid-motion-animation or the *Myrmarachne*-motion-animation. After habituation, the paper flap was lifted, revealing the stimulus.

Experimental trials lasted 15 min and were recorded using a JVC Everio Hybrid hard disk video camera (model GZ-MG575AA) placed on top of the formicarium and positioned to face directly down onto the test area. Video analysis was then completed using the multi-platform video editing software Avidemux 2.5. For the video analysis, the number of times each of the five ants entered the test area was counted and the duration of their stay was recorded in frames, which was then converted into seconds. Observations about general behaviour and whether the ants appeared oriented towards the taxa in the container were also made.

Statistical analyses were done using R v. 2.15.0 and Prism v. 5. Data were analysed using ANOVA, Kruskal-Wallis tests and Chi-square tests of independence to determine if there was a difference for the attraction of each stimuli condition to the groups of ants.

Results

There were no observable differences for the orientation propensity of ants towards the different treatments, nor were there other noticeable differences in overall behaviour. There was no significant difference for the effect of colony on the number of times weaver ants entered the test area ($F_{2,68} = 0.149$, $P = 0.862$), neither was there a significant difference for the effect of colony on how long weaver ants remained in the test area ($F_{2,68} = 1.941$, $P = 0.151$).

For live tests, there was no significant difference in the average number of times weaver ants entered the test area, irrespective of whether the stimulus was *O. smaragdina*, *M. smaragdina*, or *Cytaea* sp. ($F_2 = 1.028$, $P = 0.367$; Fig. 2), but there was a significant difference in the total number of entries made by ants depending on condition ($X^2_{28} = 156.2$, $P < 0.0001$, Fig. 3).
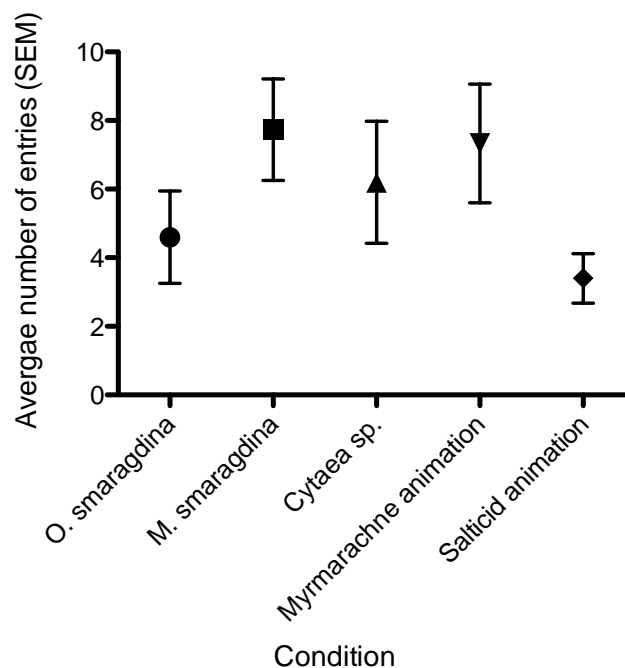

Fig. 2. Average number of times *Oecophylla smaragdina* ants entered the test area with different visual stimuli, all live (a single ant, *Myrmarachne*, or non-ant-like salticid), and in 3D animation with ant-like movement patterns (*Myrmarachne* animation) or salticid-like movement patterns (salticid animation).

In animation tests there was a significant difference in the number of times weaver ants entered the test area ($t_{28} = 2.10$, P = 0.045), with the *Myrmarachne* motion animation eliciting an average of 7.3 entries, while the salticid motion animation elicited an average of 3.9 entries into the test area (Fig. 2). This was also reflected in the total number of entries into the test area ($X^2_{14} = 42.31$, P = 0.0001, Fig. 3).
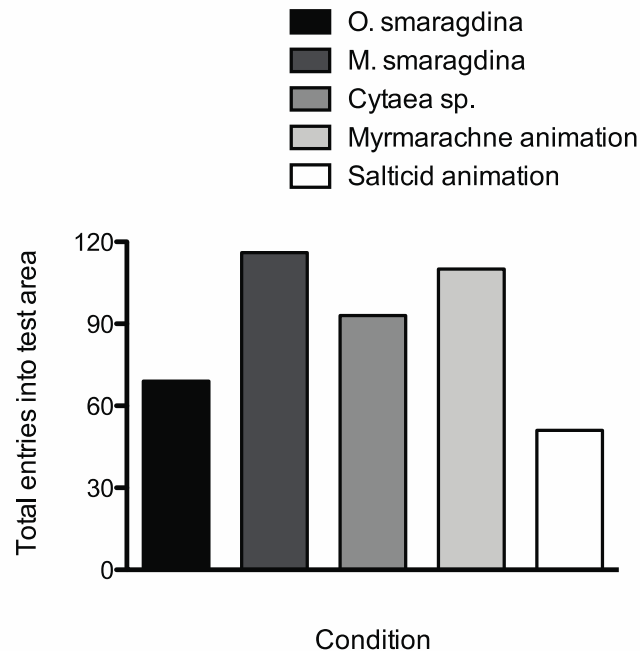

Fig. 3. Total number of entries by *Oecophylla smaragdina* ants into test area with different visual stimuli, all live (a single ant, *Myrmarachne*, or non-ant-like salticid), and in 3D animation with ant-like movement patterns (*Myrmarachne* animation) or salticid-like movement patterns (salticid animation).

Data for duration of time spent in the test area was not normally distributed and was analysed using non-parametric methods. For live tests, there was no significant difference in the time spent by weaver ants in the test area, irrespective of whether the stimulus was *O. smaragdina*, *M. smaragdina*, or *Cytaea* sp. ($H_2 = 3.415$, P = 0.18; Fig. 4). In animation tests there was also no significant difference in the number of times weaver ants entered the test area (U = 89.50, P = 0.350; Fig. 3).
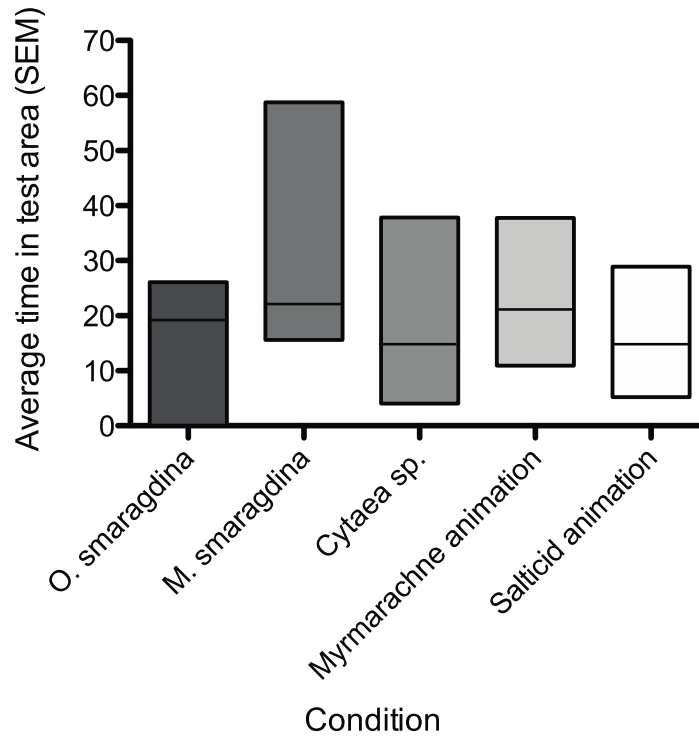
Fig. 4. Median duration of time (s) that ants spent in the test area with different visual stimuli, with live stimuli (a single ant, *Myrmarachne*, or non-ant-like salticid), and in 3D animations with ant-like movement patterns (*Myrmarachne* animation) or salticid-like movement patterns (salticid animation). Boxes represent 25% and 75% quartiles.

Discussion

Because *Myrmarachne* is expected to live among their noxious models in order to benefit from Batesian mimicry (Joron & Mallet 1998), characteristics that enabled *Myrmarachne* to get closer to the models without being detected should offer a considerable survival advantage. Previous studies demonstrate that *Myrmarachne assimilis*, an accurate mimic of *Oecophylla smaragdina*, possesses certain characteristics that enables it to survive in the proximity of its model better than do non-ant-like salticids and also compared with other myrmecomorphic spiders that are not precise mimics of this model (Nelson et al. 2004; Nelson et al. 2005). Being lab-reared, these traits could not have been due to the acquisition of cuticular carbons from its model. Following from this, the current study tested whether certain visual characteristics of another accurate mimic of *O. smaragdina*, *Myrmarachne smaragdina*, may account for the previous results. There was no difference in the duration of time

spent in the vicinity of the live ant, its mimic or a non-ant-like salticid, nor with the animations based on the morphology of *Myrmarachne* with ant-like or with salticid-like moving patterns, suggesting that these stimuli were not differentially attractive nor posed differential levels of threat, if they were perceived at all. However, that they were perceived is likely based on the results for the number of times ants approached the stimuli by entering the test area. Here there was a clear difference for animations, with ant-like movement being especially prone to elicit entries to the test area by the ants. This suggests that the movement patterns of *Myrmarachne* are potentially attractive to ants, in contrast to my prediction. In tests with live stimuli there was no difference for average number of entries. However, in these tests morphology, movement, and behaviour co-varied, making it difficult to interpret the results. Further complicating the interpretation of these results, there was a significant difference for the total number of times ants entered the test area for the live stimuli, with the ant stimulus eliciting 69 entries compared with the 116 entries elicited by *Myrmarachne,* with the non-ant-like salticid falling between these two. If the movement patterns of *Myrmarachne* are attractive to ants this may seem like a counterintuitive result for an animal that must keep its distance from its model. However, *Myrmarachne* is likely to be able to escape direct interactions with ants on most occasions. These spiders use vision to keep away from ants and usually maintain a distance of 2-3 cm from them (Ceccarelli 2007; Ceccarelli 2009) and when they do come into contact it is typically with the spider's first pair of legs, the ones that mimic antennae, and this usually leads to *Myrmarachne* running away unharmed (Ceccarelli 2007). Evidently much of *Myrmarachne*'s high survival with its model is attributable to its behaviour (Ceccarelli 2009).

The lack of differences observed in the time spent in the test area in this study may be as a result of the relatively small samples sizes, rather than the ant's inability to detect moving prey. Salticids can become prey of *O. smaragdina* (Nelson et al. 2005) and so I expected *Cytaea* sp. to have provoked predation or aggressive behaviour on the part of the ants. That this was not observed may have been due a lack of movement by the non-ant-like salticid during the test period, as research on insect eyes demonstrates that moving rather than static objects are more salient to the insect visual system (Srinivasan & Lehrer 1984; Lehrer & Srinivasan 1992). However, this seems unlikely, as the responses of ants were similar to all stimuli, and for the animations it was known that movement was essentially continuous.

Although there is evidence to demonstrate jumping spiders can see projected images for prey choice experiments (Harland & Jackson 2002; Nelson & Jackson 2006a), the 'camera' type eyes of salticids are very different to the compound eyes of insects, and this may present differences when viewing projected images or viewing objects through glass. Salticids have eight eyes composed of three pairs of secondary eyes along the edges of the cephalothorax and two large primary eyes. The secondary eyes effectively give salticids close to 360° vision and function primarily as movement detectors (Crane 1950; Land 1971, 1985a; Zurek et al. 2010). It is the primary eyes that give these spiders their exceptional spatial acuity (Land 1969; Harland et al. 1999; Harland & Jackson 2002, 2004). In insects, the receptor units in an insect's compound eye are the ommatidia, each of which requires its own lens or facet. For high spatial acuity there must be a large number of small facets, but this creates problems with diffraction (Land 1997). Despite diversity in structural modifications to optimise the eye dependent on the species' environment, compound eyes still remain limited when compared to simple eyes (Land 1997; Land & Nilsson 2002). These structural differences correspond to a lower visual acuity for insect eyes of a given size, and salticid principle eyes are usually an order of magnitude finer (Land 1985b; Land 1997). Although the spatial acuity of the eyes of *Myrmarachne* have never been directly determined, the similar size of *Myrmarachne*'s principal eyes (c. 280 um (Ceccarelli 2010)) to those of its model (c. 440 um; average from 12 ants tested) would mean that *Myrmarachne*'s vision is much better than that of *O. smaragdina*.

Armed with 360° movement detection and exceptional forward vision with ability to resolve fine detail, *Myrmarachne* could detect weaver ant workers before the weaver ant is aware of *Myrmarachne*. The difference in visual perception between ants and salticids likely posed a considerable advantage for salticids to diversify and exploit ants as a Batesian model and food source. However, better vision is not sufficient for *Myrmarachne* to survive close proximity with ants (Nelson et al. 2004; Nelson et al. 2005). The social structure and high number of ants creates a high probability of encounters between mimic and model, and a fraction of these will be fatal for *Myrmarachne* (Nelson et al. 2005). Visual ability of ant models will increase the chance of *Myrmarachne* being detected. If *Myrmarachne* could lower this detection through visual deception, as for spider-eating predators (Nelson et al. 2006a; Nelson & Jackson

2006b), it would increase *Myrmarachne*'s chance of survival. However, given the structural differences of the different types of eyes and, in particular, the limitations of compound eyes for high spatial acuity vision, teasing the effect of *Myrmarachne*'s visual deception of ants presents its own challenges.

Mimicry may only benefit *Myrmarachne* in certain specific conditions, such as when ants are distracted by a food source. If ants were at a food source they are likely to habituate to other ants of their colony moving back and forth from the food source to the nest. Under these conditions, *M. smaragdina* may pass by this group of ants without visually attracting as much attention as a non-weaver-ant modelling salticid. If they do not pose a threat, ants habituate to other ant species sharing the same trail network (Menzel et al. 2010) and presumably would habituate to ants of their colony. There is evidence showing that, in certain circumstances, exchange of food (trophallaxis) can occur between colony members of unfamiliar nests (Newey et al. 2010).

As each condition utilised species that should provoke a different reaction by weaver ants, and given the large compound eyes of the weaver ant genus *Oecophylla* (Wheeler et al. 1922), it seems possible that the inability to detect differences in these tests is attributable to limitations of the experimental design. The main identified problems are the limited understanding of how insect eyes perform regarding virtual stimuli, as this method has never been used with ants, or other insects, before. An area for further investigation is the visual ability of *O. smaragdina*, which is currently lacking in the literature. Studying the visual ability of weaver ants was beyond the scope of this thesis, but will be important for identifying any visual deception by the myrmecomorphic salticids on the model ants themselves. *O. smaragdina*, which are very common over a large part of the tropics, are sometimes used as biological control agents (Peng et al. 2012). Research on the visual ability of this species, including whether they use visual cues to navigate may provide useful information for their continued application as a biological control.

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Chapter 5: Discussion

The large jumping spider genus *Myrmarachne* is comprised of over 200 species of salticids that mimic ants in morphology (Wanless 1978; Cushing 1997, 2012; Proszynski 2007). Species in this genus often associate closely with a certain type of ant (Edmunds 1978, 2006) and this close association combined with their close mimicry offers a survival advantage when encountered by spider-eating, visual predators (Nelson & Jackson 2006; Nelson et al. 2006a). In addition to morphological mimicry, behavioural mimicry is often suggested for *Myrmarachne* (Cushing 1997, 2012). For example, *Myrmarachne* raise and wave their front pair of legs about in a manner similar to the movement of ant antennae (Ceccarelli 2008), which may be an additional component to aid in the deception. A more conspicuous component of behavioural mimicry by *Myrmarachne* is the manner in which they walk.

Batesian mimics occur as a continuum of accuracy relative to their models. At one end, mimics are described as 'general', or 'poor', and at the other, 'specific', or 'good' (Edmunds 2000, 2006; Nelson 2010). These assessments of accuracy are generally based on human observation, but research investigating mimic accuracy from the perspective of possible selecting agents is increasing (Dittrich et al. 1993; Nelson 2012), albeit slowly. So far, these experiments demonstrate that at least some selecting agents share a similar perception of accuracy as humans (Nelson 2012).

Specific mimics gain protection by animals confusing them with their harmful models, which consequently avoid them (Ruxton et al. 2004). However, the existence of general mimics has generated debate regarding the adaptive significance of partial resemblance to a model and numerous explanations have been proposed. These include evolutionary trajectories away from former specific mimicry (Azmeh et al. 1998), optimising mimicry depending on the ratio of model-eating to model-averse predators (Pekár & Jarab 2011; Pekár et al. 2011), exploiting the cognitive ability of potential predators (Kikuchi & Pfennig 2010), increased habitat availability due to resemblance to a wider

number of taxa over a greater geographical area (Edmunds 2000), or because the model species is exceptionally harmful and so even partial resemblance triggers aversive behaviour (Edmunds 2000).

If restricted to the habitat range of their particular model, specific mimics will have a greatly reduced area available to forage for resources. In the case of myrmecomorphic spiders, they may also be competing directly with their models for prey. If ant-like salticids cannot forage outside the foraging area of their model ants, they will suffer a considerable reduction in food availability compared to ordinary salticids. For example, green weaver ant (*Oecophylla smaragdina*) mimics would be restricted to a mostly arboreal, tropical, habitat, where weaver ants tend to live (Hölldobler 1983), preventing a mimic from foraging on the ground where they might find more available prey species. Conversely, a general ant mimic that shows partial resemblance to *O. smaragdina,* but also shows partial resemblance to other ant taxa that live on the ground will be able to forage for resources in both habitats.

The model of a Batesian mimic will suffer from the existence of mimics, as predators experiencing the harmless nature of the mimic may predate the model (Joron & Mallet 1998), and has resulted in mimics being referred to as parasitic (Rowland et al. 2010). Close resemblance to a model across different aspects of mimicry, such as morphology, antennal behaviour, and locomotion, may benefit the mimic in other ways: if predators confused mimic and model on one signal component, it would be advantageous for the model to evolve another signal component to escape the Batesian mimic. This would then put pressure on the mimic to evolve the new signal component in addition to the first. An arms race would then form, possibly accounting for multi-component signalling (Rowe 1999). This arms race will also occur between mimics and the selecting agent. If the selecting agent learns to differentiate mimic from model based on one signal component, the mimic should evolve close resemblance in another component. If there are multiple predators sharing habitat with *Myrmarachne*, which differ in their cognitive ability for distinguishing mimic from model, the energetic investment in locomotory mimicry (Lighton & Gillespie 1989) in addition to morphological mimicry by *Myrmarachne* may only benefit their survival when faced with the fraction of potential predators with a higher cognitive ability.

Some predators require a high degree of resemblance by the mimic to confuse it with the model (Nelson 2012) and if ant-averse predators living in sharing a habitat with the mimic possess a high ability for distinguishing mimic from model, the general mimic will be at a considerable survival disadvantage. The advantage of general versus specific mimicry can also be attributed to the ratio of model-eating and model-adverse predators living in the same habitat (Pekár & Jarab 2011; Pekár et al. 2011). If the ratio of model-eating to model-averse predators is equal then it may benefit general mimics, as partial resemblance may be enough to confuse spider-eating predators, based on either predator cognitive ability or the noxiousness of the model, and partial resemblance may be sufficient for ant-eating predators to avoid the general mimic (Pekár & Jarab 2011; Pekár et al. 2011).

In this thesis, I investigated locomotory mimicry in the salticid genus *Myrmarachne*. In particular, I attempted to identify the characteristics and the role of locomotory mimicry in the deception of visual species, and to identify any aspects of deception that improve survival among their ant models. In Chapter 2, I showed that *Myrmarachne* spp. share the locomotion pattern of ants across several measurable parameters of motion, specifically, the duration and distance of a bout of movement, the number of bouts of movement and the distance travelled per unit of time, and turning behaviour. *Myrmarachne* mimics the motion of ants across many more parameters than solely the 'speed' described for 'inaccurate' mimics (Pekár & Jarab 2011). This myrmecomorphic locomotion as an additional component to *Myrmarachne*'s morphological mimicry (Edmunds 2006; Nelson & Jackson 2006; Nelson et al. 2006a) is likely to offer better protection against visual ant-averse predators, but may place *Myrmarachne* at higher risk of being targeted by ant-eating predators (Nelson et al. 2006b; Pekár et al. 2011; Pekár & Jarab 2011). In order to ascertain if the locomotory mimicry found in Chapter 2 enhances the deceptive signal of morphological mimicry, I tested the locomotion component of *Myrmarachne*'s mimicry with ant-eating predators using computer-animated models (Chapter 3). There was no significant difference between both the salticid-motion and ant/*Myrmarachne* locomotion computer models, but there was a non-significant trend, suggesting that enhanced deception might be found with a larger sample size. The locomotory component of myrmecomorphy has been suggested to be the main protective trait of general ant mimics when faced with spider-eating predators (Pekár & Jarab 2011), and given the physiological cost of retaining locomotory mimicry

(Lighton & Gillespie 1989), its existence is expected to benefit the organism. Further research is required to identify the adaptive significance of locomotory mimicry in Batesian mimics.

Because ants are also potential predators of the ant-mimics themselves, there may be aspects of the mimicry signal that have evolved to deceive ant species, particularly those that rely more heavily on vision. The idea that *Myrmarachne* may deceive the model species has been mentioned previously in the literature (Edmunds 1974). Nelson et al. (2005) found that the weaver ant-mimicking species *M. assimilis* had a higher survival rate with its model species than with other ants. In Chapter 3 I tested the hypothesis that the visual mimicry of *Myrmarachne,* including locomotory mimicry, may fool the visual ability of green weaver ants based on its large compound eyes (Wheeler 1910). I found that the locomotory mimicry of ants may fool the ants, but is potentially maladaptive instead of adaptive, as it seemed to attract ants, placing *Myrmarachne* at greater risk of predation rather than increasing its survival. This suggests *Myrmarachne* would need additional traits to survive close encounters with its model, which may be a finely tuned aversive response.

The existence of locomotory mimicry and the increased risk of predation by the models and by ant-eating predators suggest that selective pressure for locomotory mimicry must be high in order to outweigh the potential trade-off of being attractive to its dangerous models. Possibly there are many predators with the cognitive ability to distinguish mimic from model that share their habitat with *Myrmarachne*. This aspect of deception requires more field research to understand the actual selective pressure in *Myrmarachne*'s habitat and the different species that pose the greatest threat. This will provide a clearer understanding about the cognitive ability required to distinguish *Myrmarachne* from ants. Despite birds being thought to be the major predators of spiders (Gunnarsson 2007), invertebrate predators can be both very numerous and also spider specialists (Li & Jackson 1996; Nelson et al. 2004; Cross & Jackson 2006; Jackson et al. 2008; Wignall & Taylor 2010). Some of these spider specialists are also known to possess a high cognitive ability (Jackson et al. 2001; Jackson & Nelson 2011) and thus a high degree of resemblance may be required for mimic and model to be confused (Nelson 2012). Clearly, 150 years after its discovery (Bates 1862), more research is required to understand the selective pressures on mimics in order to fully

understand the greatest post Darwinian application of natural selection (Fisher 1958), that of Batesian mimicry.

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Appendix

Table 1. Observations of *Cytaea* sp. feeding in the wild. All observations were made in Centenary Lake, Cairns, Queensland, Australia.

Observation number	Prey
1	*Oecophylla smaragdina*
2	*Oecophylla smaragdina*
3	*Polyrhachis australis*
4	*Small black ant*
5	*Small black ant*
6	*Oecophylla smaragdina*
7	*Oecophylla smaragdina*
8	*Small black ant*
9	*Polyrhachis australis*
10	*Oecophylla smaragdina*
11	*Small black ant*