

Fighting strategies and mechanisms behind contest resolution in the jumping spider *Servaea incana*



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General Abstract

Contests over limited resources are commonplace and widespread across animal taxa. Rather than unconstrained fighting, animals are expected to adopt strategies designed to reduce contest costs. One such strategy is mutual assessment, where each rival performs ritualised signals of fighting ability or resource holding potential (RHP), allowing animals to economically determine which is weaker. However, as assessment itself may also be costly or difficult, an alternative strategy to limit the costs associated with contests may be for rivals to persist until they reach an internal cost-threshold. Each strategy allows for determination of the winner while limiting the costs of fighting. Jumping spiders, with their excellent vision, elaborate displays and dangerous weapons present excellent models for the study of decision making in animal contests. In this thesis I describe the biology of the jumping spider *Servaea incana* and examine the decision rules used in male-male contests. Size is a strong predictor of contest outcome and also of whole-organism performance capacity. Correlations between size and levels of contest escalation suggest that smaller spiders are less willing to escalate, regardless of opponent size, and this suggests use of internal thresholds rather than mutual assessment. Video playback experiments reveal that visual assessment of opponent size may influence the decision to display towards or approach an opponent. Hunger may also influence contest behaviour; hungry spiders are more likely to attack conspecifics and may be more likely to engage in contests. The potential for injury, or even death, may explain the unwillingness of small spiders to engage in escalated contests.

Statement of Candidate

I certify that this thesis, entitled “Fighting strategies and mechanisms behind contest resolution in jumping spider contests” has not previously been submitted for a degree nor has it been submitted as part of requirement for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

The thesis was not subject to approval by the Macquarie University Ethics Review Committee since the organism studied is an invertebrate, the jumping spider *Servaea incana*.



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Chapter One: General Introduction

Resources are finite, so their distribution is often determined by competition among individuals. Contests for limited resources are ubiquitous across animal taxa despite the potentially high costs of physical fighting, which may include time and energetic investment (Briffa & Elwood 2004) as well as the risks of being injured (Rudin & Briffa 2011) or even killed (Reece et al. 2007). Contests are largely resolved on the basis of asymmetries in fighting ability between opponents. Strong animals, those with higher resource holding potential (RHP), are more likely to win contests and become increasingly more likely to win as the asymmetry between rivals increases. The simplest method to determine the outcome of a contest would be for animals to fight until one rival is unable fight any longer. However, animals rarely engage in such unconstrained agonistic behaviour and contests are often resolved without escalating to an all-out physical struggle, even when animals possess dangerous weapons and are capable of killing each other. Early explanations of this phenomenon suggested that such constrained agonistic behaviour was a result of group selection and exists to benefit the species or population. However, the application of game theory to animal contests identified both possible mechanisms and functions of “limited war” strategies, based on selection at the individual level; hawk-dove games and war of attrition models revealed how evolutionarily stable strategies for animal contests might exist in the absence of escalated conflict and despite asymmetries in fighting ability (Maynard Smith 1974; Maynard Smith & Parker 1976; Maynard Smith & Price 1973; Parker 1974).

Early models proposed that decision rules were the mechanisms underlying contest resolution; animals withdraw from contests under certain conditions, for example when

they reach a certain cost threshold, or as soon as they determine that their opponent is stronger than themselves. Models such as the sequential assessment model (Enquist & Leimar 1983) or the asymmetric war of attrition (Hammerstein & Parker 1982; Parker & Rubenstein 1981) proposed that rather than escalated fighting, ritualised contests with stereotyped displays may permit animals to exchange information about their relative fighting ability, allowing each rival to determine who would win an escalated struggle without bearing the costs associated with physical fighting. Models of mutual assessment predict that contests will only escalate when rivals are closely matched and will be resolved quickly when there are large asymmetries in RHP. Therefore, a negative relationship between RHP asymmetry and contest costs is consistent with mutual assessment.

Empirical studies examining the assessment strategies used in contests have relied upon the predicted correlations between RHP and contest costs to test different models. Negative correlations between RHP asymmetries and contest costs were used as support for mutual assessment in many empirical studies. However, Taylor & Elwood (2003) demonstrated that this correlation is also expected to occur in circumstances where animals are not assessing each other. Under self-assessment models such as the energetic war of attrition (Payne & Pagel 1996) and war of attrition without assessment (Mesterton-Gibbons, Marden & Dugatkin 1996), animals persist in accordance with their own abilities and do not assess the RHP of their opponent. Instead, contests are resolved when the weaker rival reaches its threshold and withdraws. Therefore, if using self-assessment, contest costs will increase with the RHP of the weaker rival. However, a negative relationship between RHP and size asymmetry still occurs because the largest asymmetries occur in contests involving the weakest rivals.

Taylor and Elwood (2003) suggested that an alternative method to distinguish between mutual and self-assessment is to examine the RHP of each rival as separate predictors of contest costs, rather than examining the composite measure of RHP asymmetry. However, the cumulative assessment model (Payne 1998) predicts similar relationships between RHP and contest costs as mutual assessment, despite the decision to withdraw being based upon an own-cost threshold. As in mutual assessment, the decision of the weaker rival to withdraw is influenced by the RHP of the stronger rival, but due to costs inflicted rather than gathering information about the opponent's RHP. Stronger rivals are expected to cause weaker rivals to give up earlier by inflicting greater costs, while the RHP of the weaker rival is expected to determine both the rival's threshold and ability to withstand costs. Therefore, relationships between RHP and contest costs that are consistent with mutual assessment may also be consistent with cumulative assessment (Arnott & Elwood 2009b; Briffa & Elwood 2009). In addition, empirical studies examining the RHP of rivals as separate predictors of contest costs suggest that there may be a continuum between self and mutual assessment (Prenter et al. 2006) and that animals may switch assessment strategy at different stages of a contest (Hsu et al. 2008).

Clearly, alternative methods of distinguishing between assessment strategies are needed (Arnott & Elwood 2009b; Briffa & Elwood 2009; Elwood & Arnott 2012, 2013; Fawcett & Mowles 2013). Empirical studies of contests have been limited in the manipulative techniques available to distinguish between assessment strategies. This is largely due to the nature of contests as they are an interaction between two rivals. Animals may be expected to assess traits that correlate with RHP, but it may be difficult to manipulate such traits without affecting actual fighting ability. However, choice experiments, playback experiments and examination of the motivation to fight may be

suitable techniques available for some animals (Arnott & Elwood 2009a; Arnott & Elwood 2010; Reichert 2014; Tibbetts & Lindsay 2008; Tibbetts, Mettler & Levy 2010).

Spiders have been important models for the study of animal contests. They were among the first empirical studies to suggest that animals may persist in accordance with their own fighting ability, rather than assessing their opponent (Bridge, Elwood & Dick 2000; Taylor, Hasson & Clark 2001; Whitehouse 1997). Contests between spiders typically start with ritualised signalling and may escalate through multiple levels of physical contact before culminating in a physical struggle. It appears that spider contests are largely resolved on the basis of self-assessment, although opponent RHP may play a role (Constant et al. 2011; Elias et al. 2008; Keil & Watson 2010; Taylor et al. 2001).

Jumping spiders make excellent subjects for the study of animal contests. Males readily engage in contests and jumping spiders possess weaponry capable of injuring or killing their conspecifics, therefore, they may be expected to have well defined strategies for engaging in, and economically resolving, contests. Jumping spiders possess excellent vision (Land 1969a, b; Williams & McIntyre 1980) and are well known for the ritualised displays that they use in intraspecific interactions, suggesting the potential for mutual assessment, however, correlative studies suggest that they rely upon self-assessment strategies to determine when to retreat from contests (Elias et al. 2008; Taylor et al. 2001).

Research objectives

The aim of this thesis is to determine the mechanisms underpinning resolution of male-male contests in the jumping spider *Servaea incana* Karsch 1878 (Araneae:

Salticidae). Little is known about the biology of this species so I describe the natural history of this species before examining contest behaviour in detail.

Thesis organisation

This thesis starts with two chapters describing the biology, natural history and behaviour of *S. incana*. Chapters 4 – 6 all focus upon contest behaviour, while chapter 7 examines why large spider might win contests. The following is a description of each chapter:

Chapter Two describes the intraspecific interactions and natural history of *S. incana* in the field and in the laboratory. This chapter is co-authored by Vivian Mendez and Phil Taylor who both contributed to the concepts and design of the chapter. Vivian and I collected the data. I analysed the data and wrote the manuscript. Phil and Vivian provided comments on revisions of the chapter. This chapter is formatted for the *Australian Journal of Zoology*.

Chapter Three describes the results of a field census examining the abundance and size *S. incana* at different life stages over a 13 month period. This chapter is co-authored by Vivian Mendez and Phil Taylor. Vivian, Phil and I planned the census. Vivian and I collected the data. Vivian analysed the data and wrote the initial draft of the manuscript. Phil and I revised the manuscript. This chapter is formatted for the *Journal of Natural History*.

Chapter Four examines correlations between RHP and measures of contest costs to determine the assessment strategies of *S. incana* in staged male-male contests in the laboratory. This chapter is co-authored by John Prenter and Phil Taylor. John, Phil and I planned the experiments. I collected and analysed the data. John and Phil provided comments and suggestions on revisions of the chapter. This chapter has been published in *Animal Behaviour*.

Chapter Five uses video playback to examine the role of visual assessment of opponents in contests of *S. incana*. This chapter is co-authored with Phil Taylor. Phil and I planned the experiments. I collected the data, ran analyses and wrote the chapter. Phil provided comments on revisions of the chapter. This chapter is formatted for *Ethology*.

Chapter Six examines the effects of hunger on contest behaviour in *S. incana*. This chapter is co-authored by Ram Krishnan and Phil Taylor. Ram, Phil and I planned the experiments. Ram and I collected the data. I analysed the data and wrote the chapter. Phil provided feedback and comments on the chapter. This chapter is formatted for *Behavioral Ecology*.

Chapter Seven explores the links between morphology and whole-organism performance in *S. incana* males. This chapter is co-authored with John Prenter and Phil Taylor. John, Phil and I planned the experiments. I collected and analysed the data and wrote the manuscript. John and Phil provided feedback and comments

on subsequent drafts of the manuscript. This chapter has been published in the *Biological Journal of the Linnean Society*.

Chapter Eight provides a general discussion of contests in *S. incana* in the context of their biology and natural history.

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Chapter Two: Natural history and display behaviour of *Servaea incana*, a common and widespread Australian jumping spider (Araneae, Salticidae)

Abstract

The natural history and intraspecific interactions of *Servaea incana*, a common jumping spider of temperate Australia, are described. Particular attention is paid to observations of behaviour in nature and in the laboratory, including interactions between male and female adults, subadults and juveniles both at and away from retreats and nests. The display repertoire of *S. incana* is broadly typical, although it is relatively simple in comparison to the behaviour of some of *Servaea*'s closest relatives. Like other jumping spiders, *S. incana* males use visual displays (Type I courtship) when they encounter females in the open. Male jumping spiders usually rely on signalling via silk borne vibrations when they encounter females at retreats and nests (Type II courtship) but this is not pronounced in *S. incana*, which largely relies on visual displays in this context. When adult males encounter subadult females at retreats, males build their own retreat near to the female's retreat and cohabit until females moult to maturity, copulating shortly afterwards. Ants make up a large portion of the diet, but *Servaea incana* prey upon a variety of small arthropods and exhibit versatility in predatory behaviour. Identified enemies of *S. incana* include other spiders, a pompilid wasp and a mantispid.

Introduction

Jumping spiders (Araneae, Salticidae) are distinguished by unique eye structure and visual acuity that far exceeds the capabilities of other spiders (Land 1985). In accord with their exceptional visual abilities, 'salticids' characteristically rely on vision-mediated behaviour in contexts where spiders from other families rely on other senses. Vision is used extensively in navigation, allowing salticids to plan long and circuitous routes that may include sophisticated detouring behaviour (Jackson *et al.* 2002; Tarsitano and Jackson 1994; Tarsitano and Jackson 1997). Rather than building webs, most salticids are cursorial hunters that rely on vision to detect, assess, and target their prey (Harland and Jackson 2002; Jackson *et al.* 2005; Li *et al.* 2003; Nelson and Jackson 2011). Some tend toward sit and wait predation, lunging at or pursuing prey that comes close (Jackson 1985b; Jackson 1990). Others are more active hunters, foraging over long distances and actively stalking their prey (Forster 1977; Jackson 1985a; Jackson 1988). Some salticids exhibit versatile hunting behaviour, using different strategies for different types of prey (Jackson and Pollard 1996; Nelson *et al.* 2005). Salticids are perhaps best known, however, for their elaborate use of complex visual displays to mediate intraspecific interactions (Clark 1994; Cross *et al.* 2008; Nelson and Jackson 2007). Intraspecific interactions, especially courtship, typically entail complex communication at a distance through sequences of postures involving legs, pedipalps, and body positions, and 'dances' whereby the spiders make a series of stepping movements while displaying with their appendages. In addition to their more readily discernable visual displays, some salticids also incorporate seismic elements as multi-modal signalling into their otherwise visual display routines (Edwards 1981; Elias *et al.* 2012; Girard *et al.* 2011; Gwynne and Dadour 1985; Maddison and Stratton 1988; Sivalinghem *et al.* 2010; Taylor and Jackson 1999).

Vision-mediated display behaviour is effective when salticids interact in the light away from their nests, but is not usually a suitable means of communication for males that encounter females in silken retreats or nests, where visual signals are usually precluded by the dense silken structure or by their dark location. Courtship versatility that accommodates the diverse sensory environment of interactions appears to be typical of salticid spiders; males primarily use visual displays when females are away from nests but instead use seismic and tactile signals when females are inside retreats or nests. When males encounter sub-adult females in retreats they commonly use seismic and tactile signals, but soon cease display and instead cohabit until the subadult female matures (Jackson 1986a; 1992).

Comparative studies of diverse species are key to understanding both the evolution of salticid behaviour and the evolution of this group of spiders as a whole (Jackson and Blest 1982). The present study is the first to describe natural history and display behaviour of a salticid spider from the genus *Servaea*. *Servaea incana* is a common Australian salticid inhabiting eastern and southern eucalypt forests of mainland Australia, from Queensland to Western Australia, as well as Tasmania, and is the largest and most widespread species of its genus (Richardson and Gunter 2012). The genus *Servaea*, members of which are primarily from temperate regions and inhabit the trunks of eucalypt trees, was revised recently (Richardson and Gunter 2012). Previously known as *Plexippus validus* and *Servaea vestita*, *S. incana* has been the subject of some important studies of arthropod vision (Blest 1983; Blest *et al.* 1981; Blest and Maples 1979; Blest *et al.* 1988; Zurek and Nelson 2012; Zurek *et al.* 2010). Despite being important as a model in these studies, detailed descriptions of this species' natural

history and behaviour have not been published previously. Studies of the natural history and behaviour of Australian jumping spiders have largely focused on tropical species.

According to the most recent phylogeny (Zhang and Maddison 2013), the genera most closely related to *Servaea* for which studies of behaviour are available include *Lycidas* (Gwynne and Dadour 1985), *Hypoblemum* (Jackson and Willey 1995), *Saitis* (Hill 2009), *Maratus* (Girard *et al.* 2011; Hill and Otto 2011) and *Thiania* (Chan *et al.* 2008; Jackson 1986b; Li *et al.* 2002). These genera all form a sister clade to *Servaea*. Within this clade, the iridescent *Thiania* are part of a separate branch to the other mentioned genera. The genus *Lycidas* currently appears to be paraphyletic and *Lycidas michaelsoni*, the only '*Lycidas*' species for which some elements of behaviour have been described (Gwynne and Dadour 1985), was not included in the phylogeny of Zhang and Maddison (2013). The appearance and behaviour of *L. michaelsoni* does not match the other species in the clade for which behaviour has been described. Males of the remaining genera (*Maratus*, *Saitis* and *Hypoblemum*) have ornamented third legs, which are used extensively in their visual display repertoires. *Maratus*, the peacock spiders, are known for particularly striking displays, making use of unusual morphological features as well as seismic signals (Girard *et al.* 2011; Hill and Otto 2011). *Thiania* are iridescent and build unusual rivet-like nests (Li *et al.* 2002). Compared with many related genera, *Servaea* has a comparatively plain appearance. Based on appearance and position in the phylogeny, *Servaea* may represent a more primitive state from which these other more colourful groups are derived.

Here we describe the display repertoire used by *S. incana* during intraspecific interactions, including interactions between males and female adults, subadults and juveniles. Sequences of behaviour are described for interactions between each sex and

age class of spiders. We also present field observations of prey, predators and predatory behaviour.

Methods

Collection & Maintenance

Servaea incana were observed on, and collected from, the trunks of eucalypt trees in parks in Sydney, NSW, Australia, between September 2010 and September 2013. Field observations were made during collecting trips and also during regular surveys carried out as part of another study (Chapter 3). Spiders were maintained in a laboratory under controlled temperature ($25 \pm 0.5^{\circ}\text{C}$) and humidity ($65 \pm 5\%$) on an 11:1:11:1 h light:dusk:dark:dawn cycle. During the light phase the laboratory was illuminated with a 50:50 mix of metal halide and halogen lights. At the commencement of the dusk phase, the metal halide lights turned off and the halogen lights lowered in intensity until switching off after 1h. At the commencement of the dawn phase, the halogen lights switched on at 5% output and then increased in intensity until at 100% output after 1h, at which time the metal halide lights turned on.

Spiders were housed individually in 1.125 L ventilated plastic cages that contained half a sheet of crumpled white A4 paper as environmental enrichment. Environmental enrichment has been found to improve the performance of jumping spiders in behavioural research (Carducci and Jakob 2000). Spiders were maintained on a two-week feeding schedule, receiving two Queensland fruit flies (*Bactrocera tryoni*) and two houseflies (*Musca domestica*) on alternate weeks. Small juveniles were fed a mixed diet of laboratory-reared *Drosophila* and various small wild insects that were

caught using a sweep net. Water was provided from a soaked cotton wick that was replaced regularly, or by spraying water through the cage at least three times each week.

Procedures for observing interactions

We use the established conventions that the terms ‘usually’ or ‘generally’, ‘sometimes’ or occasionally’, and ‘infrequently’ or ‘rarely’ refer to frequencies of more than 80%, 20-80% and less than 20%, respectively (Jackson and Hallas 1986). ‘Juvenile’ includes all active stages prior to the penultimate instar. Spiders in their penultimate instar are referred to as ‘subadults’, and at this stage can be readily identified as male or female by enlarged terminal segments of pedipalps and developing epigyne, respectively. Other than when qualified as ‘subadult’, the terms ‘male’ and ‘female’ refer only to adults.

Interactions were staged between randomly selected pairs of spiders in the laboratory, with the restriction that individual spiders were never used more than three times in any particular interaction type (e.g., male-female), never more than once with any other individual and never more than once on any day. Interactions were never staged within two hours of the end or beginning of the laboratory light phase.

Interactions were recorded with Panasonic HDC-HS700 and HS-900 High Definition digital video cameras (resolution: 1920x1080, 25 fps, codec: H264-MPEG-4-AVC) with supplementary close-up lenses. High-speed photographs were taken with the Panasonic cameras (50 s⁻¹) and high-speed photos and video (240 fps) were recorded with a Casio EX-FH25 camera. Opportunistic observations were made in the field and these were photographed and video-recorded using a Panasonic DMC-FT1 camera.

Interactions in the open

Interactions in the open were staged in an open roofed acrylic arena with 300 x 150 mm floor and 80 mm high, 5 mm thick walls (following Taylor *et al.* 2001). The arena consisted of two sections; a transparent base and opaque upper walls. The base consisted of the floor and 15 mm high transparent walls, enabling filming of interactions at ground level. The upper walls were made of white acrylic, 65 mm high and sat on top of the base. The upper walls were lightly coated with petroleum jelly to prevent spiders climbing out. A sheet of white paper covered the arena floor, and this was replaced for every interaction. Between interactions, the arena floor was sprayed with water and wiped down with tissue paper to remove silk and chemical cues that might have been left by previous pairs (Jackson 1987). For each interaction one spider was placed in each side of the arena, separated by an opaque divider. Spiders were given two minutes to settle down before the divider was removed. Interactions commenced when the spiders had oriented toward each other. Spiders were allowed to interact until one spider walked or ran away from the other. Individuals of the same age class and sex were distinguished by size and natural markings. Some additional male-female interactions away from nests were staged in a cylindrical transparent acrylic arena (150 mm diameter, 120 mm height), the upper portion of which was lightly coated with petroleum jelly and surrounded with paper, leaving a 15mm window to film through at the bottom.

Interactions at retreats and nests

The terms 'retreat' and 'nest' have been used inconsistently in the literature, and we here define 'retreat' as a thin silken structure that is often constructed as a shelter by

any stage and sex of *S. incana* and define 'nest' as a denser silken structure only constructed by adult females (see Results for further details of retreat and nest structure).

Interactions at retreats and nests were staged in 150 mm diameter Petri dishes. Subadult and adult females were housed in these Petri dishes with a 50 x 40 mm piece of brown paper folded into a tent like shape as a shelter, with an entrance at each end, and fixed to the base of the Petri dish with Blu-tack adhesive putty (Bostik, Australia). Interactions were staged in open Petri dishes after resident spiders had built retreats or nests under the pieces of paper. To start a trial, an intruder was introduced to the Petri dish while the resident was in the retreat or nest. Interactions began when the spiders oriented towards each other or when the intruder interacted with the retreat or nest. Trials ended when one spider left the Petri dish. Trials were terminated after 1 hour if both spiders remained in the Petri dish but were not interacting, except in interactions between males and subadult females. To observe cohabitation between males and subadult females these trials were terminated when one spider left the Petri dish or if males were not under the paper shelter with the female by the end of the light phase.

Seismic communication during visual displays

We used laser vibrometry to ascertain whether *S. incana* include seismic elements in their 'visual' display routines. Vibrations were recorded using a digital laser vibrometer (Polytec PDV100, Germany) and were encoded using a Digital Rapids DC 1500 board using Stream 1.5.23 (Digital Rapids, Canada) on a Windows computer (Dual 3.0 GHz Xeon, 4 GB RAM). Video was recorded with a 540TVL GoVideo camera (Digital Products International Inc., USA). The AES output of the laser vibrometer was converted

to EBU (Midiman CO3, M-Audio, USA) and synchronised to the audio track of the video. Vibrations were recorded at 44.1 KHz/16 bits. Nylon fabric was stretched over the base and window section of the rectangular acrylic arena that was used to observe interactions in the open. Three rows of 16 equally spaced spots of reflective paint were applied onto the fabric as target points for the vibrometer. Pairs of males or males and females were placed on the nylon in the arena and allowed to interact.

Morphological measures

Spiders were restrained against the lid of a Petri dish with clear plastic film (Glad Products, Padstow, Australia) and then photographed with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany) focussed through an Olympus SZX12 stereomicroscope (Olympus Corporation, Tokyo, Japan). Measurements of cephalothorax width and length, to the nearest 0.1 mm, were taken from digital images using ImageJ 1.36b (National Institute of Health, Bethesda, MD, USA).

Observations

Morphology and appearance

Servaea incana is a medium sized salticid; adult female body length of collected spiders ranged between 6.9 and 10 mm while adult male body length ranged between 5.4 and 10.3 mm. *S. incana* has a round abdomen of similar dimensions to the cephalothorax. The abdomen is of similar size in males and females, but can become much larger when females are gravid. Sexual size dimorphism is modest in *S. incana*; in terms of size, the sexes have similar mean cephalothorax width, but males are more

variable (male: $N = 286$, range: 1.97 – 3.84 mm, Mean \pm SD = 2.80 ± 0.37 ; female: $N = 286$, range: 2.33 – 3.25 mm Mean \pm SD = 2.81 ± 0.16 ; fig. 1). Males tend to be darker, usually grey in colouration. Chelicerae and Legs I and II are larger and thicker in males than in females, and almost black in colouration (figs. 2, 3). Juveniles are similar in appearance to adult females, being pale to dark brown in colour (Richardson and Gunter 2012). Spiders tended to be redder for the first few days after moulting. Variation in colouration, patterns and markings on the dorsal surface of the body were substantial enough that similar sized pairs of spiders could be easily be distinguished by eye.

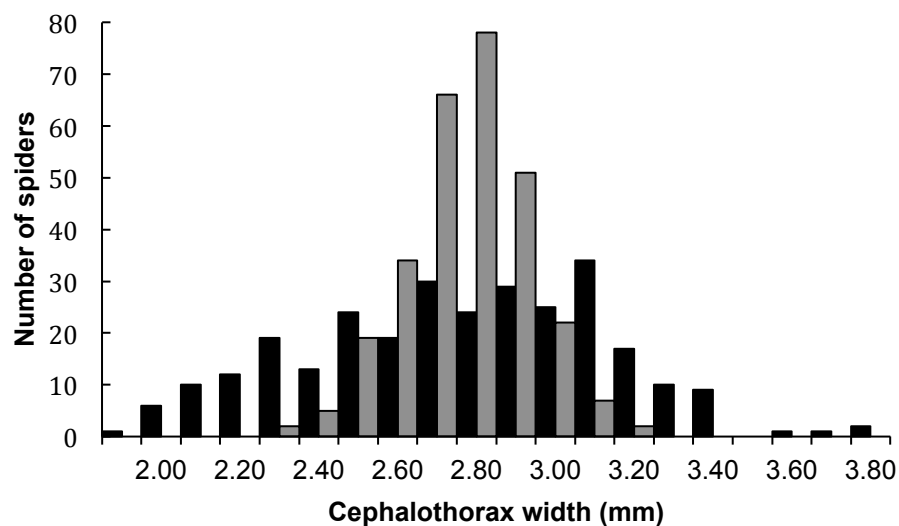


Figure 1: Size distribution of 286 adult male (black) and 286 adult female (grey) *S. incana*.



Figure 2: Adult female *S. incana* standing with cephalothorax tilted, the right palp in the neutral position and the left palp slightly lowered.

Locomotion

Routine locomotion was typically by intermittent bouts of walking, usually of distances less than 200 mm. Pauses usually lasted between 1 and 30 seconds, during which spiders often turned on the spot and tilted their cephalothorax, apparently surveying their surroundings. Palps were usually held still while walking and during pauses. Spiders rarely jumped, usually only doing so to move from one surface to another. When startled in the field, *S. incana* typically ran across the trunk of the tree and then hid under loose bark. Startled spiders occasionally leaped off the tree and either landed on the trunk further down or fell to the ground. Once on the ground, *S. incana* usually remained still for several minutes before moving towards the tree and climbing up the trunk again.



Figure 3: Adult male *S. incana* standing with retracted palps.



Figure 4: An unreceptive adult female in a retreat in nature. The female's body is raised, her palps are downwards and her legs are semi-erect in position 3. A courting male is behind the curvature of the bark. Photograph taken from above, tree trunk is at the top of the photograph, the base of the female's retreat is on the bark.



Figure 5: Adult male above the retreat of a subadult female in nature. The female is visible inside the retreat.

Location and structure of retreats and nests

Servaea incana were observed on the trunks of eucalypt trees including *Eucalyptus amplifolia*, *E. haemastoma*, *E. racemosa*, *E. saligna* and *Angophora costata*. Spiders were most commonly found standing or walking on areas of smooth bark that were adjacent to areas of loose bark where they built their retreats and nests. In the field, retreats and nests were usually built between two pieces of loose bark or between loose bark and the trunk (fig. 4). Occasionally, retreats and nests were only attached to a single surface of bark. Retreats comprised a loosely spun tube of silk with an entrance at each end and

were approximately 10 – 15 mm in length and width, for adults, just large enough for one spider to sit inside, although they were flexible and so could accommodate copulating pairs. Spiders were easily visible through the silk walls of the retreat (fig. 5). When females were preparing to oviposit, they spun denser, larger opaque nests, so that the eggs and spider could not usually be seen from outside (fig. 6). Eggs were deposited under a layer of silk at the bottom of the nest and some females used the same nest to deposit up to three clutches of eggs, laying between 7 and 36 eggs in each clutch. Nests had larger chambers than retreats, allowing the adult female to walk around inside. Nests were often roughly circular in shape, but could be more oval, usually with a length between 20 and 35 mm and width of approximately 20 mm.

Elements of behaviour in intraspecific interactions

We identified 40 body postures and movements that were associated with intraspecific interactions.

1. Raised and lowered cephalothorax – Spiders normally held their cephalothorax 1 – 2 mm above, and parallel to, the substrate (figs. 3, 5, 7). A raised cephalothorax was held 2 – 4 mm above the substrate, sometimes with legs fully extended (figs. 4, 7, 8, 9, 10, 11). When lowered, the sternum was positioned less than 1 mm above the substrate (fig. 7).

2. Lean, tilt, rotate & pivot – To lean, a spider flexed its legs on one side or end of the body and extended legs on the other side or end, without moving its tarsi, so that the cephalothorax was moved anteriorly ('lean forward'), posteriorly ('lean backward') or to one side ('lean sideways'). To tilt, a spider raised the anterior end of its cephalothorax so that it angled up as much as 60° from the posterior end (figs. 2, 9). Spiders rotated the

cephalothorax so that it was lowered on one side and raised on the other side by as much as 30° from horizontal. Spiders pivoted by lifting and repositioning their legs on the substrate to turn their body on the spot around a mid-cephalothorax axis.



Figure 6: Nest of an adult female *S. incana* in nature, between the bark and trunk of a eucalyptus tree.



Figure 7: Mounting sequence of *S. incana*. Receptive female with lowered body is on the left. Starting with body in the neutral position and Legs I in semi-erect position 3, the male approaches the female, extending Legs I forward into position 1 while raising the body.

3. Neutral, lowered and bent abdomen – Spiders usually held their abdomen in the neutral position, in line with their cephalothorax, although gravid females sometimes let their distended abdomen rest on the substrate. When lowered, abdomens were flexed down 45 – 90° with the cephalothorax in the raised position, sometimes so that the spinnerets made contact with the substrate (figs. 7, 8). Lowered abdomens were

sometimes bent by positioning the distal end as much as 45° to the left or right of the sagittal plane.

4. Opened chelicerae – The chelicerae were held open with the basal segments spread apart and often with fangs extended between 0 - 90° (fig. 9).

5. Palp postures –

Normal palps – At rest, palps were held with the femur directed upward c. 60° to the front and the rest of the palp angled down in front of the chelicerae, converging slightly towards each other (figs. 2,8).

Retracted palps – Retracted palps were held with the femur directed upward and the rest of the palp flexed straight down so that the tarsi were positioned to the side of the chelicerae (fig. 3).

Arched palps – Arched palps were held with the femur c. 45° forward and c. 60° below horizontal. Segments distal to the patella were extended downwards with the tarsi slightly bent towards each other.

Lateral erect palps – All joints were extended, so that the palps were held approximately perpendicular to the sagittal plane and parallel to the substrate (fig. 11).

Forward erect palps – Palps were held with all joints extended forward, parallel to each other and the substrate, with the tarsi angled down slightly (fig. 9).

Downward erect palps – Palps were held at full extension angled down towards the substrate (figs. 4, 12).

Downward lateral palps – With palps downwards, the tarsi were extended away from the sagittal plane of the body (figs. 10, 13).

6. *Wave palps* – Starting in the normal, arched or downward lateral palp positions, spiders made sweeping movements with their palps, moving them down then sweeping horizontally away from the centre of the body and then up and around to the starting position in a triangular pattern. These movements were made in an alternating phase pattern usually in bouts of 2 – 4 cycles in c. 0.5 s. Pauses between bouts of waving were highly variable.



Figure 8: Subadult female *S. incana* with raised body, hunched legs and abdomen lowered.

7. *Palpate* – To palpate, spiders moved palps similar to the waving palp pattern, but tarsi touched and slid across the substrate. If silk was present, spiders sometimes plucked at it by slowly raising tarsi away from the substrate, lifting the silk with it. Palps would often move independently of each other when plucking at silk. From the normal palp position, palps would be extended and lowered so that the tips of the tarsi touched the substrate.

8. *Quiver palps* – While two spiders embraced with locked chelicerae (see below), lateral erect palps moved rapidly ($4 - 8 \text{ s}^{-1}$), primarily up and down but also forwards and back, so that the tarsi of each spider touched those of the other (fig.11).

9. *Erect legs* – All joints distal to the femur were fully extended. Erect legs were held in 3 different positions.

Position 1 – Legs I held forwards parallel to each other and to the substrate (fig. 7)

Position 2 – Legs I held c. 45° to the side with the tarsi pointing down and either touching or slightly above the substrate.

Position 3 – Legs I held $20 - 60^\circ$ to the side and $20-90^\circ$ upward.

10. *Semi-erect legs* – Legs I were held with c. 135° flexion at the femur-patella joint and the distal joints fully extended, or slightly bent. Erect Legs positions 2 (fig. 13) and 3 (figs. 4, 7, 10, 12, 14) were also observed with semi-erect legs.

11. *Hunched legs* – Hunched Legs I were held $60 - 90^\circ$ away from sagittal plane of the body with the femur angled upwards $45 - 90^\circ$, the femur-patella joint flexed at c. 90° , and the distal joints flexed slightly (figs. 8, 14). Hunching spiders always held their cephalothorax in the raised position and usually with the abdomen lowered and bent. Legs II and III were usually positioned perpendicular to the sagittal plane with similar flexion of joints as Legs I, although tarsi remained on the substrate. Legs IV angled rearward about 45° from the sagittal plane.

12. *Posture* – Spiders postured by standing or stepping with erect, semi-erect or hunched legs.

13. *Gesture* – While displaying with either erect or semi-erect Legs I, spiders gestured by raising and then lowering their legs by c. 10° through flexion and extension at the trochanter or femur-patella joint. This was often done while standing, but also while leaning or stepping. Legs usually moved up faster than they came back down, the whole cycle taking c. 0.1 s. Pauses between gestures were highly variable, between 1 and 15 seconds.



Figure 9: The adult female *Servaea incana* on the right is fending off an adult male that is attempting to mount. The male's body is raised and palps and Legs I are extended forwards. The female's cephalothorax is tilted upwards with chelicerae open and fangs extended. The female has raised her first two pairs of legs to prevent the male from mounting.

14. *Wag* – Legs moved in matching phase and were extended from a hunched to semi-erect position. Wagging was usually performed while stepping forward or to the side. Legs moved smoothly throughout the motion and returned to the original hunched position once stepping stopped.

15. *Quiver legs* – Erect or semi-erect Legs I, were moved up and down rapidly (c. 50 s^{-1}) by extension and flexion at the trochanter-femur joint in bouts of c. 0.5 s with c. 1 s between bouts. Palps were usually held still in the downward lateral position while quivering legs, but were often waved at the end of bouts.



Figure 10: Adult male *S. incana* posturing with raised body, downwards lateral palps and legs in semi-erect position 3.

16. *Quiver body* – With Legs I erect or semi-erect in position 3, spiders raised and lowered their body by extending and flexing legs in cycles lasting c. 0.05 s, followed by a pause of c. 0.05 s, performing up to 20 cycles per bout. Spiders usually pivoted away from the other spider at the end of a bout, keeping Legs IV in place. Spiders sometimes stepped as they quivered their body, giving them a jerky gait as they walked. Legs II were sometimes lifted and quivered briefly with Legs I.

17. *Stalk* – Stalking spiders lowered their body and slowly approached conspecifics with legs held close to the body, similar to how they would stalk prey. Spiders usually only

stalked while the other spider was turned away from them and would remain still if the other spider oriented.

18. Veer and sidestep – Rather than approach another spider directly, a spider veered by stepping to one side as it approached, while still facing the other spider. To sidestep, spiders stepped to one side without approaching.

19. Zigzag dance – While facing a female, males stepped to one side in an arc, quivering Legs 1 as they walked. Males usually paused briefly before stepping in the other direction, but sometimes they only slowed down before performing another arc. Arcs became narrower as males approached females.

20. Long leap – Usually starting from a crouched position, a spider made a long leap by leaping 30 – 50 mm, usually landing very close to the other spider and sometimes making contact with them.

21. Truncated leap – The spider made a truncated leap by suddenly jumping 10 – 20 mm towards the other spider but without making contact. Spiders sometimes performed up to three truncated leaps in succession, or a long leap followed by truncated leaps.

22. Charge – Charging spiders ran rapidly 10-100 mm towards the other spider, sometimes with hunched legs or semi-erect legs in position 3, before stopping abruptly in front of the other spider without making contact. Truncated leaps were sometimes interspersed with charging.

23. *Ram* – Ramming was like charging, except that the spider continued so that they ran into the other spider, rather than stopping. If the other spider did not decamp, the spiders would end up with their faces in contact and often the ramming spider would push the other spider backwards.

24. *Lunge* – Spiders lunged at each other when within 20 mm. Lunging spiders stepped and leaned rapidly forward c. 5 mm, without the tarsi of Legs IV leaving the substrate. Legs I started either hunched or in a semi-erect position 3 and were extended and raised rapidly at all joints distal to the femur, as spiders moved forward, and were then lowered to their original position as spiders moved back. Chelicerae were often open and fangs extended during lunges and spiders usually made contact with the other spider's legs or face.

25. *Propulsive displays* – These included long leaping, truncated leaping, charging, ramming and lunging.



Figure 11: A pair of adult male *Servaea incana* embracing.

26. *Embrace* – Two spiders approached each other, with Legs I hunched or in semi-erect position 3, and locked chelicerae usually so that each spider was holding one chelicera of the other in its own (fig. 11). Occasionally, spiders locked chelicerae with only the ends of the chelicerae touching, apparently holding on to each other with their fangs. Legs I were usually held out to the side, parallel to the substrate and 90° from the sagittal plane with palps in the lateral erect position. Legs II, III and usually IV were held close to parallel to each other. Embracing often occurred after bouts of lunging if neither spider decamped. While embracing, spiders often raised Legs I above parallel to the substrate, up to 90°, but in intervals of no more than 20° at a time. After each movement, spiders held their legs in the new position for 1 – 5 seconds before either raising or lowering them again and spiders usually matched each other's movements. Embracing usually ended when spiders grappled (see below).

27. *Push and pull* – While embracing, spiders pushed by stepping, or by leaning forward and pulled by stepping or leaning backwards. Sometimes spiders pushed their opponent backwards, but kept their legs out to the sides of the body.

28. *Grapple* – While embracing, one or both spiders extended one or both Legs I, and sometimes Legs II, over the legs of the other spider. Spiders then pushed and pulled each other, repositioning their legs on the substrate. Grappling ended when spiders released their grip on each other's chelicerae and one decamped or when spiders clasped (see below).

29. *Clasp* – Clasping spiders were positioned venter-to-venter with their legs wrapped around each other and with open chelicerae. Both spiders moved their legs and body

rapidly. They often rolled around on the substrate, apparently attempting to bite at each other. Clasping ended when one spider broke free and decamped. When they broke apart, spiders often had to right themselves and were no longer oriented towards each other. One spider then usually decamped and the other usually re-oriented towards the other spider and followed.

30. Decamp – Spiders usually decamped by turning and running away from the other spider. Sometimes spiders stepped backwards while still facing the other spider before turning and running away.



Figure 12: An adult female *Servaea incana* steps out of the entrance to her retreat in response to a courting male in the foreground of the image. The female's palps are held in the downwards erect position.

31. Watch and follow – Spiders watched conspecifics as they decamped by pivoting on the spot, maintaining orientation towards them. Sometimes spiders followed conspecifics by running after them as they decamped.

32. *Chew and tug* – Spiders chewed by palpating silk of retreats or nests and pulling the silk towards their chelicerae with their palps and biting it. Spiders tugged by raising or tilting their cephalothorax away from the silk while holding it in their chelicerae.

Chewing and tugging resulted in distinct tears in the silk.

33. *Probe* – While standing at retreats or nests, spiders probed by pushing and pulling silk with the tarsi of Legs I. Spiders also probed with their first two pairs of legs by making forward and lateral movements against the silk, usually in alternating phase.



Figure 13: Adult male *Servaea incana* displaying towards a subadult female (out of frame). Legs I are in semi-erect position 2 and palps are in the downwards lateral position.

34. *Fend* – Females prevented males from mounting by raising Legs I to erect or semi-erect position 3. Fending females often held their palps in the forward erect position and tilted their cephalothorax upward, sometimes with open chelicerae and fangs extended (fig. 9). Fending was generally combined with quivering body and legs.

35. Mount and post-mount courtship – Males mounted females by raising their body with Legs I erect in position 1 and palps in the forward erect position, and then walking forward until positioned over the female (fig. 7). Males usually started mounting a female from in front, while they were facing each other, but sometimes mounted from the side, reorienting after positioning themselves over the female's body. Once tarsi of the male's Legs I were in line with the distal end of the female's abdomen the male flexed Legs I curling them towards the female's body. Once the male's cephalothorax was over the female's pedicel the male then leaned to the left or right to engage the right or left palp respectively.

36. Post-mount tap with legs – Males tapped at the female's abdomen with the tarsi of Legs I out of phase and in no obvious pattern.

37. Post-mount tap with palps – Starting with palps in the normal position, tarsi were lowered one at a time to contact the female's body in no consistent pattern. Males usually leaned to one side of the female's body as they tapped with palps.

38. Lift leg IV and rotate abdomen – Males leaned to one side of the female and placed both Legs I between the female's Legs III and IV. Males then placed one Leg I against the female's Leg III and reached under the female's Leg IV and abdomen with their other Leg I, pulling the abdomen up. The female's Leg IV lifted as her abdomen rotated (fig. 15).

39. Apply palp – Males inserted their embolus into the female's genitalia by holding their palp against the ventral surface of the female's abdomen, posterior to her genitalia. The cymbium then bent towards the male's body as the hematodocha expanded allowing the

embolus to engage with the female's epigynum. As males applied their palps, they were sometimes observed to open their chelicerae and extend the fangs slightly.

40. Copulation – As is typical of salticids, *Servaea incana* copulated with the male and female facing in opposite directions, with the male's ventral surface against the female's dorsal surface (fig. 15). After the first insertion, males returned to the female's midline, then leaned to the other side of the female's abdomen to insert his other palp. When the palp was initially inserted, hematodochae pulsed 4 – 6 times over 3 – 4 seconds and then usually once every 2-5 seconds after that. The bodies of both spiders rocked with each pulse and the spines of the male's legs also erected and then lowered with each pulse.

Organisation of behaviour

Interactions began when each spider oriented to face the other, or when a spider walked onto the retreat or nest of another and began to display. Interactions ended when one spider decamped. A summary of the contexts in which each elements of behaviour was observed appears in table 1. Durations of interactions between adult *S. incana* are provided in table 2.

Male-male interactions

Upon orienting towards another male, males sometimes turned away and resumed wandering around the arena without the other spider orienting. Alternatively, a male that oriented first sometimes maintained orientation until the other male also oriented and an interaction began. After orienting towards a male conspecific, *S. incana* males usually postured with raised body, hunched legs, lowered abdomen and arched

palps. Sometimes males adopted a neutral posture or lowered their body upon orientation and some walked toward the other spider before posturing. Once the two males were oriented towards each other, they usually postured with hunched legs, unless one spider immediately decamped. Sometimes only one spider hunched, while the other watched without displaying. During an interaction, males sometimes plucked at silk on the substrate and then repeatedly plucked at silk and waved their palps throughout the interaction. Alternatively, if spiders did not pluck at silk, palps remained in the retracted or arched position.

After at least one spider began posturing, either one or both males usually walked towards the other, maintaining the posture that they were in. Males that lowered their body upon orienting occasionally made truncated leaps towards the other spider, rather than walking, and some males charged or rammed. Sometimes one male decamped when the other spider started to approach.

When within 20 – 30 mm of each other, males usually lifted their Legs I from a hunched position to erect or semi-erect position 3 and lunged, often making contact with their legs and sometimes also their faces. Between lunges males returned their legs to either a hunched position or semi-erect position 3. Often after 1 – 5 lunges one spider decamped and the other usually followed. Males often opened their chelicerae during lunges and sometimes locked chelicerae and embraced. Embracing spiders sometimes pushed and pulled each other or grappled until one broke free, at which point they either clasped or one decamped. Clasping more often occurred directly after lunging, without the spiders embracing.



Figure 14: Two adult male *Servaea incana* during an interaction. The male on the left is in a hunched posture, with lowered abdomen and hunched Legs I. The male on the right has Legs I semi-erect in position 3.



Figure 15: A pair of *Servaea incana* copulating, the male is facing towards the camera, while the female is facing away. The male has just disengaged his left palp from the female's left genital opening and is holding the female's rotated abdomen with his left Leg I.

Table 1. Major elements of intraspecific behaviour of *Servaea incana* and the interactions in which they occurred, at (N) and away from (X) retreats and nests (M: adult male, F: adult female, SF: subadult female, SM: subadult male, J: juvenile. M-F is male behaviour.)

Behaviour	M-F	F-M	M-M	F-F	M-SF	SF-M	F-SF	SF-F	M-SM	SM-M	F-SM	SM-F	M-J	J-M	F-J	J-F	J-J
Charge	X	X	X	X	X	X	X	-	X	-	X	X	X	-	X	-	X
Chew	N	-	-	-	N	-	-	-	-	-	-	-	-	-	-	-	-
Clasp	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Embrace	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gesture	X,N	-	-	-	X,N	-	-	-	X	-	-	-	X	-	-	-	-
Grapple	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hunched legs	X,N	X,N	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Leg postures																	
Position 1	X,N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Position 2	X,N	-	-	-	X,N	-	-	-	X	-	-	-	X	-	-	-	-
Position 3	X,N	X	X	X	X,N	X	-	-	X	X	X	X	X	X	X	-	X
Long leap	-	X	X	X	-	-	-	-	-	-	X	X	-	-	-	-	-
Lunge	X	X,N	X	X	X	N	X	X	X	X	X	X	X	-	X	-	X
Palpate	X,N	-	X	-	X,N	-	-	-	X	-	-	-	X	-	X	-	-
Palp postures																	
Retracted	X	X,N	X	X	X	-	-	-	X	-	-	-	X	-	-	-	-
Arched	X	-	X	-	X	-	-	-	X	-	-	-	X	-	-	-	-
Lateral erect	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forward erect	X,N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Downward erect	-	X,N	-	X	-	X,N	-	-	-	X	X	-	-	X	-	-	-
Downward lateral	X,N	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-
Probe	N	-	-	-	X,N	-	-	-	-	-	-	-	-	-	-	-	-
Push	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Quiver body	-	X,N	-	-	-	X,N	-	-	-	X	-	-	-	X	-	-	-
Quiver legs	X,N	-	-	-	X,N	-	-	-	X	-	-	-	X	-	-	-	-
Ram	-	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Truncated leap	-	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tug	N	-	-	-	N	-	-	-	-	-	-	-	-	-	-	-	-
Wag	-	-	X	X	-	-	-	-	X	X	X	X	-	-	X	X	X
Zigzag dance	X,N	-	-	-	X	-	-	-	X	-	-	-	X	-	-	-	-

Table 2. Durations of intraspecific interactions between adult *Servaea incana* in the laboratory

In the open	Male-unreceptive female	Male-receptive female	Male-male	Female-female
Number of interactions	31	10	36	48
Maximum duration	9 min 8 s	40 min 9 s	1 min 54 s	36 s
Minimum duration	2 s	3 min 42 s	1 s	1 s
Median duration	1 min 26 s	6 min 10 s	8 s	6.5 s
Mean duration	1 min 58 s	11 min 50 s	15.8 s	8.6 s
At retreats				
Number of interactions	13	13		
Maximum duration	56 min 59 s	80 min 32 s		
Minimum duration	1 min 27 s	9 min 5 s		
Median duration	6 min 20 s	14 min 47 s		
Mean duration	14 min 29 s	26 min 44 s		
At nests				
Number of interactions	20			
Maximum duration	20 min 20s			
Minimum duration	14 s			
Median duration	5 min 34 s			
Mean duration	7 min 15 s			

Female-female interactions

Interactions between adult females were generally simpler and shorter than those between males (table 2), with fewer displays, and they usually ended without any physical contact. Females that oriented towards another usually lowered their body and watched the other female, but sometimes adopted a hunched posture. Infrequently, the first female to orient stalked or made long or truncated leaps towards the other. When the other female oriented, often only one spider postured, but sometimes neither or both spiders postured. Rather than approach, some females hunched and sidestepped while wagging, usually while the other spider watched without displaying. Females occasionally decamped immediately after orienting. Some females followed decamping conspecifics but usually for no more than 50 mm. Females rarely came into contact with each other during interactions, and when they did it was usually through lunges. We never observed females embracing and only observed clasping once.

Male-female interactions in the open

Males usually postured, gestured and waved palps within seconds of orienting towards a female. Males also usually raised their body and raised Legs I to semi-erect position 3 with downwards lateral palps. If they were more than 100 mm away, males often ran towards females, with a raised body and waving palps, before they started to posture. After initially posturing, males usually approached the female by walking and gesturing or by zig-zag dancing. Males zig-zag danced with quivering legs and waving palps, and held legs and palps still in between bouts of stepping. As males approached females, they tended to bring Legs I forward from position 3 to position 1 and legs

tended to become erect, rather than semi-erect. Infrequently, males adopted a hunched posture.

If females oriented first, they usually watched the male briefly before turning away. Infrequently, they hunched or stalked the male. After males had commenced displays, females often quivered their body as they walked towards the male for a few steps and then turned away. Males usually kept their Legs I in position 3 while females performed these displays and sometimes approached or remained stationary, but if the female was close they sometimes stepped or leaned backwards while maintaining orientation. Palps were usually extended downwards as females quivered their legs and body. Usually after a few bouts of quivering or fending, females walked away from the male. Males usually followed females, often positioning themselves in front of the female, but they also postured and zig-zag danced while the female was oriented away from them. Infrequently, interactions between males and unreceptive females were similar to intrasexual contests, with both spiders exhibiting behaviours more characteristic of intraspecific interactions rather than courtship. Receptive females never performed propulsive displays.

As males got to within 20 mm of females, they usually extended their Legs I forward to position 1 erect and approached the female, while at the same time raising their body. Unreceptive females usually fended and turned away. Receptive females usually remained still and lowered their body to the substrate, allowing the male to mount. Some females allowed males to mount after initially fending. After males mounted, females occasionally started to step away. If this occurred, males usually stepped to remain mounted on the female. If the female moved away from the male, the

male usually recommenced courtship displays and immediately attempted to mount again.

Once mounted, males leaned to one side as they tapped the female's abdomen with their palps. Males then lifted the female's Leg IV and rotated the female's abdomen to apply their palp, initiating copulation. Durations and numbers of palp applications are summarised in table 3. During copulation, both spiders usually remained still, other than both of their bodies pulsing as the male's haematodocha inflated and deflated. After each palp application, the male and the female's abdomen returned to the central position. The male then leaned to the other side to insert his palp into the female's other genital opening or dismounted. Females sometimes stepped after palp applications, causing males to dismount. After males dismounted, females sometimes became aggressive, quivering and fending, but occasionally decamped or remained still without display. Males sometimes recommenced courtship and approached to mount again, but usually desisted within 10 seconds and decamped.

Male-female interactions at retreats and nests

As females inside retreats were visible from outside, both males and females sometimes started displaying visually before the male made contact with the retreat. Females usually raised and quivered their bodies while inside their retreats, with legs semi-erect in position 3 and palps downward (fig. 12). As females quivered, the silk of the retreat moved and sometimes females stood in the entrance to their retreat while quivering. Occasionally, females lunged at males from inside the retreat when males touched the silk. Males postured and gestured in a manner similar to that observed during interactions in the open. Males palpated the silk at the periphery of retreats and

sometimes probed. Unreceptive females usually prevented males from entering the retreat by standing at the entrance and performing propulsive displays. Infrequently, unreceptive females abandoned the retreat. Receptive females sometimes performed propulsive displays but later permitted males to enter the retreat. Males extended their Legs I in position 1 through the retreat entrance and stepped forward to mount. After copulating, females stepped and pivoted and males decamped from the retreat. Some males left immediately whereas others stayed until females became aggressive, performing propulsive displays.

Females at nests usually became aggressive when males stepped onto the nest. Lunging and quivering of the body were the primary behaviours of females in nests. As males moved around the outside of nests, females moved around inside the nest to remain close to the male. The whole silk structure usually shook and bulged outwards with the female's propulsive displays. Males palpated, probed, tugged and chewed at nests, but usually left soon afterwards. If females were visible, males sometimes used the same visual displays as were used during courtship interactions away from nests, including posturing, gesturing and zig-zag dancing. Females generally responded with quivering and lunging inside the nest. Females in nests were usually not receptive and males rarely entered nests. In one interaction a male entered a nest and appeared to mount the female but it was not clear whether they copulated. Both spiders remained in the nest for 4 hours, after which the female left and then re-entered the nest before the male decamped.

Table 3. Number of palp applications, duration of palp applications and total duration of copulations in the open, at retreats and with cohabiting pairs soon after females matured.

	In the open	At retreats	Cohabiting pairs
Number of copulations	10	13	4
<i>Number of palp applications</i>			
Maximum	3	6	2
Minimum	1	1	2
Median	2	2	2
<i>Palp application duration</i>			
Maximum	20 min 45 s	39 min 49 s	15 min 41 s
Minimum	4 min 48 s	4 min 23 s	6 min 15 s
Median	8 min 20 s	11 min 5 s	7 min 46 s
<i>Copulation duration</i>			
Maximum	38 min 23 s	54 min 59 s	28 min 50 s
Minimum	7 min 4 s	9 min 28 s	12 min 41 s
Median	19 min 4 s	22 min 10 s	15 min 36 s

Male-subadult female interactions in the open

After orienting toward a subadult female, males usually raised their body and approached while quivering with erect or semi-erect legs in position 3, often holding legs in position 2 between bouts. They either waved their palps or held their palps in the downwards lateral position. Zig-zag dances were rarely performed. Subadult females usually quivered their legs or body and decamped, or decamped without displaying. After these initial displays, some males pivoted to remain oriented towards subadult females as they walked around but rarely followed, instead posturing and gesturing while stationary with erect legs in position 2 and downwards lateral palps. Subadult females walked about the arena, occasionally re-orienting to the male. Males eventually turned away from the subadult female. Infrequently, subadult females hunched and

males usually responded with propulsive displays, after which the subadult females decamped.

Male-subadult female interactions at retreats

Interactions between males and subadult females at retreats were similar to interactions between males and adult females. Spiders usually oriented to face each other before the male made contact with the retreat. Subadult females often oriented first and started displaying. Subadult females usually quivered their legs and body while remaining inside the retreat. Sometimes males commenced courtship displays as they did during interactions with adult females. Infrequently, subadult females left the retreat. Males sometimes followed subadult females that left their retreats while quivering their legs and performing zigzag dances, but sometimes they instead remained next to or entered the retreat. More often, after displays by both spiders, the male remained next to the retreat for the rest of the day, sometimes posturing again. Males sometimes tugged and pulled silk at the periphery of the retreat, but did not enter the retreat while the female was inside. Males and females sometimes began spinning silk towards the end of the laboratory light phase. We observed the duration of cohabitation for five pairs of spiders in the laboratory. Each of the subadult females in these pairs had failed to cohabit with a male on the day prior to cohabiting, but on the following opportunity cohabited until they moulted to maturity. The duration of these five cohabitations were 3, 4, 4, 7 and 8 days.

On four occasions we observed subadult females moult to maturity in the presence of a male. Two of these observations were with pairs that had been cohabiting, the other two were during interactions at subadult female nests where pairs had not

cohabited but males were nearby when females began moulting. Males remained outside retreats while females moulted. After separating from the exuvia, females initially remained almost motionless with a lowered abdomen and all legs extended ventrally, parallel to each other, for approximately 10 minutes. Females then began moving about within the retreat, extending and flexing legs in an irregular pattern for approximately one minute before flexing all leg joints so that their legs curled close to the body. Females remained in this curled position for approximately 30 minutes, with their legs twitching slightly and gradually extending from tightly curled to a loosely flexed position. Throughout this period, males remained outside the retreat, occasionally stepping around the periphery of the retreat but usually maintaining orientation towards the female. Females then pivoted or walked about within the retreat after which males commenced probing, chewing and tugging on silk. Females did not display and only stepped slightly as the male entered the retreat and mounted. Copulations were similar to those described previously for copulations at retreats (table 3). After mating, one male remained near the retreat and inducted sperm into his palps (for detailed description, see below), two males left the retreat but remained nearby for the rest of the day and one male walked away immediately, leaving the Petri dish arena.

Female-subadult female interactions in the open

Interactions between adult and subadult females in the open were similar to interactions between adult females, although subadult females generally decamped first. Both adult and subadult females sometimes hunched Legs I, but occasionally neither spider displayed during an interaction. Subadult females never charged and rarely approached adult females. Adult females sometimes performed propulsive displays and sometimes stalked subadult females.

Male-subadult male interactions in the open

Interactions between adult and subadult males were sometimes similar to interactions between males and subadult females, and were sometimes similar to female-female interactions. Some males courted subadult males, raising their semi-erect legs to position 2 or 3 and gesturing or zig-zag dancing. When males performed courtship behaviours, some subadult males quivered their legs and body and then decamped whereas others hunched their legs before decamping. Adult males usually continued to court as the subadult males decamped. In some interactions either the male or the subadult male adopted a hunched posture. Usually this was immediately followed by the subadult male decamping, but sometimes one or both spiders approached the other first. Infrequently, spiders stalked each other. Adult males rarely decamped before the subadult males.

Female-subadult male interactions in the open

Interactions between adult females and subadult males were similar to interactions between adult females, as adult females and subadult males exhibited similar behaviours. Subadult males that approached females usually performed propulsive displays. Females sometimes approached without displaying and then long leaped towards the subadult males. Subadult males tended to hunch more often and also decamped more often than females. Females sometimes hunched their legs but in some interactions neither spider displayed. Spiders rarely came into contact with each other in these interactions.

Male-juvenile interactions in the open

Males sometimes hunched upon orienting towards juveniles but sometimes commenced courtship displays. If males hunched, juveniles generally decamped immediately but infrequently also hunched and then immediately decamped. Some juveniles waited until the male stepped toward them before decamping. If males gestured or quivered Legs I juveniles usually either hunched or quivered Legs I before decamping. Infrequently, juveniles charged or long leaped towards males before decamping. Males sometimes followed decamping juveniles.

Female-juvenile interactions in the open

Most interactions between adult females and juveniles proceeded in one of two ways. After orienting towards each other, some females showed little interest in the juvenile and turned away after several seconds. Juveniles usually continued to watch the female and as the female started to walk, juveniles sometimes hunched their legs and approached the female. Females usually reoriented and then the juvenile decamped. In other interactions, females were more aggressive and stalked, charged and long leaped towards juveniles. In these interactions the juveniles usually decamped as soon as the female approached and females usually followed them.

Juvenile-juvenile interactions in the open

Interactions between juveniles were similar to interactions between adult females. Interactions often started after a period of one spider watching the other. Occasionally, spiders oriented simultaneously and one or both immediately fled. The

spider that oriented first often maintained the same body position, without displaying and usually did not approach the other spider. Sometimes juveniles adopted a hunched posture. Juveniles rarely made contact with each other and rarely performed propulsive displays.

Recordings of vibrations

There was no evidence of seismic elements to visual displays other than those generated in the production of those displays. In particular, impact sounds were recorded from the substrate during footsteps. When males gestured towards females the movements of the legs generated weak seismic components, which had much lower amplitude than footsteps. All detected vibrations in male-male interactions appeared to be associated with footsteps.

Sperm Induction

On four occasions males were observed recharging their palps with sperm after copulation. In one instance the male was observed immediately after copulating with a female in a retreat in a Petri dish; two males inducted sperm when they were placed in Petri dishes after they mated with recently moulted females; and one male inducted his palps while standing adjacent to a recently moulted female. To induct sperm, males first spun a small sheet of silk, shorter than their body length and slightly wider than their body width, between the wall and floor of the Petri dish. Males stood still while spinning the web, lowering their abdomen and bending it from side to side without repositioning their tarsi. Males spent approximately two minutes spinning the web. Males then lowered and raised their abdomen so that it tapped against the posterior end of the web.

As they moved their abdomen they also flexed their legs slightly, so that their cephalothorax moved both forward and downwards less than 1 mm then up and back. These movements were performed 10 – 20 times over approximately 30 seconds. Spiders then paused for 10 - 20 seconds before lowering their body again as they expelled a white drop from their genital pore and deposited it onto the web. Males then stepped backwards so that their chelicerae were positioned over the drop of ejaculate and touched the drop with the end of each palp for 1 – 10 seconds at a time in alternating phase. When touching the drop, males moved the palp up and down less than 1 mm at a rate of 10 s^{-1} , causing the drop to move as they did so. These movements were repeated about 20 times per palp, the drop becoming smaller as they did so.

Observations of interactions in nature

More than 900 person-hours were spent in the field collecting and observing *S. incana*. Although we sometimes found more than 10 *S. incana* inhabiting the same tree, interactions were rarely observed in the field. We only observed one male-male interaction in the field. A large male was walking on the trunk of a tree when he encountered a piece of bark under which there were two retreats of *S. incana*. As the male approached the retreats from below, another, smaller, male exited from the uppermost opening of the higher retreat and approached the intruder. Both males hunched their legs and approached each other. The two spiders lunged at each other and the smaller resident decamped, running around to the other side of the tree trunk. The larger intruder then entered the retreat that had previously been occupied by the smaller male. An adult female with a soft cuticle, indicating that she had recently moulted, was found inside the other retreat.

We observed one interaction between an adult male and a subadult female in the field. Both spiders were on the outside surface of a loose piece of bark, oriented towards each other, approximately 20 mm apart with the male above the subadult female. The subadult female turned away and after about 35 seconds the male stepped forward and to his right while quivering Legs I. The subadult female oriented to the male and displayed with quivering legs, the male stepped back and both spiders paused before the subadult female turned away again. After about 10 seconds the subadult female walked away, moved underneath the piece of bark and entered a retreat. Approximately 90 seconds later the male walked off the bark in the opposite direction to the female and onto the tree trunk. Later the male walked back around the bark to where the female had entered a retreat and stopped in front of the retreat while the female displayed from inside. There was at least one empty retreat visible under the bark close to the retreat containing the female.

All other observed interactions in nature were between adult males and adult females. We observed one male visit two females at their retreats and interact with a female in the open twice, all within 18 minutes. This male was first observed peering around the edge of a piece of bark to where a female's retreat was located, with a female inside. The male then left and interacted with an unreceptive adult female in the open. The female quivered her body and legs as the male approached. The male approached rapidly with Legs I semi-erect in position 3 but then hunched before lunging at the female, making contact and immediately returning to the original position. Both spiders then decamped. The female walked under an adjacent piece of bark and the male walked away across the tree trunk. The male next encountered an adult female in a retreat under a piece of bark. The male entered the retreat and the female backed away while facing the male and quivering her body and legs. The female then left the retreat. The

male walked through one entrance of the retreat and came out the other entrance in front of the female. The female decamped around to the opposite side of the loose piece of bark under which the retreat was built and then returned to the inside but decamped again as the male approached. The female returned once more to the lower surface of the bark and quivered her body and legs in front of the male then decamped, walking into the open on the tree trunk. The male then left the piece of bark in the opposite direction and encountered the same female that he had previously interacted with in the open. This time the male raised Legs I to position 3 and quivered his Legs I while stepping sideways to position himself above the female on the trunk. The female stepped c. 10mm from side to side while quivering her body and legs, and then retreated to under the piece of loose bark that she was standing on. The female came back out and quivered again before moving to the trunk underneath the bark. The male approached and looked under the bark but the female continued to quiver and the male did not move to beneath the bark. The male passed the female on the outer side of the bark and then left to walk across the tree trunk.

We observed another two interactions between males and females in the open and three at retreats, all of which proceeded in a similar manner to that described above. Males palpated the tree trunk as they approached retreats. Once oriented towards a female, males displayed with quivering Legs I, while the females quivered their body and legs and decamped if they were outside their nest. In one interaction that occurred close to dusk at the retreat of an adult female, a male began to spin silk, apparently building his own retreat.

More than 20 males were found in retreats close to those of both subadult and adult females in the field ('cohabitation'). On one occasion we observed three retreats

together under a single piece of bark. In one retreat was a subadult male, below a subadult female and in the lowest retreat there was an adult male.

Prey and hunting behaviour

In the field, we recorded 72 individual prey items from 6 different arthropod orders (Table 4). Hymenoptera were the most common prey items; 33 of the 72 prey items were ants, while four were wasps. Ant genera included *Calomyrmex*, *Camponotus*, *Iridomyrmex*, *Linepithema*, *Myrmicinae*, *Podomyrma*, *Rhytidoponera* and *Technomyrmex*. Three of the ant specimens were alate. Other prey included Hemiptera (13), other spiders (10), including other salticids, Diptera (7), Coleoptera (5) and Neuroptera (1). Spiders were usually larger than their prey, in terms of body length. Although *Iridomyrmex* ants were common in many areas where *S. incana* were collected, we never found *S. incana* feeding upon them.

Foraging behaviour of *S. incana* seems to primarily involve waiting on the trunk of a tree until a potential prey item comes into view. When outside their nests or retreats, females and juveniles were usually observed on the trunks of trees within 50 mm of a piece of bark where a retreat was located. Spiders usually oriented towards the ground often with their cephalothorax lowered and legs held close to the body. We observed five prey capture attempts by *S. incana* in the field. Three of these occurred while *S. incana* was standing on a tree trunk close to a piece of bark and flying insects landed close to the spider. The spiders oriented and leaped without stalking, however, only one of these attempts was successful. On two occasions we observed *S. incana* hunting ants that ran up the trunks of trees. On both occasions, the spider pivoted to retain orientation toward the ant as it passed, and then ran around in front of the ant

and lunged down over the head of the ant, biting the anterior end of the thorax. In the laboratory, when prey was stationary *S. incana* engaged in the typical salticid hunting sequence of orienting, pursuing until within striking distance, crouching and then jumping (Forster 1977). If prey was running, or struggling with silk in the cage, spiders usually ran towards the prey and leaped onto it.

Table 4. Observed prey items of *S. incana*

ORDER	TOTAL
Hymenoptera	37
Ant	33
Wasp	4
Hemiptera	13
Cicadellidae	11
Pentatomidae	2
Araneae	10
Salticidae	3
Thomisidae	2
Sparassidae	1
Theridiidae	1
Unknown	3
Diptera	7
Coleoptera	4
Elateridae	3
Weevil	1
Unknown	1
Neuroptera	1

Enemies

We observed two instances of predators feeding on *S. incana* in the field. One was a juvenile huntsman spider (Sparassidae) feeding on an adult male *S. incana*, and the other was an adult male salticid (*Sandalodes superbus*) feeding on a juvenile *S. incana*. We also observed an adult female *Sandalodes superbus* chase an adult female *Servaea incana* across the trunk of a tree. Adult *S. superbus* are generally larger than adult *S.*

incana, however, the size of the adult males do overlap. We have observed *S. incana* feeding on both juvenile *S. superbis* and juvenile sparassids.



Figure 16: Larva of the mantispid *Spaminta minjerribae* on the ventral surface of an adult male *Servaea incana*. The anterior end of the larva is positioned near the spider's pedicel, and the larva's body extending over the spider's left book lung.

The most commonly observed enemy of *S. incana* was the mantispid *Spaminta minjerribae*. In the field we found *S. incana* nests containing mantispid pupae, and some adults and subadult *S. incana* of both sexes collected from the field were later found to be carrying mantispid larvae (Fig. 10). Adult mantispids also emerged from nests built in the laboratory by female spiders collected from the field. Adult mantispids did not appear to interact with *S. incana* in the laboratory, but they did feed on the flies provided as food for the spiders. Under a microscope we observed mantispid larvae feeding on the hemolymph of *S. incana* at the pedicel. We did not observe any obvious behaviours in *S. incana* that may help to remove mantispids from their body or nest. We

also observed mantispid larvae on *Sa. superbis*, a salticid that was both a predator and prey of *S. incana*.



Figure 17: This subadult *S. incana* has been parasitised by a pompilid wasp, of the genus *Epipompilus*, but remains active. The larva is attached to the right side of the spider's abdomen.

We staged an interaction in the open between an adult male *S. incana* that was harbouring a mantispid larva and an adult female that had recently moulted. The pair copulated, the male inserting each palp once, and the mantispid could be seen crawling on the side of the female's abdomen during the second palp application. The male was mounted on the female for 20 minutes, the palp applications lasting 394s and 699s. Both spiders were checked under a microscope after the copulation and the mantispid larva was positioned on the dorsal side of the female's pedicel. An interaction was also staged between a female *S. incana* that was harbouring a mantispid larva and a female *Sa. superbis*. The larger *Sa. superbis* attacked and consumed the *S. incana*. The mantispid

larva was observed leaving the body of the *S. incana* and crawling across the chelicerae and then cephalothorax of the *Sa. superbis*.

We also found adult and subadult *S. incana* of both sexes in the field that had been parasitised by the pompilid wasp *Epipompilus* sp. indet. Larvae of these wasps were attached to the side of the spider's abdomen, near the pedicel. Spiders remained active with the pompilid larva attached (fig. 17). Larvae always consumed and killed the spiders while in the retreat, leaving behind only the dorsal carapace. Larvae then pupated within the silk left behind by the spider. We did not observe any predation of *S. incana* eggs by *Epipompilus* larvae, female *S. incana* that were brought in to the laboratory were consumed before they laid any eggs. We successfully removed larvae from three *S. incana*. Larvae were pierced at the anterior end of the body and then removed with forceps, while the spiders were restrained with cling film. All three *S. incana* survived and appeared to behave normally after removal of the larvae.

Discussion

Interactions between *Servaea incana* are more or less typical of jumping spiders, although the displays appear relatively simple compared to some other salticids. This allowed us to adopt terminology similar to that used for previous studies of other salticids. Adult females, subadults and juveniles had similar repertoires, but males were distinctive. Only males gestured, zig-zag danced and quivered their legs, and they used these displays during interactions with adult females and immatures of both sexes. Adult females and immature spiders quivered their legs and body in response to these courtship displays from males, and this quivering was only used towards adult males. Apart from interactions between males and other sex and age classes of conspecifics,

intraspecific interactions were similar at the early stages. Highly ritualised agonistic behaviour was only pronounced at the later stages of male-male interactions. Therefore, it appears that males undergo a marked shift in their behaviour and display repertoire upon maturity, whereas females retain the same repertoire through at least the later juvenile instars and then into adulthood.

Aggression towards adult males by immature males and females was generally reciprocated, ending with decamping by the subadult or juvenile spiders. Immature spiders that were not aggressive and either did not display at all or only performed quivering displays were often able to continue wandering around the arena, while the male watched and displayed at a distance. Subadult males quivered their body in the same way that adult females did, but this behaviour was never observed in adult males. By behaving similar to females, immature spiders may be able to avoid aggressive interactions with adult males, possibly similar to how males of some animals, such as the giant cuttlefish *Sepia apama* (Norman *et al.* 1999) and the flat lizard *Platysaurus broadleyi* (Whiting *et al.* 2009), avoid aggression from conspecific males by masquerading as females. While juveniles may not represent as significant a threat to males as another adult male would, they may still impose costs in terms of competition for food and retreat sites, as well as potentially attracting predators, so we would not expect males to tolerate them.

As is typical of jumping spiders, *S. incana* exhibits courtship versatility, although it may not be as pronounced as in some other species. When males encounter females (as well as subadults and juveniles) in the open they engage in visual courtship displays (type 1 courtship; Jackson 1977). At retreats, most salticids studied so far interact primarily by silk vibrations (type 2 courtship), but these behaviours appear minimal in

S. incana. Instead, *S. incana* seems to rely largely upon visual communication at retreats, where males and females are often able to communicate using visual signals while the female is still within the retreat. Presumably, ample light levels between the loose layers of bark facilitate this behaviour in *S. incana*, unlike in other salticids, such as *Trite planiceps* (Taylor and Jackson 1999) and *Phidippus johnsoni* (Jackson 1977) that build retreats and nests in darker places. Like many other spiders (Jackson 1986a), when male *S. incana* encounter subadult females at retreats, they cohabit with the female, copulating soon after the female moults to maturity. However, it appears that subadult females are not always willing to cohabit and males are not always successful, possibly allowing for female choice.

Among its closest relatives, *Servaea* appears most similar to *Thiania* in both morphology and behaviour, although only male-male interactions have been described for *Thiania*. Males of both *Servaea* and *Thiania* possess dimorphic first pairs of legs which they make use of during their displays, unlike *Maratus*, *Saitis* and *Hypoblemum* which primarily use their sexually dimorphic third pair of legs. *Servaea incana* were never observed raising their abdomen, while the rest of these genera are all known to raise their abdomen while displaying during interactions. *Maratus* are also known to produce distinct seismic signals (Girard *et al.* 2011). Seismic signalling is an important mode of communication in many spiders, including some salticids. However, we did not find any evidence that *S. incana* produce sounds or substrate borne signals away from retreats or nests and the use of tactile signals through silk appears to be minimal. Whether the presence of these behaviours in *Maratus* or the absence in *Servaea* represents the ancestral state remains to be seen, as the behaviour of many species remains to be described. Aside from the Euophryinae, sound production or substrate borne signals have also been documented for the subfamilies Pelleninae and

Dendryphantinae. The salticids that produce these signals all live on leaf litter or foliage, which may permit better transmission of sounds than tree trunks and bark usually occupied by *S. incana* (Elias *et al.* 2004).

Mantispid larvae were the most frequently observed enemy of *S. incana*. Bearing mantispid larvae is potentially costly for *S. incana* as larvae sustain themselves by feeding on the spider's haemolymph. When larvae of the mantispid, *Dicromantispa sayi*, parasitise subadults of the lycosid spider, *Rabidosa rabida*, the spiders take longer to mature and mature at smaller size, with females maturing after one less instar (Redborg 1982). To complete their lifecycle, mantispids must feed upon spider's eggs, so they need to find the nest of a female spider and enter the egg sac. However, as we found with *S. incana*, mantispid larvae board adults and subadults of both sexes (Redborg 1998). Some species of mantispid are known to transfer between spiders during copulation (Redborg 1998; Scheffer 1992) and this was the case with *Spaminta minjerribae* that parasitised *S. incana*. If females mate with multiple males, they may increase the risk of acquiring a larval mantispid, and so risk of parasitism and egg predation may be an important cost of polyandry in this species. A single mantispid is capable of eating all the eggs in a spider's nest (Rienks 2000) and guarding of the eggs by females likely has little effect upon egg predation by mantispids (Vieira and Romero 2008; Willey and Adler 1989). As *S. incana* females only produce up to three batches of eggs, losing one batch represents a very high fitness cost. However, females that mate once and produce temporally spaced clutches of eggs may minimise the impact of mantispid predation on their eggs. For males, the benefits of polygyny are increased as they can get rid of mantispid larvae during copulation. Long copulation times may also benefit males and be more costly to females as this means that mantispid larvae have more opportunity to transfer (O'Brien and Redborg 1997). This possibly results in sexual conflict over both

the number and duration of copulations. Female spiders would be advantaged by an ability to detect whether males are carrying mantispid larvae, however, both males and their mantispids would benefit by being able to conceal such cues from females. It is unknown whether mantispids influence display behaviour or mate choice of either sex in *S. incana* or any other spider. The function and condition-dependence of salticid courtship display remains poorly understood, although given our observations it seems possible that complex and energetic displays serve at least in part as indicators of parasite absence.

We also observed mantispid larvae on a predator of *S. incana*, the salticid, *Sandalodes superbus*. Some species of mantispid are known to transfer between prey and predator during araneophagy (O'Brien and Redborg 1997) and in this study we observed *Sp. minjerribae* transfer from *S. incana* to *Sa. superbus*. *Servaea incana* and other cursorial spiders may be generally at risk of acquiring mantispids when they prey upon other spiders. Despite predation of the eggs of all major families of cursorial spiders and the implications for sexual and natural selection highlighted here, there has been little research into the effects of mantispids on the behaviour and ecology of spiders.

Salticids are an abundant and diverse family of spiders and many interesting questions remain to be answered about the evolution and ecology of salticid behaviour. The behaviour of many more species still remains to be described and more studies are required in order to map the evolution of behaviour onto newly available phylogenies (Zhang and Maddison 2013). Further research is also required to determine what selection pressures could cause often-substantial variation in behaviour of closely related species.

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Chapter Three: Seasonal variation in sexual opportunities of *Servaea incana* jumping spiders

Abstract

Male reproduction is often constrained by the availability of females, and more specifically by opportunities to fertilize the ova that females carry. For species in which the availability and reproductive value of females varies seasonally, it is anticipated that male phenology will adapt to maximise access to the most productive females. In the jumping spider *Servaea incana*, virgin females are at a premium because once mated, females only rarely accept subsequent suitors. We studied a population of *S. incana* for 13 months and found strong seasonal patterns in population structure, with a distinct peak of sexual maturation in the autumn months. Males matured earlier than females (protandry) such that most males were already mature and ready to mate as females began maturing. Males were also found to cohabit with subadult females that were about to mature, waiting for them to mature before mating. As the season progressed subadult females became less abundant and males were sometimes found cohabiting with mature females. Despite protandry, male size decreased through the year, suggesting that males maturing at the beginning of the year tend to be larger than males maturing later. We discuss the implications of protandry, cohabitation and mating-induced sexual inhibition in the mating system and life history of this spider.

Introduction

Reproductive opportunities can vary substantially both in space and in time, and mating systems evolve in response to the selection pressures imposed by this variation (Emlen & Oring 1977; Clutton-Brock & Parker 1992). Because females carry the burden of providing material resources for developing ova and offspring they are expected to benefit from choosing the best mates. Female reproduction may also be influenced by the suitability of the environment between locations and through the year for the material requirements associated with production of eggs and development of offspring (Davies 1991). On the other hand, males are expected to maximize fitness by competing for access to females. The timing and success of male reproduction may be linked more to the availability or quality of mating partners (Emlen & Oring 1977; Ims 1988; Pröhl & Berke 2001; Pröhl 2002; Shuster & Wade 2003). Accordingly, male distribution and seasonality might come to match periods of peak sexual opportunity rather than material resources.

In species that show distinct seasonality, reproductive opportunities available to males can be linked to timing of maturation. For example, males that mature early in a season might have more mating opportunities than males that mature later, simply because their period of sexual activity coincides to the greatest extent with the availability of females (Bulmer 1983; Thornhill & Alcock 1983; Andersson 1994). The benefits of early male maturation are even greater for species in which virgin females are more abundant early in a season and are at a premium (Thornhill & Alcock 1983; Simmons 2001).

There are several reasons why virgin females might be at a premium. In some

species, virgin females show higher receptivity, lower choosiness or lower aggression than mated females (Carrière & McNeil 1990; Miyatake et al. 1999). Accordingly, males that mature early in the season, when virgins are more abundant, will encounter females that are on average more likely to mate and less likely to be aggressive. Benefits of male maturation that coincides with maximum availability of virgin females may extend beyond probability of copulation and risk of injury. In species that store sperm and show first male sperm precedence or low remating tendency, males that mate with virgins rather than previously mated females will be advantaged in terms of fertilization success (e.g. Simmons et al. 1994). Mated females may carry sexually transmitted diseases and parasites, and so males that mate with virgins might also benefit from lower risk of exposure (Hurst et al. 1995; Thrall et al. 1997).

Protandry, whereby males tend to mature and prepare for mating before females, is common in butterflies (Wiklund & Fagerström 1977), crickets (Murray & Cade 1995), and spiders (Gunnarsson & Johnsson 1990; Masumoto 1994; Maklakov et al. 2004) and is thought to arise as an evolutionary response to the benefits of access to virgin females (Wiklund and Fagerström 1977; Thornhill & Alcock 1983; Morbey and Ydenberg 2001; Simmons 2001). Supporting this view, protandry tends to be negatively associated with propensity of females of a species to mate with multiple males ('polyandry') (Wiklund and Forsberg 1991). Protandry can also be negatively correlated with male size because size and development time are interdependent (Zonneveld 1996). For species with determinate growth, if males and females grow at the same rate as juveniles, then to mature earlier males must shorten their development time and complete their growth at a smaller size (Singer 1982). For example, Maklakov et al. (2004) found that early maturing males of *Stegodyphus lineatus* (Eresidae) spiders were smaller than those that matured later. On the other hand, selection for large size can result when male mating

success increases with male size (Morbey 2013). For example, if large males are more likely to win in contests, and winning a contest allows access to virgin females, then there will be selection pressure for large size in males. In this context, selection pressure for large male size may oppose selection for protandry (Zonneveld 1996).

Spiders have served as useful subjects for the study of mating system evolution. Protandry has been found in many spiders (for a review, see Elias et al. 2011), which suggests a premium on virgin females as a reproductive resource. Associated with protandry, many spiders exhibit ‘cohabitation’ whereby mature males guard immature females that are close to maturing, and then mate soon after the females mature (Jackson 1986). For example, the lyniphiid *Nerienne litigiosa* (Watson 1986) and the salticid *Phidippus johnsoni* (Jackson 1981) exhibit both protandry and cohabitation. Consistent with the expected premium on virgin females, these species have distinct reproductive seasons and exhibit high levels of monandry (Jackson 1980; Watson 1986).

In the present study we are interested in the seasonal nature of mating opportunities in a jumping spider, *Servaea incana* Karsch, 1878 (= *Servaea vestita* (L. Koch 1879)) (Araneae, Salticidae), which lives on eucalyptus trees in temperate regions of Australia (Richardson and Gunter 2012). We have observed cohabitation in the field and have also found virgin females to be much more receptive to mating than are mated females (Mendez et al. unpublished). Here we describe seasonal demographic changes in a population of *S. incana* and discuss the implications of protandry, cohabitation and remating inhibition in the mating system and natural history of this spider.

Methods

Study sites and sampling

A population of *Servaea incana* at Mirambeena Regional Park, in Sydney, Australia (33° 54' 0.7482" S, 150° 58' 27.9876" E), was surveyed from December 2010 until December 2011. The study site contained 67 eucalyptus trees surrounded by areas of maintained lawn and short grass.

From December 2010 until June 2011 (summer, autumn) a census was carried out every two weeks. Pilot data from previous seasons indicated that this is the peak maturation period in *S. incana* and so this sampling frequency was estimated as sufficient to detect protandry. From June until December (winter, spring) a census was carried out once each month.

During each census, trees were searched from ground level to 2.5 m, lifting loose pieces of bark where *S. incana* usually build nests and retreats. On each census date we counted the number of adult males, adult females, sub-adult males, sub-adult females and juveniles. Sub-adult males and females were those that needed only one moult to become adults, as is evident from enlarged palps in males and visible development of epigynum beneath the cuticle in females. Juveniles included all earlier stages, for which it was not possible to reliably ascertain sex from morphology. We recorded any instances of cohabitation, whereby males are found sheltering together with an adult or subadult female.

Sex and developmental stage were determined in the field, but genitalia of each spider were also photographed for later confirmation. Dorsal and ventral views of each collected spider were photographed in the field using a digital camera (Panasonic DMC-FT1, 12 megapixels; Panasonic Corp., Japan). Each spider found on a tree was placed inside a plastic vial and held in place against the bottom of the vial with a circular piece of sponge. A paper scale marked in millimetres was placed next to the spider for each photograph. After photographing the ventral or dorsal side of the spider, the sponge was removed and the spider was flipped over to photograph the other side. Using ImageJ 1.36b (National Institute of Health, USA), these photographs were used to measure cephalothorax width, using the paper scale to calibrate size. After identification of species, stage and sex, and photographing, each spider was immediately replaced on the tree where it had been collected.

Results

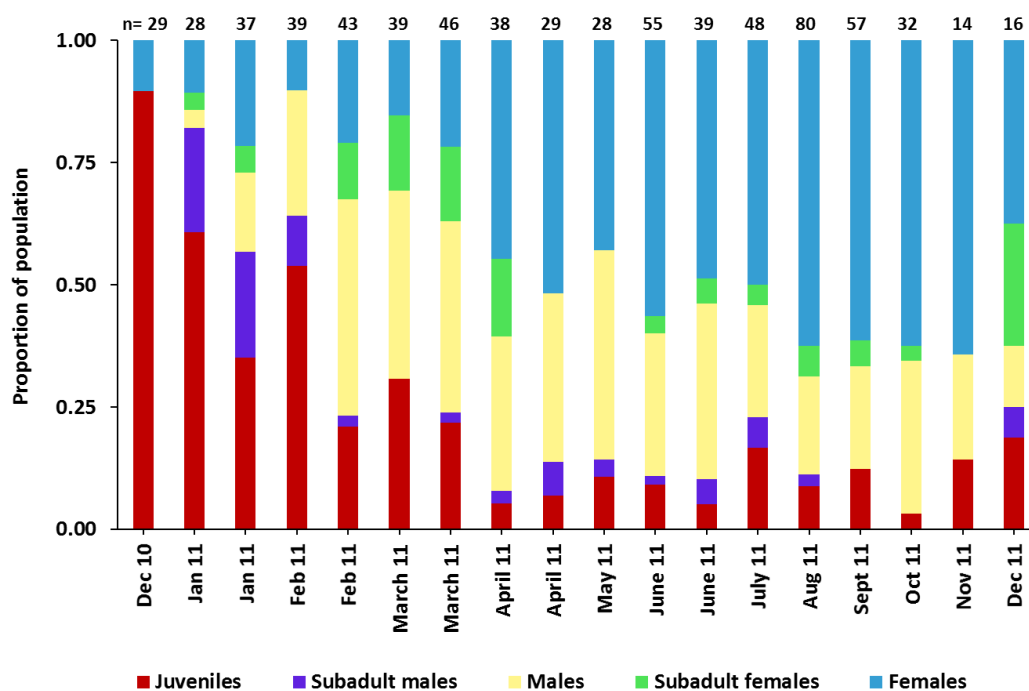


Figure 1. Relative abundance of each sex and age category of *Servaea incana* jumping spiders over the year from December 2010 to December 2011

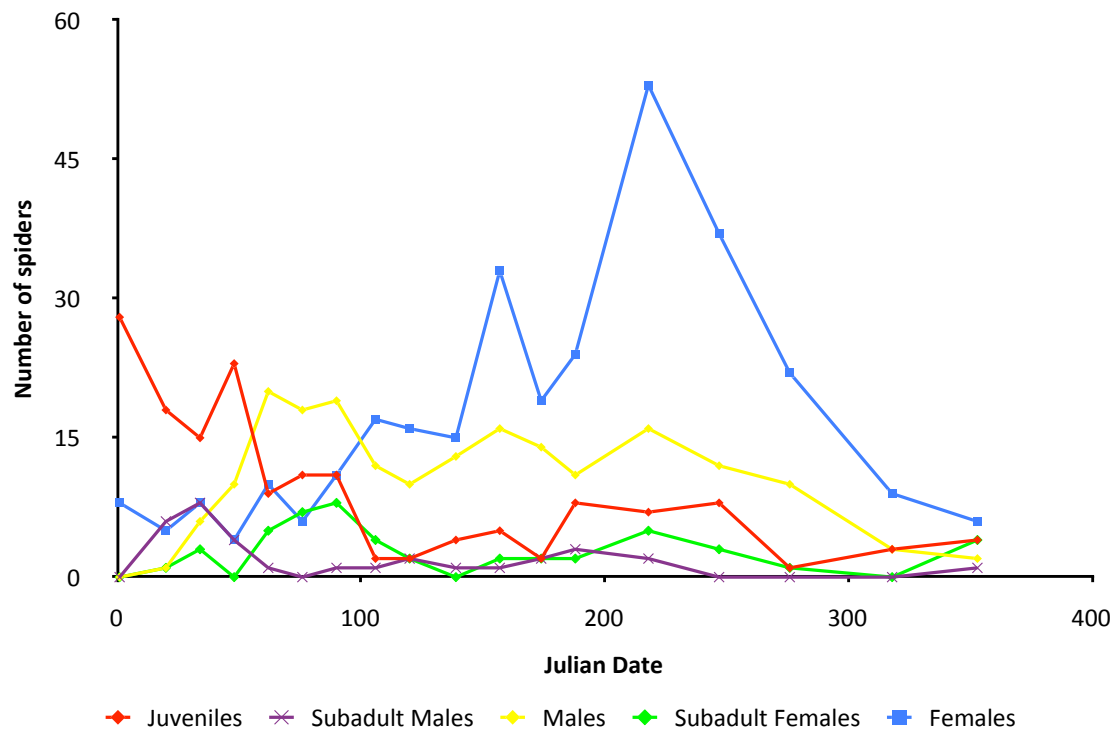


Figure 2. Absolute abundance of each sex and age category of *Servaea incana* jumping spiders over the year from December 2010 to December 2011.

Population composition and protandry

All developmental stages of both males and females were recorded through most of the year. However, there were distinct seasonal patterns in absolute and relative abundance of the developmental stages and sexes.

Juveniles were by far the most prevalent class at the beginning of the study (December 2010) when they comprised approximately 90% of the recorded population. Abundance of juveniles declined sharply over following sampling dates until the second half of March, after which, they were always present but were of comparatively low abundance. The decline in abundance of juveniles over this period was matched by an increase in abundance of the subsequent stages of subadults and adults. Sex differences

in the replacement of juveniles with these subsequent stages indicate a distinct pattern of protandry (Figs. 1, 2).

The decline in abundance of juveniles from January through to March was matched by increased abundance of subadult and then adult males. This was the only period during the year when the sex ratio of the adult population was male biased (Fig. 3). As subadult males matured into adult males, the continuing decline in juvenile numbers was apparently maintained by continuing development of juveniles to subadult males. From February, only small numbers of subadult males were recorded as abundance of adult males plateaued and declined only slightly through until October, when numbers dropped sharply to match the low numbers recorded in the previous December (Figs. 1, 2). No males were found in December 2010 or in the first half of January 2011, and only two males were found in December 2011 (Figs. 1, 2).

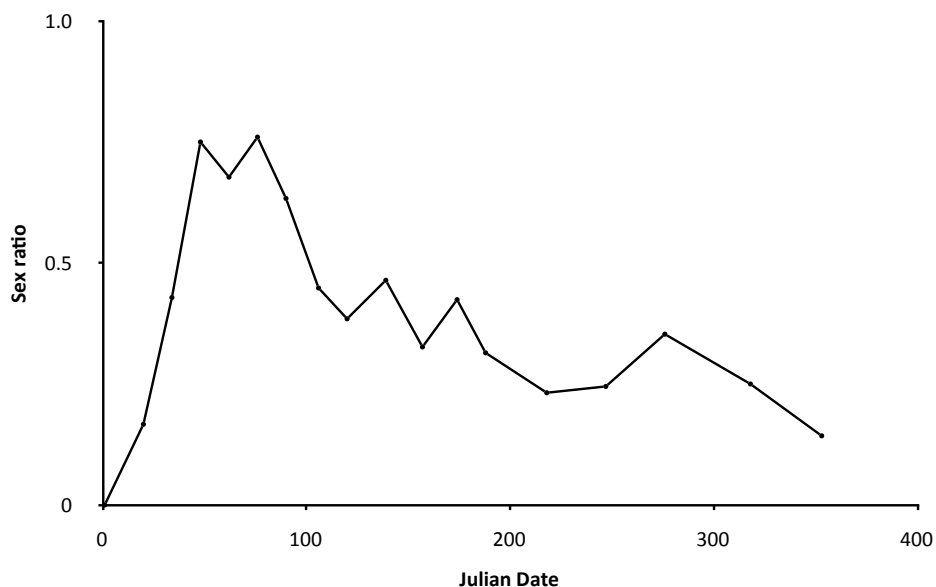


Figure 3. Sex ratio (proportion of males) of adult *Servaea incana* jumping spiders over the year from December 2010 to December 2011.

In February, just as abundance of sub-adult males declined and abundance of adult males reached its peak, abundance of juveniles dropped with increased prevalence of subadult females. In March, the abundance of adult females increased sharply while abundance of juveniles dropped to a similar extent. That the abundance of subadult females was maintained through this period indicates that the continuing decline in juvenile numbers was at this time driven by on-going development of juveniles to subadult females. From late April only small numbers of subadult males and females were recorded and the overall population profile remained comparatively stable through the autumn and winter months (Figs. 1, 2). Mature females were most abundant in August, but after this peak the number of females declined sharply. All sex and age classes were found only in very low numbers in November and December.

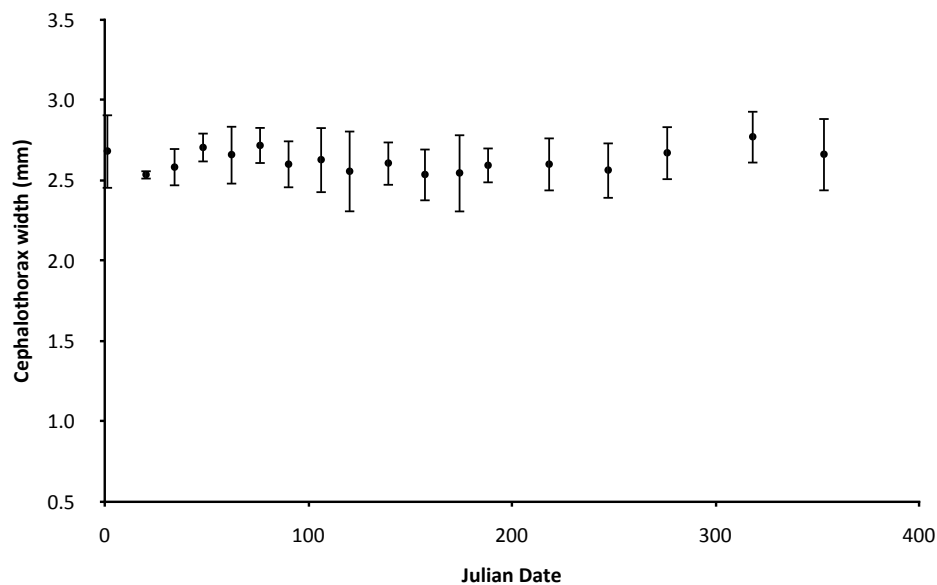


Figure 4. Size of adult females from December 2010 to December 2011 ($\bar{X} \pm \text{SD}$). There were no significant changes in adult female size over the year (ANOVA: $F_{17,265} = 1.569$ $P < 0.0722$).

Body size through the year

On average, females and males did not differ in cephalothorax width ($X \pm SE$: females = 2.599 ± 0.015 mm, $N = 283$; males = 2.595 ± 0.018 mm, $N = 195$; $t_{476} = 0.148$, $P = 0.882$). Size of females appeared to stay relatively constant through the year (Fig. 4), while male size appeared to decrease (Fig. 5), suggesting that early maturation by individual males does not entail a trade-off of reduced body size. Cephalothorax width appeared to increase slightly through the year for both subadult females and subadult males (Figs. 6, 7).

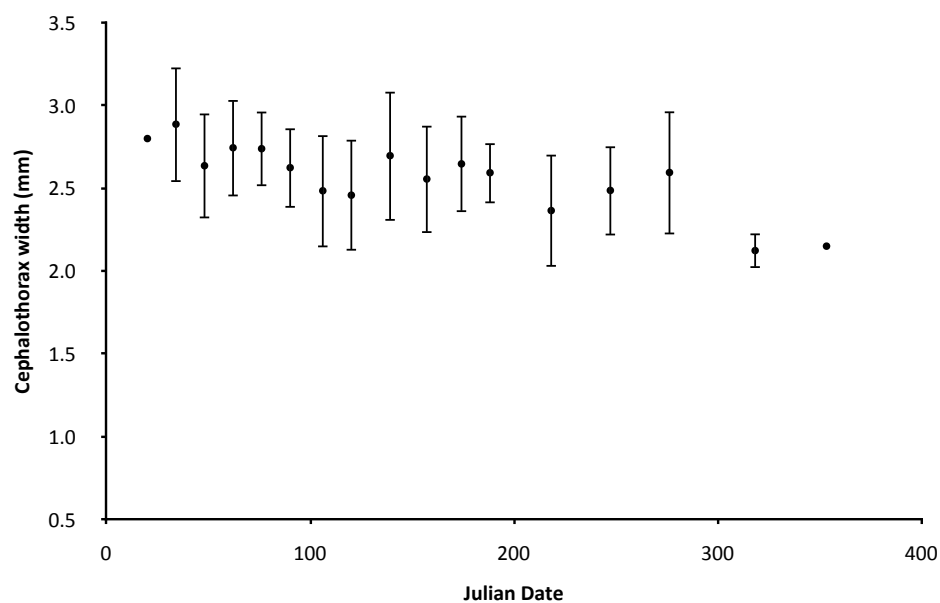


Figure 5. Size of adult males from December 2010 to December 2011 ($X \pm SD$: points without error bars represent single individuals). Male size varied through the year (ANOVA: $F_{16,178} = 2.531$, $P = 0.0016$).

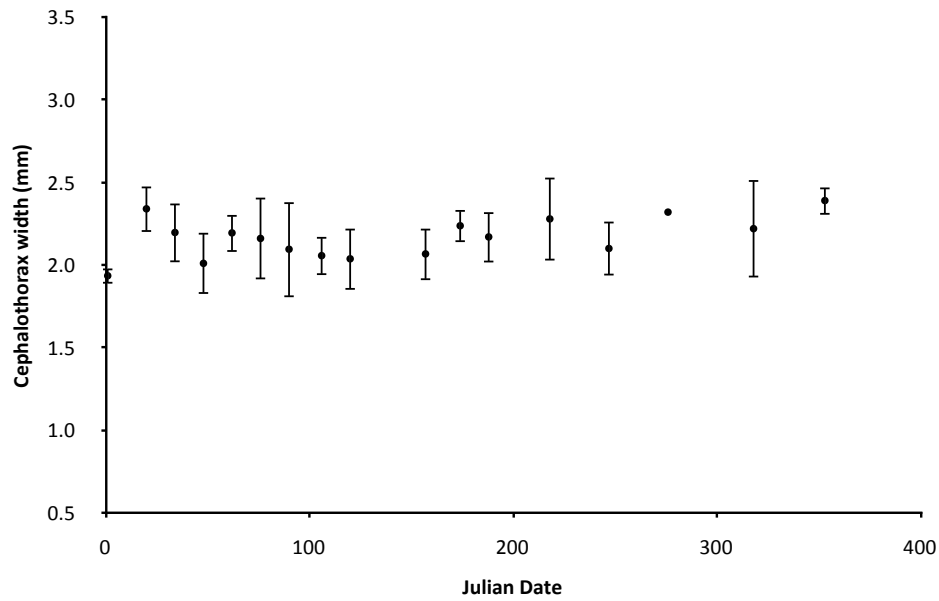


Figure 6. Size of subadult females from December 2010 to December 2011 ($X \pm SD$; points without error bars represent single individuals). Subadult female size varied over the year (ANOVA: $F_{16,90} = 1.758$, $P = 0.0499$).

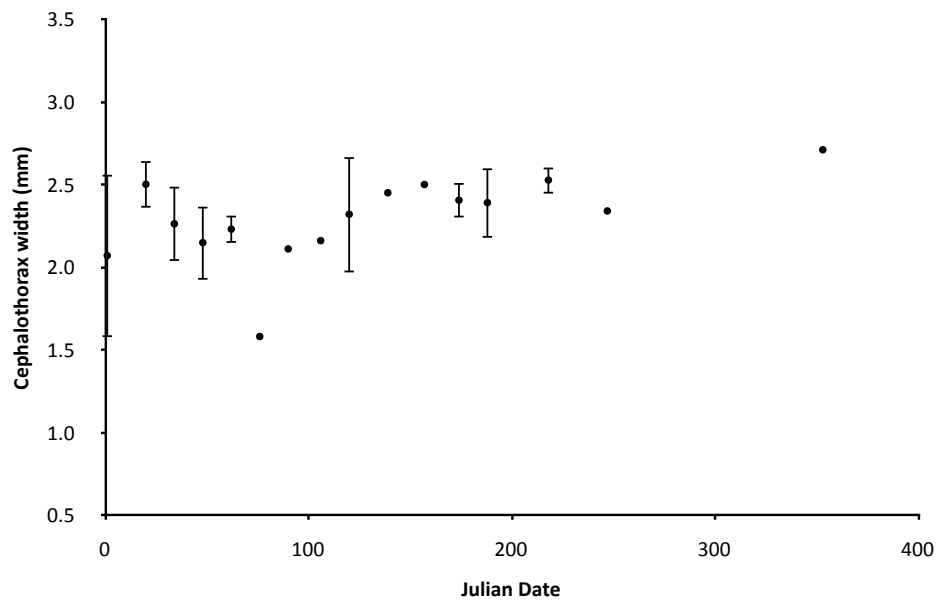


Figure 7. Size of subadult males from December 2010 to December 2011 ($X \pm SD$; points without error bars represent single individuals). Subadult male size varied throughout the year (ANOVA: $F_{15,38} = 2.418$, $P = 0.0141$).

Cohabitation

Twelve instances of cohabitation were observed. Cohabiting pairs consisted of a subadult female and an adult male ($N = 6$), or an adult female and an adult male ($N = 6$). We only found cohabiting pairs during the first half of the year; the first pair was found in January and the last pair in June. In the first census of January 2011 we found a cohabiting pair of a subadult female and an adult male. In the second census of January 2011 we found a cohabiting pair of an adult female and an adult male. Between February and April 2011 we found four cohabiting pairs, all of which involved subadult females. In contrast, between April and June 2011 we found four cohabiting pairs, all of which involved adult females. We only found males cohabiting with adult females during times of the season when subadult females were rare (January, April, May, June) (Figs. 1, 2).

Size-assortative cohabitation

There was limited evidence of size-assortative cohabitation in *S. incana*. In an ANCOVA predicting cohabiting male size as a function of female stage (subadult vs. adult) and female size, we found that female size ($F_{1,8} = 0.235$, $P = 0.641$) and stage ($F_{1,8} = 0.025$, $P = 0.879$) did not predict male size and this tendency was not significantly different for subadult and adult females (female size x stage: $F_{1,8} = 0.071$, $P = 0.796$; overall model: $N = 12$, $R^2 = 0.141$, $F_{3,8} = 0.438$, $P = 0.732$).

To increase sample size to further explore this relationship, we added data of 14 cohabiting pairs of males and subadult females that had been opportunistically collected

from other nearby populations in Sydney (additional pairings of males and adult females were not found). After increasing the sample size to 22, we still found no evidence of a relationship (female size $F_{1,19} = 2.81$, $P = 0.110$; female stage $F_{1,19} = 0.292$, $P = 0.595$; female size x stage $F_{1,19} < 0.001$, $P = 0.978$; overall model $N = 22$, $R^2 = 0.218$, $F_{3,19} = 1.765$, $P = 0.188$).

We were interested in comparing the size of males cohabiting with females with the size of males found alone. If male ability to defend females depends on his size, then cohabiting males would tend to be larger than single males. The cephalothorax width of males cohabiting with subadult females was 2.632 ± 0.450 mm, $N = 6$, while the size for those cohabiting with adult females was 2.788 ± 0.241 mm, $N = 6$. The size for males found alone was 2.588 ± 0.321 , $N = 183$. However, scarcity of cohabiting pairs precluded statistical analysis.

Discussion

Population composition and protandry

We found a distinct pattern of protandry in the studied population of *Servaea incana*; the peak in the abundance of subadult males was followed by simultaneous peaks in the abundance of subadult females and adult males (Fig. 2). This was also when the sex-ratio was male biased (Fig. 3), indicating that males tended to mature earlier in the season than females. *Servaea incana* females are less receptive and more aggressive towards males after their first copulation and, in the laboratory, many females only mate once during their entire life (Mendez et al. unpublished). Therefore, males maturing earlier in the season will be advantaged by greater access to subadult females that they

can guard and later mate with. The evolution of protandry is most readily explained by these advantages to males.

Benefits to males are not the only potential drivers of protandry, however. Protandry might also be promoted by selection on females to delay maturation and prolong development (Thornhill and Alcock 1983), such as to achieve larger size that is also commonly associated with higher fecundity (Simpson 1995). However, adult female size did not vary throughout the year in *S. incana*. To mature later in the season, females may pass through more juvenile instars, spend longer in juvenile instars, or both (Levy 1970; Head 1995). In *Phidippus johnsoni*, a North American jumping spider with protandry similar to that of *S. incana* (Jackson 1978), females undergo more instars than males before completing development. Lacking reliable information of the evolutionary starting point of protandry, we are currently unable to ascribe this aspect of life history to selection for early maturation in males (e.g., for increased access to subadult females) or late maturation of females (e.g., for greater fecundity through larger size).

The pattern of protandry found in *S. incana* naturally evokes questions of mechanism. The obvious possibilities include fixed sex differences in developmental requirements or schedule. Other possibilities include seasonal variation in sex ratio of eggs of the previous season. Sex bias in egg production is known to occur in spiders (Gunnarsson and Andersson 1996; Avilés *et al.* 1999, 2000; Gunnarsson *et al.* 2004) such that protandry could result from male bias in the early batches of eggs and female bias in later batches. Social factors may also play a role. Experience of subadult females with adult males can affect female mate choice (Hebets 2003) and propensity for pre-copulatory sexual cannibalism (Johnson 2005). Subadult females could base decisions of when to moult to maturity on the presence and abundance of adult males. By this

mechanism, the final stages of female development would not proceed until a large proportion of males were already mature.

Body size of spiders through the year

Male size decreased through the year, suggesting that males maturing at the beginning of the year tend to be larger than males maturing later. There was much more variation in male size than observed for adult and subadult females (see Figs. 4, 5, 6, 7). Given the pattern of protandry in *S. incana* and that early maturation most likely means less development time, we expected that male size would increase through the season. Seasonal variation in male size is not easily explained by developmental trade-offs associated with protandry in *S. incana*.

Seasonal patterns in male size may be better explained by links between male size and performance in male-male contests early in the season, when subadult females are most abundant. Size is a very strong predictor of outcome in contests between male salticids (Wells 1988; Taylor et al. 2001; Taylor & Jackson 2003; Hoefler 2007; Chapter 4) even if prior ownership offers an advantage (Kasumovic et al. 2011) and is also linked generally with physical performance capacity in *S. incana* (McGinley et al. 2013). It is likely that male size would confer ability to defend subadult females against rival males. For example, in *Zygiella x-notata* (Araneidae) large males were more likely to succeed in their guarding attempts and are more likely to succeed in evicting a guarding male (Bel-Venner and Venner 2006). Males of *S. incana* may evict guarding males (Chapter 2). If size advantage in male-male contests over subadult females is the main driver for seasonal variation in size of *S. incana* males, then we would expect to find cohabitation to be more prevalent in large males and absence of relation between size of male and

subadult females in cohabiting pairs; our limited sample size suggests that this could be the case.

Size-linked mortality patterns could also underpin seasonal variation in male size. Mate search is often associated with a high risk of mortality in male spiders (Vollrath and Parker 1992; Andrade 2003; Kasumovic et al. 2007; Berger-Tal and Lubin 2011). If large males are more susceptible to predation, or other sources of mortality, then this would lead to a gradual loss of large males from the population and produce a gradual decline in mean size of remaining males, as was found in the present study.

Cohabitation

Male *S. incana* were sometimes found cohabiting with subadult females at the beginning of the season, between January and April. In salticid spiders, such cohabitation typically lasts one to two weeks (Jackson 1986) and so represents a very sizeable investment. We have observed male *S. incana* guarding females for up to 8 days in the laboratory (Chapter 2). The scale of this investment provides a measure of the high value male salticids place on copulations with virgin females. The time males spend guarding a female could be spent searching for and potentially mating with other females. However, if previously mated females are reluctant to mate compared to virgin females, or are aggressive, then guarding a subadult female would be a more rewarding tactic in terms of fitness (Jackson 1986). In general, pre-copulatory guarding is expected in species with first-male sperm precedence and post-copulatory guarding in species with last male sperm precedence (Miyashita 1993). The sperm precedence pattern for *S. incana* is not known. In *Phidippus johnsoni* (Salticidae) there is mixed sperm precedence,

pre-copulatory cohabitation, protandry and remating inhibition (Jackson 1978, 1980), and this general pattern may hold for a large proportion of salticids, including *S. incana*.

In salticids, males mate with the subadult female they are guarding shortly after the female moults to maturity (Jackson 1980; Jackson and Hallas 1986; Taylor and Jackson 1999; Hoefler 2007), and this is the case for *S. incana* (Chapter 2). Remating inhibition is strong in *S. incana*, with females showing greatly reduced receptivity and increased aggressiveness immediately after their first mating (Mendez et al. unpublished data). Given high levels of mating-induced sexual inhibition in *S. incana* females, a male's ejaculate is quite well defended by female unwillingness to accept competing ejaculates from rival males. After mating with newly adult females, cohabiting males are hence expected to seek additional mating opportunities elsewhere rather than continue to guard a female they have already mated with. Indeed, during the times of year when subadult females were most abundant we found males cohabiting with subadult females but not with adult females. In the laboratory, males also leave females shortly after copulating (Chapter 2).

Given the low reproductive value of previously mated females (low mating propensity, presence of competing ejaculate) and lack of precedents from other salticid species, we did not expect to find adult females being guarded by adult males. Yet six instances of adult males cohabiting with adult females were recorded. It is important to note, however, that we only found males cohabiting with adult females when subadult females were rare (January, April, May, June; Fig. 1, 2). Cohabitation of males with adult females was not observed during February and March, when sub-adult females were at their peak of abundance (Fig. 1, 2). At times of year when subadult females are scarce, the lack of preferred mating partners may make males more inclined to invest in

guarding of adult females. Although mated females are generally reluctant to remate and offer a smaller paternity return than virgins, some females do remate (especially if within their nest; Mendez et al. unpublished) and so this might be the best prospect of reproductive returns at times when subadult females and virgins are not available. From our field data we cannot ascertain whether males cohabiting with adult females (1) had previously cohabited with those females when they were subadult and were hence defending sole paternity of her offspring, (2) were cohabiting in speculation of a potential mating opportunity as the female's second mate, or (3) had already copulated as the female's second mate and were then defending their share of a mixed paternity.

Even at times when subadults were very scarce, most adult females were not attended by an adult male and most adult males were found alone. It would be interesting to consider whether the males and adult females of cohabiting pairs are in some way distinct from solitary conspecifics. For example, it might be that a comparatively high remating propensity of some mated females can be detected by males such that males are able to decide whether time invested in cohabitation with a particular mated female is warranted on the basis of likely payoff.

Size assortative pairing has been reported in other spiders (Rubenstein 1987, Masumoto 1999, Maklakov et al. 2004), including one salticid (Hoefer 2007). Size assortative cohabitation might be the result of male choice, with males having a preference for females of large size (Hoefer 2007). In the present study we found limited evidence of size assortative cohabiting in *S. incana*, perhaps due to the low numbers of co-habiting pairs observed during this study. In *Phidippus clarus* (Salticidae), Hoefer (2007) found a male preference for larger females and a large male advantage in

male-male contests, and suggested that the combination of these two conditions could have resulted in size assortative pairing.

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Chapter Four: Assessment strategies and decision-making in male-male contests of *Servaea incana* jumping spiders

Abstract

Animals often engage in contests that have potential to impose substantial costs in time, energy and risk of injury. To reduce the costs of contests, animals are expected to assess the resource holding potential of their rivals and compare it to their own ('mutual assessment') as a means of economically determining a winner. If information about the rival is difficult or costly to obtain, rivals may instead reduce the costs of fighting by withdrawing when an individual cost threshold is reached ('self-assessment'). Here we investigate the assessment strategies used by *Servaea incana* jumping spiders to resolve male-male contests. To examine the effects of body size on contest outcome and strategy, contests were staged between size unmatched and size-matched pairs. Contests comprised a series of distinct stages of escalation and body size was a strong predictor of contest outcome. To gain insight to assessment strategy, we consider duration and escalation as measures of cost accrual. Overall, the relationships of body size to contest duration and escalation suggest that the decision of whether to retreat during the early non-contact contest phase is largely determined by size-associated internal cost thresholds while the timing of this decision may be determined by opponent size. We highlight the need to consider appropriateness of proxies used for costs and whether game theoretical predictions for whole contests apply to separate stages within a contest.

Introduction

Conflict over resource distribution is widespread in animals, and as a consequence many species engage in contests that expose rivals to costs that might include time and energy as well as risk of injury, death or predation (Andersson 1994). To more efficiently resolve conflicts rivals may assess each other's fighting ability, or resource holding potential (RHP), so that the weaker rival can retreat when sufficiently certain of its inferior status ('mutual assessment'; Maynard Smith & Parker 1976; Parker 1974). The ability to obtain information about a rival during a contest may be constrained by physical and cognitive abilities such that assessment itself may be costly or even beyond the capacity of some animals (Elwood & Arnott 2012, 2013; Fawcett & Mowles 2013). Under such circumstances, animals may reduce contest costs by retreating when they reach an individual cost threshold ('self-assessment'; Prenter et al. 2006; Taylor et al. 2001).

Game theoretical models predict that different fighting strategies produce different relationships between contest costs and RHP. In models assuming mutual assessment, e.g. the sequential assessment model, decisions are based upon assessment of RHP asymmetries between rivals (Enquist & Leimar 1983). Costs decrease with increasing asymmetry, because larger asymmetries are easier to detect. However, such a relation may also be expected for self-assessment (Taylor & Elwood 2003). This is because in self-assessment models, e.g. energetic war of attrition, animals with low RHP have lower thresholds and withdraw first (Payne & Pagel 1996), so contest costs increase with increasing RHP of the weaker rival. The negative correlation between cost

and RHP asymmetry occurs because the largest asymmetries can only occur between the weakest and strongest members of a population.

Alternative fighting strategies are better distinguished by examining the RHP of rivals separately (Taylor & Elwood 2003). Under mutual assessment, contest costs are expected to have a positive relation with the weaker rival's RHP and an equal but negative relation with the RHP of the stronger rival. If animals are using self-assessment there should be a positive relation between contest costs and the weaker rival's RHP but little relation with the stronger rival's RHP.

The predictions for self-assessment apply to situations where the accumulation of costs is determined only by an individual's own actions. However, if costs are also inflicted by the rival, as under the cumulative assessment model (CAM) (Payne 1998), then the same relations predicted for mutual assessment can occur without rival assessment taking place, because the decision to withdraw is influenced by the RHP of both rivals. Mutual assessment differs from cumulative assessment in that it predicts no relationship between costs and RHP when rivals are RHP-matched, therefore, such a relationship would exclude mutual assessment as a putative strategy (Arnott & Elwood, 2009).

While estimating RHP can be relatively straightforward, accurately estimating the costs of contests can be more difficult (Briffa et al. 2013). Time is commonly used as a measure of cost (Arnott & Elwood, 2009) and may be appropriate in contests where the actual costs accrue linearly with time, for example when contests consist of extended energetically expensive displays (wars of attrition). However, contests often escalate through distinct stages, typically starting with stereotyped displays at a distance, and

later escalating to physical fighting, where the rates of energetic costs and risks of injury are higher. The level of escalation reached may, therefore, be a better indication of costs than duration. Indeed, some studies that use duration and escalation as measures of contest cost have reported results for each measure (e.g. Constant et al. 2011; Keil & Watson 2010). Furthermore, animals may use different strategies at different stages of a contest (Hsu et al. 2008). Also, self and mutual assessment may represent extremes in a continuum rather than two discrete alternatives (Prenter et al. 2006). When animals have no information about their rivals they can only use self-assessment, but as information about the rival becomes available there is increasing opportunity for mutual assessment (Mesterton-Gibbons & Heap 2014).

In this study we investigate whether and when males of a jumping spider, *Servaea incana*, use information about themselves and their rivals during contests. Studies of spiders have made significant contributions to the study of contest behaviour (reviewed in Elwood & Prenter 2013) and number among the first empirical studies to suggest that animals may persist in accordance with their own abilities (Bridge et al. 2000; Taylor et al. 2001; Whitehouse 1997) rather than relying solely on mutual assessment. Although jumping spiders are known for their acute vision and elaborate visual displays during intraspecific interactions, they appear to rely substantially on self-assessment during contests (Taylor et al. 2001), with a comparatively minor role for mutual assessment (Elias et al. 2008; Kasumovic et al. 2011). Like spiders from most other families, jumping spider contests progress through distinct levels of escalation (Table 1) (Elwood & Prenter 2013) and so escalation may prove a more useful than duration as a measure of contest cost. After initially orienting towards each other, rivals initiate stereotyped displays. Rivals may then approach each other and engage in potentially injurious physical combat (Jackson 1988; Jackson & Hallas 1986; Wells

1988). By examining the relationships between size, a measure of RHP, and contest costs we here aim to determine the extent to which decisions of contest persistence (duration and escalation stage) of male *S. incana* depend on self or mutual assessment.

Methods

Study animals and maintenance

Servaea incana is a medium sized jumping spider native to temperate regions of eastern and southern Australia (Richardson & Gunter 2012). Male spiders were collected between March 2009 and August 2013, from the trunks of eucalypt trees, in parks in Sydney, NSW, Australia. Spiders were maintained in the laboratory under controlled temperature (24-26°C) and relative humidity (65-75%). Individuals were housed individually in 1.125 L ventilated cages on a 12:12h light:dark cycle. Spiders were fed two Queensland fruit flies (*Bactrocera tryoni*) or two houseflies (*Musca domestica*) on alternating weeks. Water was provided in a 6 ml vial attached to the base of the cage, stoppered with a dental wick. Spiders were also provided with half a crumpled sheet of white A4 paper for environmental enrichment (Carducci & Jakob 2000). Spiders were housed under these conditions for at least one week prior to use in experiments.

Contest protocol

To examine the effects of size difference versus individual size on decisions of persistence, 85 dyadic contests were staged between different sized males that were paired at random from the laboratory population ('size unmatched'). To further distinguish between effects of size difference and individual size, we staged an

additional 73 contests in which the effects of size difference were experimentally reduced by size-matching of spiders ('size matched'). All pairs were novel and each male was used no more than once in each experiment. Contests were staged in an open roofed 300 x 150 x 80 mm Perspex arena, identical in dimensions to that used by Taylor et al. (2001). The bottom 15 mm of the arena walls were transparent, facilitating filming from the side (Panasonic HDC-HS700, Panasonic Corp., Japan). The opaque white upper walls of the arena were lightly coated with petroleum jelly in order to restrict spiders to the floor of the arena. Contests were conducted under fluorescent laboratory lighting supplemented with full spectrum incandescent lamps (Crompton Lighting, Sydney Australia). A sheet of white paper was used to cover the base of the arena and was replaced between contests. The arena was also washed with water and wiped clean between contests to remove silk draglines and possible chemical cues (Jackson 1987). For each contest, a spider was introduced to each end of the arena, separated by a white opaque divider, and given two minutes to settle down before the divider was removed. Spiders were allowed to interact until one retreated from its rival. Individual spiders were distinguished on the basis of size and natural markings. Contests escalated through 6 clearly identifiable sequential levels of increasing risk and intensity (Table 1). For each contest, we recorded whole contest duration, duration of the precontact phase (levels I-III) and contact phase (levels IV-VI) (Table 1), maximum level of escalation and the winner. We also noted which spider was first to orient to face, display to and proximate toward the other. Contests were deemed to have begun when both spiders oriented and ended when one, the loser, retreated.

Morphological measurements

Following contests between size unmatched pairs, spiders were weighed to the

nearest 1 mg with an electronic balance (Shimadzu Corporation, Japan; Model N595, Type AX200). Spiders were also photographed with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany) focussed through an Olympus SZX12 stereo-microscope (Olympus Corporation, Japan). Measurements of cephalothorax width and length, to the nearest 0.1 mm, were taken from digital images using ImageJ 1.36b (National Institute of Health, Bethesda, MD, USA). For size-matched pairs, all spiders had been measured at least three days prior to the contests and were fed two Queensland fruit flies three days prior to the contests. Any uneaten flies were removed the following day. On the morning of the contest all spiders were weighed and contests were staged between spiders that differed in cephalothorax width, cephalothorax length, and weight by less than 5% $((\text{Measure of individual A} - \text{Measure of individual B}) / (\text{Mean of A and B}) * 100)$.

Table 1: The stages of escalation in contests between male *S. incana*. The first three levels make up the precontact phase, the last three make up the contact phase. Contests may end at any level of escalation.

Phase	Stage	Escalation	Description
Precontact	I	Orient	Spiders turn to face rival.
	II	Hunch	Spider raises body above substrate and raises first pair of legs into an arched position.
	III	Proximate	Spider approaches rival, usually maintaining the hunched posture.
Contact	IV	Spar	When within two body lengths, spiders lunge towards each other, flicking the first pair of legs vertically, and making contact with the legs and body and pushing against the rival.
	V	Embrace	Spiders lock chelicerae and push and pull against each other.
	VI	Struggle	Spiders roll around on the substrate grasping and biting at each other.

Statistical analyses

We used multiple regression to examine assessment, following the practice of Taylor and Elwood (2003), with duration or level of escalation as dependent variables

and measures of rival size as predictors. We use cephalothorax width as our measure of size as it can be more accurately determined than cephalothorax length and is a fixed measure for adult spiders, unlike weight, which fluctuates with physical state. To ascertain determinants of outcome during the pre-contact phase we only include those contests that ended prior to making contact. To ascertain speed of escalation to the contact phase, we also examined the pre-contact phase of contests that continued beyond the pre-contact phase. Contest duration data required log transformation to meet the assumptions of parametric tests. We also examined contest behaviour in terms of the level of escalation, rather than duration, using multiple stepwise logistic regressions, with escalation as the dependent and rival size and an interaction term (relative size) as predictors. For contests between spiders that were matched for size we used simple regressions with mean size of the rivals as the predictor variable. All tests were two-tailed. Analyses were carried out using JMP 5.0.1.2 for Macintosh (SAS Institute Inc., Cary, NC, USA).

Results

Outcome of contests between size unmatched pairs

Spiders interacted in every trial. Contests were brief, ranging between 1 and 35 seconds. Thirty-four contests escalated to physical contact (i.e. sparring or struggling). These contact phases were brief compared to the precontact phase (Table 2). Smaller and larger rivals were similarly likely to orient first (47 smaller, 38 larger; binomial test: $P = 0.386$), present 'hunch' displays first (47 smaller, 38 larger; $P = 0.386$) and proximate first (37 smaller, 35 larger; $P = 0.906$). The larger spider won 68 of 85 (80.0%) contests. The likelihood of the larger spider winning increased with size of the

larger rival ($\beta = 3.726$, $\chi^2_1 = 8.256$, $P = 0.0041$) and decreased with the size of the smaller rival ($\beta = -3.999$, $\chi^2_1 = 6.917$, $P = 0.0085$; final model: $R^2 = 0.110$, $\chi^2_1 = 9.369$, $P = 0.0092$), but was not affected by which spider oriented, hunched or proximated first (for all, $P > 0.1$). Using size difference, rather than the size of the larger and smaller rivals, yielded similar results, the probability of the larger rival winning increased with the absolute size difference between rivals ($R^2 = 0.109$, $\chi^2_1 = 9.307$, $P = 0.0023$) Size difference was a strong predictor of outcome in both contests that terminated during the precontact phase ($R^2 = 0.096$, $\chi^2_1 = 5.337$, $P = 0.0209$) and contests that escalated to the contact phase ($R^2 = 0.203$, $\chi^2_1 = 5.762$, $P = 0.0164$).

Table 2: Summary statistics for the duration (s) of whole contests and the pre-contact and contact phases of contests between size matched and unmatched *S. incana* males. IQR = Interquartile range.

	Unmatched				Matched			
	N	Median	IQR	Range	N	Median	IQR	Range
Whole Contest	85	8	4.5 - 13	1 - 35	73	11	7 - 14	1 - 61
Precontact phase (terminated)	51	5	3 - 10	1 - 35	21	8	4.5 - 12.5	1 - 52
Precontact phase (escalated)	34	8.5	5 - 12	1 - 24	52	9	6 - 11	2 - 59
Contact phase	34	1.5	1 - 3.75	1 - 6	52	2	1 - 3.75	1 - 38

Table 3: Regression models of the relationships between size of the smaller and larger rivals and contest escalation and likelihood of transitioning from one stage of escalation to the next. All contests that escalated to embracing continued to struggling. Statistically significant effects in bold.

	Smaller rival's size		Larger rival's size		Whole model			
	$\beta \pm S.E.$	P	$\beta \pm S.E.$	P	N	R^2	χ^2_2	P
Maximum level of escalation	2.61 \pm 0.95	0.005	-0.26 \pm 0.76	0.738	85	0.051	10.10	0.006
Hunch-Proximate	2.35 \pm 1.34	0.073	-1.45 \pm 1.06	0.174	85	0.048	3.49	0.175
Proximate-Spar	2.19 \pm 1.15	0.050	1.03 \pm 0.99	0.292	72	0.105	10.44	0.005
Spar-Struggle	0.88 \pm 2.49	0.718	-0.49 \pm 2.03	0.805	34	0.005	0.13	0.936

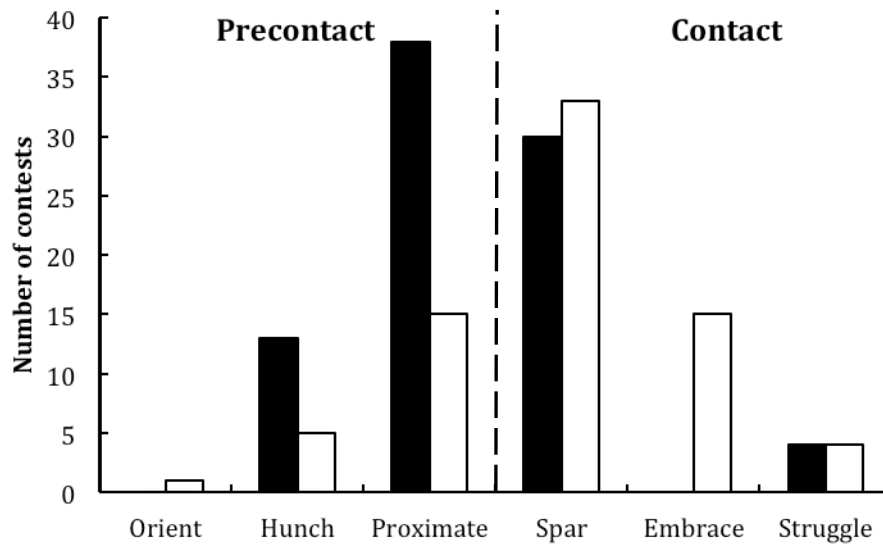


Figure 1: Distribution of the maximum levels of escalation in contests between randomly paired male *S. incana* (black bars) and contests between males matched for size (white bars).

Factors affecting contest escalation

Only the size of the smaller rival predicted the overall maximum level of escalation (Table 3). Hunch displays occurred in all (N=85) interactions. The size of the smaller rival was a marginally non-significant predictor of whether contests ended prior to proximation (13 out of 85 contests; Table 3). Spiders proximated in 72 contests and 34 pairs escalated to the contact phase. Only size of the smaller rival predicted whether the contest escalated to the contact phase (Table 3, Fig. 2). Of the contests that escalated to the contact phase, 30 terminated after sparring, while 4 escalated further to struggling. However, neither size difference nor the size of either rival predicted whether this occurred (Table 3).

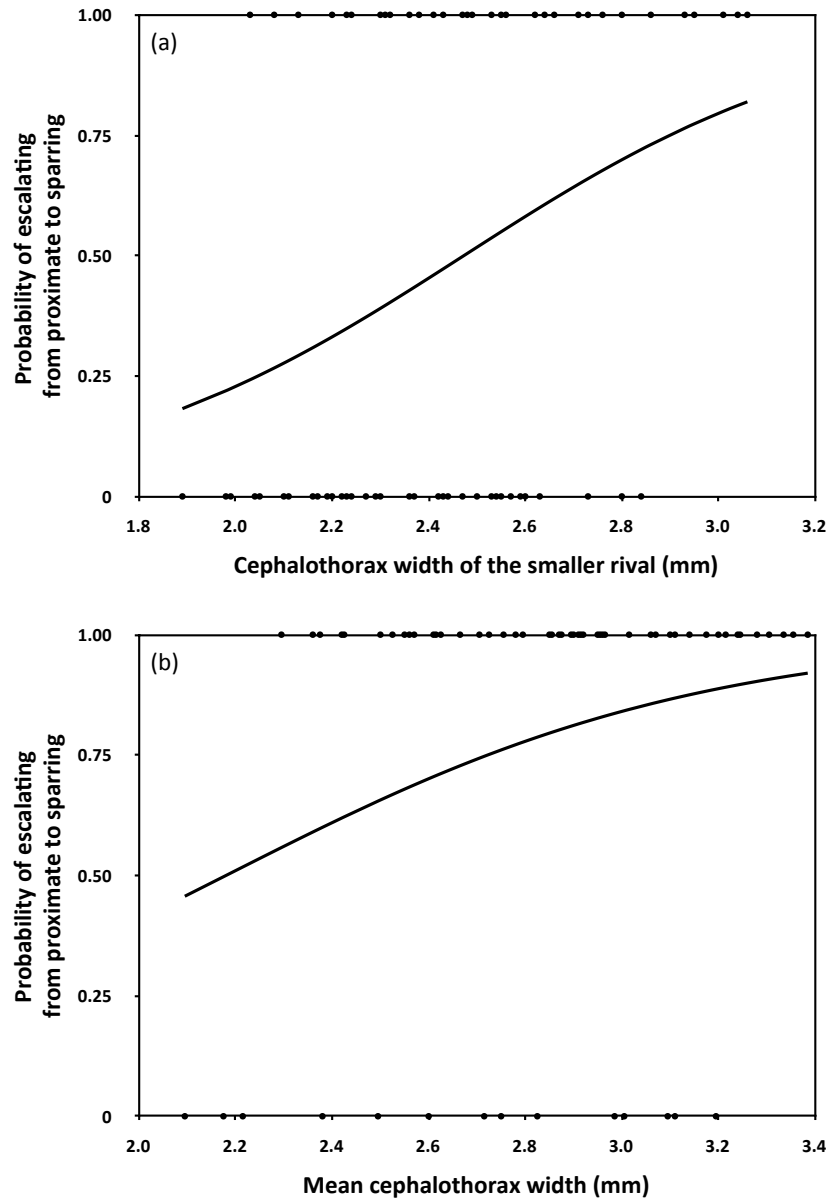


Figure 2: Simple logistic regressions illustrating that the probability of escalating from proximate to sparring increased with size of the smaller male in size unmatched contests (a) and increased with the mean size of the pair in size matched contests (b).

Factors affecting contest duration

Neither size of the larger nor smaller rival predicted the total contest duration (Table 4). A separate one-way analysis found a marginally non-significant negative relationship between absolute size difference and total contest duration ($R^2 = 0.043$, $F_{1,83} = 3.706$, $P = 0.0576$).

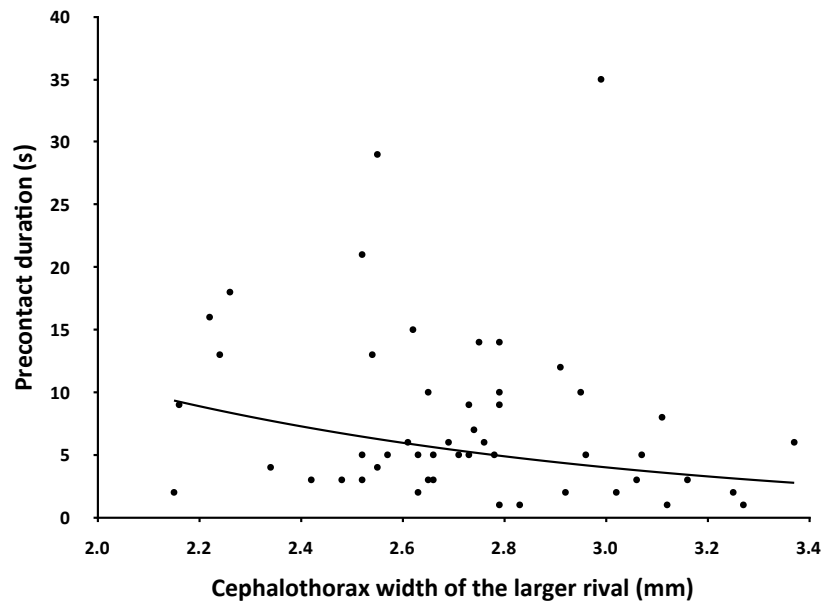


Figure 3: Back-transformed simple regression illustrating the relationship between larger rival size and duration of contests between size unmatched pairs that did not escalate to physical combat.

Duration of the 51 contests that ended during the pre-contact phase decreased with increasing size of the larger rival ($R^2 = 0.105$, $\beta = -0.998$, $F_{1,49} = 5.763$, $P = 0.0202$; Table 4, Fig. 3) but was not related to the size of the smaller rival. Neither size of the larger nor smaller rival predicted how quickly contests escalated to the contact phase (Table 4). For the 34 contests that escalated to the contact phase, neither size of the larger or smaller rival predicted the duration of the contact phase (Table 4).

Contests between size-matched pairs

The duration of contests between size-matched males ranged from 1 to 61 seconds ($N = 73$, $X \pm SE = 12.33 \pm 1.16$ s, Median = 11 s). Fifty-two contests (71.2%) escalated to the contact phase (Fig 1). There were no significant differences in any of the size measurements between winners and losers (Table 5), confirming that spiders were closely matched. Winners and losers were just as likely to be the first to orient (36 vs.

37; binomial test: $P = 1.00$), hunch (39 vs. 33 ; binomial test: $P = 0.556$) or proximate (30 vs. 37; binomial test: $P = 0.464$).

Table 4: Regression models of the relationships between size of the smaller and larger rivals and whole contest duration, precontact phase duration of contests that terminated prior to the contact phase, precontact phase duration of contests that escalated to contact and contact phase duration. Statistically significant effects in bold.

	Smaller rival's size		Larger rival's size		Whole model			
	$\beta \pm S.E.$	P	$\beta \pm S.E.$	P	N	R^2	F	P
Whole Contest	0.70 ± 0.38	0.072	-0.51 ± 0.32	0.116	85	0.044	1.91	0.155
Precontact phase (terminated)	0.72 ± 0.57	0.210	-1.25 ± 0.46	0.009	51	0.134	3.73	0.031
Precontact phase (escalated)	-0.73 ± 0.55	0.197	0.64 ± 0.45	0.163	34	0.071	1.19	0.317
Contact phase	0.71 ± 0.42	0.102	-0.52 ± 0.34	0.136	34	0.096	1.64	0.136

Table 5: Comparison of mean \pm SE cephalothorax width, cephalothorax length and body mass of winners and losers in contests between unmatched (randomly paired) males and contests between size-matched males (paired t-tests).

	Unmatched				Matched			
	Winner	Loser	t_{84}	P	Winner	Loser	t_{72}	P
Width (mm)	2.75 ± 0.04	2.46 ± 0.03	6.99	<0.001	2.86 ± 0.04	2.85 ± 0.04	0.85	0.399
Length (mm)	3.41 ± 0.04	3.06 ± 0.04	6.86	<0.001	3.51 ± 0.04	3.50 ± 0.04	1.06	0.293
Body mass	48.64 ± 1.90	35.02 ± 1.37	6.72	<0.001	52.37 ± 1.86	52.26 ± 1.85	0.89	0.377

The mean size of pairs of spiders did not predict maximum escalation ($R^2 = 0.002$, $\beta = 0.419$, $\chi^2_1 = 0.376$, $P = 0.540$). Only one contest (between spiders that were two standard deviations below the mean size) ended at the orienting stage without exchange of hunch displays. Of the 72 contests in which spiders displayed, 67 proceeded to proximate. Smaller pairs of spiders tended to be more likely to proximate, although the trend was non-significant ($R^2 = 0.082$, $\beta = -3.086$, $\chi^2_1 = 22.988$, $P = 0.084$). Once spiders had proximated, larger pairs were more likely to escalate to the contact phase ($R^2 = 0.064$, $\beta = 2.194$, $\chi^2_1 = 4.565$, $P = 0.0388$; Fig 3b). Size of spider pair did not predict

probability of further escalation between escalation levels within the contact phase (spar – embrace: $R^2 = 0.010$, $\beta = -0.814$, $\chi^2_1 = 0.657$, $P = 0.418$; embrace – struggle: $R^2 = 0.114$, $\beta = -3.660$, $\chi^2_1 = 2.230$, $P = 0.135$). Mean size of pairs was not related to total contest duration (simple linear regression: $R^2 = 0.007$, $F_{1,71} = 0.521$, $\beta = 0.176$, $P = 0.473$), duration of the precontact phase in contests that did not escalate ($R^2 = 0.008$, $F_{1,19} = 0.147$, $\beta = 0.202$, $P = 0.705$) or escalated ($R^2 = 0.003$, $F_{1,50} = 0.153$, $\beta = 0.114$, $P = 0.697$) or duration of the contact phase ($R^2 = 0.017$, $F_{1,50} = 0.887$, $\beta = 0.338$, $P = 0.351$).

Discussion

Mutual or self assessment?

Our results suggest that during early stages of contests between male *Servaea incana* jumping spiders, the decision to persist or retreat is determined principally by each spider's individual cost threshold, that is by self assessment, rather than by mutual assessment. When spiders differed in size, the probability of escalation from the precontact phase to the contact phase was predicted by the size of smaller rival rather than size difference between the pair; the larger the size of the smaller spider in a dyad, the higher the probability that it would persist until the contest escalated to the contact phase (Fig. 3). Further, when spiders were size matched, contests between larger pairs were more likely to escalate from proximating to the contact phase. These patterns are predicted by self-assessment but are inconsistent with predictions of mutual assessment models (i.e., equal and opposite effects of larger and smaller rival size). Because there was no association between smaller rival size and duration of size-unmatched contests that ended during the pre-contact phase, and no relationship between spider size and

duration of size-matched contests that ended during the pre-contact phase it seems unlikely that these decisions of smaller spiders are based on accumulated physiological costs of persistence (e.g., lactate accumulation from anaerobic respiration). Instead, it seems more likely that the tested spiders expressed size-dependent aversion to the risks of persisting to the contact phase.

For contests resolved during the precontact phase there was a negative relationship between contest duration and size of the larger spider in a pair. That is, although there was a tendency for the smaller spider in a pair to determine whether a contest would terminate at this stage, the timing of this decision was associated with the size of the larger spider. This may arise from size dependent behaviour that does not influence outcome. For example, if smaller rivals are less willing to escalate then contests may last longer when both rivals are small and reluctant to escalate.

Alternatively, if larger rivals escalate contests quicker, then RHP of the larger rival may indirectly influence the timing of the decision to retreat by the smaller rival without any assessment necessarily taking place. Such patterns have been interpreted as a form of cumulative assessment (Morrell et al. 2005; Payne 1998), but whether this represents a true form of assessment is the subject of ongoing debate (Elwood & Arnott 2012, 2013; Fawcett & Mowles 2013). Although larger and smaller rivals were equally likely to initiate proximation, there may be other cues associated with size of larger rivals that are used by smaller rivals, such as a more rapid or direct approach.

For both size unmatched and size matched contests resolved during the post-contact phase we found no patterns of persistence or escalation tendency that might support either self- or mutual-assessment linked to size that might explain the tendency of larger spiders to win. A lack of patterns in size matched contests is consistent with

mutual assessment, and may also be consistent with cumulative assessment if the rate of cost accrual depends on both the ability of the rivals to inflict costs as well as withstand damage (Payne 1998). The lack of predicted patterns in size unmatched contests could also be consistent with cumulative assessment.

Difficulties arise in determining assessment mechanisms at later contests stages owing to changes in sample size and RHP as contests progress. First, sample sizes are usually smaller for analysis of escalation stages that occur later in contests as pairs that resolve an outcome at earlier stages are depleted from the initial sample. With diminishing sample size it become increasingly difficult to detect significant effects. Second, the non-random depletion of certain pairings as contests progress can restrict variation in the remaining pairings. For example, if an individual's own size determines persistence at each level of escalation then only the largest of the smaller rivals will persist to the higher levels, reducing both variation in size of individuals and size difference between rivals as contests progress (Taylor et al 2001). If animals use mutual assessment at earlier stages, pairings with large size differences will tend to resolve more often at earlier contest stages, resulting in size assortative fighting amongst the remainder (Fawcett & Mowles 2013). While the size range of individuals may be maintained, the range of size differences will be reduced and the correlation between the size of the opponents will be stronger, making it difficult to examine the effects of size of each rival separately. Some experimental approaches rely on size-matched pairings but because animals at the extremes of the distribution are more difficult to match there can be a tendency for under-representation of the largest and smallest individuals. In the present study, smaller spiders were more likely to withdraw during the pre-contact phase of contests, potentially restricting the size range of smaller rivals in both contests that terminated at this stage and those that continued, and possibly

inflating the effect of larger rival size on pre-contact duration, resulting in a relationship that appears to be suggestive of opponent only rather than mutual assessment. To study assessment mechanisms at later contest stages, a larger and more broadly representative sample might be obtained by encouraging pairs to escalate to higher levels through increasing the value of contested resources (Elias et al. 2008; Hoefler et al. 2009; Magellan & Kaiser 2010; Mager et al. 2008; Wells 1988).

Measures of costs

Our results add to a growing appreciation that different measures of contest cost can lead to contradictory support for alternative theories of assessment. In the golden orb-web spider, *Nephila clavipes*, no relations were found between contest duration and body size of rivals but escalation increased with the size of the smaller rival, consistent with self-assessment (Constant et al. 2011). Keil and Watson (2010) found support for self-assessment in terms of escalation and intensity (an estimate of the energetic costs of a contest using the time spent performing different actions) in the sierra dome spider, *Neriene litigosa*. However, they also found evidence for mutual assessment; duration of the whole contest and different phases within the contest diminished with size asymmetry between rivals (although they did not separate contests that terminated during one phase from those that escalated to the next phase). Studies of animal contests have typically chosen one or two common measures of cost, such as duration and escalation, but generally the strength of association between these metrics and actual underlying costs and constraints on contest behaviour is not known. One metric may be a more or less accurate means of estimating costs and this might add to variance in the analyses. Of greater concern, one metric may be a more reliable means of estimating cost such that results and conclusions obtained from a poor choice may then

be unreliable. There appears a need for greater attention to the suitability of cost metrics chosen for studies of contest behaviour.

Duration is used as a measure of cost for four main reasons: (1) it is a readily accessible and convenient measurement, (2) many theoretical models involve predictions about contest duration (Enquist & Leimar 1983; Taylor & Elwood 2003), (3) time spent fighting could be allocated to other activities and (4) physical and physiological costs accumulate with time (Hack 1997; Prenter et al. 2006). Costs are unlikely to accumulate linearly with time, however, especially when contests escalate through phases of different intensity. As contests between male *S. incana* were brief and rapidly progressed through different stages, the level of escalation may be a better indicator of costs than contest duration. Escalation appears to be a more consistent indicator of assessment strategy in other spiders (Bridge et al. 2000; Constant et al. 2011; Taylor et al. 2001; Wells 1988; Whitehouse 1997). For mutual assessment, theoretical predictions relate to the timing of a decision, therefore time is a suitable variable to examine, however, for models that explicitly depend on cost thresholds and the accumulation of costs, time may not be the most appropriate metric. Contests are likely to be physiologically expensive for spiders as they have limited metabolic capacity (Prestwich 1983; McGinley et al. 2013). Measures of the physiological costs of fighting (e.g. Briffa & Elwood 2004; DeCarvalho et al. 2004; Prenter et al. 2006) or risks of injury may give a better indication of the true costs of contests as well as the capabilities and decisions of the animals involved.

Interpretation of assessment strategy in the separate phases of complex multistage contests may also depend on whether contests are analysed as a single entity or instead are analysed as a series of distinct decisions. In particular, treating the whole

contest as a single entity in analyses may mask variation (Morrell et al. 2005). In contests that consist of escalating phases, separate examination of the phases can uncover varying assessment strategies within the same contests. For example, in their investigation of display and fighting phases of contests between mate guarding and intruder males of the hermit crab, *Pagurus middendorffi*, Yasuda et al. (2012) reported that smaller intruders were less likely to escalate to physical fighting, consistent with self assessment. However, the duration of the escalated fighting phase increased with decreasing difference in cheliped size between opponents, consistent with mutual assessment. Thus, animals may shift from mutual assessment to self assessment, or vice versa, over the course of a contest. By examining escalation through different stages of a contest, Hsu et al. (2008) found that killifish, *Kryptolebias marmoratus*, use mutual assessment during precontact stages and self-assessment during escalated fighting. If the analysis had been confined to examining total contest duration, results observed would have suggested that they use mutual assessment throughout the contest. Because of diminishing sample sizes as contests progress, analyses of whole contest patterns tend to over-emphasise the assessment strategies used in early contest stages.

In summary, our results suggest that contests between male *S. incana* are largely resolved by own cost thresholds. Size of the opponent may influence the timing of the decision to withdraw, however it is unclear whether this is due to opponent assessment or reluctance of smaller opponents to act. These results were only revealed by considering multiple measures of cost at different stages of the contests. Therefore we highlight the need to consider carefully which are the most appropriate proxies of costs and to understand that the theoretical predictions for a whole contest do not necessarily apply to each of its constituent parts.

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Chapter Five: Video playback experiments support a role for visual assessment of opponent size in male-male contests of *Servaea incana* jumping spiders

Abstract

Jumping spiders (Salticidae) are known both for their excellent vision and for the elaborate visual displays they use to mediate intraspecific interactions. Despite appearing well adapted for visual exchange of information, several correlative studies have suggested that jumping spiders may not visually assess opponent size during agonistic interactions. To more directly examine whether jumping spiders are able to visually assess opponent size, we examined how males of *Servaea incana* respond to videos of agonistic displays from conspecifics. The size of video opponents was manipulated so that each exemplar was presented at four sizes that spanned the range of natural variation. Responses to videos were related to both the final size of the video opponents and the size of the live spiders, but not the original size of the opponents in the videos. Jumping spiders appear sensorially capable of assessing opponent size, but their slow visual system and dynamic behaviour during contests may often impede assessment.

Introduction

Animals often engage in contests that potentially expose them to substantial costs, such as injury, energy expenditure or exposure to enemies. To limit the costs incurred during contests, animals are expected to gather and use information efficiently to guide decisions of whether to persist or retreat. In particular, animals are expected to assess fighting ability, or resource holding potential (RHP), of their opponents (Maynard Smith & Parker 1976; Enquist & Leimar 1983). However, there is increasing evidence that this source of information may not be as widely used as was once thought (Taylor & Elwood 2003; Arnott & Elwood 2009). Instead, perhaps because of assessment costs or lack of sensory capability, some animals may simply persist in contests until they reach an internal threshold, regardless of opponent quality.

Studies of mechanisms underlying contest resolution have relied greatly on interpreting patterns of persistence and behaviour in staged encounters, a correlative approach. Theoretical models make predictions about the nature of correlations between RHP and the costs involved in contests; if animals are assessing each other's RHP then the costs of contests should increase with the RHP of the weaker rival and decrease with the RHP of the stronger rival, however, if using pure self-assessment the costs should be determined only by the RHP of the weaker rival (Arnott & Elwood 2009). However, empirical studies often fail to meet the predictions of these models, or produce results that are consistent with multiple models (Jennings et al. 2004; Morrell et al. 2005). As a complement to correlative studies of live pairings, more experimental approach can allow for clearer discrimination between alternative assessment strategies and better reveal what sources of information are used to make decisions in

contests (Tibbetts & Lindsay 2008; Arnott & Elwood 2010; Tibbetts et al. 2010; Reddon et al. 2013; Reichert 2014).

Jumping spiders (Salticidae) present interesting subjects for the study of animal contests. Possessing a well developed visual system (Land 1969a,b), jumping spiders are able to make fine visual discriminations (Jackson et al. 2005; Nelson & Jackson 2012) although it may take some time for a response or to make a decision (Harland et al. 2012; Zurek & Nelson 2012). Jumping spiders are also well known for their use of elaborate visual displays to mediate intraspecific interactions. These displays, combined with high acuity vision, lead naturally to an expectation of opponent assessment during contests (Wells 1988; Faber & Baylis 1993). However, tests of this hypothesis suggest that decisions in jumping spider contests are instead determined largely by a spider's own RHP rather than assessment of the opponent (Taylor et al. 2001; Elias et al. 2008). In the jumping spider *Servaea incana*, there is large variation in the size of adult males (Chapter 2) and size is positively associated with fighting ability (Chapter 4) as well as physical performance (McGinley et al. 2013). We may therefore expect strong selection for male ability to assess size of their opponents and to compare these estimates with estimates of their own size or ability. However, results of staged contests between *S. incana* males suggest that small spiders are less likely to participate in escalated contests irrespective of the size of their opponent, although the decision to retreat tends to be made earlier if the opponent is larger.

Because contest dynamics depend on both opponents, correlative studies such as have been the mainstay of investigations into jumping spider contests (Chapter 3; Taylor et al. 2001; Wells 1988; Faber & Baylis 1993; Elias et al. 2008) often yield results that cannot clearly reveal information state or assessment ability of individuals (Briffa &

Elwood 2009; Elwood & Arnott 2013; Fawcett & Mowles 2013). Rather than using live opponents, to more directly test whether *S. incana* jumping spiders are capable of assessing opponent size we here examine whether and how behaviour of individual spiders changes in response to size of video-presented opponents. Video playback has proven highly effective as a tool to study assessment by jumping spiders in the contexts of courtship (Clark & Uetz 1990; Tedore & Johnsen 2013) and predation (Harland & Jackson 2002; Nelson & Jackson 2006; Bednarski et al. 2012), but remains to be employed as a standard tool for the study of jumping spider contests.

Methods

Collection and maintenance of spiders

Adult male *Servaea incana* were collected from the trunks of eucalypt trees in parks in Sydney, NSW, Australia, between October 2011 and August 2013. Spiders were maintained in a laboratory under controlled temperature ($25 \pm 1^\circ\text{C}$) and humidity ($65 \pm 5\%$) on a 12:12h light:dark cycle. Spiders were housed individually in 1.125 L ventilated plastic cages with half a crumpled sheet of white A4 paper as environmental enrichment (Carducci & Jakob 2000). Water was provided *ad libitum* via a 5 mL vial attached to the base of the cage, stoppered with a cotton dental wick that carried moisture into the cage. Prior to the experiment, spiders were fed two Queensland fruit flies (*Bactrocera tryoni*) every two weeks and two houseflies (*Musca domestica*) in alternate weeks.

Morphological Measures

Each spider was photographed no less than three days prior to any trials taking

place with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany), focussed through an Olympus SZX12 dissecting microscope (Olympus Corporation, Tokyo, Japan). To ensure consistent presentation, spiders were restrained on the lid of a 50 mm Petri dish using clear plastic film (Glad Products, Australia). We scaled and measured cephalothorax width from digital images using ImageJ 1.36b (National Institute of Health, Bethesda, MD, USA). Descriptive statistics for morphology of the spiders used in this study are presented in figure 1.

Creation of playback stimuli

When jumping spiders see their reflection in a mirror, they often behave as if they are interacting with a same-sex conspecific (Harland et al. 1999). To generate realistic videos of the displays that *Servaea incana* use in contests, live spiders were recorded while displaying at their reflection in a two-way mirror. The mirror consisted of a pane of glass with window tinting film (Alpena Fade Shade, Marklyn Co. Inc. Brampton, Ontario, Canada) on one side. On the untinted side of the glass was an arena with a length of 100 mm and a width of 80 mm at the end away from the mirror, narrowing to 20 mm at the mirror. On the tinted side of the glass was a black cardboard box, 200 x 80 x 80 mm, with a 20 x 30 mm hole at the end against the glass. At the other end of the box a hole was cut to the size of the lens of a digital video camera (Panasonic HDC-HS700, Panasonic, Japan) that was used to record the displays of the spiders. Spiders were placed at the wide end of the arena and allowed to make their way towards the mirror. Upon seeing their reflection some spiders displayed as if towards a same-sex conspecific. We recorded the displays of 3 large and 3 small *S. incana* males (see figure 1) for use as stimuli in video playback experiments.

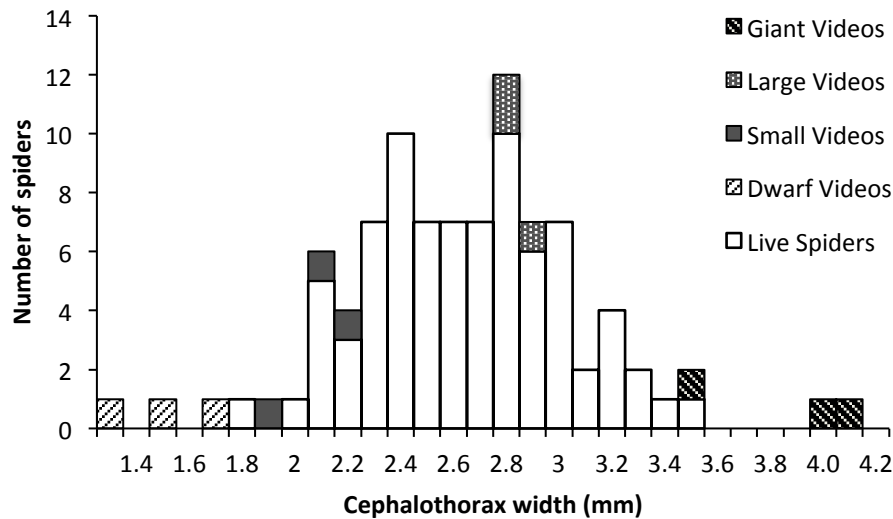


Figure 1. Size distribution of the live spiders ($N = 81$, $X \pm SD = 2.69 \pm 0.36$ mm) and videos used in playback trials.

Videos were converted from the original MPEG-2 Transport Stream (M2TS) format to MPEG-4 Part 14 (MP4) with Aimersoft Video Converter Ultimate for Mac (Aimersoft Software Co., Ltd.) so that they could be edited with Final Cut Express 4.0 (Apple Inc., Cupertino, CA, USA). Videos of displays were cropped and edited so that they could be played in a continuous loop. Each video was scaled to match the size of the corresponding live spider when viewed on the screen of an iPod touch 4 (Apple Inc., Cupertino, CA, USA). The recorded display of each large spider was paired with that of a small spider. Size-modified videos were generated by scaling each recording to the size of the other spider in the pair, giving a total of twelve videos; three of a large spider at its original size (large video), three of a large spider at the size of its smaller partner (small video), three of a small spider at its original size (small video) and three of a small spider at the size of its larger partner (large video). Additional videos that were larger and smaller than the two natural sizes were created such that the ratio between the smallest (dwarf) and small video, and the large and largest (giant) video were the same as the ratio between the small and large video. This resulted in a total of 24 videos; three sets

of exemplars x two original sizes (small or large) x four final sizes (dwarf, small, large and giant).

Playback trials

The arena comprised a ramp with a level viewing platform at the top, constructed of foam board (Fig. 2). The ramp was 120 mm long, 80 mm wide and sloped upward at an angle of 30°. At the top of the ramp the viewing platform was 100 mm long and narrowed from 80 mm at the top of the ramp to 40 mm at the end closest to the screen. The walls of the arena were 100 mm high at the bottom of the ramp and 35 mm high at the viewing platform. Videos were played on an iPod touch 4 screen that was positioned in a slot cut into the walls of the arena at the narrow end of the viewing platform. For each trial a new piece of 10 mm grid paper, cut to the shape of the arena was placed on the arena floor. The walls of the arena were lightly coated with petroleum jelly to prevent spiders from climbing out. The arena was constructed so that spiders would make their own way towards the videos. Spiders were placed at the bottom of the ramp and allowed to make their own way to the top. Trials began when spiders oriented towards the video and ended when they retreated from the video or attempted to escape the arena. Between trials the arena was sprayed with water and wiped down with tissue paper to remove pheromones and silk draglines (Jackson 1987). All trials were video recorded (Panasonic HDC-HS700, Panasonic, Japan). From recordings, we assessed whether spiders performed hunch displays typical of the precontact phase of contests between *S. incana* males (Chapter 3). We also assessed whether spiders approached to within 30 mm of the screen. At this distance, live pairings of *S. incana* males usually escalate from visual displays to lunging and make contact with each other (Chapter 3).

Each spider participated in one trial every second day until they had watched a complete set of eight videos. Two days before the first trial, spiders were provided two *B. tryoni* flies as food. The following day flies were removed. To maintain the same level of hunger throughout the experiment, spiders were provided two flies after each trial and flies were removed on the day between trials.



Figure 2. The arena used for the playback trials. A *Servaea incana* male is oriented towards a video of a conspecific on an iPod screen after walking up the ramp to the viewing platform.

Statistical Analyses

We used generalised estimating equations to examine the effects of a spider's own size and the original and final size of the video on a spider's response to the videos. Our independent variables were final video size (4 levels; dwarf, small, large, giant), original size of the recorded spider (2 levels; small, large) and exemplar set (3 levels)

with focal spider size as a covariate. We entered either whether spiders displayed or whether they approached to within 30 mm of the screen as binary dependent variables. We started with a full factorial model, removing interaction terms with p-values greater than 0.10 until we reached the final model. Analyses were performed in IBM SPSS v. 20 (IBM Corp., Armonk, NY, USA).

Results

Eighty one live *S. incana* were tested in this study, each participating in 8 trials (27 spiders for each exemplar set). Spiders appeared to interact with the videos as they usually would with live conspecific males. Several spiders continued to lunge at the screen even after coming into contact with it. However, in the majority of trials with dwarf videos, spiders did not behave as they usually would with conspecifics. Many spiders watched the dwarf videos for long periods, sometimes for several minutes, without displaying or walked around the arena several times before eventually orienting towards the video.

Table 1. Results of generalised estimating equations showing the effects of a spider's own size and the video opponent's final and original size on the tendency to display.

Effect	χ^2	d.f.	P
Spider size	2.664	1	0.103
Opponent's final size	10.666	3	0.014
Opponent's original size	0.703	1	0.402
Exemplar set	1.025	2	0.599
Spider size x Opponent's final size	11.996	3	0.007

Spiders displayed towards the screen in 401 of 648 trials (62%); of the 162 trials with each size class of video, spiders displayed in 55 (34%) with dwarf spider videos,

114 (70%) with the small spider videos, 119 (73%) with the large spider videos and 113 (70%) with the giant spider videos. Spiders displayed in 205 of 324 (63%) trials when the spider in the video was originally large and 196 of 324 (60%) trials when the spider in the video was originally small. The final size of the video and an interaction between final video size and size of the live spider predicted whether spiders displayed towards the screen (Table 1). Investigation of the parameter estimates revealed that when the video spider was giant sized, there was a positive correlation between spider size and probability of displaying ($\beta = 2.073 \pm 0.595$, $\chi^2_1 = 12.143$, $P < 0.001$; Fig. 3). When the video spider was large sized, there was a similar trend, however, it was non-significant ($\beta = 0.926 \pm 0.546$, $\chi^2_1 = 2.881$, $P = 0.090$). Size of the live spider did not predict whether spiders displayed when the video was small ($\beta = -0.457 \pm 0.568$, $\chi^2_1 = 0.647$, $P = 0.421$) or dwarf sized ($\beta = -0.163 \pm 0.524$, $\chi^2_1 = 0.097$, $P = 0.756$).

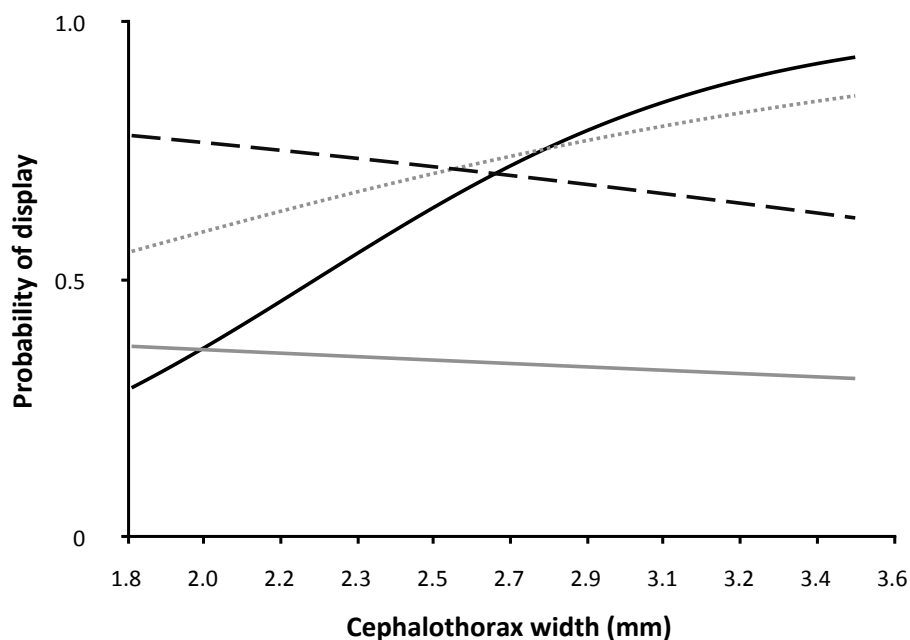


Figure 3. Relationships between size of the live spiders and their tendency to display towards dwarf (solid grey line), small (dashed black line), large (dotted grey line) and giant (solid black line) sized videos.

Overall numbers of displays were similar towards small, large and giant videos (70 -73%), therefore, as the probability of displaying reduced for some spiders, for others it must have increased (Fig. 3). We examined pairwise comparisons of the estimated marginal means for the different sized videos, while varying live spider size to determine at what size the difference between the probability of displaying towards a small versus a large or giant video becomes significant ($\alpha = 0.05$). At the mean spider size, the probability of a display was similar for each of the video sizes ($P > 0.6$ for all comparisons). We found that live spiders with a cephalothorax width greater than 3.24 mm were significantly more likely to display towards large sized videos than smaller sized videos. Spiders smaller than 2.19 mm were significantly more likely to display towards the small sized videos than the large ($P > 0.05$ within the range 2.19 – 3.24 mm). When spiders were between 2.37 and 3.01 mm there were not significant differences in the probability of display between giant and small sized videos, spiders above this range were more likely to display towards giant videos while spiders below were more likely to display towards the small video than the giant.

Table 2. Results of generalised estimating equations results showing the effects of own size and the video opponent's original and final size on the tendency to approach within 30 mm of the screen.

Effect	χ^2	d.f.	P
Live spider size	5.518	1	0.019
Final video size	12.836	3	0.005
Original video size	0.123	1	0.725
Exemplar	4.188	2	0.123

Spiders approached to within 30 mm of the screen in 248 of 648 trials (38%); of the 162 trials with each size class of video, spiders approached in 59 (36%) with dwarf spider videos, 77 (48%) with the small spider videos, 64 (40%) with the large spider videos and 48 (30%) with the giant spider videos. Spiders approached in 122 of 324

(38%) trials with videos of spiders that were originally large and 126 of 324 (39%) trials with videos of spiders that were originally small. Size of the live spider and size of the final video were significant predictors of whether spiders approached to within 30 mm of the screen (Table 2). The probability of approaching increased with the size of the live spider (Fig. 3). Pairwise comparisons of the estimated marginal means revealed that spiders were significantly less likely to approach dwarf and giant sized videos than small sized videos ($P = 0.022$ and 0.001 respectively) and less likely to approach giant than large videos ($P = 0.036$). All other pairwise comparisons were non-significant ($P > 0.1$).

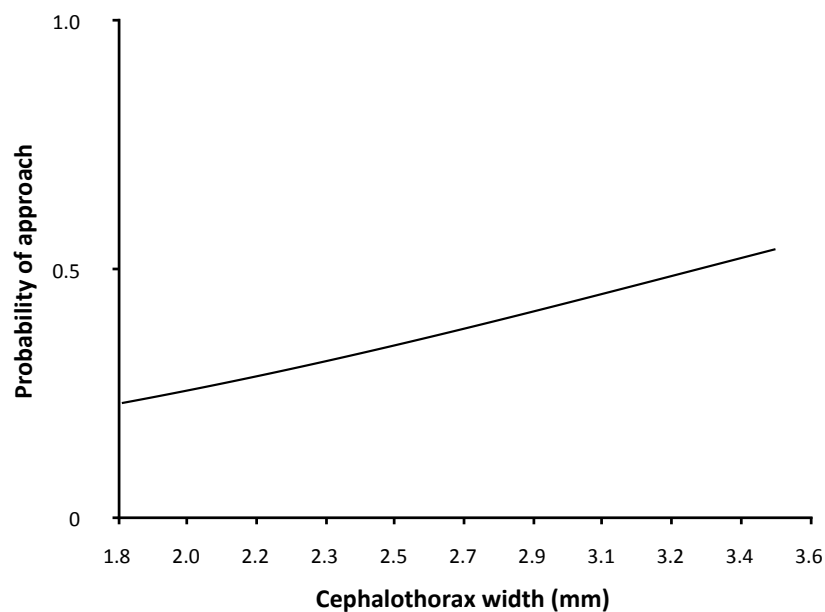


Figure 4. Relationship between live spider size and the probability of approaching to within 30 mm of the screen. Larger spiders were more likely to approach all videos.

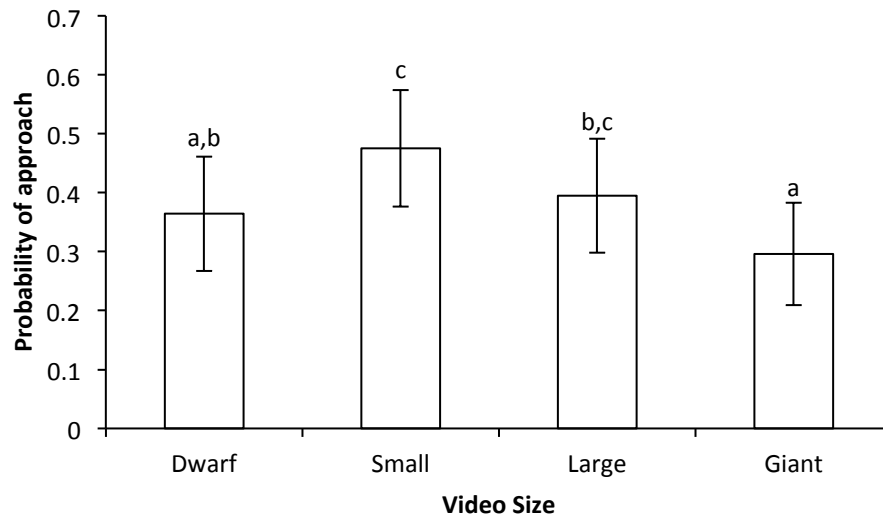


Figure 5. Probability of spiders approaching within 30 mm of video opponents of different sizes. Presented are the estimated marginal means with the standard error computed from generalised estimating equations with spider size set at the mean. Non-significant differences share the same letter.

Discussion

Servaea incana males modulated their response to the size of displaying same-sex conspecifics that were presented as video images, altering both their tendency to return display and their tendency to approach the screen. These results suggest that *S. incana* are capable of visually assessing the size of their opponents during the precontact phase of contests with live opponents. A spider's own size also influenced these decisions. We detected a significant interaction between the effects of test spider size and video opponent size on the probability of display. Spiders were least likely to display towards the smallest 'dwarf' videos. If the video opponent was small there was no evidence of relation between test spider size and display tendency, but as the size of the video opponent was increased, smaller spiders became less likely to display, while large spiders were increasingly likely to display. Effects of both test spider size and video opponent size were also detected in tendency to approach the screen. Spiders were less likely to approach video presentations of large opponents, but were also less likely to

approach if of small size themselves. The original size of the spiders used to generate the video stimuli did not affect whether spiders displayed towards or approached a video. This indicates that *S. incana* assess actual size, rather than assessing other cues or characteristics that may correlate with size in live spiders, such as morphological allometry or size-associated behaviour.

The results of this study contrast with those of previous experiments examining the role of opponent assessment in male-male contests in *S. incana* (Chapter 4). In staged contests, decisions of persistence appear to be determined primarily by a spider's own size; smaller spiders are less likely to escalate towards physical fighting, regardless of opponent size. However, the decision to retreat is made earlier with increasing size of the larger spider, but it is unclear whether this is due to the reluctance of the larger spider in a pair to escalate when they are small or whether it is due to opponent assessment by the smaller rival. The results of the present study provide evidence in support of the latter explanation.

The reliance upon self-assessment observed in live contests in contrast to the support for mutual assessment in the present study may be explained by the differences in behaviour of live and video-presented spiders. The video opponents used as stimuli in the present study all displayed continuously, which may allow greater opportunity for assessment of opponent size than might be the case for live pairings. Although jumping spiders possess an exceptional visual system, it may not operate as fast as in other arthropods (Zurek & Nelson 2012). The principal eyes have a narrow field of view, but jumping spiders possess movable retina, allowing them to scan an object to obtain a complete image (Land 1969a). Such a system may be very useful for identifying relatively stationary prey items and when spiders have the time to carefully assess an

opponent, but may not be so useful when a rapid decision of whether to flee a potentially dangerous opponent needs to be made. In addition, because the video played continuously, the video opponent was always the first to orient and display so the results of the present study may only reflect a spider's behaviour when an opponent orients and displays first. Spiders engaged in contests with live conspecifics may perform other behaviours that influence the decisions of their opponent; for example, they may orient without displaying or may approach the opponent, actions that the video opponents did not perform in the present study. Video opponents also continued to display regardless of their own size or the size of their live opponents; we found that the live spider's tendency to display changed with both of these factors.

An alternative explanation for the apparent differences in results between this study and previous experiments with live opponents (Chapter 4), is that the experiments addressed different types of decisions made during contests. Chapter 4 focused upon the decision to withdraw from a contest; smaller spiders were more likely to withdraw prior to making physical contact, regardless of the size of their opponent. The present study allows us to examine decisions that may be related to initiating contests and different information may be used to make these decisions. Indeed, other animals appear to use different sources of information at different stages of a contest (Hsu et al. 2008).

It appears that *S. incana* do not interpret conspecifics under a certain size as a threat. Test spiders tended not to respond to the dwarf-sized videos as opponents. It is possible that spiders did not recognise these small videos as conspecifics, however, we did detect a similar effect with the larger spiders; large spiders being less likely to display towards small videos than large videos. In contests between live spiders, the

tendency of larger spiders to not display may hinder the ability of small spiders to accurately assess opponent size.

Agonistic displays may provide at least three types of information in jumping spider contests: (1) inform the receiver that they have been detected; (2) inform the receiver that they are considered a threat; and (3) facilitate assessment of the signaller's size. When jumping spiders fail to display towards conspecifics they may be more likely to be attacked (Jackson & Harding 1982) so spiders may display in order to deter an attack, similar to how prey may display to deter attacks from predators by use of 'pursuit deterrent signals' (Hasson 1991; Caro 1995). However, when small spiders encounter substantially larger spiders, a display that advertises detection or size may not influence their larger opponent's decision of whether to attack. This appears to be the case in tephritid flies that mimic the agonistic displays of salticids (Hasson 1995); the displays of the fly reduce the probability of an attack by small spiders but are not effective deterrents for large spiders. Therefore we may expect that small spiders should flee rather than display when they encounter large conspecifics, consistent with the results of the present study.

For small spiders, both large and small opponents may be dangerous, but for large spiders only other large spiders are a threat. Large spiders may not display towards smaller conspecifics because they are not considered a threat. If large spiders display towards rivals that are significantly smaller than themselves, they may make themselves more conspicuous to other enemies, may expend energy, and may allow the smaller male to quickly determine their disadvantage, resulting in an early withdrawal. By not displaying, the larger male may reduce risk of attack by other enemies, save

energy and may increase the chances of success in attacking the smaller rival, potentially resulting in both a meal and the elimination of a rival for mates.

Servaea incana are unlikely to encounter conspecifics as large as the ‘giant’ videos they were presented with here, but the results obtained may still be biologically relevant. The populations of *S. incana* collected for this study share their habitat with other salticids that may be as large or even much larger than themselves (Chapter 2). Jumping spiders typically use the display repertoire of intrasexual interactions to mediate interactions with other jumping spider species (Jackson & Wilcox 1990; Nelson et al. 2006), and this is the case in *S. incana* (McGinley, personal observation). Another jumping spider, *Sandalodes superbus*, lives on the same trees as *S. incana* and adults are usually larger than adult *S. incana*. These two species do prey upon each other (Chapter 2), therefore selection is expected to favour an ability of each species to assess size in the other.

The present study is among the first to supplement the correlative study of jumping spider contests with an experimental approach that more directly investigates the assessment capabilities of individual spiders. Through the control over stimulus parameters that video playback permitted, we were able to assess sources of information that may influence behavioural decisions during interactions between *S. incana*. Although *S. incana* appear capable of assessing opponent size, this information may not be readily accessible or identifiable during interactions between live spiders.

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Chapter Six: Hunger influences behaviour but not outcome in male-male contests of *Servaea incana* jumping spiders

Abstract

Animals engaged in contests may base their decisions on a diverse array of factors, some are fixed in individuals, others are variable. Body size is the most often studied fixed property of individuals, and is an important predictor of outcome in jumping spider contests. Here we examine the effects of a flexible factor, hunger, on decisions during male-male contests of *Servaea incana* jumping spiders. Hunger may impair fighting ability through energetic constraints, but hungry spiders may also be more inclined to fight because rivals are also prospective meals. We investigated the contest behaviour of spiders that had either been fed within the previous two days or deprived of food for at least seven days. Contests were staged between spiders that were (1) matched for both size and hunger state, (2) matched for size but not matched for hunger state, and (3) not matched for either size or hunger. Contests between hungry spiders were similar to contests between spiders that had recently fed. In contests between hungry and fed spiders, spiders were similarly likely to have seen each other first, but hungry spiders were more likely to have oriented first at the outset of a contest and more often engaged in predatory behaviour. Interactions between spiders may be more likely to occur when spiders are hungry. Overall, although hunger had clear effects on behaviour in contests, it did not affect fighting ability.

Introduction

Animal contests sometimes escalate to potentially injurious fights, but are more often resolved efficiently and without injury on the basis of asymmetries between rivals (Vieira & Peixoto 2013). Some asymmetries are fixed properties of individuals, and others are more variable factors associated with individuals and context. For example, body size (Briffa 2008; Rudin & Briffa 2011) and weapon size (Sneddon et al. 1997; Yoshino et al. 2011) are fixed qualities of individuals. Residency (Kemp & Wiklund 2004; Umbers et al. 2012), and resource value (Mohamad, Monge & Goubault 2010; Sultana et al. 2013) are variable aspects of context. Age (Kemp 2003; Lailvaux et al. 2004), physiological state (Briffa & Sneddon 2007; Chelliah & Sukumar 2013), and experience (Garcia et al. 2014; Hsu et al. 2014) are variable qualities of individuals. Some asymmetries between rivals might be important determinants of decisions during the course of contests, such as whether to engage in a contest at all or whether to initiate escalation, but not influence the final decision of whether and when to retreat (i.e., contest outcome) (Prenter et al. 2008).

Hunger presents as an interesting flexible individual quality that may have contrasting effects on decisions during animal contests. Contests are often energetically expensive and so hunger may make animals less willing to invest the energy required to perform displays or to physically overcome an opponent, resulting in reduced contest success, reduced tendency to engage in contests, or reduced tendency to initiate escalation once engaged in contests. On the other hand, hunger may increase motivation and aggression (Laidre & Elwood 2008; Lamba et al. 2008; Machmer & Ydenberg 1998) and willingness to engage in high-risk behaviours (Barnard & Brown 1985; Fraker 2008; Laidre & Elwood 2008; Walker & Rypstra 2003) or contest escalation (Sheldon 1974)

such that hungry animals are more likely to initiate and win contests, particularly if fighting for food (Barnard & Brown 1984; Nosil 2002).

Spiders are interesting models for studying the effects of hunger on behaviour. Spiders live a feast and famine lifestyle, being well adapted to survive long periods with little or no food, but capable of rapid and massive consumption when food is available (Anderson 1974), and even capable of consuming the specific nutrients that they require from a prey item (Mayntz et al. 2005). While some spiders are quite selective in their prey choice, most are generalist predators that will eat almost any small invertebrate that they can subdue with their venom and silk, including each other (Foelix 2010). When, in addition to being potential rivals or mates, conspecifics comprise potential meals, hunger can play a particularly important role in intra-specific interactions. Sexual cannibalism is well documented in spiders (Andrade 1998; Elgar 1992) and both long and short term feeding history may influence female aggression towards males (Moskalik & Uetz 2011). Males of some sexually cannibalistic species wait until females are feeding before courting (Austin & Anderson 1978; Prenter et al. 1994a,b) while males of the pisaurid, *Pisaura mirabilis*, use nuptial gifts to turn female voracity to their advantage (Bilde et al. 2007). Cannibalism may be an important regulator of population size in some populations (Samu et al. 1999; Wagner & Wise 1997; Wise 2006) and cannibalism rates may increase with hunger or food limitation (Samu et al. 1999).

Cannibalism among jumping spiders (Araneae: Salticidae) has received less attention than in some other spider families, but has been reported for numerous species, occurring between and within sexes and age classes (Allan & Elgar 2001; Clark & Biesiadecki 2002; Cross et al. 2008; Elias et al. 2005; Jackson 1977, 1980, 1985, 1986, 1988; Jackson & Hallas 1986; Jackson & Harding 1982; Jackson & Macnab 1989; Jackson

et al. 1990; Nelson & Jackson 2007; Rienks 2000; Taylor & McGraw 2013; Taylor & Jackson 1999). Cannibalism among jumping spiders most commonly occurs when one spider stalks the other without being noticed, using the same behaviours as when hunting other prey, or when one spider is caught as it attempts to retreat after an interaction. Contests between potential cannibals can present high risk, especially if one or both are hungry and if hunger of rivals is variable and difficult to discern.

In the present study we examine the effects of hunger on decisions made during male-male contests of a jumping spider, *Servaea incana*. In *S. incana* hunger is known to reduce the threshold required to induce an orientation response to moving objects (Zurek et al. 2010). In other jumping spiders, hunger increases the tendency to attack heterospecific prey (Gardner 1964, 1966). For example, some jumping spiders exhibit clear prey preferences when well-fed but are increasingly willing to accept non-preferred prey as hunger increases (Jackson & Olphen 1991; Jackson 2000; Jackson et al. 1998; Jackson & van Olphen 1992; Li 2000; Li, Jackson & Harland 1999). Size of prey also influences attack behaviour; as hunger increases, spiders may be more willing to attack larger prey (Drees 1952). Size is a strong predictor of contest outcome in jumping spiders (Elias et al. 2008; Faber & Baylis 1993; Taylor et al. 2001; Wells 1988) including *S. incana* (Chapter 3), but the effects of hunger on decisions made by jumping spiders during contests have not been investigated previously.

Methods

Collection and maintenance

Males of *S. incana* were collected from parks in Sydney, Australia, between August 2012 and November 2013 and maintained in a controlled environment laboratory at 25°C, 65% RH where they were housed in 1.125 L ventilated plastic cages. Spiders were fed two Queensland fruit flies, *Bactrocera tryoni*, every two weeks and with two houseflies, *Musca domestica*, in alternate weeks. For moisture, cages were sprayed with water at least three times each week. Spiders were visually isolated from each other with paper taped onto the outside of three sides of their cages.

To measure size, each spider was restrained against the lid of a 50 mm Petri dish with the aid of cling film (following McGinley et al. 2013). Spiders were then photographed with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany) focussed through an Olympus SZX12 stereomicroscope (Olympus Corporation, Japan). Cephalothorax width and length were measured from photographs to the nearest 0.01 mm using ImageJ 1.36b (National Institute of Health, Bethesda, MD, USA).

All spiders were provided with two *B. tryoni* as prey, nine days prior to contests taking place. Uneaten flies were removed from the cages two days later. For the size-matched contests, spiders were weighed to the nearest 0.1 mg with an electronic balance (Shimadzu Corporation, Kyoto, Japan; Model N595, Type AX200) two days prior to contests taking place. Spiders were then paired to be within 5% of each other for the three measures (mass, cephalothorax width, cephalothorax length). When size matched in this way, these measures do not predict the outcome of contests (Chapter 3). Spiders in the fed treatments were offered another two flies two days prior to the contests, whereas spiders in the hungry treatment were not, such that the hungry spiders had not fed in at least seven days when experiments took place.

Three types of contest were staged to examine the effects of feeding state on both contest outcome and behaviour. In experiment one we staged contests between spiders that were matched for both size and feeding state to ascertain whether contests between hungry spiders culminate in more cannibalism attempts and higher costs (escalation, time) than contests between spiders that have fed recently. In experiment two we staged contests between spiders that were matched for size but differed in hunger state to ascertain the effects of feeding state asymmetry on contest outcome and behaviour independent of size. In experiment three, contests were staged between spiders that differed in both size and hunger state to ascertain the combined effects on contest outcome and behaviour.

For all experiments, contests were staged using the protocols described in Chapter 4. Briefly, arenas were open roofed 300 x 150 x 80 mm plexiglass boxes. The walls of the arena were white, except for the bottom 15 mm, which were transparent. Arenas also had a moveable white barrier that could slide in and out mid-way along the arena length to separate spiders. The upper (opaque white) 65 mm of the walls were lightly coated with petroleum jelly to prevent spiders from climbing out. A sheet of white paper was placed on the floor of the arena. Between trials the paper was replaced and arenas were wiped down with water to remove silk draglines and pheromones left by spiders (Jackson 1987). To stage a contest a spider was transferred from its cage with the aid of a vial and a paintbrush to each side of the arena with the barrier in place. Spiders were allowed to settle down for two minutes before the barrier was then removed and spiders were allowed to interact. Contests started when the two spiders had oriented towards each other and ended when one decamped (the loser). Spiders were separated and returned to their cages after one spider decamped. Individual spiders were distinguished by size (experiment 3) and natural markings (all

experiments). All contests were recorded at ground level with a digital video camera (Panasonic HDC-HS700, Panasonic, Japan).

We assessed both initial orientation order (which spider was first to orient towards the other regardless of whether they maintained orientation until the other spider also oriented) as well as orientation order at the beginning of contests (which spider oriented first in cases where orientation was maintained continuously until the other spider also oriented), as some spiders orient and then turn away without the other spider orienting. We also recorded which spider displayed first, which spider proximated first (approaching the rival), contest duration and the highest level of escalation (Table 1). We also noted pre-contest predatory behaviour, whereby one spider hunted the other prior to the other spider orienting. *Servaea incana* either stalk their prey slowly or chase and leap upon their prey (Chapter 2). We recorded whether spiders stalked or ran without displaying and leaped towards the other spider prior to the beginning of the contest.

Statistical Analyses

We sought to determine whether hunger and the occurrence of certain behaviours predicted contest outcome and the occurrence of other behaviours. Binomial tests to investigate the probability of binary events and contingency analyses with Fisher's exact tests were used for examining relationships between pairs of binary variables. To investigate the effects of multiple factors on probability of an event we used logistic regression. When determining whether certain behaviours predict contest outcome, we have included multiple tests because not all behaviours occur in all contests. The behaviours (orienting, displaying, proximating) occur in a sequential

pattern in contests, so as each variable was added as predictors of later events, contests in which the behaviour did not occur were removed from the analyses. To investigate differences in duration under different conditions we used t-tests. We present descriptive statistics as frequencies for binary outcomes and as means \pm standard error for continuous variables. All analyses were run in JMP 5.0.1.2.

Table 1: The stages of escalation in contests between male *S. incana*. The first three levels make up the pre-contact phase, the last three make up the contact phase. Contests may end at any level of escalation.

Phase	Stage	Escalation	Description
Pre-contact	I	Orient	Spiders turn to face rival.
	II	Hunch	Spider raises body above substrate and raises first pair of legs into an arched position.
	III	Proximate	Spider approaches rival, usually maintaining the hunched posture.
Contact	IV	Spar	When within two body lengths, spiders lunge towards each other, flicking the first pair of legs vertically, and making contact with the legs and body and pushing against the rival.
	V	Embrace	Spiders lock chelicerae and push and pull against each other.
	VI	Struggle	Spiders roll around on the substrate grasping and biting at each other.

Results

Experiment 1: Contests between hunger and size matched spiders

Pre-contest

The tendency to orient and then turn away did not differ between pairs of hungry or pairs of sated spiders. One spider oriented towards the other and turned away at

least once without the other spider orienting prior to 6 of 26 contests between fed spiders and 7 of 24 contests between hungry spiders (Fisher's exact test: $P = 0.751$). The spider that initially oriented but turned away later won 5 of the 6 contests between fed spiders and 3 of the 7 contests between hungry spiders (Fisher's exact test: $P = 0.266$).

Initial orientation order did not predict outcome in contests between fed spiders (won 16, lost 10; binomial test: $P = 0.327$) or between hungry spiders (won 11, lost 13; binomial test: $P = 0.839$) (Fisher's exact test: $P = 0.395$).

Pre-contest predatory behaviour was observed in 8 out of 26 (31%) contests between fed spiders and 12 out of 24 (50%) contests between hungry spiders (Fisher's exact test: $P = 0.248$). Pre-contest predatory behaviour did not predict contest outcome; spiders that engaged in predatory behaviour went on to win 11 out of 20 contests (binomial test: $P = 0.824$).

Contest

Orientation order at the beginning of the contest did not predict outcome in contests between hungry spiders (win 12, lose 12; binomial test, $P = 1.00$) or contests between fed spiders (win 14, lose 12; binomial test, $P = 0.845$). Contests between fed and between hungry spiders did not differ in the relationship between orientation order at the beginning of contests and outcome (Fisher's exact test: $P = 1.00$).

Which spider displayed first did not predict contest outcome (win 28, lose 22; binomial test, $P = 0.480$). Hunger and orientation order at the beginning of contests did not predict whether the spider that displayed first would win (logistic regression: $R^2 =$

0.029, $\chi^2_2 = 1.988$, $P = 0.370$; hunger: $\beta = -0.059 \pm 0.291$, $\chi^2_1 = 0.041$, $P = 0.840$,
orientation: $\beta = 0.400 \pm 0.291$, $\chi^2_1 = 1.925$, $P = 0.165$).

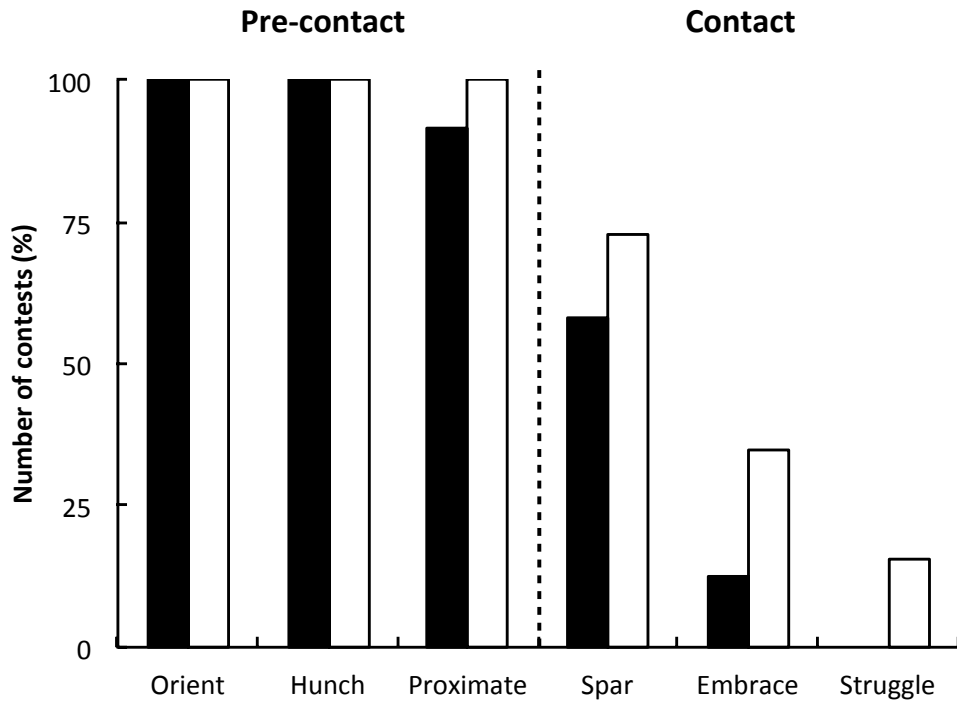


Figure 1. Proportion of contests persisting to each level of escalation when pairs of hungry (black; $N = 24$) and fed (white; $N = 26$) spiders were size-matched.

Spiders that proximated first were just as likely to win contests as those that did not (win 27, lose 21; binomial test, $P = 0.471$). Hunger, orientation order and display order did not predict whether spiders that proximated first would win (logistic regression: $R^2 = 0.037$, $\chi^2_3 = 2.411$, $P = 0.492$; hunger: $\beta = 0.330 \pm 0.305$, $\chi^2_1 = 1.197$, $P = 0.274$, orientation: $\beta = 0.256 \pm 0.304$, $\chi^2_1 = 0.716$, $P = 0.397$, display: $\beta = 0.228 \pm 0.303$, $\chi^2_1 = 0.570$, $P = 0.450$).

Total contest duration and duration of the pre-contact and contact phases were similar for pairings of fed spiders and hungry spiders (Table 2). We found a marginally non-significant difference between the two types of contests in maximum escalation,

with contests between fed spiders tending to reach higher levels (ordinal logistic regression: $R^2 = 0.028$, $\chi^2_1 = 3.821$, $P = 0.051$). Hunch displays were observed in all contests and only two contests, both between hungry spiders, terminated at this stage. Struggling, the maximum level of escalation, occurred in 4 contests, all of which were between fed spiders. Similar numbers of contests terminated at the other levels of escalation for both hungry and fed contests (Fig. 1). The proportion of contests that escalated to the contact phase was similar for the two types of contests (hungry 14 of 24, fed 19 of 26).

Table 2. Differences in contest duration and duration of the pre-contact and contact phases ($X \pm SE$) in contests between size-matched spiders when pairs were either hungry or recently fed.

	Hungry		Fed		<i>t</i>	<i>P</i>
	Ln duration (s)	<i>N</i>	Ln duration (s)	<i>N</i>		
Whole contest	2.21 \pm 0.20	24	2.23 \pm 0.19	26	0.085	0.932
Precontact phase	1.90 \pm 0.19	24	1.93 \pm 0.16	26	0.124	0.902
Contact phase	1.31 \pm 0.33	14	1.06 \pm 0.19	19	0.495	0.495

Experiment 2: Effects of hunger asymmetries independent of size

Pre-contest

Hungry spiders were the first to initially orient in 37 trials and fed spiders were first to orient in 26 trials (binomial test, $P = 0.207$). Being the first to initially orient did not predict whether hungry or fed spiders won (Fisher's exact test: $P = 1.00$). Spiders oriented and then turned away at least once prior to 14 contests; 9 times by the fed spider and 5 times by the hungry spider, this behaviour tended to be more common when the fed spider oriented first (9 of 26) than when the hungry spider oriented first (5 of 37) (Fisher's exact test: $P = 0.066$).

Pre-contest predatory behaviour was observed in 28 trials. In 23 of these instances it was the hungry spider that hunted the fed spider (binomial test, $P < 0.001$). Pre-contest predatory behaviour tended to be more common when the hungry spider was the first to initially orient; 20 of the 37 trials in which hungry spiders oriented first, compared to 8 of the 20 trials in which the fed spider oriented first (Fisher's exact test: $P = 0.078$). Spiders that engaged in predatory behaviour won 18 of 28 contests (binomial test, $P = 0.185$).

Contest

Hunger differences did not predict the outcome of contests between size-matched males; hungry spiders won 36 of the 63 contests and fed spiders won 27 (binomial test, $P = 0.314$).

Hungry spiders were more likely to be the first to orient at the beginning of contests (hungry 43, fed 20; binomial test, $P = 0.005$). Being the first to orient at the beginning of contests did not predict the contest outcome (winner 33, loser 30; binomial test, $P = 0.801$). Whether the hungry or fed spider oriented first, did not predict whether the hungry or fed spider won (Fisher's exact test: $P = 0.791$).

Hunger state did not predict which spider displayed first (hungry 30, fed 29; binomial test, $P = 1.00$). Orientation order did not predict which spider would display first; when hungry spiders were the first to orient, they were the first to display in 22 of 40 contests. In the 19 contests where fed spiders were the first to orient they were the first to display 7 times (Fisher's exact test: $P = 0.267$). Display and orientation order did

not predict whether the hungry or fed spider won (logistic regression: $R^2 = 0.002$, $\chi^2_2 = 0.173$, $P = 0.917$; orientation: $\beta = -0.116 \pm 0.291$, $\chi^2_1 = 0.162$, $P = 0.688$, display: $\beta = -0.010 \pm 0.269$, $\chi^2_1 = 0.001$, $P = 0.970$).

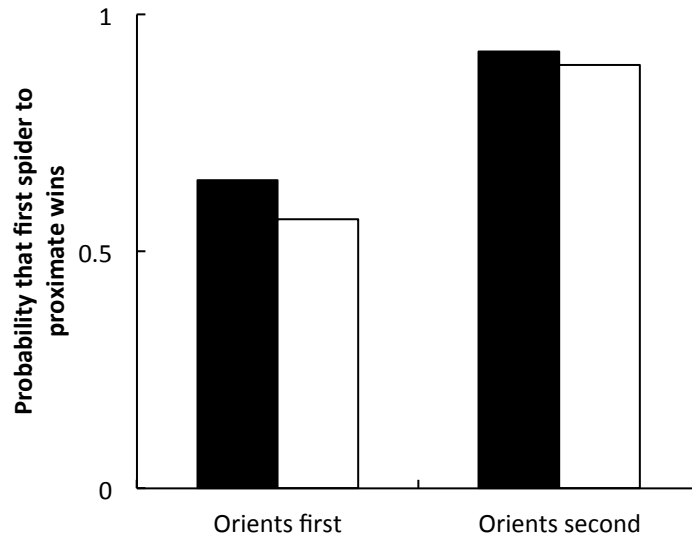


Figure 2. Probability of the spider that proximates first going on to win, in contests between size-matched spiders that differed in hunger. Both hungry (black) and fed (white) spiders were more likely to win when their opponent oriented first but did not proximate first.

Hungry spiders were more likely to proximate before fed spiders (hungry 39, fed 13; binomial test, $P < 0.001$). Orientation order, but not display order predicted which spider would proximate first (logistic regression: $R^2 = 0.171$, $\chi^2_2 = 9.974$, $P = 0.0068$; orientation: $\beta = 1.061 \pm 0.365$, $\chi^2_1 = 9.045$, $P = 0.0026$, display: $\beta = 0.166 \pm 0.365$, $\chi^2_1 = 0.206$, $P = 0.650$). Hungry spiders were the first to proximate in 33 of 38 contests where they were the first to orient, while fed spiders were the first to proximate in 8 of the 14 contests that they were the first to orient in (Fisher's exact test: $P = 0.0026$). Orientation order and proximation order both predicted whether hungry or fed spiders won, but display order did not (logistic regression: $R^2 = 0.141$, $\chi^2_3 = 9.865$, $P = 0.0197$; orientation: $\beta = -0.941 \pm 0.568$, $\chi^2_1 = 3.904$, $P = 0.0482$, display: $\beta = 0.068 \pm 0.318$, $\chi^2_1 = 0.046$, $P =$

0.831, proximation: $\beta = 1.368 \pm 0.559$, $\chi^2_1 = 9.560$, $P = 0.002$). Spiders were more likely to win when they proximated first after the opponent was the first to orient (Fig. 2).

There was no evidence of difference in the duration of contests won by the hungry spider ($N = 36$, $X \pm SE = 12.72 \pm 1.82$ s) and contests won by the fed spider ($N = 27$, $X \pm SE = 10.78 \pm 2.10$ s) ($t_{61} = 0.173$, $P = 0.863$). Levels of escalation were similar for contests won by the hungry spider and those won by the fed spider (ordinal logistic regression: $R^2 = 0.005$, $\chi^2_1 = 0.902$, $P = 0.342$; Fig. 3). Contests won by the hungry or fed spider were similarly likely to have escalated to the contact phase (hungry spider won: 20 of 36, fed spider won, 12 of 27) (Fisher's exact test: $P = 0.450$).

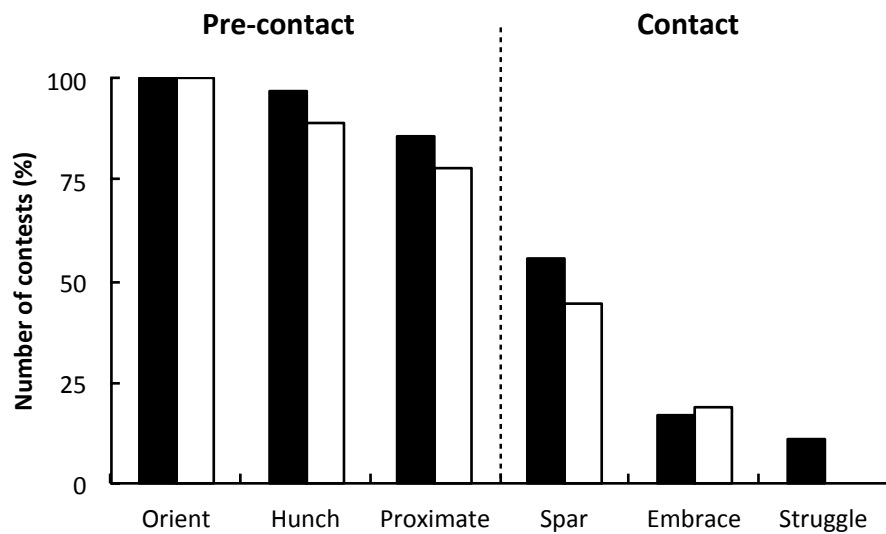


Figure 3. Proportion of contests persisting to each level of escalation when spiders were size-matched and either the hungry (black; $N = 36$) or fed (white; $N = 27$) spider won the contest.

Table 3. Differences in contest duration and duration of the pre-contact and contact phases ($X \pm SE$) in contests between size-matched spiders when pairs differed in hunger and either the hungry or recently fed spider won.

	Hungry spider won		Fed spider won		<i>t</i>	<i>P</i>
	Ln duration (s)	<i>N</i>	Ln duration (s)	<i>N</i>		
Whole contest	2.20 ± 0.13	36	2.17 ± 0.15	27	0.173	0.863
Pre-contact phase	2.00 ± 0.14	36	1.95 ± 0.17	27	0.248	0.805
Contact phase	0.93 ± 0.15	19	1.18 ± 0.19	12	1.05	0.301

Experiment 3: How hunger and size interact

One spider was killed in this experiment; a larger hungry spider stalked and attacked a smaller fed spider that failed to orient towards the attacker. This trial has been excluded from further analyses. The larger spider was the hungry spider in a further 30 contests, while the smaller spider was hungry in another 29. Overall, the larger spider won 46 out of the 59 contests (78%). Hungry spiders won in 27 contests (46%). Hungry spiders won 22 of 30 contests, when the larger spider was hungry. When the larger spider was fed, hungry spiders won 5 of 29 contests. Only size predicted outcome, larger spiders being more likely to win with increasing size difference and hunger having no significant influence on which spider won (logistic regression: $R^2 = 0.239$, $\chi^2_2 = 14.863$, $P < 0.001$; size: $\beta = -7.583 \pm 2.725$, $\chi^2_1 = 14.094$, $P < 0.001$, hunger: $\beta = -0.131 \pm 0.364$, $\chi^2_1 = 0.131$, $P = 0.717$).

Pre-contest

Larger and smaller spiders were similarly likely to be the first to initially orient (29 vs. 30, respectively; binomial test, $P = 1.00$), regardless of whether the larger spider was hungry (15 vs. 15) or fed (14 vs. 15) (Fisher's exact test: $P = 1.00$). Initial orientation

order did not influence the tendency of large spiders to win ($\beta = -0.569 \pm 0.381$, $\chi^2_1 = 2.368$, $P = 0.124$).

One spider oriented and then turned away prior to 22 of 59 contests, 12 times by the larger spider and 10 times by the smaller spider. Initial orientation order and hunger predicted whether spiders oriented and then turned away (logistic regression: $R^2 = 0.237$, $\chi^2_3 = 18.452$, $P < 0.001$; hunger: $\beta = -0.833 \pm 0.363$, $\chi^2_1 = 6.286$, $P = 0.012$, orientation: $\beta = -0.019 \pm 0.363$, $\chi^2_1 = 0.003$, $P = 0.958$, hunger*orientation: $\beta = -1.136 \pm 0.363$, $\chi^2_1 = 12.776$, $P < 0.001$). This behaviour occurred more often when the spider that oriented first was fed (17 of 29 when the fed spider oriented first vs. 5 of 30 when the hungry spider oriented first). Spiders were most likely to orient and turn away when the larger spider was fed and oriented first while this behaviour was least likely to occur when the larger spider was hungry and oriented first (Fig. 4). When the larger spider oriented first they turned away in 11 of 14 trials when fed but only 1 of 15 when hungry. When smaller spiders were the first to initially orient they turned away in 4 out of 15 trials when hungry and 6 of 15 trials when fed.

We observed 21 instances of pre-contest predatory behaviour in this experiment, with similar tendency when the large or small spider was hungry (12 of 30 and 9 of 29 respectively) (Fisher's exact test: $P = 0.589$). Hunger predicted which spider performed the predatory behaviour; when the larger spider was hungry it performed the predatory behaviour in 9 of the 12 occurrences. When the smaller spider was hungry it performed this behaviour 8 out of the 9 times (Fisher's exact test: $P = 0.008$).

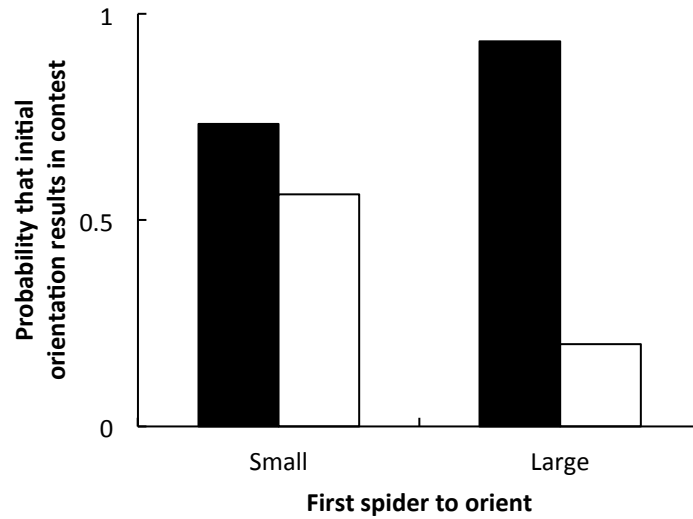


Figure 4. Probability of the initial orientation leading to a contest when the smaller spider or larger spider orients first and are either hungry (black) or fed (white).

Contest

Smaller and larger spiders did not differ in tendency to be the first to orient at the beginning of contests (smaller 34, larger 25; binomial test, $P = 0.298$). However, hunger predicted whether the larger or smaller spiders were more likely to orient first at the beginning of contests; the larger spider oriented first in 19 of 30 contests when it was hungry and 6 of 29 contests when the smaller spider was hungry (Fisher's exact test: $P = 0.0098$). The tendency of larger spiders to win did not vary with orientation order when it was added to the logistic regression ($\beta = -0.095 \pm 0.378$, $\chi^2_1 = 0.063$, $P = 0.802$).

Smaller spiders displayed first more often than larger spiders (large 16, small 35; binomial test, $P = 0.011$). Hunger and orientation order at the beginning of contests did not affect whether the larger or smaller spider displayed first (logistic regression: $R^2 = 0.027$, $\chi^2_2 = 1.729$, $P = 0.421$; hunger: $\beta = -0.379 \pm 0.338$, $\chi^2_1 = 1.2863$, $P = 0.257$, orientation: $\beta = -0.049 \pm 0.336$, $\chi^2_1 = 0.021$, $P = 0.885$). Display order did not affect whether larger spiders would win ($\beta = 0.291 \pm 0.438$, $\chi^2_1 = 0.436$, $P = 0.509$).

Larger and smaller spiders were similarly likely to proximate first (22 and 20 respectively binomial test, $P = 0.878$). Orientation order, but not hunger or display order predicted which spider would proximate first (logistic regression: $R^2 = 0.118$, $\chi^2_3 = 6.846$, $P = 0.077$; hunger: $\beta = 0.224 \pm 0.393$, $\chi^2_1 = 0.336$, $P = 0.562$, orientation: $\beta = 0.933 \pm 0.395$, $\chi^2_1 = 6.463$, $P = 0.011$, display: $\beta = 0.050 \pm 0.358$, $\chi^2_1 = 0.019$, $P = 0.889$), spiders that oriented first being more likely to proximate first (29 of 42, binomial test: $P = 0.020$). Whether the larger or smaller spider was first to proximate did not have a significant effect upon the probability of the larger spider winning ($\beta = 0.484 \pm 0.554$, $\chi^2_1 = 0.795$, $P = 0.373$).

The duration of contests where the larger spider was hungry were not significantly different to contests where the smaller spider was hungry ($t_{57} = 1.108$, $P = 0.272$). Levels of escalation were similar whether the larger spider was the hungry or fed spider (ordinal logistic regression: $R^2 = 0.002$, $\chi^2_1 = 0.287$, $P = 0.592$; Fig. 5). Contests where the larger or smaller spider was hungry were similarly likely to escalate to the contact phase (larger spider hungry, 13 of 31, smaller spider hungry, 12 of 30) (Fisher's exact test: $P = 1.00$).

Table 4. Differences in contest duration and duration of the pre-contact and contact phases ($X \pm SE$) in contests where the larger or smaller spider was hungry.

	Larger spider hungry		Smaller spider hungry		<i>t</i>	<i>P</i>
	Ln duration (s)	<i>N</i>	Ln duration (s)	<i>N</i>		
Whole contest	2.30 \pm 0.17	30	2.03 \pm 0.18	29	1.108	0.272
Pre-contact phase	2.15 \pm 0.17	30	1.90 \pm 0.17	29	1.080	0.285
Contact phase	1.03 \pm 0.26	13	0.76 \pm 0.28	11	0.715	0.482

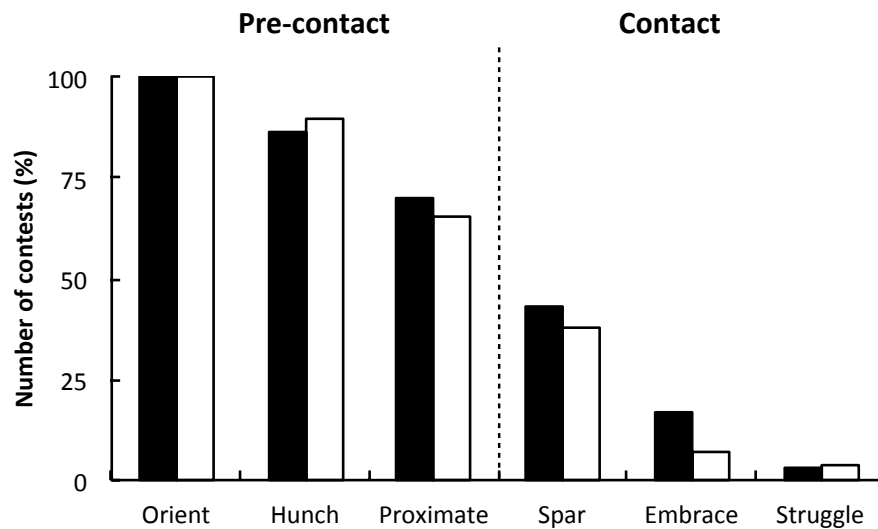


Figure 5. Proportion of contests that persisted to each level of escalation when spiders differed in both size and hunger and either the larger (black; N = 30) or smaller spider was hungry (white; N = 29).

Discussion

Feeding state did not predict contest outcome, but we did detect effects of feeding state on behaviour at the beginning of contests. When there were asymmetries in feeding state, hungry and fed spiders were just as likely to be the first to orient toward their rival. However, spiders that had recently fed were more likely to turn away after orienting, especially when they were the larger spider, whereas hungry spiders were more likely to maintain orientation until the other spider also oriented and contests began. If fed spiders are more likely to avoid interactions then perhaps interactions in nature are more likely to occur when spiders are hungry. Being the first spider to orient confers an advantage in contests of the jumping spider *Plexippus paykulli* (Taylor et al. 2001), however, being the first to orient initially or at the

beginning of contests did not predict outcome in this study, or in a previous study of *S. incana* (Chapter 4).

We detected evidence of a link between hunger, proximation and outcome when spiders were matched for size but differed in hunger. In these contests, spiders that oriented first but were not the first to proximate were more likely to go on to lose the contest. These spiders may have been at a disadvantage at the outset of the contest and reluctant to escalate, alternatively, the failure to proximate first may have put them at a disadvantage. Spiders that proximated first were more likely to go on to win contests and hungry spiders were more likely to initiate proximation. Hungry spiders won more contests, although the difference was not significant. In *P. paykulli* larger spiders are more likely to initiate escalation by being the first to proximate (Taylor et al. 2001) and in *S. incana*, smaller spiders are less likely to escalate to physical fighting (Chapter 4). If hunger causes spiders to behave more like larger spiders by proximating first, they may have a slight advantage over size-matched rivals that are not as willing to escalate. However, contests between pairs of hungry spiders were not more escalated than contests between fed spiders.

A previous study examining the responses of *Servaea incana* males to video-presented rivals suggests that spiders show little interest in conspecifics that are much smaller than themselves (Chapter 5). Small spiders were also less likely to display towards or approach rivals that were significantly larger than themselves. In that study, spiders were given the opportunity to feed every two days. The present study illustrates that tendency to maintain attention on smaller spiders may be restored when the larger spider is hungry. This suggests that *S. incana* may respond to small conspecifics as if they are prey and large conspecifics as if they are rivals or enemies. Larger spiders

rarely turned away from smaller spiders when they were hungry, but frequently turned away when they were well fed. The effect of hunger was similar but weaker for smaller spiders. Previous experiments examining contest behaviour in *S. incana* all involved spiders that had been fed within a week (Chapters 4, 5).

When there was a difference in hunger level, hungrier spiders were more likely to engage in predatory behaviour, even when the hungrier spider was at a size disadvantage. Pre-contest hunting also occurred more often among pairs of hungry spiders than pairs of fed spiders, although the difference was non-significant. Although actual cannibalism is usually performed by the larger spider and may become more likely with increasing size difference (Samu et al. 1999), we demonstrate here that size-disadvantaged spiders are just as likely to make cannibalism attempts as size-advantaged spiders.

Out of 70 incidences of pre-contest hunting, only one was successful, involving a larger, hungrier spider killing a smaller rival. Despite the size difference and the homogenous setting in the arena, the larger male was able to stalk and leap upon the smaller male without the smaller male orienting towards the larger male. Interactions similar to this may be more common in nature, where the heterogeneous environment would better facilitate successful stalking of conspecifics and spiders are likely to be hungry (Taylor et al. 2000; Wise 2006). There is also the potential for cannibalism to occur at the end of contests. In this study spiders were separated as soon as one withdrew, as they were unable to escape the arena. However, *S. incana* often chase down decamping conspecifics at the end of agonistic interactions (Chapter 2). The potential for injury or death in jumping spider contests is likely a primary reason why small spiders are less willing to escalate to physical fighting. While animals with limited

capacity to kill or injure each other may base decisions upon energetic constraints (Briffa & Elwood 2005; Mowles et al 2009; Prenter et al. 2006) decisions in fights between dangerous rivals are more likely to be determined by risks.

If spiders that have recently fed do not engage in interactions unless attacked, then most contests in nature may fall into two categories; (1) contests at the retreats of females or (2) contests away from retreats, where a hungry spider attacks another. Contests in nature may not necessarily follow the same rules as in the laboratory, where animals receive food regularly; the costs of encountering a conspecific in the field are likely higher than observed in laboratory studies.

There is growing evidence that animals may have limited ability or opportunity to assess each other during contests, despite the diversity of ritualised signals associated with animal contests (Arnott & Elwood 2009). If this is the case then what role do these displays play? At the very least, displays inform receivers that they have been detected. Displays also likely convey information about the identity and intent of the signaller and have been suggested to function to decrease cannibalism in spiders (Jackson & Harding 1982; Stoltz et al. 2008; Wignall & Herberstein 2013). Detection of predators by potential prey decreases the chance of successful predation, so prey may use pursuit deterrent signals to prevent an attack before it occurs, benefitting both prey and predator (Caro 1995; Hasson 1991). Species that are potential prey and mimics of jumping spiders appear to exploit such signals to deter predation (Greene et al. 1987; Hasson 1995; Mather & Roitberg 1987; Rao & Díaz-Fleischer 2012; Rota & Wagner 2006; Zolnerowich 1992). Jackson and Harding (1982) found that *Holoplatys* jumping spiders will attack each other when they do not display, and also attacked more often

when hungry. In the present study, small *S. incana* were more likely to display first in contests.

The lack of relation between hunger and contest outcome may be explained by the relative costs and benefits of fighting for hungry and fed spiders. The costs of losing to a hungry cannibal (death) outweigh any benefits that the cannibal may gain from winning, therefore the value of winning a contest may be high even for fed spiders. Even if well-fed spiders avoid contests prior to them occurring, once they are involved in one, they may be expected to fight just as intensely as hungry spiders.

The risk of cannibalism may explain why jumping spiders engage in ritualised contests even when no apparent resources are at stake. Smaller spiders are more vulnerable to cannibalism and appear to be more averse to escalated contests than larger spiders (Chapter 4). Therefore, the risks of being killed or injured may be the primary costs that determine the behaviour of *S. incana* in contests. The results of the present study illustrate the importance of considering the behaviour of animals with regards to their biology.

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Chapter Seven: Whole-organism performance in a jumping spider, *Servaea incana* (Araneae: Salticidae): links with morphology and between performance traits

Abstract

Studies of whole-organism performance are central to understanding the links between animal behaviour, morphology, and fitness. Invertebrates have been popular models for studies of behaviour, but there have been few detailed studies of their whole-organism performance, links between performance and morphology, or trade-offs amongst different performance dimensions. In the present study, we investigate four facets of whole-organism performance (running speed, climbing speed, endurance and pulling force) in males of a jumping spider (*Servaea incana*). We consider links between these performance traits and their association with three morphological measures expected to influence maximum performance capacity: body size, relative leg length and relative body mass (condition). Running speed, climbing speed and pulling force were all positively related, suggesting that selection for one may positively effect all. By contrast, endurance capacity decreased with running and climbing speed, suggesting conflict in mechanism and evolutionary trade-off. Associations amongst performance measures cannot be explained solely as correlates of morphology: large size conferred greater sprint speed, climbing speed, and pulling force, but was not associated with endurance; relative leg length was linked to pulling force, but not to other performance traits; relative mass was linked to climbing speed and endurance, but not sprint speed or pulling force.

Introduction

Behaviour and morphology evolve in concert, as variation in each is constrained by the other. Through detailed studies of links with morphology, substantial gains have been made in understanding the behaviour and physical capabilities of animals from a large taxonomic range, including squamate reptiles, amphibians, fish, and primates (for reviews, see Koehl 1996; Irschick et al. 2008). For example, in *Anolis* lizards, longer legs are advantageous for running on broad surfaces whereas shorter legs are better for narrow surfaces and, as a result, individuals with preferences for substrates appropriate for their morphology have higher survival rates (Calsbeek & Irschick 2007). In mosquito fish (*Gambusia affinis*), variation in swimming performance between populations is associated with differences in both body shape and predation pressure (Langerhans et al. 2004; Langerhans 2009). Whole-organism performance capacity has been linked with foraging (Huey et al. 1984; Herrel et al. 2008), predator evasion (Watkins 1996; Downes & Shine 2001), sexual competition, and territoriality (Lailvaux et al. 2004; Husak et al. 2006). Contrasting the detailed understanding that has developed in some vertebrate systems, our understanding of links between whole-organism performance and morphology is generally less advanced in invertebrate systems. While some groups have been studied in varying degrees of detail (e.g., ants, Weihmann & Blickhan 2009; crabs, Weinstein 1998, Mowles, Cotton & Briffa 2010; crickets, Dangles et al. 2007; fleas, Krasnov et al. 2003; locusts, Kirkton & Harrison 2006; scorpions, Prestwich 2006; Shaffer & Formanowicz 2000), others have received little attention to date.

We predict that spiders will provide particularly interesting models for the study of links between morphology and whole-organism performance, as well as the

relationships between different performance traits. Spiders have unique morphology and musculoskeletal systems such that advances in the study of performance in other invertebrate taxa do not transfer readily. In particular, spiders have an unusual mechanism for limb movement; whereas flexion of all leg joints is achieved by muscles, extension at several major joints is instead achieved by hydraulic pressure of hemolymph generated by contraction of muscles in the cephalothorax (Parry and Brown 1959a,b; Anderson & Prestwich 1975; Weihmann et al. 2010) and elastic energy stored during flexion (Sensenig & Shultz 2003). Therefore, unlike other many animals, muscles in the body, rather than the limbs, may be important in terms of locomotor performance. Body pressures developed during locomotion can severely impede circulation, and hence place limits on aerobic metabolism (Paul et al. 1994; Paul & Bihlmayer 1995). Spiders rely on anaerobic respiration for sustained activity, and recovery to basal lactate levels can be slow (Anderson & Prestwich 1985).

Morphology has a bearing on many fitness-related activities in spiders, including foraging (Rovner, 1980), searching for mates (Foellmer & Fairbairn, 2005), courtship (Framenau & Hebets, 2007), and conspecific contests (Wells 1988; Faber & Baylis 1993; Taylor et al. 2001; Taylor & Jackson 2003; Elias et al. 2008). Although whole-organism performance is central to these activities, there has been little investigation into the links between morphology and performance in spiders and whether these relationships underly the observed relationships between morphology and fitness. Recent studies of spider performance have examined the relationships between size, locomotor speed and habitat, principally to explain patterns of sexual size dimorphism (Moya-Laraño, Halaj & Wise 2002; Foellmer & Fairbairn 2005; Brandt & Andrade 2007; Moya-Laraño et al. 2008, 2009; Prenter, Perez-Staples & Taylor 2010a,b; Prenter, Fanson & Taylor 2012). Other studies have similarly dealt with sprint speed in the context of prey capture,

fleeing from predators or effects of injury on performance (Amaya, Klawinski & Formanowicz 2001; Nelson & Formanowicz 2005; Pruitt & Husak 2010; Pruitt & Troupe 2010).

These narrowly framed studies of sprint speed present a very limited perspective of whole-organism performance in spiders; important dimensions of whole-organism performance, in particular endurance and strength, have been almost entirely neglected. Endurance capacity may be a particularly important target for selection, as spiders have very few mitochondria in leg muscles and have extremely limited physiological capacity for sustained activity (Prestwich 1983, 1988b; Shillington & Peterson 2002). Such limits are expected to constrain activity when foraging or when searching for mates (e.g. Kramer & McLaughlin 2001), and especially during courtship and contests, which tend to be energetically expensive (Watson & Leighton 1994; Kotiaho et al. 1998; DeCarvalho, Watson & Field 2004). Strength is surely relevant in spider contests, which typically entail ritualized pushing, grabbing and wrestling activities (for a review, see Elwood & Prenter 2013). Strength is also likely to be important when grasping and subduing prey and defending against enemies, including aggressive and potentially cannibalistic females.

Jumping spiders (Salticidae) may be particularly intriguing and tractable models for the study of whole-organism performance. They are generally diurnal, wandering predators that actively pursue prey or wait to lunge at prey that passes within range (reviewed by Jackson & Pollard 1996). Despite their common name, walking is the primary mode of locomotion in most jumping spiders, with jumping largely reserved for bridging gaps, attacking prey, rapid escape from predators and other danger, and ritualized leaps during intraspecific interactions. Males roam widely in search of mates,

and females routinely leave their nests to hunt. Vigorous and highly ritualised intraspecific interactions, comprising complex displays and routines, are common in jumping spiders (Taylor, Hasson & Clark 2000; Lim & Li 2004; Hoefler 2007; Sivalinghem et al. 2010). Escalated contests typically entail bouts of pushing, grasping and biting of a rival's limbs and body, sometimes to deadly effect (Wells 1988; Taylor, Hasson & Clark 2001; Elias et al. 2008). Unreceptive females commonly attack courting males, which must then defend themselves or flee (Jackson & Hallas 1986; Taylor & Jackson 1999).

Several recent studies of sprint speed and climbing speed have included a jumping spider, *Jacksonoides queenslandica* (Prenter et al. 2010a,b, 2012). However, as with other spiders, to date there has been no investigation of links between morphology and either endurance or strength, or potential trade-offs involving these abilities. The present paper takes a substantially expanded view of whole-organism performance in spiders, examining four performance traits - vertical climbing, horizontal running, locomotor endurance and pulling force (the force required to pull a spider off a surface) - in males of a common Australian jumping spider, *Servaea incana* Karsch (Fig. 1). We address: (1) relationships between morphological measures and performance, (2) relationships among performance traits, and (3) repeatability of performances over short (1 day) and medium (up to 6 days) timescales. Measuring repeatability establishes the potential for selection on performance traits (Boake 1989; Lynch & Walsh 1998), validates experimental methods (Losos, Creer & Schulte 2002), and facilitates future investigation of underlying proximate mechanisms (Bennett, Garland & Else 1989; Rhodes, Garland & Gammie 2003). Very few studies have examined the repeatability of performance over periods longer than one day (Oufiero & Garland 2009), with only a single example for spiders (Pruitt 2010). Examining relationships among performance

traits will establish whether they might be linked to the same underlying physiology or morphology, or if higher performance in one trait compromises performance in another.

Materials and methods

Maintenance

Adult male *Servaea incana* were collected from the trunks of eucalypt trees in parks in Sydney, NSW, Australia, between April 2009 and March 2010. Spiders were maintained in a laboratory under controlled temperature ($25 \pm 1^\circ\text{C}$) and humidity ($70 \pm 5\%$) on a 12:12h light:dark cycle. Spiders were housed individually in 1.125 L ventilated plastic cages with a folded piece of paper for environmental enrichment (Carducci & Jakob 2000). Water was provided *ad libitum* via a 5 mL vial attached to the base of the cage, stoppered with a cotton dental wick that carried moisture into the cage. Prior to the experiment, spiders were fed three Queensland fruit flies (*Bactrocera tryoni*) per week.

General methods

Performance trials were conducted under fluorescent ceiling lighting supplemented with two 60W full spectrum incandescent bulbs (Crompton Lighting, Sydney, Australia) positioned 0.5 m above the test apparatus. To standardise feeding state, spiders were offered two flies, two days prior to trials. Food was removed on the day before trials, leaving 24 hours to clear the gut. The same 44 spiders took part in four types of performance trial: running, climbing, endurance and pulling force. Each day that trials took place was preceded by two rest days, one for feeding and one for fasting. The sequence of trials started with the first day of climbing trials, followed by the first day of

running trials and then the second days of the climbing and running trials. These were followed by the endurance trials, one a day on three separate days and finally one day of pulling force trials. The entire study spanned 24 days from the first day of feeding to the final trial. This order of trials was chosen so that the spiders took part in the putatively less demanding trials first. Running and climbing trials are short bursts of activity that are unlikely to affect later performances, whereas endurance trials are much more demanding. Pulling force trials required attachment of an apparatus to subjects, which could result in permanent damage.

Running

We measured maximum horizontal running speed of male *S. incana* by making them run along a raceway (Brandt & Andrade 2007; Prenter et al. 2010b, 2012). Raceways were 700 mm long, 50 mm wide, with walls 50 mm high. They were constructed from white foam board and had a 240 grit sandpaper base for traction. Spiders were placed in a 50 x 50 mm staging area at one end of the raceway and were then chased with a soft sable hair paintbrush over a distance of 600 mm to an identical staging area at the other end. Spiders were encouraged to run continuously by gently brushing the hind legs if they attempted to pause. The time taken to run 600 mm was recorded with a digital stopwatch and was used to calculate speed (mms^{-1}). These trials were performed three times in one day with 3 hours between trials, and were repeated with the same spiders six days later. Although *S. incana* is able to jump, its normal mode of locomotion is by walking and spiders were not observed to jump in any of the trials.

Climbing

Maximum climbing speed was estimated using established techniques (Brandt & Andrade 2007; Prenter et al. 2010b). Spiders were transferred to a 10 mm staging area at the base of a vertical wooden dowel (diameter 25 mm) that had been coated with textured Spray Stone Paint (White Knight Paints, Australia). Using a soft sable hair paintbrush, spiders were chased 250 mm to the top of the dowel. The time taken to climb this distance was recorded with a digital stopwatch and was used to calculate speed (mms^{-1}). Spiders were encouraged to run continuously by gently brushing the hind legs if they attempted to pause. *S. incana* live on tree trunks, so they readily climbed to the top of the dowel. On the rare occasion that they did not climb straight to the top of the dowel, spiders were returned to their cages for several minutes before re-running the trial. These trials were performed three times in one day with 3 hours between trials and were repeated six days later with the same spiders. To validate the use of manual timing we confirmed strong correlation between manual timing with timing taken from video recordings of additional climbing trials ($r = 0.998$, $N = 22$, $P < 0.0001$).

Endurance

To examine endurance we adapted general methods used previously in both vertebrates and invertebrates (see Lailvaux, Alexander & Whiting 2003; Lailvaux et al. 2005).

Spiders were forced to run continuously around a circular raceway (185 mm diameter, circumference 580 mm), by chasing them with a soft-haired paintbrush, until they were exhausted. In these trials the spiders almost always followed the outer wall of the raceway and movement away from this wall was rare. A spider was deemed to have reached exhaustion when it failed to move despite being repeatedly touched on the hind

legs with the brush, or it was unable to right itself, having collapsed onto its dorsum. We recorded both time elapsed and distance moved until exhaustion. Trials were performed three times over 7 days, with two days recovery between trials.

Pulling force

We assessed pulling force of male *S. incana* by adapting methods used previously in insects (Lailvaux et al. 2005). A small piece of cork, approximately 1 x 1 x 2 mm, with a copper wire twisted into the shape of a hook inserted at the top, was fixed to the dorsal carapace of each spider using melted beeswax (Fig. 1). A 1.2 m length of nylon fishing line was tied at one end to the hook and at the other end to a 15 mL plastic specimen jar. Spiders were placed on a horizontal wooden dowel of 2 mm diameter, with the fishing line running over a smooth aluminium rod positioned 600 mm above the dowel, so that the specimen jar was hanging adjacent to the spider. Water was gradually added to the specimen jar from a 3 mL syringe, until the downward force exerted by the weight of the water caused the spider to be pulled up and off the dowel. We recorded the combined weight of the specimen jar and water required to pull the spider free of the dowel and later converted this value to millinewtons. Trials were repeated three times on each individual spider in one day, with three hours rest between trials. Because spider motility and hunting would be impeded by the cork and hook, and because repeated removal and reapplication of the cork and hook could cause damage, these trials were not repeated over longer time scales.



Figure 1. A male jumping spider, *Servaea incana*, ready to perform in a pulling force trial. Photograph by Rowan H. McGinley.

Morphological Measures

Each spider was photographed no less than two days prior to any trials taking place with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany), focussed through an Olympus SZX12 dissecting microscope (Olympus Corporation, Tokyo, Japan). To facilitate image capture, spiders were restrained on the lid of a Petri dish using clear plastic film (Glad Products, Padstow, Australia). We measured cephalothorax width and length as well as tibia length of the first leg ('leg length') from digital images using ImageJ 1.36b (National Institute of Health, Bethesda, MD, USA). While it is relatively easy

to obtain measures of tibia length in live *S. incana*, it is more difficult to obtain accurate measures of total leg length. However, we found a strong correlation between tibia length and total leg length of $N = 44$ deceased *S. incana* males ($r = 0.968$, $P < 0.0001$), validating our general interpretation of tibia length as a measure of overall leg length. Spiders were also weighed to the nearest 1 mg, at the end of each trial day with an electronic balance (Shimadzu Corporation, Kyoto, Japan; Model N595, Type AX200) and we used the average measure across the trials for analysis. Descriptive statistics for morphology of the spiders used in this study are presented in table 1.

Statistical Analyses

Cephalothorax width and length were entered into a principal components analysis to generate a PC1 score that provides an overall measure of size (following Prenter et al. 2010a,b, 2012). We then calculated relative tibia length by taking residuals from the regression of tibia length on body size. These residuals comprise the portion of leg length that is not explained by variation in body size, allowing us to examine how length of legs for a given body size is related to performance. We were also interested in the effect of mass after controlling for both body size and leg length; such relative mass is often interpreted as ‘condition’ but also incorporates unmeasured size dimensions (Prenter et al. 2012). We took residuals from the regression of body mass on body size and then used those residuals in a regression on residual tibia length, calculated previously, to generate residuals that give a measure of relative mass after removing variation of both body size and leg length (Prenter et al. 2012). To examine the morphological predictors of performance, we performed multiple linear regressions, using type III tests, entering body size, relative leg length and relative mass as predictors of performance (Type I tests, with body size, leg length and mass as predictors, in that

order, yielded closely comparable results). When investigating predictors of performance we used the maximum performances to minimise error from low motivation and sub-maximal performances (Losos et al. 2002). Bivariate relationships among performance traits were examined using Pearson's product moment correlations. Data for time and distance until exhaustion in endurance trials required log transformation to meet the requirements for parametric analysis. To quantify short-term (within a day) repeatability of performances we calculated the intraclass correlation coefficients (I_{cc}) (Brandt & Andrade 2007; Prenter et al. 2010b). As mean performances may change between days, which would reduce the I_{cc} , we used Pearson's product moment correlations to measure repeatability of performances across days (Oufiero & Garland 2009). Regression analyses were performed in JMP 5.0.1.2 (SAS Institute, Cary N.C., USA) and intraclass correlation coefficients were calculated in SPSS v.16 (SPSS Institute, Chicago, IL, USA). When describing raw distributions we present mean \pm s.d., but when estimating means we present mean \pm s.e.m.

Table 1. Summary of morphological data for the male *S. incana* used in the performance trials ($N = 44$).

Measurement	Minimum	Maximum	Mean \pm s.d.
Cephalothorax length (mm)	2.57	4.34	3.56 \pm 0.39
Cephalothorax width (mm)	1.94	3.50	2.83 \pm 0.31
Tibia length (mm)	1.07	2.33	1.71 \pm 0.25
Average weight (mg)	19.88	101.63	53.64 \pm 17.10

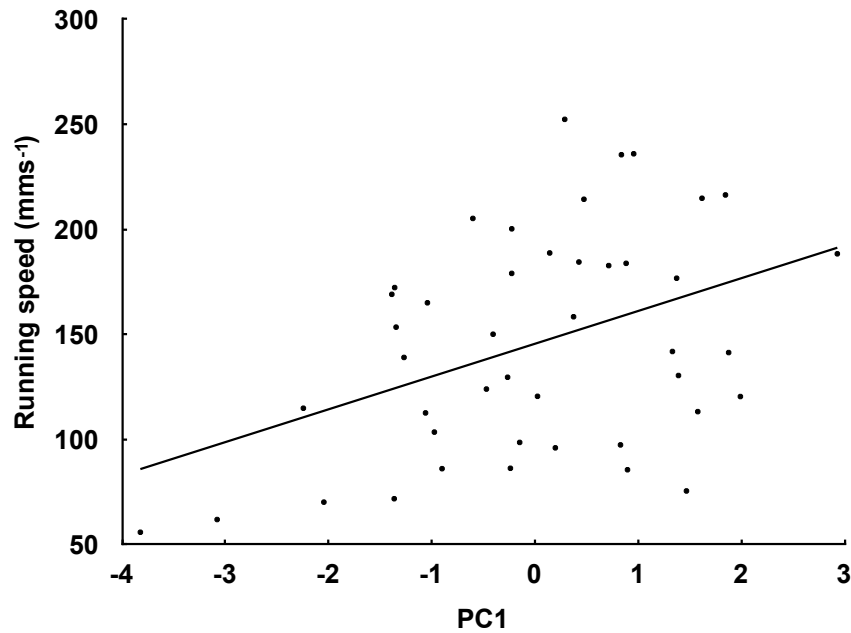


Figure 2. Partial regression plot showing size-dependent performance in male *S. incana*. Body size (PC1) was positively related to running speed.

Results

Running speed

Mean maximum running speed on the horizontal runway was 145.6 ± 7.9 mms⁻¹.

Running performances were consistent throughout the trials (Table 2), being highly repeatable within both days of trials (Day 1: $I_{cc} = 0.641$, $P < 0.0001$; Day 2: $I_{cc} = 0.616$, $P < 0.0001$) as well as between days ($r = 0.636$, $N = 44$, $P < 0.0001$). Individual maximum speed on the first day of trials was not significantly different from the second day of trials (paired t-test: $t_{43} = 0.865$, $P = 0.392$), indicating that sufficient time had been available for recovery. Running speed increased with body size (Fig. 2) and showed no evidence of a relationship with relative leg length or relative mass (Table 3).

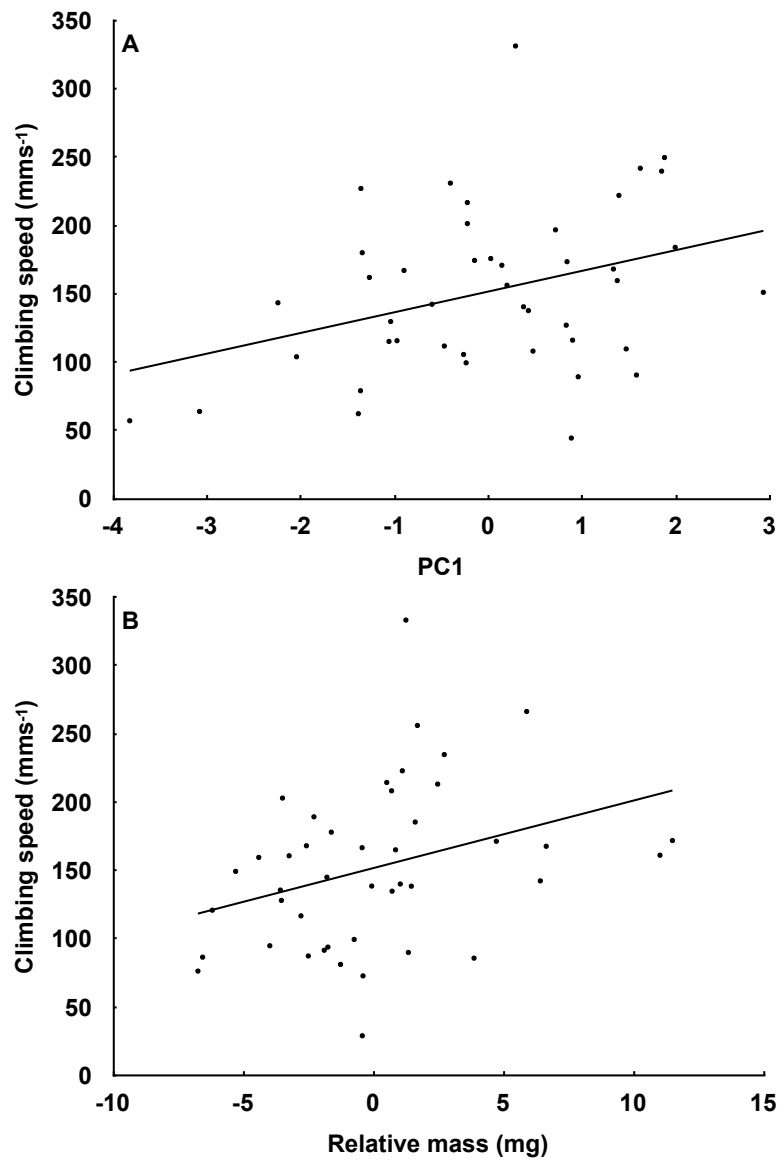


Figure 3. Partial regression plots showing the morphological predictors of vertical climbing speed. Climbing speed increased with both (A) body size (PC1) and (B) relative mass, after controlling for size and relative leg length, in male *S. incana*.

Table 2. Performances of male *S. incana* ($N = 44$) over the different days of trials (means \pm s.e.m.). Performances were generally consistent across the running, climbing and pulling force trials. However, performances in endurance tests decreased significantly after the first trial.

	Day 1			Day 2			Day 3		
	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3
Running speed (mms^{-1})	102.5 \pm 7.6	108.3 \pm 6.1	98.3 \pm 7.0	117.9 \pm 8.1	101.8 \pm 6.5	104.1 \pm 6.6			
Climbing speed (mms^{-1})	109.8 \pm 8.0	115.8 \pm 9.6	114.1 \pm 6.8	118.5 \pm 8.4	108.2 \pm 7.6	114.2 \pm 8.8			
Time to exhaustion (s)	202.56 \pm 33.14			102.96 \pm 16.97			114.29 \pm 16.46		
Distance to exhaustion (m)	8.55 \pm 1.02			4.75 \pm 0.41			5.72 \pm 0.47		
Pulling force (mN)	25.91 \pm 1.22	27.94 \pm 1.12	27.85 \pm 1.22						

Climbing speed

Spiders climbed up poles at a mean maximum speed of $151.7 \pm 9.6 \text{ mms}^{-1}$. Climbing speed was highly repeatable within both days of trials (Day 1: $I_{cc} = 0.701$, $P < 0.0001$; Day 2: $I_{cc} = 0.784$, $P < 0.0001$) as well as between days ($r = 0.803$, $N = 44$, $P < 0.0001$). Individual maximum speed on the first day of trials was not significantly different from that on the second day of trials (paired t-test: $t_{43} = 0.239$, $P = 0.813$), again indicating that sufficient time had been available for recovery. Maximum climbing speed increased with both body size and relative mass, but showed no evidence of relationship with relative leg length (Table 3, Fig. 3).

Endurance

Mean maximum time taken to exhaust spiders in circular runways was $239.35 \pm 33.92 \text{ s}$ and the mean maximum distance travelled before exhaustion was $9.76 \pm 1.01 \text{ m}$. The time taken to exhaust spiders was repeatable between the first and second trial ($r = 0.539$, $N = 44$, $P = 0.0002$) but not between the second and third trial ($r = 0.1824$, $N = 44$, $P = 0.236$), or between the first and third trial ($r = 0.1069$, $N = 44$, $P = 0.490$). Similar results were obtained for the repeatability of distance travelled before exhaustion (trials 1 and 2: $r = 0.408$, $N = 44$, $P = 0.0059$; trials 2 and 3: $r = 0.084$, $N = 44$, $P = 0.587$; trials 1 and 3: $r = 0.129$, $N = 44$, $P = 0.406$). Twenty-seven spiders (61.36%) ran the furthest distance in the first trial, five (11.36%) in the second trial and twelve (27.27%) in the third trial. Both the time and distance until exhaustion were significantly higher in the first trial than the second and third trials (Fig. 4). These results indicate that spiders did not fully recover their endurance capacity between trials, even when provided two days

to rest. We found no significant predictors of time until exhaustion, however, relative mass was positively related to the distance travelled prior to exhaustion (Table 3, Fig. 5).

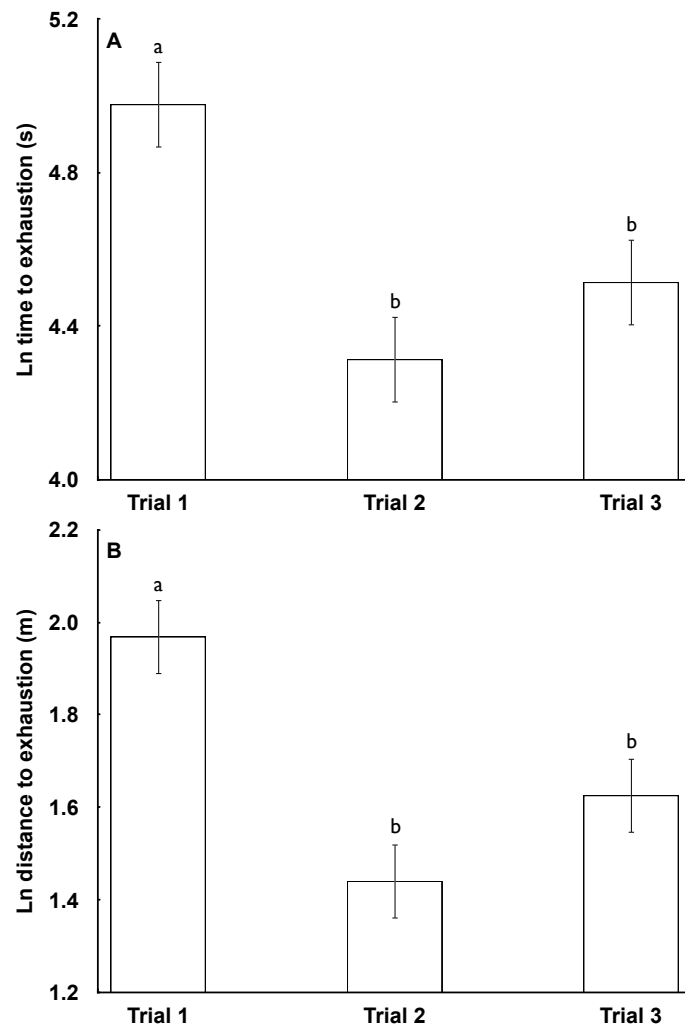


Figure 4. Male *S. incana* spiders exposed to exhaustion showed long-lasting reductions in endurance capacity. Performance, measured as (A) time and (B) distance travelled prior to exhaustion, decreased after the first endurance trials (trials that did not differ are marked by the same letter; Tukey's HSD).

Table 3. Relationships between performance capacity and morphology in male *S. incana*. All estimates are from multiple linear regressions, using type III sums of squares. Significant regressions are presented in bold.

Performance trait	Variable	Estimate	Error	$F_{1,40}$	P
Running speed	PC1	15.60	5.323	8.60	0.0055
	Tibia	66.22	69.21	0.92	0.3444
	Mass	0.91	1.83	0.25	0.6202
Climbing speed	PC1	15.15	6.32	5.75	0.0212
	Tibia	67.07	82.17	0.67	0.4192
	Mass	4.94	2.17	5.18	0.0282
Ln time to exhaustion	PC1	-26.66	24.39	1.21	0.2784
	Tibia	20.57	56.79	0.05	0.8275
	Mass	16.71	8.08	2.27	0.1398
Ln distance to exhaustion	PC1	0.02	0.05	0.09	0.7683
	Tibia	-0.18	960.73	0.07	0.7879
	Mass	0.05	0.02	9.26	0.0041
Pulling force	PC1	3.54	0.50	49.48	<0.0001
	Tibia	17.38	6.55	7.03	0.0114
	Mass	0.18	0.17	1.08	0.3060

Pulling force

Spiders were able to resist an average maximum upward force of 31.10 ± 1.05 mN before being pulled off the wooden dowel. Maximum pulling force was highly repeatable within the single day of testing ($I_{cc} = 0.641$, $P < 0.0001$). Both body size and relative leg length predicted pulling force (Table 3), larger spiders and those with long legs for their size being able to resist stronger forces (Fig. 6).

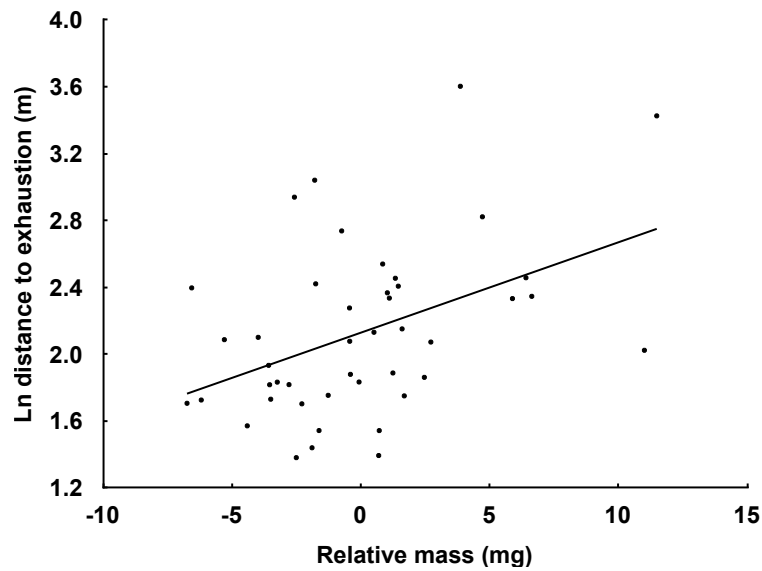


Figure 5. Partial regression plot for the effect of relative mass on the distance run prior to exhaustion. Individuals that were heavy for their size ran further before becoming exhausted, suggesting that endurance capacity varies with body condition in male *S. incana*.

Table 4. Pearson's product moment correlations (r) between pairs of different measures of performance in male *S. incana*. Values in bold indicate statistically significant correlations ($\alpha = 0.05$, 2-tailed tests, $N = 44$).

	Climbing speed	Ln time to exhaustion	Ln distance to exhaustion	Pulling force
Running speed	0.4726	-0.4209	-0.2500	0.3928
Climbing speed		-0.2989	-0.0464	0.3237
Ln time to exhaustion			0.8836	-0.0975
Ln distance to exhaustion				0.0476

Relationships among performance measures

The relationships among performance traits are summarised in Table 4. Maximum sprint speeds on horizontal runways were positively correlated with vertical climbing speed (Fig. 7), and both had similar positive relationships with pulling force (Fig. 8). Horizontal and vertical sprint speed were both negatively correlated with the time to exhaustion (Fig. 9), suggesting a trade-off between speed and endurance capacity. The

two measures of endurance (distance travelled and time elapsed, before exhaustion) were strongly correlated (Table 4).

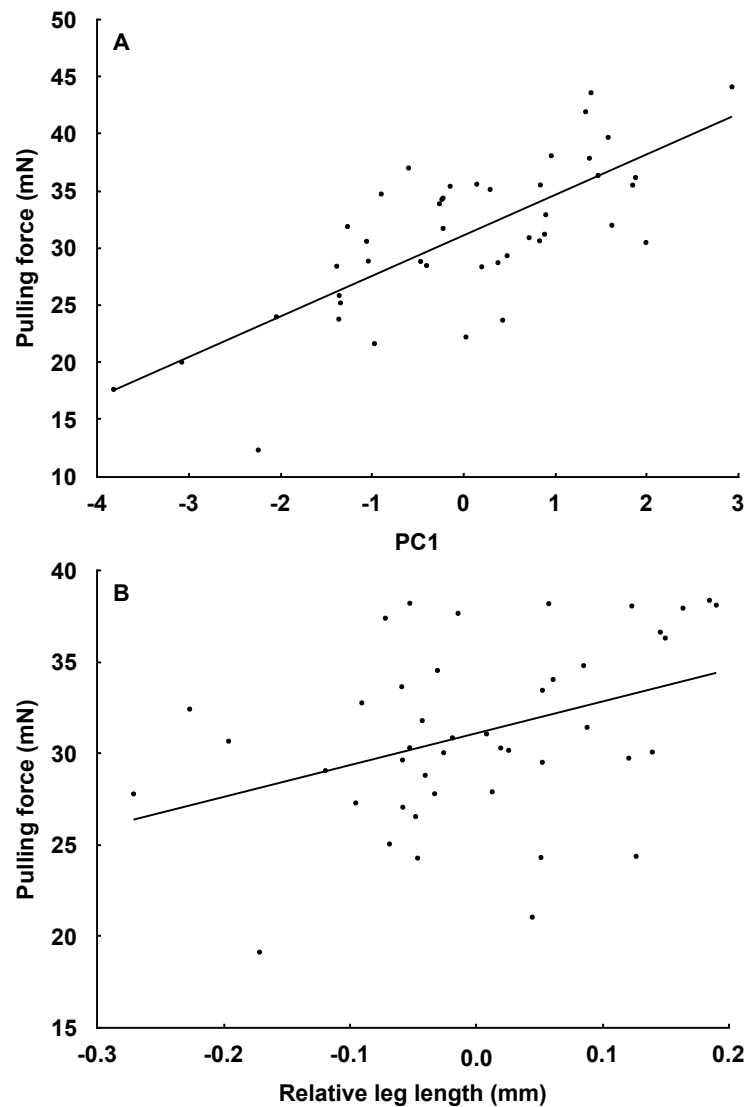


Figure 6. Partial regression plots of the relationship between morphology and pulling force in male *S. incana*. Pulling force increased with both (A) body size (PC1) and (B) relative leg length.

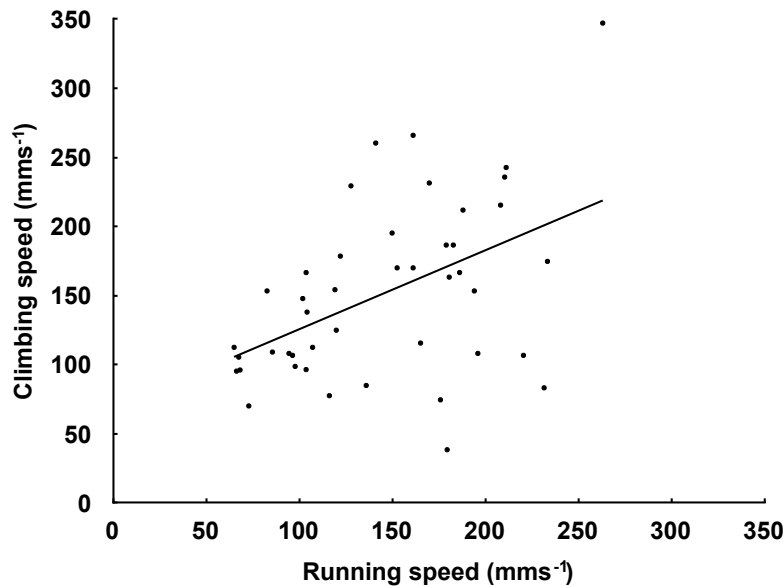


Figure 7. Bivariate relationship between running and climbing speed in male *S. incana*.

Discussion

High repeatability in running and climbing speed in the present study confirms individually characteristic locomotor traits through which selection may act to influence fitness and morphology in *S. incana* jumping spiders, and matches recent findings for other spiders (Brandt & Andrade 2007; Prenter et al. 2010b, 2012; Pruitt 2010; Pruitt and Husak 2010). Whereas individual spiders were very consistent in horizontal and vertical sprints (short and medium term) and tests of pulling force (short term), they showed low repeatability for endurance performance owing to a sharp decrease in performance after the first trial (Fig. 4). Spiders are characterized by rapid fatigue and slow recovery from activity (Prestwich 1988a), but failure to recover even after two days of rest is extraordinary. Previous studies of endurance by exhaustion in arthropods have only performed a single trial for each individual, offering no estimate of repeatability or recovery (Ramos et al. 2004; Lailvaux et al. 2005). Investigations of repeatability in endurance by exhaustion in spiders may require substantial intervals

between repetitions (Dohm 2002), if complete recovery occurs at all. Accurate short term estimates of endurance repeatability may be possible through techniques that stop short of exhaustion, such as direct measurement of metabolic rates (e.g. heart rate, Coelho & Amaya 2000; or respirometry, Prestwich, 1983), in combination with treadmills (Schmitz 2005) or fixed distance runs (Mowles et al. 2010).

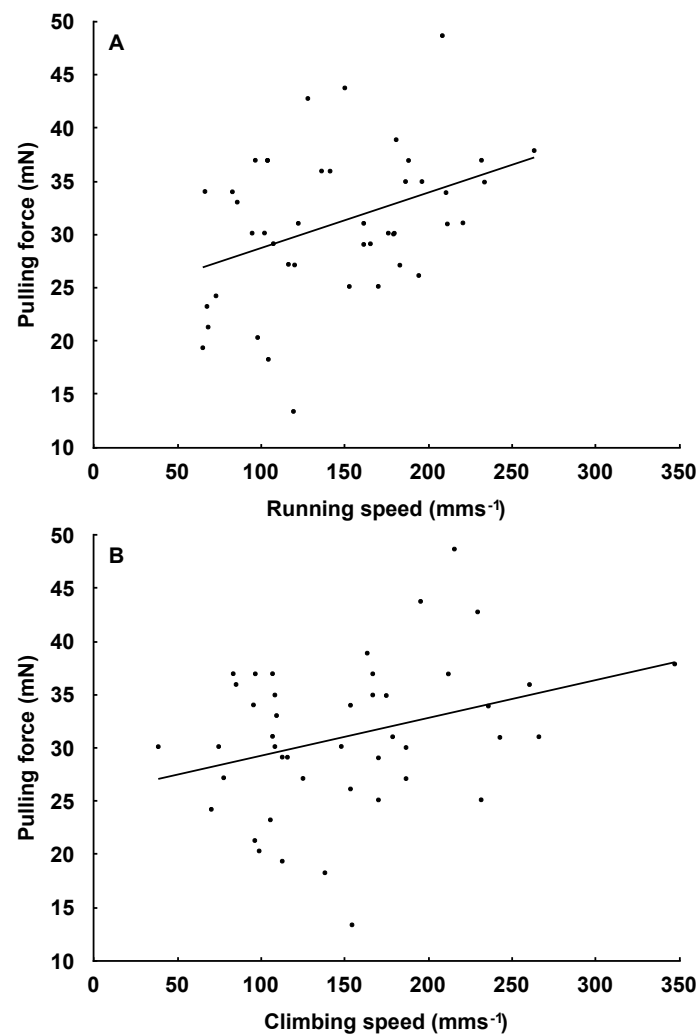


Figure 8. Bivariate relationships between pulling force and (A) climbing and (B) running performance. Both measures of speed were positively correlated with pulling force.

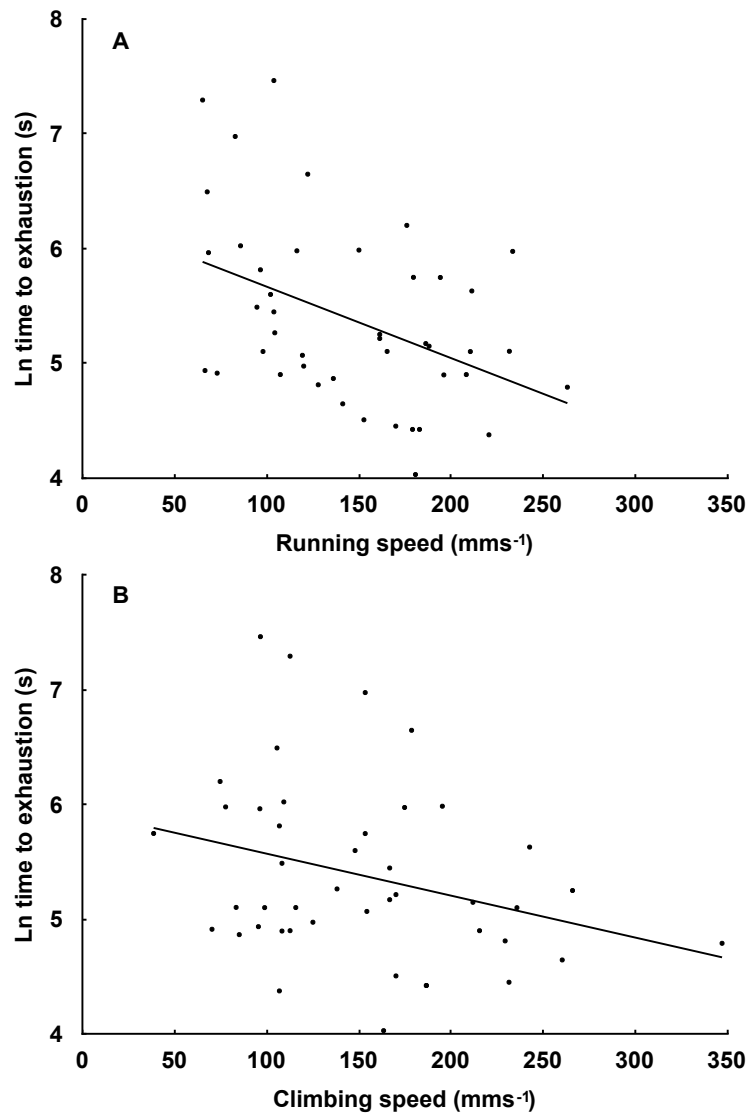


Figure 9. Bivariate relationships between the time until exhaustion and (A) climbing and (B) running performance. Both measures of speed were negatively correlated with this measure of endurance capacity.

Trade-offs between performance traits

Individual *S. incana* with high sprinting performance tended to have low endurance capacity (and vice versa) (Fig. 9); this appears to be the first study to suggest a trade-off between sprint speed and endurance in an invertebrate. Climbing and running speeds were both negatively correlated with the time elapsed to exhaustion. We found no

evidence that this apparent sprint speed-endurance trade-off results from gross morphological constraints. Whereas horizontal sprint speed increased with body size and was not related to relative mass, endurance capacity was quite the opposite; positively related to relative mass and unrelated to body size.

Trade-offs between sprint speed and endurance capacity are well known in vertebrates, and have been attributed to anatomical constraints or muscle fibre composition (lizards, Bonine, Gleeson & Garland 2001; Vanhooydonck, Van Damme & Aerts 2001, fish, Langerhans 2009; Reidy, Kerr & Nelson 2000, humans, Bottinelli & Reggiani 2000; Van Damme et al. 2002). Less is known about invertebrate muscle fibre types. Slow and fast twitch muscle fibres similar to those found in vertebrates have been identified in the walking legs of crabs (Perry et al. 2009), scorpions (Wolf & Harzsch 2002), the wandering spider *Cupiennius salei* (Maier, Root & Seyfarth 1987), and the tarantula *Eurypelma californicum* (Paul, Zahler & Werner 1991). Leg muscles of the wandering spider *C. salei* have few mitochondria to sustain aerobic respiration (Linzen & Gallowitz 1975), and the dominant fibres present are analogous to vertebrate fast-twitch fibres (Maier et al. 1987) that use anaerobic metabolism to generate short, powerful bursts of action, but fatigue rapidly. Variation in aerobic and anaerobic capacity may, therefore, underlie the trade-off between individual ability for speed and endurance in *S. incana*. Low levels of aerobic metabolism in spiders are thought to represent an adaptation for surviving extended periods of starvation (Anderson 1974), however, this may come at the cost of reduced endurance capacity and help explain the intermittent mode of locomotion typically adopted by spiders (reviewed in Kramer & McLaughlin 2001). Intermittent locomotion is thought to improve endurance through facilitating partial recovery during pauses.

An alternative explanation is that the observed relationships between speed and endurance are a result of the order in which the trials were carried out. All of the short running and climbing trials were carried out prior to the endurance trials, so that perhaps the spiders that ran fastest in the short trials could have already been tired for the exhaustion trials. However, each spider took part in 12 of these trials, within a 10 day period, and there was no evidence that these sprint trials had an influence on sprint performance in future trials (Table 2). Thus, we expect that these trials will have a minimal effect upon endurance capacity, if at all.

Links between morphology and whole-organism performance

The present study suggests performance advantages for large size, relatively long legs and high relative mass in male *S. incana* jumping spiders. Larger spiders were faster on both the horizontal and vertical surfaces and also appear to be capable of greater pulling force than smaller spiders. The positive relation between body size and horizontal sprint speed in *S. incana* males (Fig. 2) is consistent with those identified in several other ground living and low dwelling spiders, including other jumping spiders (Brandt & Andrade 2007; Prenter et al. 2010b). Sprint speed has also been related to body size in the jumping spider, *Jacksonoides queenslandica*. However, unlike *S. incana*, *J. queenslandica* males showed; positive relation between relative leg length and climbing speed; no relation between relative mass and maximum speed; and no relation between horizontal and vertical sprint speed (Prenter et al. 2010a,b). Species differences in relations between performance and morphology may reflect adaptations to specific habitats, as in *Anolis* lizards (Calsbeek & Irschick 2007). *Servaea incana* typically live on tree trunks, whereas *J. queenslandica* principally inhabit rocks and flatter surfaces and these differences in habitat may have evolutionary implications for

performance. Whereas *S. incana* is a quite stout and short-legged spider, *J. queenslandica* is comparatively gracile, and these overall species differences in shape may have implications for how each dimension of size and shape influence performance.

We can expect that there are fitness benefits for being large since large size is associated with increased performance. Assays of sprint speed as performed here are thought to assess the ability to flee from predators (Prenter et al. 2010b) or chase down prey. Most jumping spiders are cursorial hunters (Forster 1977) and strength is particularly relevant for restraint of prey (Clarke 1986). Owing to their greater speed and strength, we may expect large spiders to be more adept at prey capture. Whole-organism performance is correlated with success in intrasexual contests in some animal groups (e.g. Huyghe et al. 2005; Lailvaux & Irschick 2007; Mowles et al. 2010). In the dung beetle, *Euoniticellus intermedius*, horn length is a strong predictor of both pulling force and fighting ability (Lailvaux et al. 2005). Jumping spiders also commonly engage in apparent ‘trials of strength’ during escalated contests, pushing against one another (Taylor & Jackson 1999; Taylor et al. 2001), therefore the ability to grasp onto a surface and resist being pushed or pulled off may influence contest outcomes. Both size and relative leg length predict pulling force in *S. incana* males, and are also predictors of fighting ability in jumping spiders (Wells 1988; Faber & Baylis 1993; Taylor et al. 2001; Taylor & Jackson 2003; Elias et al. 2008; Tedore & Johnsen 2012); therefore the advantage of large body size and long legs evident in jumping spider contests likely arises from the links between these morphological measures and strength (Fig. 6).

Given that small spiders are slower and weaker, and by implication may not be as successful at prey capture, predator escape and conspecific agonistic interactions, what compensating factors might promote the wide range of sizes recorded in *S. incana*

(Table 1) and the maintenance of small size? Perhaps large and small spiders are more adept at capturing different types of prey. Large size is sometimes associated with increased viability costs due to longer development time. Female jumping spiders commonly have reduced receptivity after their first mating and are suggested to exhibit first male sperm priority patterns (Jackson 1980). For species with distinct seasonality, maturing at a particular time of year, males may have a mating advantage if they mature early in the season when virgin females are more abundant than aggressive mated females. However, to mature quickly may also mean developing quickly and maturing with a small size (Maklakov, Bilde & Lubin, 2004). Small spiders might also be favoured by reduced conspicuousness to enemies (e.g. Vollrath & Parker 1992; Blanckenhorn 2000).

Low mass has been hypothesised to be advantageous in spiders when moving against gravity (Moya-Laraño et al. 2009; Corcobado et al. 2010). Contradicting the ‘gravity hypothesis’, larger male *S. incana* and those heavier for their size climbed faster (see also Prenter et al. 2010b). As we averaged individual mass across trials and feeding experience was standardized, our measure of relative mass is unlikely to represent variation in gut contents or recent feeding history. Differences in relative mass may largely represent variation in overall condition (Jakob, Marshall & Uetz 1996), reflecting longer-term energy stores and/or muscle mass. Thus, it appears that spiders in better condition were able to pull themselves against gravity more effectively, despite their greater relative mass.

The present study brings the evolutionary trade-offs of jumping spider performance capacity into focus, illustrating the complexity of forces at play in defining performance capacity of individuals. Performance and morphology are intertwined such

that selection for one will commonly lead to evolution of the other. For example, selection for small size may lead to reduced strength and slower sprint speed in a population. Different dimensions of performance are similarly intertwined; selection for fast sprint speeds may also be selection for poor endurance. Little is known about the mechanisms that underlie relationships between morphology and whole-organism performance in spiders. Investigation of these underlying mechanisms, and the selection forces that drive them, is required to understand the evolutionary constraints on morphology and performance.

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Chapter Eight: General Discussion

Animal contests are usually resolved when the loser makes the decision to withdraw. This decision may be influenced by diverse sources of information available during a contest. To limit the costs of contests, animals may gather information about their opponents and withdraw when they determine that the opponent is stronger (Enquist & Leimar 1983; Hammerstein & Parker 1982; Parker & Rubenstein 1981). Alternatively, they may persist in a contest until they reach a cost threshold (Payne 1998; Payne & Pagel 1996). The degree to which animals assess their opponents can vary depending on the sensory and cognitive capabilities of the animal as well as the costs of sharing or gathering information, and may even vary within a contest (Mesterton-Gibbons & Heap 2014; Prenter et al. 2006). Therefore, knowledge of an animal's abilities, the nature of their contests and the potential costs involved in contests are required to understand the contest behaviour of animals.

The focus of this thesis was to determine how males of the jumping spider *Servaea incana* resolve intrasexual contests. To understand the context within which contests take place and the display repertoire involved, I first examined the biology, phenology and display behaviour of *S. incana* to determine what factors and selection pressures might influence behaviour in contests. In a correlative study of contests between *S. incana* males I then found that large spiders win contests and that *S. incana* males appear to rely upon size associated cost thresholds in order to determine when to withdraw. A manipulative experiment, using video playback to simulate opponents, revealed that *S. incana* are capable of opponent assessment but may have limited opportunity to express this ability. Examination of the effects of hunger on contest behaviour suggests that the risk of cannibalism may be a high cost of contests in *S.*

incana and may explain the reliance upon self-assessment. Finally, the relationships between morphology and performance capacity may explain why large spiders tend to win contests.

Natural history of Servaea incana

The behaviour of *S. incana* is generally similar to that of many other jumping spiders (Jackson 1988; Jackson & Macnab 1989; Jackson & Willey 1995). While the display repertoire is not as complex as in some other species (Clark & Uetz 1993; Cross & Jackson 2008; Girard et al. 2011), *S. incana* males possess distinct signals for use in courtship and in agonistic interactions. Unlike some other jumping spiders (Elias et al. 2012; Jackson 1977; Maddison & Stratton 1988; Taylor & Jackson 1999), substrate and silk borne tactile signalling do not appear to play a major role in communication in this species. The exposed tree trunks inhabited by *S. incana* may preclude the necessity for the elaborate displays or multi-modal signalling found in some other jumping spiders that inhabit darker or more complex habitats (Elias et al. 2004; Jackson 1979; Taylor & Jackson 1999). As *S. incana* do not produce substrate borne signals, visual displays are likely to be the primary means of communication in *S. incana* contests.

In many spiders, including jumping spiders, males may secure mating opportunities by maturing earlier than females and guarding subadult females until they mature (Elgar & Bathgate 1996; Jackson 1986). Although protandry was evident in the population studied in Chapter 3, there was no evidence that early maturation results in small body size due to shorter development time (Maklakov et al. 2004; Kasumovic & Andrade 2009; Zonneveld 1996). The advantage of large body size in male-male contests may select for large males at this time of the season when there may be

increased competition for access to virgin females (Hoeftler 2007; Kasumovic et al. 2011).

Competition among *S. incana* males may be magnified due to a brood parasite, the mantispid *Spaminta minjerribae*. Mantispid larvae must transfer to female spiders in order to feed upon spider eggs and complete their life cycle (Redborg 1998); however, larvae were found on both male and female *S. incana*. In other spider species, mantispids are known to transfer from the male to the female during copulation (Scheffer 1992). This may simultaneously promote polygyny in males and monandry in females; a male carrying a mantispid must mate at least twice to secure reproductive fitness, while females increase the risk of acquiring a mantispid with each new copulation. This may lead to increased competition among males for a small number of receptive females.

Large *S. incana* males win contests (Chapter 4) and have greater performance capacity (Chapter 7; McGinley et al. 2013). Despite the large variation in adult male size, no advantages for small males have been directly identified in *S. incana*. There was large overlap of the different life stages throughout the year and females produce multiple batches of temporally spaced eggs, so smaller males could be those that hatched later and matured earlier in their development to coincide with the maturation of females (Kasumovic & Andrade 2006, 2009). Small male *S. incana* may also be subject to lower mortality (Chapter 3) and small male size may be associated with the costs of mate searching (Vollrath & Parker 1992); large spiders may be more vulnerable to predation (Gunnarsson 1998) and in spiders, the sex that wanders in search of mates tends to be smaller (Aisenberg et al. 2007). However, direct evidence supporting the advantage of small males in mate search is lacking (Berger-Tal & Lubin 2011; Foellmer & Fairbairn 2005; Kasumovic et al. 2007). Regardless of whether they are better adapted for mate

search, it is a strategy that small *S. incana* males may be forced to adopt due to their disadvantage in direct competition with larger males.

Contest behaviour in Servaea incana

Contest strategies in *S. incana* males appear more complex than the strategies described in theoretical models. While the most important decision in contests is whether to persist or withdraw, *S. incana* may make other decisions that influence the dynamics of contests. Similar to other spiders (Constant et al. 2011; Elias et al. 2008; Faber & Baylis 1993; Wells 1988) and many other animals (Briffa 2008; Jenssen et al. 2005; Prenter et al. 2008; Reece et al. 2007) body size is a strong predictor of contest outcome in *S. incana* (Chapters 4,6). Large spiders are more likely to win contests and the probability of larger spiders winning increases with increasing size asymmetry between the smaller and larger spider. The link between size and fighting ability may be related to performance capacity, as large males demonstrate greater pulling force, as well as faster running and climbing speed (Chapter 7). To economically resolve contests, we may expect *S. incana* to assess the size of their opponent and withdraw when they determine that their opponent is larger than themselves. We may also expect that the substantial variation in size of *S. incana* males (Chapter 2) combined with their signalling repertoire and the exceptional vision that jumping spiders possess (Land 1969a,b; Zurek & Nelson 2012) may facilitate assessment of opponent size. However, correlations between spider size and levels of contest escalation provide little support for the role of mutual assessment in *S. incana* contests. Instead, it appears that the decision to withdraw prior to an escalated contest is related to a spider's own size. The size of the opponent does not appear to influence this decision directly, but may influence its timing, as spiders withdrew more quickly against larger opponents.

However, such a correlation is not necessarily evidence for opponent assessment as the same relationship could be achieved due to pairs of smaller spiders both being hesitant to escalate.

Despite the lack of evidence for opponent assessment in contests with live spiders, video playback experiments demonstrated that *S. incana* are capable of visually assessing the size of their opponents, at least under certain conditions, and that information about the size of an opponent may influence decisions in contests. Other sources of information are known to influence the behaviour of jumping spiders in contests; cues from prey (Cross & Jackson 2011, 2014) and from females (Cross et al. 2006, 2007; Wells 1988) may result in higher levels of contest escalation and past experiences of winning or losing may affect future contest behaviour (Kasumovic et al. 2009, 2010). Why then do *S. incana* seem to ignore information about the fighting ability of their opponent? As might be expected if animals are using mutual assessment, smaller spiders were less likely to display towards or approach videos of larger conspecifics than videos of smaller conspecifics. However, all spiders were unlikely to display towards or approach very small video opponents, and larger spiders were more likely to display towards the largest videos than the smaller videos. Theoretical models of mutual assessment do not predict this type of behaviour, strong opponents are expected to benefit by advertising their advantage, leading to an early withdrawal by weaker opponents and avoiding escalation (Enquist & Leimar 1983; Mesterton-Gibbons & Heap 2014). That larger spiders are less likely to display towards smaller opponents when asymmetries are large, may reduce the opportunity for mutual assessment in contests between live spiders.

Theoretical models are useful for describing general patterns of contest behaviour that may be applicable to a wide range of animals and for predicting how animals might modify their behaviour with changing circumstances. However, the underlying biology of a species is also an important factor to consider when seeking to understand the behaviour of animals in contests. Escalation in contests is expected to be costly, and honest displays of RHP are expected to benefit large individuals (Mesterton-Gibbons & Heap 2014). However, as size asymmetries between opponents increase, the costs of escalation likely reduce for the larger opponent. The substantial variation in body size observed in *S. incana* males may result in large asymmetries in some contests. At a certain size threshold it may not be worth sharing information with a small opponent in order to deter an attack. Displays could be costly in terms of energy (DeCarvalho et al. 2004; Kotiaho et al. 1998a) or the risk of attracting a predator (Kotiaho et al. 1998b; Taylor et al. 2005) therefore, the costs of displaying for a large spider may outweigh the risks of an escalated contest with a small opponent. If large *S. incana* males do not display towards smaller opponents then there may be an added benefit of increasing the opportunity to attack the opponent, eliminating a competitor and providing a meal.

Just as theoretical models may fail to capture the complexity of behaviour in the real world, studies in the laboratory under controlled conditions may fail to capture the complex and diverse sources of variation in nature. The risks of being attacked by a conspecific, in *S. incana* and in other spiders, are likely influenced by hunger (Wise 2006). Even after a relatively short period of food deprivation, larger *S. incana* show increased attention toward their smaller opponents. Hungry spiders were more likely to stalk conspecific males and were less likely to turn away after orienting towards them. Levels of hunger are likely much higher in nature than in most laboratory studies

(Taylor et al. 2000; Wise 2006), therefore, costs associated with intraspecific interactions may be much higher than is usually observed in the laboratory.

Variation in assessment strategy in jumping spider contests may best be explained by the costs and benefits of mutual and self-assessment. Cannibalism may shift the balance of the costs and benefits involved in contests; increasing the costs of contests for small spiders while increasing the benefit for large spiders. The potential for cannibalism may explain why small males are averse to physical fighting and why large *S. incana* may not fight according to the rules predicted by theory for non-cannibalistic animals. Although not addressed in this thesis, the costs and benefits of opponent assessment could also change depending on the value of a resource (Mesterton-Gibbons & Heap 2014). In another jumping spider, *Phidippus clarus*, males guarding females appear to use self-assessment during contests with intruders, while the behaviour of intruding males appears to depend on the size of their opponent (Kasumovic et al. 2011). If a resource is at stake, making a wrong decision and withdrawing early could be more costly, therefore, intruders may invest more in mutual assessment in this context and only escalate when they determine that they have the advantage. The risk of cannibalism is also likely lower in this context.

Sharing information to aid assessment may not be the only function of displays in contests. Although large spiders were more likely to display towards the largest videos, they were less likely to approach them than small videos and in Chapter 6, smaller opponents of size-asymmetric pairs were more likely to display first. This suggests that these displays are used when spiders perceive a threat. In another jumping spider *Evarcha culicivora*, cannibalism of females by males is common and *E. culicivora* females take a more active role in signalling during intersexual interactions than females of

other jumping spiders (Cross & Jackson 2008). Displays used by *S. incana* in contests may function to deter attacks, either as threat displays or as pursuit deterrent signals (Caro 1994; Hasson 1991). However, these signals may not be effective against substantially larger opponents or predators (Hasson 1995) and small *S. incana* males were more likely to retreat without displaying when presented with video opponents that were substantially larger than themselves. In live contests this behaviour may give small spiders a head start as they try to escape larger spiders that would otherwise be capable of chasing them down due to their faster speed (Chapter 7). For small spiders, there may be a trade-off between displaying in order to deter an attack and sharing information about their small size. As *S. incana* share their habitat with other jumping spiders, both larger and smaller, it may be interesting to examine whether interactions with other species are mediated in a similar way to interactions with conspecifics.

Conclusions

When animals have limited information about their opponent, they are expected to base decisions of persistence on their own fighting ability. However, as information becomes available during the course of a contest there is increasing opportunity to base decisions on opponent assessment (Prenter, Elwood & Taylor 2006). Errors in assessment of opponents are expected to lead to shifts from mutual assessment to self-assessment and the costs and benefits of mutual and self-assessment may not be the same for large and small spiders (Mesterton-Gibbons & Heap 2014). Video playback experiments show that when information is readily available (for example, when opponents stand and display continuously), *S. incana* may use this information to guide their decisions in contests. However, in contests between live *S. incana* there may be limited opportunity to assess the fighting ability of the opponent due to the opponent's

behaviour and the amount of time it may take for the primary eyes of a jumping spider to gather information about an object (Land 1969a).

Mutual assessment is more likely to result in ideal decision making in animal contests. However, weak individuals are expected to benefit from self-assessment as they do not share information about their weak state with a stronger opponent, increasing the probability that the stronger opponent makes a wrong decision and withdraws from a contest that it could have won (Mesterton-Gibbons & Heap 2014). For small *S. incana* any benefits of mutual assessment (i.e. reducing the risk of withdrawing from other small spiders) are likely outweighed by the increased risk of being injured or killed by larger spiders. Mutual assessment may allow for accurate determination of an opponent's fighting ability, but may also increase the opportunity for an opponent to attack, the results of which are more costly for smaller spiders. Rather than advertise their small size, an early withdrawal may increase survival.

Strong opponents are expected to benefit from mutual assessment as it increases the chance of a weak opponent making the correct decision and withdrawing while also increasing the chance that the stronger opponent makes the correct decision by not withdrawing early (Mesterton-Gibbons & Heap 2014). However, for large *S. incana*, the costs of a small opponent making a wrong decision and escalating may be small, and may even be beneficial due to the opportunity for cannibalism. Therefore, the lack of mutual assessment in *S. incana* may be explained by the benefits for both large and small spiders.

The findings of this thesis highlight the limitations of correlative techniques for studying behaviour in animal contests. While they are useful and an important first step

in describing patterns of behaviour, it is difficult to draw firm conclusions about the causation of the observed patterns (Briffa & Elwood 2009; Elwood & Arnott 2013; Fawcett & Mowles 2013). Identified patterns should be used to decide which manipulations might be the most informative in follow up experiments (Reichert & Gerhardt 2011, 2013; Reichert 2014). However, the power and limitations of manipulative experiments lie in the fact that they are not natural contests (Arnott & Elwood 2010; Reichert 2014). Consideration of theoretical predictions and the biology of the species being studied, and the combination of both correlative studies and manipulative experiments will likely produce the clearest understanding of the decisions and behaviour of animals in contests.

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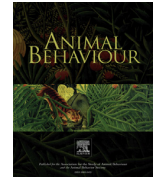
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Appendices

Appendix I

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Assessment strategies and decision making in male–male contests of *Servaea incana* jumping spiders



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Animals often engage in contests that have the potential to result in substantial costs in time, energy and risk of injury. To reduce the costs of contests, animals are expected to assess the resource-holding potential of their rivals and compare it to their own as a means of economically determining a winner ('mutual assessment'). If information about the rival is difficult or costly to obtain, rivals may instead reduce the costs of fighting by withdrawing when an individual cost threshold is reached ('self-assessment'). Here we investigated the assessment strategies used by *Servaea incana* jumping spiders to resolve male–male contests. To examine the effects of body size on contest outcome and strategy, contests were staged between size-unmatched and size-matched pairs. Contests escalated through distinct stages that were of increasing intensity, and body size was a strong predictor of contest outcome. To gain insight into assessment strategy, we considered duration and escalation as measures of cost accrual. Overall, the relations of body size to contest duration and escalation suggest that the decision of whether to retreat during the early noncontact contest phase is largely determined by size-associated internal cost thresholds. Body size was not related to either duration or escalation in the contact phase of contests. We highlight the need to consider appropriateness of proxies used for contest costs and whether game-theoretical predictions for whole contests apply to stages within a contest.

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Contests for resources expose rivals to costs that might include time and energy as well as risk of injury or death (Andersson, 1994). To efficiently resolve conflicts, rivals may assess traits that are associated with each other's fighting ability, or resource-holding potential (RHP), so that the weaker rival can retreat when sufficiently certain of its inferior status ('mutual assessment'; Maynard Smith & Parker, 1976; Parker 1974). However, the ability to obtain information about a rival during a contest may be constrained by physical and cognitive abilities such that assessment may be costly or even beyond the capacity of some animals (Elwood & Arnott, 2012, 2013; Fawcett & Mowles, 2013). Under such circumstances, animals may reduce contest costs by retreating when they reach an individual cost threshold ('self-assessment'; Prenter, Elwood, & Taylor, 2006; Taylor, Hasson, & Clark, 2001).

Game-theoretical models predict that different fighting strategies produce different relations between contest costs and RHP. In models assuming mutual assessment, e.g. the sequential

assessment model, decisions are based upon assessment of RHP asymmetries between rivals (Enquist & Leimar, 1983). Costs are expected to decrease as RHP asymmetry increases, because larger asymmetries are easier to detect. However, a negative relation between costs and RHP asymmetry may also be expected for self-assessment (Taylor & Elwood, 2003), because in self-assessment models, e.g. energetic war of attrition, animals with low RHP have lower thresholds and tend to withdraw early in the interaction (Payne & Pagel, 1996). Overall contest costs increase with RHP of the weaker rival and so a negative correlation between cost and RHP asymmetry occurs because the largest asymmetries can only occur in contests between the weakest and strongest members of a population.

Alternative assessment strategies are better distinguished by examining the RHP of rivals separately (Taylor & Elwood, 2003), assuming that the assortment of opponents in contests is random (Fawcett & Mowles, 2013). Under mutual assessment, contest costs are expected to have a positive relation with the weaker rival's RHP and an equal but negative relation with the RHP of the stronger rival. If animals are using self-assessment there should be a positive relation between contest costs and the weaker rival's RHP but little relation with the stronger rival's RHP.

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The predictions for self-assessment apply to situations in which the accumulation of costs is determined only by an individual's own actions. However, if the rival also inflicts costs, as under the cumulative assessment model (CAM; Payne, 1998), then the decision to withdraw is influenced by the RHP of both rivals. Therefore, the same relations predicted for mutual assessment can occur without information about the RHP asymmetry being gathered. Under the CAM, the decision to withdraw is based upon a cost threshold; therefore, an individual will fight up until this threshold, regardless of the RHP of the opponent. Under mutual assessment an individual's decision to withdraw is based upon information about RHP asymmetry, such that an individual will pay higher costs in contests against similarly matched opponents. Mutual assessment predicts no relation between costs and RHP when rivals are matched for RHP; therefore, such a relation would exclude mutual assessment as a putative strategy (Arnott & Elwood, 2009).

While estimating RHP can be straightforward through association with outcome, estimating the costs of contests is often more difficult (Briffa et al., 2013). Time is commonly used as a measure of cost (Arnott & Elwood, 2009) and may be appropriate in contests in which contest costs accrue linearly with time, for example when contests consist of extended energetically expensive displays (wars of attrition) or only involve one type of behaviour (Kemp & Wiklund, 2001; Zenner, O'Callaghan, & Griffin, 2014). However, contests often escalate through distinct stages, typically starting with stereotyped displays at a distance, and later escalating to physical fighting, where the rates of energetic cost and risks of injury are higher. The level of escalation reached may, therefore, be a better indication of costs than duration. Indeed, some studies using duration and escalation as measures of contest cost have reported different results for these measures. For example, assessment of contest duration suggested neither mutual assessment nor self-assessment in the golden orb web spider, *Nephila clavipes* (Constant, Valbuena, & Rittschof, 2011) and suggested mutual assessment in the sierra dome spider, *Neriene litigiosa* (Keil & Watson, 2010). However, both studies found support for self-assessment when escalation was used as a measure of contest costs rather than duration. Many studies have inferred assessment strategies by considering relations between RHP proxies and overall contest costs, but such approaches may be misleading if animals use different strategies at different stages of a contest (Hsu, Lee, Chen, Yang, & Cheng, 2008). Furthermore, self- and mutual assessment may represent extremes in a continuum rather than two discrete alternatives (Prenter et al., 2006). When animals have no information about their rivals they can only use self-assessment, but as information about the rival becomes available there is increasing opportunity for mutual assessment (Mesterton-Gibbons & Heap, 2014).

In this study we investigated whether and when males of a jumping spider, *Servaea incana*, use information about themselves and their rivals during contests. Studies of spiders have made significant contributions to the study of contest behaviour (reviewed

in Elwood & Prenter, 2013) and number among the first empirical studies to suggest that animals may persist in contests in accordance with their own abilities (Bridge, Elwood, & Dick, 2000; Taylor et al. 2001; Whitehouse, 1997) rather than relying solely on mutual assessment. Although jumping spiders are known for their acute vision and elaborate visual displays during intraspecific interactions, they appear to rely substantially on self-assessment during contests (Taylor et al. 2001), with a comparatively minor role for mutual assessment (Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Kasumovic, Mason, Andrade, & Elias, 2011). Like spiders from most other families, jumping spider contests progress through distinct levels of escalation (Table 1; Elwood & Prenter, 2013) and so escalation may prove more useful than duration as a measure of contest cost. After initially orienting towards each other, rivals initiate stereotyped displays. They may then approach each other and engage in potentially injurious physical combat (Jackson, 1988; Jackson & Hallas, 1986; Wells, 1988). By examining the relations between size, a measure of RHP, and contest costs we aimed to determine the extent to which decisions of contest persistence (duration and escalation level) of male *S. incana* depend on self- or mutual assessment.

METHODS

Study Animals and Maintenance

Servaea incana is a medium-sized jumping spider that is native to temperate regions of eastern and southern Australia (Richardson & Gunter, 2012). Adult males were collected from the trunks of eucalypt trees in Sydney, NSW, Australia. Spiders were housed individually in 1.125-litre ventilated cages on a 12:12 h light:dark cycle, and were maintained in a laboratory with controlled temperature (24–26 °C) and relative humidity (65–75%). Spiders were fed two Queensland fruit flies, *Bactrocera tryoni*, or two house flies, *Musca domestica*, on alternating weeks. Water was provided in a 6 ml vial attached to the base of the cage, stoppered with a cotton dental wick. Half a crumpled sheet of white A4 paper was provided as environmental enrichment (Carducci & Jakob, 2000). Spiders were housed under these conditions for at least 1 week prior to use in experiments.

Contest Protocol

To examine the effects of size difference versus individual size on decisions of persistence, 85 dyadic contests were staged between *S. incana* males that were paired at random from the laboratory population ('size-unmatched' pairings). To further distinguish between effects of size difference and individual size, we staged an additional 73 contests in which the effects of size difference were experimentally reduced by size matching of spiders ('size-matched' pairings). All pairs were novel and each male was used no more than once in each experiment. Contests were staged

Table 1
The levels of escalation in contests between male *S. incana*

Phase	Level	Activity	Description
Precontact	I	Mutual orientation	Spiders turn to face rival
	II	Hunch	Spider raises body above substrate and raises first pair of legs into an arched position
	III	Approach	Spider moves towards rival, usually maintaining the hunched posture
Contact	IV	Spar	When within two body lengths, spiders lunge towards each other, flicking the first pair of legs vertically, and making contact with the legs and body and pushing against the rival
	V	Embrace	Spiders lock chelicerae and push and pull against each other
	VI	Struggle	Spiders roll around on the substrate grasping and biting at each other

The first three levels make up the precontact phase; the last three make up the contact phase. Contests may end at any level of escalation.

in an open-roofed Perspex arena (300 × 150 mm and 80 mm high), identical in dimensions to that used by Taylor et al. (2001). The bottom 15 mm of the arena walls were transparent, facilitating filming from the side (Panasonic HDC-HS700, Panasonic Corp., Japan). The opaque white upper walls of the arena were lightly coated with petroleum jelly in order to restrict spiders to the floor of the arena. Contests were conducted under fluorescent lighting supplemented with full-spectrum incandescent lamps (Crompton Lighting, Sydney, Australia). A sheet of white paper covered the base of the arena and was replaced between trials. The arena was also washed with water and wiped clean between trials to remove silk draglines and chemical cues (Jackson, 1987). To stage a contest, a white opaque divider was positioned at the arena midpoint and a spider was introduced to each end of the arena. After 2 min of acclimation the divider was removed and spiders were allowed to interact until one retreated from its rival. Individual spiders were distinguished on the basis of size and natural markings. Contests escalated through six clearly identifiable sequential levels of increasing risk and intensity (Table 1). For each contest, we recorded whole contest duration, duration of the precontact phase (levels I–III) and contact phase (levels IV–VI) (Table 1), maximum level of escalation and the winner. We also noted which spider was first to orient to face, display to and approach the other. Contests were deemed to have begun when both spiders oriented and ended when one, the loser, retreated.

Morphological Measurements

Following contests between size-unmatched pairs, spiders were weighed to the nearest 1 mg with an electronic balance (Shimadzu Corporation, Japan; Model N595, Type AX200). Spiders were also photographed with a ProgResC10 digital camera (Jenoptik LOS GmbH, Germany) focused through an Olympus SZX12 stereomicroscope (Olympus Corporation, Japan). Cephalothorax width and length were measured to the nearest 0.1 mm from digital images using ImageJ 1.36b (National Institute of Health, Bethesda, MD, U.S.A.). For size-matched pairs, all spiders had been measured at least 3 days prior to the contests and were fed two *B. tryoni* 3 days prior to the contests. Any uneaten flies were removed the following day. On the morning of the contest all spiders were weighed and contests were staged between spiders that differed in cephalothorax width, cephalothorax length and weight by less than 5% ((measure of individual A – measure of individual B)/(mean of A and B) × 100).

Statistical Analyses

To examine the determinants of outcome in contests between unmatched spiders, we used multiple logistic regression with outcome as the response variable and size of the larger and smaller rival and whether the larger or smaller spider oriented first, displayed first or approached first as predictor variables. Nonsignificant predictor variables were removed from the model. Multiple regression was used to examine assessment mechanisms, following the practice of Taylor and Elwood (2003), with duration or level of escalation as dependent variables and measures of rival size as predictors. Therefore, the whole model included the size of the larger rival and the size of the smaller rival as predictor variables. We used cephalothorax width as our measure of size as it can be more accurately determined than cephalothorax length and is a fixed measure for adult spiders, unlike weight, which fluctuates with physiological state. To ascertain assessment strategies used during the precontact phase we only included those contests that ended prior to making contact. To investigate speed of escalation to the contact phase, we examined the precontact phase of contests

that continued beyond the precontact phase. Contest duration data required log transformation to meet the assumptions of parametric tests. We also examined contest behaviour in terms of the level of escalation using multiple logistic regression (ordinal when assessing overall contests, nominal when assessing tendency to escalate from one stage to the next), with escalation as the dependent variable and rival sizes as predictors. For contests between spiders that were matched for size we used simple regressions with mean size of the rivals as the predictor variable. All tests were two tailed. Analyses were carried out using JMP 5.0.1.2 for Macintosh (SAS Institute Inc., Cary, NC, U.S.A.).

Ethical Note

Spiders were separated as soon as one withdrew from the interaction. Five individuals were injured during contests: four lost a leg and one was bitten on the abdomen, but all survived these injuries. Leg autotomy is a natural and widespread phenomenon among spiders and probably functions to facilitate escape from predators. Although injury may affect future performance in contests, it has little effect upon survival (Taylor & Jackson, 2003). After experiments, spiders were released at the sites where they were collected.

RESULTS

Outcome of Contests Between Size-unmatched Pairs

Spiders interacted in every trial. Although on rare occasions one spider displayed at or approached the other prior to both spiders orienting, spiders were never attacked without first orienting towards their rival. Contests were brief, ranging from 1 to 35 s. Of 85 contests, 34 escalated to physical contact (i.e. sparring or struggling; Fig. 1). These contact phases were brief compared to the precontact phase (Table 2). Smaller and larger rivals were similarly likely to orient first (47 smaller, 38 larger; binomial test: $P = 0.386$), present 'hunch' displays first (47 smaller, 38 larger; $P = 0.386$) and approach first (37 smaller, 35 larger; $P = 0.906$). Size predicted the outcome of contests (Table 3), the larger spider winning 68 of 85 contests (80.0%). The likelihood of the larger spider winning increased with size of the larger rival (ln odds ratio = 6.409, 95% CI = 1.843 – 12.182, $\chi^2_1 = 8.256$, $P = 0.004$) and decreased with the size of the smaller rival (ln odds ratio = –4.799, 95%

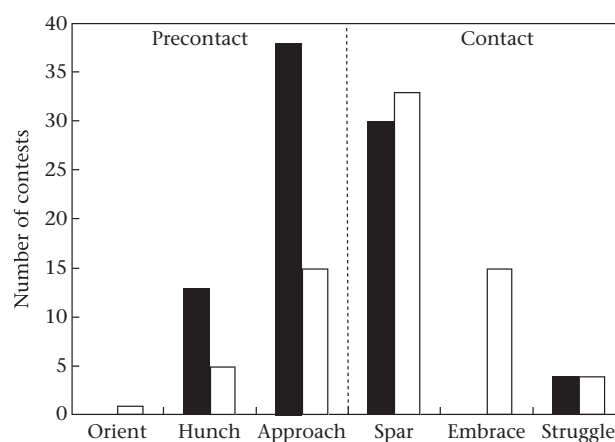


Figure 1. Distribution of the maximum escalation in contests between male *S. incana* in size-unmatched (black bars) and size-matched (white bars) pairings.

Table 2

Summary statistics for the duration (s) of whole contests, the precontact phase of contests that terminated prior to the contact phase and those that escalated to contact, as well as contact phases of contests between size-matched and unmatched *S. incana* males

	Unmatched				Matched			
	N	Median	IQR	Range	N	Median	IQR	Range
Whole contest	85	8	4.5–13	1–35	73	11	7–14	1–61
Precontact phase (terminated)	51	5	3–10	1–35	21	8	4.5–12.5	1–52
Precontact phase (escalated)	34	8.5	5–12	1–24	52	9	6–11	2–59
Contact phase	34	1.5	1–3.75	1–6	52	2	1–3.75	1–38

IQR = interquartile range.

CI = $-9.345 - -1.128$, $\chi^2_1 = 6.917$, $P = 0.009$; final model: $R^2 = 0.110$, $\chi^2_1 = 9.369$, $P = 0.009$, but was not affected by which spider oriented, hunched or approached first (for all, $P > 0.1$). Using size difference, rather than the size of the larger and smaller rivals, yielded similar results: the probability of the larger rival winning increased with the absolute size difference between rivals (ln odds ratio = 4.434, 95% CI = 1.416 – 8.321, $R^2 = 0.109$, $\chi^2_1 = 9.307$, $P = 0.002$). Size difference was a strong predictor of outcome regardless of whether contests terminated during the precontact phase (ln odds ratio = 3.747, 95% CI = 0.513 – 7.934, $R^2 = 0.096$, $\chi^2_1 = 5.337$, $P = 0.021$) or escalated to the contact phase (ln odds ratio = 8.735, 95% CI = 1.152 – 21.045, $R^2 = 0.203$, $\chi^2_1 = 5.762$, $P = 0.016$).

Contest Escalation in Size-unmatched Pairs

Only the size of the smaller rival predicted the overall maximum level of escalation (whole model: $R^2 = 0.051$, $\chi^2_1 = 10.10$, $P = 0.006$; smaller rival's size: $\beta = 2.613 \pm 0.953$, $\chi^2_1 = 7.882$, $P = 0.005$; larger rival's size: $\beta = -0.261 \pm 0.763$, $\chi^2_1 = 0.112$, $P = 0.738$). Hunch displays occurred in all ($N=85$) interactions. The size of the smaller rival was a marginally nonsignificant predictor of whether contests ended prior to approach (13 of 85 contests; Table 4). Spiders approached in 72 contests and 34 pairs escalated to the contact phase. Only size of the smaller rival predicted whether the contest escalated to the contact phase (Table 4, Fig. 2a). Of the contests that escalated to the contact phase, 30 terminated after sparring, while four escalated further to struggling; however, neither size of the larger nor that of the smaller rival predicted whether this occurred (Table 4).

Contest Duration in Size-unmatched Contests

Neither size of the larger nor that of the smaller rival predicted total contest duration (Table 5). Duration of the 51 contests that ended during the precontact phase decreased with increasing size of the larger rival ($R^2 = 0.105$, $\beta = -0.998$, $F_{1,49} = 5.763$, $P = 0.020$; Table 5, Fig. 3) but was not related to the size of the smaller rival. Neither size of the larger nor that of the smaller rival predicted how

quickly contests escalated to the contact phase (Table 5). For the 34 contests that escalated to the contact phase, neither size of the larger nor that of the smaller rival predicted the duration of the contact phase (Table 5).

Contests Between Size-matched Pairs

The duration of contests between size-matched *S. incana* males ranged from 1 to 61 s ($N = 73$, mean \pm SE = 12.33 ± 1.16 s, median = 11 s). Fifty-two contests (71.2%) escalated to the contact phase (Fig. 1). There were no significant differences in any of the size measurements between winners and losers (Table 3), confirming that spiders were closely matched. Winners and losers were just as likely to be the first to orient (36 winners, 37 losers; binomial test: $P > 0.99$), hunch (39 versus 33; binomial test: $P = 0.556$) or approach (30 versus 37; binomial test: $P = 0.464$).

The mean size of pairs of spiders did not predict maximum escalation ($R^2 = 0.002$, $\beta = 0.419$, $\chi^2_1 = 0.376$, $P = 0.540$). Only one contest (between spiders that were two standard deviations below the mean size) ended after orienting, without exchange of hunch displays. Of the 72 contests in which spiders displayed, 67 proceeded to approach. There was a nonsignificant tendency for smaller pairs of spiders to be more likely to approach ($R^2 = 0.082$, ln odds ratio = 3.982, 95% CI = $-0.475 - 9.964$, $\chi^2_1 = 22.988$, $P = 0.084$). Once spiders had approached, larger pairs were more likely to escalate to the contact phase ($R^2 = 0.064$, ln odds ratio = -2.617 , 95% CI = $-6.103 - -0.213$, $\chi^2_1 = 4.565$, $P = 0.039$; Fig. 2b). Size of the spider pair did not predict the probability of further escalation within the contact phase (spar – embrace: $R^2 = 0.010$, ln odds ratio = 0.888, 95% CI = $-1.262 - 3.113$, $\chi^2_1 = 0.657$, $P = 0.418$; embrace – struggle: $R^2 = 0.114$, ln odds ratio = 3.130, 95% CI = $-0.948 - 8.282$, $\chi^2_1 = 2.230$, $P = 0.135$). Mean size of pairs was not related to total contest duration (simple linear regression: $R^2 = 0.007$, $F_{1,71} = 0.521$, $\beta = 0.176$, $P = 0.473$), duration of the precontact phase in contests that did not escalate ($R^2 = 0.008$, $F_{1,19} = 0.147$, $\beta = 0.202$, $P = 0.705$), that did escalate ($R^2 = 0.003$, $F_{1,50} = 0.153$, $\beta = 0.114$, $P = 0.697$) or the duration of the contact phase ($R^2 = 0.017$, $F_{1,50} = 0.887$, $\beta = 0.338$, $P = 0.351$).

DISCUSSION

Mutual or Self-assessment?

Our results suggest that during precontact stages of contests between male *S. incana* jumping spiders, the decision to persist or retreat is determined principally by each spider's individual size-associated cost threshold, that is by self-assessment, rather than by mutual assessment. When spiders differed in size, the probability of escalation from the precontact phase to the contact phase was predicted by the size of the smaller rival rather than the size difference between the pair; the larger the size of the smaller spider in a dyad, the higher the probability that it would persist until the contest escalated to the contact phase (Fig. 2a). Further, when spiders were size-matched, contests between larger pairs were

Table 3

Comparison of mean \pm SE cephalothorax width, cephalothorax length and body mass of winners and losers in contests between unmatched (randomly paired) males and contests between size-matched males (paired t tests)

	Unmatched				Matched			
	Winner	Loser	t_{84}	P	Winner	Loser	t_{72}	P
Width (mm)	2.75 \pm 0.04	2.46 \pm 0.03	6.99	<0.001	2.86 \pm 0.04	2.85 \pm 0.04	0.85	0.399
Length (mm)	3.41 \pm 0.04	3.06 \pm 0.04	6.86	<0.001	3.51 \pm 0.04	3.50 \pm 0.04	1.06	0.293
Body mass (mg)	48.64 \pm 1.90	35.02 \pm 1.37	6.72	<0.001	52.37 \pm 1.86	52.26 \pm 1.85	0.89	0.377

Table 4

Regression models of size of the smaller and larger rivals as predictors of whether contests transitioned from one level of escalation to the next

	<i>N</i>	Whole model			Smaller rival's size			Larger rival's size				
		<i>R</i> ²	<i>F</i>	<i>P</i>	ln odds ratio	95% CI	<i>P</i>	ln odds ratio	95% CI	<i>P</i>		
Hunch-Approach	85	0.048	3.49	0.175	−2.82	−6.16	0.26	0.073	2.49	−1.12	6.17	0.174
Approach-Spar	72	0.105	10.44	0.005	− 2.56	− 5.36	> −0.01	0.050	−1.78	−5.26	1.52	0.292
Spar-Struggle	34	0.005	0.13	0.936	−0.91	−6.87	3.84	0.718	0.85	−5.41	9.17	0.805

All contests that escalated to embracing continued to struggling. Bold indicates statistically significant effect.

more likely to escalate from approaching to the contact phase (Fig. 2b). These patterns are predicted by self-assessment but are inconsistent with predictions of mutual assessment models (i.e. equal and opposite effects of larger and smaller rival size). Because there was no association between smaller rival size and duration of size-unmatched contests that ended during the precontact phase, and no relation between mean spider size and duration of size-matched contests that ended during the precontact phase, it seems unlikely that these decisions of smaller spiders are based on accumulated physiological costs of persistence (e.g. lactate accumulation from anaerobic respiration). Instead, it seems more likely that the spiders expressed size-dependent aversion to entering the contact phase, perhaps as a result of prior experience or physiology that is correlated with size.

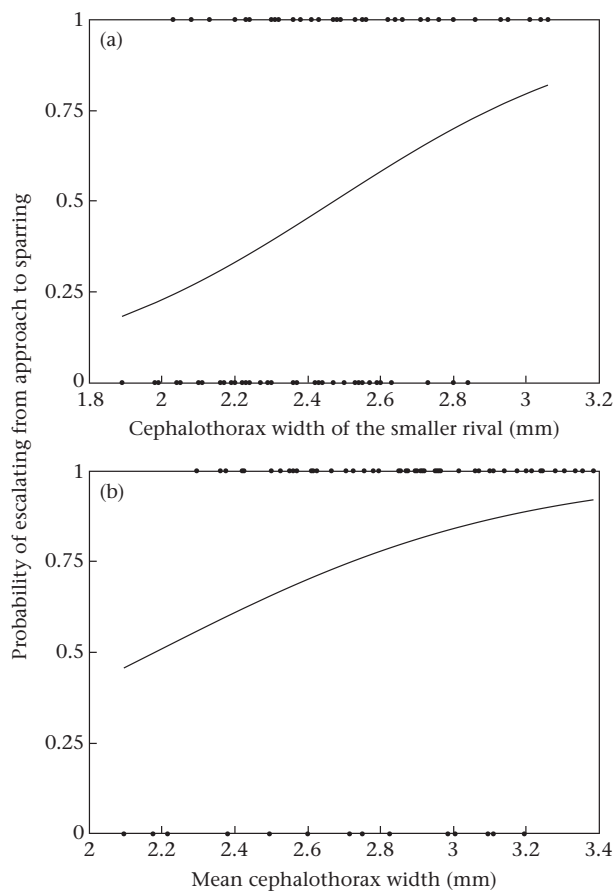


Figure 2. Simple logistic regressions for the probability of escalating from approach to sparring in (a) size-unmatched pairings in relation to the size of the smaller male and (b) size-matched pairings in relation to the mean size of the pair.

For contests between size-unmatched spiders that were resolved during the precontact phase, there was a negative relation between contest duration and size of the larger spider in a pair. That is, although there was a tendency for the smaller spider in a pair to determine whether a contest would terminate at this stage, the timing of this decision was associated with the size of the larger spider. Such a relation is consistent with assessment of only the opponent, without persistence being based upon own-RHP ('opponent-only assessment'); however, this unexpected pattern may arise from size-dependent behaviour that does not influence outcome. For example, if smaller rivals are less willing to escalate then contests may last longer when both rivals are small and reluctant to escalate. Alternatively, if larger rivals escalate contests quicker, then RHP of the larger rival may indirectly influence the timing of the decision to retreat by the smaller rival without a more direct assessment of size taking place. Such patterns have been interpreted as a form of cumulative assessment (Morrell, Backwell, & Metcalfe, 2005; Payne, 1998), but whether this represents a form of assessment is the subject of ongoing debate (Elwood & Arnott, 2012, 2013; Fawcett & Mowles, 2013). Although larger and smaller rivals were equally likely to initiate an approach, there may be other more subtle behavioural cues associated with size of larger rivals that are used by smaller rivals, such as a more rapid or direct approach.

For contests between both size-unmatched and size-matched pairs that were resolved during the contact phase, we found no patterns of persistence or escalation tendency linked to the size of either opponent. A lack of patterns in size-matched contests is consistent with mutual assessment, and may also be consistent with cumulative assessment if the rate of cost accrual depends on the ability of the rivals both to inflict costs and to withstand damage (Payne, 1998). The lack of predicted patterns in size-unmatched contests could also be consistent with cumulative assessment during the contact phase of contests as the decision to withdraw may depend upon the ability of rivals both to inflict and to withstand costs. Difficulties often arise in determining assessment mechanisms at later contest stages owing to changes in sample size and RHP distribution of rivals as contests progress. First, sample sizes are usually smaller for analysis of escalation stages that occur later in contests as pairs that resolve an outcome at earlier stages are depleted from the initial sample. With diminishing sample size it becomes increasingly difficult to detect significant effects. Second, the nonrandom depletion of certain pairings as contests progress can restrict variation in the remaining pairings. For example, if an individual's own size determines persistence at each level of escalation then only the largest of the smaller rivals will persist to the higher levels, reducing both variation in size of individuals and size difference between rivals as contests progress (Taylor et al. 2001). If animals use mutual assessment at earlier stages, pairings with large size differences will tend to be resolved more often at earlier contest stages, resulting in size-assortative contests among the remainder (Fawcett & Mowles, 2013). While the size range of contest participants may be maintained, the range of size differences will be reduced and the correlation between the

Table 5

Regression models of size of the smaller and larger rivals as predictors of the duration (s) of whole contests, the precontact phase (for contests that terminated prior to the contact phase and also those that escalated to contact) and the contact phase

	N	Whole model			Smaller rival's size		Larger rival's size	
		R^2	F	P	$\beta \pm \text{SE}$	P	$\beta \pm \text{SE}$	P
Whole contest	85	0.044	1.91	0.155	0.70 \pm 0.38	0.072	–0.51 \pm 0.32	0.116
Precontact phase (terminated)	51	0.134	3.73	0.031	0.72 \pm 0.57	0.210	–1.25\pm0.46	0.009
Precontact phase (escalated)	34	0.071	1.19	0.317	–0.73 \pm 0.55	0.197	0.64 \pm 0.45	0.163
Contact phase	34	0.096	1.64	0.136	0.71 \pm 0.42	0.102	–0.52 \pm 0.34	0.136

Bold indicates statistically significant effects.

size of the rivals will be stronger, making it difficult to examine the effects of size of each rival separately. Some experimental approaches rely on size-matched pairings, but because animals at the extremes of the distribution are more difficult to match there can be a tendency for underrepresentation of the largest and smallest individuals. In the present study, smaller spiders were more likely to withdraw during the precontact phase of contests, potentially restricting the size range of smaller rivals in both contests that terminated during this phase and those that continued, and possibly inflating the effect of larger rival size on precontact duration. This can result in a relation that appears to be suggestive of opponent only rather than mutual assessment. To study assessment mechanisms at later contest stages, a larger and more broadly representative sample might be obtained by encouraging pairs to escalate to higher levels through increasing the value of contested resources (Elias et al. 2008; Hoefler, Guhanarayan, Persons, & Rypstra, 2009; Magellan & Kaiser, 2010; Mager, Walcott, & Piper, 2008; Wells, 1988).

Measures of Contest Costs

Our results add to a growing appreciation that different measures of contest cost can lead to contradictory support for alternative theories of assessment. In *N. clavipes*, Constant et al. (2011) found no relation between contest duration and body size of rivals but escalation increased with the size of the smaller rival, consistent with self-assessment. Keil and Watson (2010) found support for self-assessment in terms of escalation and intensity (an estimate of the energetic costs of a contest using the time spent performing different actions) in *N. litigiosa*. However, they also

found evidence for mutual assessment; duration of whole contests and the first phase of contests diminished with increasing size asymmetry between rivals when size of the smaller rival and size difference were included in the same model (although contests that terminated during one phase were not analysed separately from those that escalated to the next phase). Studies of animal contests have typically chosen one or two common measures of cost, such as duration and escalation, but generally the strength of association between these metrics and actual underlying costs and constraints affecting contest behaviour is not well known. One metric may be a less accurate means of estimating costs and this might add to variance in the analyses (Jennings, Gammell, Carlin, & Hayden, 2004). Of greater concern, one metric may be a more appropriate means of estimating cost such that results and conclusions obtained from a poor choice may then be unreliable. There appears to be a need for greater attention to the suitability of cost metrics chosen for studies of contest behaviour. Researchers should ensure that they are aware of both the limitations and the advantages of each metric.

Duration is used as a measure of cost for four main reasons: (1) it is a readily accessible and convenient measurement; (2) many theoretical models involve predictions about contest duration (Enquist & Leimar, 1983; Taylor & Elwood, 2003); (3) time spent fighting could be allocated to other activities; and (4) physical and physiological costs accumulate with time (Hack, 1997; Prenter et al. 2006). Costs are unlikely to accumulate linearly with time, however, especially when contests escalate through phases of different intensity. As contests between male *S. incana* were brief and rapidly progressed through different stages, the level of escalation may be a better indicator of costs than contest duration. Escalation appears to be a more consistent indicator of assessment strategy in other spiders (Bridge et al., 2000; Constant et al., 2011; Taylor et al., 2001; Wells, 1988; Whitehouse, 1997). Contests are likely to be physiologically expensive for spiders as they have limited metabolic capacity (McGinley, Prenter, & Taylor, 2013; Prestwich, 1983). Measures of the physiological costs of fighting (e.g. Briffa & Elwood, 2004; DeCarvalho, Watson, & Field, 2004; Prenter et al., 2006) or risks of injury may better indicate the costs of contests as well as the capabilities and decisions of the animals involved.

Interpretation of assessment strategy in the separate phases of complex multistage contests may also depend on whether contests are analysed as a single process or as a series of distinct decisions. In particular, treating the whole contest as a single process in analyses may mask important variation (Morrell et al., 2005). In contests that consist of distinct phases, separate examination of the phases can uncover marked changes in assessment strategies within a contest. For example, in their investigation of display and fighting phases of contests between mate-guarding and intruder males of the hermit crab, *Pagurus middendorffi*, Yasuda, Takeshita, and Wada (2012) reported that smaller intruders were less likely to escalate to physical fighting, consistent with self-assessment. However, the duration of the escalated fighting phase was related to the difference in cheliped size between opponents, rather than the RHP of

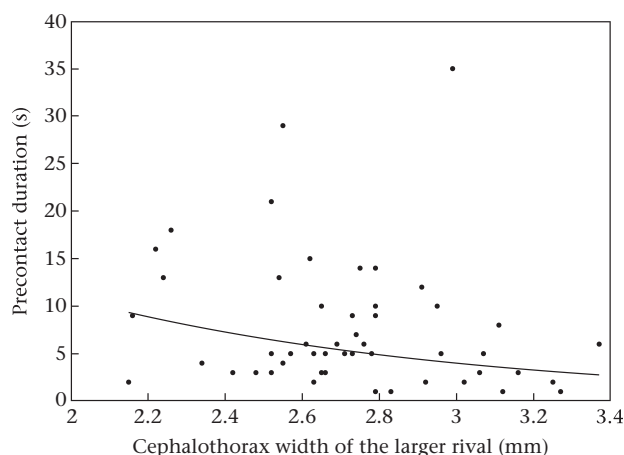


Figure 3. Back-transformed simple regression illustrating the relation between larger rival size and duration of contests between size-unmatched pairs that did not escalate to the contact phase.

either individual, consistent with mutual assessment. Thus, animals may shift from self-assessment to mutual assessment, or vice versa, over the course of a contest. By examining escalation through different stages of a contest, Hsu et al. (2008) found that killifish, *Kryptolebias marmoratus*, use mutual assessment during precontact stages and self-assessment during escalated fighting. If their analysis had been confined to examining total contest duration, observed results would have suggested that they use mutual assessment throughout the contest. Because of diminishing sample sizes as contests progress, analyses of whole contest patterns tend to overemphasize the assessment strategies used in early contest stages.

In summary, our results suggest that contests between male *S. incana* jumping spiders are largely resolved by individual size-associated cost thresholds. These results were only revealed by considering multiple measures of cost at different stages of the contests. Therefore, we highlight the need to consider carefully which are the most appropriate measures of costs and to understand that the theoretical predictions for a whole contest do not necessarily apply to each of its constituent parts.

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Appendix II

Published version of Chapter Seven.

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Whole-organism performance in a jumping spider, *Servaea incana* (Araneae: Salticidae): links with morphology and between performance traits

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Studies of whole-organism performance are central to understanding the links between animal behaviour, morphology, and fitness. Invertebrates have been popular models for studies of behaviour, although there have been few detailed studies of their whole-organism performance, links between performance and morphology, or trade-offs amongst different performance dimensions. In the present study, we investigate four facets of whole-organism performance (running speed, climbing speed, endurance, and pulling force) in males of a jumping spider (*Servaea incana*). We consider links between these performance traits and their association with three morphological measures expected to influence maximum performance capacity: body size, relative leg length, and relative body mass (condition). Running speed, climbing speed, and pulling force were all positively related, suggesting that selection for one may positively effect all. By contrast, endurance capacity decreased with running and climbing speed, suggesting an evolutionary trade-off. Associations amongst performance measures cannot be explained solely as correlates of morphology: large size was associated with greater running speed, climbing speed, and pulling force but not with endurance; relative leg length was associated with pulling force but not other performance traits; relative mass was associated with climbing speed and endurance but not running speed or pulling force. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **110**, 644–657.

ADDITIONAL KEYWORDS: climbing – endurance – locomotion – pulling force – repeatability – running – salticid – speed – trade-off.

INTRODUCTION

Behaviour and morphology evolve in concert because variation in each is constrained by the other. Through detailed studies of links with morphology, substantial gains have been made in understanding the behaviour and physical capabilities of various animals, including squamate reptiles, amphibians, fish, and primates (Koehl, 1996; Irschick *et al.*, 2008). Whole-organism performance capacity (i.e. the ability to conduct an ecologically relevant task, such as running; Irschick *et al.*, 2008) has been linked with foraging behaviour (Huey *et al.*, 1984; Herrel *et al.*, 2008), predator evasion (Watkins, 1996; Downes & Shine, 2001),

sexual competition, and territoriality (Lailvaux *et al.*, 2004; Husak *et al.*, 2006). Contrasting the detailed understanding that has developed in some vertebrate systems, our understanding of links between whole-organism performance and morphology is generally less advanced in invertebrate systems. Although some groups have been studied in varying degrees of detail (ants: Weihmann & Blickhan, 2009; crabs: Weinstein, 1998; Mowles, Cotton & Briffa, 2010; crickets: Dangles *et al.*, 2007; fleas: Krasnov *et al.*, 2003; locusts: Kirkton & Harrison, 2006; scorpions: Prestwich, 2006; Shaffer & Formanowicz, 2000), others have received little attention to date.

We predict that spiders will provide particularly interesting models for the study of links between morphology and whole-organism performance, as well as the relationships between different performance

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traits. Spiders have unique morphology and musculoskeletal systems, such that advances in the study of performance in other invertebrate taxa do not transfer readily. In particular, spiders have an unusual mechanism for limb movement; although flexion of all leg joints is achieved by muscles, extension at several major joints is achieved by hydraulic pressure of haemolymph generated by contraction of muscles in the cephalothorax (Parry & Brown, 1959a, b; Anderson & Prestwich, 1975; Weihmann *et al.*, 2010) and elastic energy stored during flexion (Sensenig & Shultz, 2003). Body pressures developed during locomotion can severely impede circulation, and hence place limits on aerobic metabolism (Paul *et al.*, 1994; Paul & Bihlmayer, 1995). Spiders rely on anaerobic respiration for sustained activity, and recovery to basal lactate levels can be slow (Anderson & Prestwich, 1985).

Morphology has a bearing on many fitness-related activities of spiders, including foraging (Rovner, 1980), searching for mates (Foellmer & Fairbairn, 2005), courtship (Framenau & Hebets, 2007), and intraspecific contests (Wells, 1988; Faber & Baylis, 1993; Taylor, Hasson & Clark, 2001; Taylor & Jackson, 2003; Elias *et al.*, 2008). Although whole-organism performance is central to these activities, there has been little investigation into the links between morphology and performance in spiders, or whether these relationships underly the observed relationships between morphology and fitness. Recent studies of spider performance have examined the relationships between size, running and climbing speed, and habitat, principally to explain patterns of sexual size dimorphism (Moya-Larano, Halaj & Wise, 2002; Foellmer & Fairbairn, 2005; Brandt & Andrade, 2007; Moya-Larano *et al.*, 2008, 2009; Prenter, Pérez-Staples & Taylor, 2010a, b; Prenter, Fanson & Taylor, 2012). Other studies have similarly dealt with running speed in the context of prey capture, fleeing from predators or effects of injury on performance (Amaya, Klawinski & Formanowicz, 2001; Nelson & Formanowicz, 2005; Pruitt & Husak, 2010; Pruitt & Troupe, 2010). These narrowly framed studies of running speed provide very limited insight to whole-organism performance in spiders; important dimensions of whole-organism performance, in particular endurance and strength, have been almost entirely neglected. Endurance capacity may be a particularly important target for selection because spiders have very few mitochondria in leg muscles and have extremely limited physiological capacity for sustained activity (Prestwich, 1983, 1988b; Shillington & Peterson, 2002). Such limits are expected to constrain activity when foraging or when searching for mates (Kramer & McLaughlin, 2001), and especially during courtship and contests, which tend to be energetically expensive (Watson & Lighton,

1994; Kotiaho *et al.*, 1998; DeCarvalho, Watson & Field, 2004). Strength is surely relevant in spider contests, which typically entail ritualized pushing, grabbing, and wrestling activities (Elwood & Prenter, 2013). Strength is also likely to be important when grasping and subduing prey and defending against enemies, including aggressive and potentially cannibalistic females.

Jumping spiders (Salticidae) may be particularly intriguing and tractable models for the study of whole-organism performance. Most are diurnal, wandering predators that ambush or actively pursue prey (Jackson & Pollard, 1996). Despite their common name, walking is the primary mode of locomotion in most jumping spiders, with jumping largely reserved for bridging gaps, attacking prey, rapid escape from predators and other danger, and ritualized leaps during intraspecific interactions. Males tend to roam more than females, presumably in search of mates, although females must routinely leave their nests to hunt (Jackson, 1978, 1979; Hoefler & Jakob, 2006; Hoefler, 2007). Vigorous and highly ritualized intraspecific interactions are common in jumping spiders (Taylor, Hasson & Clark, 2000; Lim & Li, 2004; Hoefler, 2007; Sivalingham *et al.*, 2010). Escalated contests typically entail bouts of pushing, grasping, and biting of a rival's limbs and body, sometimes to deadly effect (Wells, 1988; Taylor *et al.*, 2001; Elias *et al.*, 2008). Unreceptive females commonly attack courting males, which must then defend themselves or flee (Jackson & Hallas, 1986; Taylor & Jackson, 1999).

Several recent studies of running speed and climbing speed have included a jumping spider, *Jacksonoides queenslandica* (Prenter *et al.*, 2010a, b, 2012). However, as with other spiders, to date there has been no investigation of links between morphology and either endurance or strength, or potential trade-offs involving these abilities. Examining relationships among performance traits will establish whether they might be linked to the same underlying physiology or morphology, or whether higher performance in one trait compromises performance in another. The present study takes a substantially expanded view of whole-organism performance in spiders, examining four performance traits, namely vertical climbing, horizontal running, locomotor endurance and pulling force (i.e. the force required to pull a spider off a surface), in males of a common Australian jumping spider, *Servaea incana* Karsch (Fig. 1). We address: (1) relationships between morphological measures and performance; (2) relationships among performance traits; and (3) repeatability of performances over short (1 day) and medium (up to 6 days) timescales. Measuring repeatability establishes the potential for selection on performance traits (Boake, 1989; Lynch & Walsh, 1998) and validates



Figure 1. A male jumping spider, *Servaea incana*, ready to perform in a pulling force trial. Photograph by Rowan H. McGinley.

experimental methods (Losos, Creer & Schulte, 2002). Very few studies have examined the repeatability of performance over periods longer than one day (Oufiero & Garland, 2009), with only a single example for spiders (Pruitt, 2010).

MATERIAL AND METHODS

MAINTENANCE

Adult male *S. incana* were collected from the trunks of eucalypt trees in parks in Sydney, NSW, Australia, between April 2009 and March 2010. Spiders were maintained in a laboratory with controlled temperature ($25 \pm 1^\circ\text{C}$) and humidity ($70 \pm 5\%$) under a 12 : 12 h light/dark cycle. Spiders were housed individually in 1.125-L ventilated plastic cages with a folded piece of paper for environmental enrichment (Carducci & Jakob, 2000). Water was provided *ad libitum* via a 5-mL vial attached to the base of the cage, stoppered with a cotton dental wick that carried moisture into the cage. Prior to the experiment, spiders were provided three Queensland fruit flies (*Bactrocera tryoni*) as food on a single day each week.

GENERAL METHODS

Performance trials were conducted under fluorescent ceiling lighting supplemented with two 60-W full spectrum incandescent bulbs (Crompton Lighting, Sydney, Australia) positioned 0.5 m above the test apparatus. To standardize feeding state, spiders were offered two flies, two days before the trials. The initial pair of flies, before the first day of trials, was offered 5 days after a regular feeding day. Flies were removed on the day before trials. The same 44 spiders took part in four types of performance trial: running, climbing, endurance, and pulling force. Each day that the trials took place was preceded by 2 days in which trials were not run: one for feeding and one for fasting. The entire study spanned 24 days from the first day of feeding to the final trial. The sequence of trials started with the first day of climbing trials (day 3) followed by the first day of running trials (day 6) and then the second days of the climbing and running trials (days 9 and 12, respectively). These were followed by the endurance trials, one a day on three separate days (days 15, 18, and 21) and, finally, 1 day of pulling force trials (day 24). This order of trials was chosen so that the spiders took part in the putatively less demanding trials first. Running and climbing trials comprise short bursts of activity that are unlikely to affect later performances, whereas endurance trials are much more demanding. Pulling force trials required the attachment of an apparatus to subjects, which could result in permanent damage. Although *S. incana* is able to jump, its normal mode of locomotion is by walking and spiders were not observed to jump in any of the trials.

RUNNING

We measured maximum horizontal running speed of male *S. incana* by making them run along a raceway (Brandt & Andrade, 2007; Prenter *et al.*, 2010b, 2012). Raceways were 700 mm in length and 50 mm in width, with walls 50 mm high. They were constructed from white foam board and had a 240 grit sandpaper base for traction. To begin each trial, a spider was placed in a starting area (50 × 50 mm) at one end of the raceway and was then chased with a soft sable hair paintbrush over a distance of 600 mm to an identical area at the other end. Spiders were encouraged to run continuously by gently brushing the hind legs if they paused. The time taken to run 600 mm was recorded with a digital stopwatch and was used to calculate speed (mm s^{-1}). These trials were performed three times in one day with 3 h between trials, and were repeated with the same spiders 6 days later.

CLIMBING

Maximum climbing speed was estimated using established techniques (Brandt & Andrade, 2007; Prenter *et al.*, 2010b). Spiders were transferred to a 10-mm staging area at the base of a vertical wooden dowel (diameter 25 mm) that had been coated with textured Spray Stone Paint (White Knight Paints). Using a soft sable hair paintbrush, spiders were chased 250 mm to the top of the dowel. The time taken to climb this distance was recorded with a digital stopwatch and was used to calculate speed (mm s^{-1}). Spiders were encouraged to run continuously by gently brushing the hind legs if they paused. *Servaea incana* live on tree trunks, and readily climbed to the top of the dowel. On the rare occasion that they did not climb straight to the top of the dowel, spiders were returned to their cages for at least 5 min before re-running the trial. These trials were performed three times in 1 day with 3 h between trials and were repeated 6 days later with the same spiders. To validate the use of manual timing, we confirmed strong correlation between manual timing with timing taken from video recordings of additional climbing trials ($r = 0.998$, $N = 22$, $P < 0.0001$).

ENDURANCE

To examine endurance, we adapted general methods used previously in both vertebrates and invertebrates (Lailvaux, Alexander & Whiting, 2003; Lailvaux *et al.*, 2005). Spiders were forced to run continuously around a circular raceway (diameter 185 mm, circumference 580 mm), by chasing them with a soft-haired paintbrush, until they were exhausted. In these trials, the spiders almost always followed the outer wall of the raceway and movement away from this wall was rare. A spider was deemed to have reached exhaustion when it failed to move despite being repeatedly touched on the hind legs with the brush, or it was unable to right itself, having collapsed onto its dorsum. We recorded both time elapsed and distance moved until exhaustion. Trials were performed three times over 7 days, with 2 days of recovery between trials.

PULLING FORCE

We assessed the pulling force of male *S. incana* by adapting methods used previously in insects (Lailvaux *et al.*, 2005). A small piece of cork, approximately $1 \times 1 \times 2$ mm, with a copper wire twisted into the shape of a hook inserted at the top, was fixed to the dorsal carapace of each spider using melted beeswax (Fig. 1). A 1.2 m length of nylon fishing line was tied at one end to the hook and at the other end to a 15-mL plastic specimen jar. Spiders were placed

on a horizontal wooden dowel (diameter 2 mm), with the fishing line running over a smooth aluminium rod positioned 600 mm above the dowel, so that the specimen jar was hanging adjacent to the spider. Water was gradually added to the specimen jar from a 3-mL syringe, until the downward force exerted by the weight of the water caused the spider to be pulled up and off the dowel. We recorded the combined weight of the specimen jar and water required to pull the spider free of the dowel and later converted this value to millinewtons. Trials were repeated three times on each individual spider in 1 day, with 3 h of rest between trials. Because spider motility and hunting would be impeded by the cork and hook, and because repeated removal and reapplication of the cork and hook could cause damage, these trials were not repeated over longer time scales.

MORPHOLOGICAL MEASURES

Each spider was photographed no less than 2 days before any trials taking place with a ProgResC10 digital camera (Jenoptik LOS GmbH), focussed through an Olympus SZX12 dissecting microscope. To facilitate image capture, spiders were held still on the lid of a Petri dish using clear plastic film (Glad Products). We measured cephalothorax width and length, as well as tibia length of the first leg ('leg length'), from digital images using IMAGEJ, version 1.36b (National Institute of Health). For each spider, we measured the tibia that we were better able to align with the Petri dish. Although it is relatively easy to obtain measures of tibia length in live *S. incana*, it is more difficult to obtain accurate measures of total leg length. However, we found a strong correlation between tibia length and total leg length for 44 deceased *S. incana* males ($r = 0.968$, $P < 0.0001$), validating our general interpretation of tibia length as a measure of overall leg length. Spiders were also weighed to the nearest 1 mg, at the end of each trial day with an electronic balance (Model N595, Type AX200; Shimadzu Corporation) and we used the mean weight across the trials for analysis. Descriptive statistics for morphology of the spiders used in this study are provided in Table 1.

STATISTICAL ANALYSIS

Cephalothorax width and length were entered into a principal components analysis to generate a PC1 score that provides an overall measure of size (*sensu* Prenter *et al.*, 2010a, b, 2012). We then calculated relative tibia length by taking residuals from the regression of tibia length on body size. These residuals comprise the portion of leg length that is not

Table 1. Summary of morphological data for the male *Servaea incana* used in the performance trials ($N = 44$)

Measurement	Minimum	Maximum	Mean \pm SD
Cephalothorax length (mm)	2.57	4.34	3.56 ± 0.39
Cephalothorax width (mm)	1.94	3.50	2.83 ± 0.31
Tibia length (mm)	1.07	2.33	1.71 ± 0.25
Mean weight (mg)	19.88	101.63	53.64 ± 17.10

Table 2. Performances of male *Servaea incana* ($N = 44$) over the different days of trials (mean \pm SEM)

	Day 1			Day 2			Day 3
	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3	
Running speed (mm s ⁻¹)	102.5 ± 7.6	108.3 ± 6.1	98.3 ± 7.0	117.9 ± 8.1	101.8 ± 6.5	104.1 ± 6.6	
Climbing speed (mm s ⁻¹)	109.8 ± 8.0	115.8 ± 9.6	114.1 ± 6.8	118.5 ± 8.4	108.2 ± 7.6	114.2 ± 8.8	
Time to exhaustion (s)	202.56 ± 33.14			102.96 ± 16.97			114.29 ± 16.46
Distance to exhaustion (m)	8.55 ± 1.02			4.75 ± 0.41			5.72 ± 0.47
Pulling force (mN)	25.91 ± 1.22	27.94 ± 1.12	27.85 ± 1.22				

Performances were generally consistent across the running, climbing, and pulling force trials. However, performances in endurance tests decreased significantly after the first trial.

explained by variation in body size, allowing us to examine how length of legs for a given body size is related to performance. We were also interested in the effect of mass after controlling for both body size and leg length; such relative mass is often interpreted as 'condition' but also incorporates unmeasured size dimensions (Prenter *et al.*, 2012). We took residuals from the regression of body mass on body size and then used those residuals in a regression on residual tibia length, calculated previously, to generate residuals that give a measure of relative mass after removing variation of both body size and leg length (Prenter *et al.*, 2012). To examine the morphological predictors of performance, we performed multiple linear regressions, using type III tests, entering body size, relative leg length, and relative mass as predictors of performance (Type I tests, with body size, leg length, and mass as predictors, in that order, yielded closely comparable results). When investigating predictors of performance, we used the maximum performances to minimize error from low motivation and submaximal performances (Losos *et al.*, 2002). Bivariate relationships among performance traits were examined using Pearson's product moment correlations. Data for time and distance until exhaustion in endurance trials required log transformation to meet the requirements for parametric analysis. To quantify short-term

(within a day) repeatability of performances, we calculated the intraclass correlation coefficients (I_{cc}) using the best two performances on that day (Brandt & Andrade, 2007; Prenter *et al.*, 2010b). To measure repeatability of performances across days, we used Pearson's product moment correlations (Oufiero & Garland, 2009). Regression analyses were performed in JMP, version 5.0.1.2 (SAS Institute) and intraclass correlation coefficients were calculated in SPSS, version 16 (SPSS Institute). We present the mean \pm SD when describing raw distributions and the mean \pm SEM when estimating means.

RESULTS

RUNNING SPEED

The mean maximum running speed on the horizontal runway was 145.6 ± 7.9 mm s⁻¹. Running performances were consistent throughout the trials (Table 2), being highly repeatable within both days of trials (day 1: $I_{cc} = 0.727$, $P < 0.0001$; day 2: $I_{cc} = 0.773$, $P < 0.0001$), as well as between days ($r = 0.636$, $N = 44$, $P < 0.0001$). Individual maximum speed on the first day of trials was not significantly different from the second day of trials (paired t -test: $t_{43} = 0.865$, $P = 0.392$), indicating that sufficient time had been

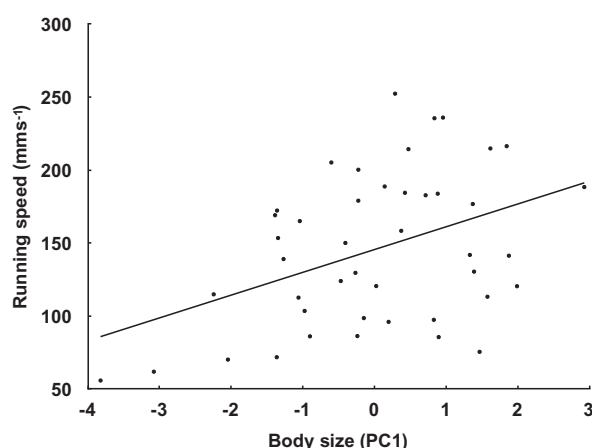


Figure 2. Partial regression plot showing size-dependent performance in male *Servaeae incana*. Body size (PC1) was positively related to running speed.

available for recovery. Running speed increased with body size (Fig. 2) and showed no evidence of a relationship with relative leg length or relative mass (Table 3).

CLIMBING SPEED

Spiders climbed up poles at a mean maximum speed of $151.7 \pm 9.6 \text{ mm s}^{-1}$. Climbing speed was highly repeatable within both days of trials (day 1: $I_{cc} = 0.799$, $P < 0.0001$; day 2: $I_{cc} = 0.852$, $P < 0.0001$), as well as between days ($r = 0.803$, $N = 44$, $P < 0.0001$). Individual maximum speed on the first day of trials was not significantly different from that on the second day of trials (paired t -test: $t_{43} = 0.239$, $P = 0.813$), again indicating that sufficient time had been available for recovery. Maximum climbing speed increased with both body size and relative mass but showed no evidence of relationship with relative leg length (Fig. 3, Table 3).

ENDURANCE

Mean maximum time taken to exhaust spiders in circular runways was $239.35 \pm 33.92 \text{ s}$ and the mean maximum distance travelled before exhaustion was $9.76 \pm 1.01 \text{ m}$. The time taken to exhaust spiders was repeatable between the first and second trial ($r = 0.539$, $N = 44$, $P = 0.0002$) but not between the second and third trial ($r = 0.182$, $N = 44$, $P = 0.236$), nor between the first and third trial ($r = 0.107$, $N = 44$, $P = 0.490$). Similar results were obtained for the repeatability of distance travelled before exhaustion (trials 1 and 2: $r = 0.408$, $N = 44$, $P = 0.0059$; trials 2 and 3: $r = 0.084$, $N = 44$, $P = 0.587$; trials 1 and 3: $r = 0.129$, $N = 44$, $P = 0.406$). Twenty-seven

spiders (61.36%) ran the furthest distance in the first trial, five (11.36%) ran the furthest distance in the second trial and twelve (27.27%) ran the furthest distance in the third trial. Both the time and distance until exhaustion were significantly higher in the first trial than the second and third trials (Fig. 4). These results indicate that spiders did not fully recover their endurance capacity between trials, even when provided 2 days to rest. We found no significant predictors of time until exhaustion, however, relative mass was positively related to the distance travelled before exhaustion (Fig. 5, Table 3).

PULLING FORCE

Spiders were able to resist an average maximum upward force of $31.10 \pm 1.05 \text{ mN}$ before being pulled off the wooden dowel. Maximum pulling force was highly repeatable within the single day of testing ($I_{cc} = 0.796$, $P < 0.0001$). Both body size and relative leg length predicted pulling force (Table 3), with larger spiders and those with long legs for their size being able to resist stronger forces (Fig. 6).

RELATIONSHIPS AMONG PERFORMANCE MEASURES

The relationships among performance traits are summarized in Table 4. Maximum running speeds on horizontal runways were positively correlated with vertical climbing speed (Fig. 7) and both had similar positive relationships with pulling force (Fig. 8). Running and climbing speeds were both negatively correlated with the time to exhaustion (Fig. 9), suggesting a trade-off between speed and endurance capacity. The two measures of endurance (distance travelled and time elapsed before exhaustion) were strongly correlated (Table 4).

DISCUSSION

High repeatability in running and climbing speed in the present study confirms individually characteristic locomotor traits through which selection may act to influence fitness and morphology in *S. incana* jumping spiders, and matches recent findings for other spiders (Brandt & Andrade, 2007; Pruitt, 2010; Pruitt & Husak, 2010; Prenter *et al.*, 2010b, 2012). Although individual spiders were very consistent in running and climbing trials (short and medium term) and tests of pulling force (short term), they showed low repeatability for endurance performance owing to a sharp decrease in performance after the first trial (Fig. 4). Spiders are characterized by rapid fatigue and slow recovery from activity (Prestwich, 1988a), although failure to recover even after 2 days of rest is extraordinary. Previous studies of endurance by

Table 3. Relationships between performance capacity and morphology in male *Servaea incana*

Performance trait	Variable	Estimate	Error	$F_{1,40}$	P
Running speed	Body size (PC1)	15.60	5.32	8.60	0.0055
	Relative leg length	66.22	69.21	0.92	0.3444
	Relative mass	0.91	1.83	0.25	0.6202
Climbing speed	Body size (PC1)	15.15	6.32	5.75	0.0212
	Relative leg length	67.07	82.17	0.67	0.4192
	Relative mass	4.94	2.17	5.18	0.0282
Ln time to exhaustion	Body size (PC1)	-26.66	24.39	1.21	0.2784
	Relative leg length	20.57	56.79	0.05	0.8275
	Relative mass	16.71	8.08	2.27	0.1398
Ln distance to exhaustion	Body size (PC1)	0.02	0.05	0.09	0.7683
	Relative leg length	-0.18	960.73	0.07	0.7879
	Relative mass	0.05	0.02	9.26	0.0041
Pulling force	Body size (PC1)	3.54	0.50	49.48	< 0.0001
	Relative leg length	17.38	6.55	7.03	0.0114
	Relative mass	0.18	0.17	1.08	0.3060

All estimates are from multiple linear regressions, using type III sums of squares. Significant regressions are shown in bold.

exhaustion in arthropods have only performed a single trial for each individual, offering no estimate of repeatability or recovery (Ramos, Irschick & Christenson, 2004; Lailvaux *et al.*, 2005). Investigations of repeatability in endurance by exhaustion in spiders may require substantial intervals between repetitions (Dohm, 2002), if complete recovery occurs at all. Accurate short term estimates of endurance repeatability may be possible through techniques that stop short of exhaustion, such as direct measurement of metabolic rates (e.g. heart rate: Coelho & Amaya, 2000; respirometry: Prestwich, 1983), in combination with treadmills (Schmitz, 2005) or fixed distance runs (Mowles *et al.*, 2010).

TRADE-OFFS BETWEEN PERFORMANCE TRAITS

Individual *S. incana* with high running and climbing speeds tended to have low endurance capacity (and vice versa) (Fig. 9); this appears to be the first study to provide evidence of a trade-off between speed and endurance in an invertebrate. Climbing and running speeds were both negatively correlated with the time elapsed to exhaustion. We found no evidence that this apparent speed-endurance trade-off results from gross morphological constraints. Although running speed increased with body size and was not related to relative mass, endurance capacity was quite the opposite; positively related to relative mass and unrelated to body size.

Trade-offs between maximal running speed and endurance capacity are well known in vertebrates, and have been attributed to anatomical constraints or the abundance of different muscle fibre types (lizards:

Bonine, Gleeson & Garland, 2001; Vanhooydonck, Van Damme & Aerts, 2001; fish: Reidy, Kerr & Nelson, 2000; Langerhans, 2009; humans: Bottinelli & Reggiani, 2000; Van Damme *et al.*, 2002). Less is known about invertebrate muscle fibre types. Slow and fast twitch muscle fibres similar to those found in vertebrates have been identified in the walking legs of crabs (Perry *et al.*, 2009), scorpions (Wolf & Harzsch, 2002), the wandering spider *Cupiennius salei* (Maier, Root & Seyfarth, 1987), and the tarantula *Eurypelma californicum* (Paul *et al.*, 1991). Leg muscles of the wandering spider *C. salei* have few mitochondria to sustain aerobic respiration (Linzen & Gallowitz, 1975), and the dominant fibres present are analogous to vertebrate fast-twitch fibres (Maier *et al.*, 1987) that use anaerobic metabolism to generate short, powerful bursts of action but fatigue rapidly. Variation in aerobic and anaerobic capacity may therefore underlie the trade-off between individual ability for speed and endurance in *S. incana*. Low levels of aerobic metabolism in spiders are considered to represent an adaptation for surviving extended periods of starvation (Anderson, 1974); however, this may come at the cost of reduced endurance capacity and help explain the intermittent mode of locomotion typically adopted by spiders (Kramer & McLaughlin, 2001). Intermittent locomotion is thought to improve endurance by facilitating partial recovery during pauses.

An alternative explanation is that the observed relationships between speed and endurance are a result of the order in which the trials were carried out. All of the short running and climbing trials were carried out before the endurance trials, so that

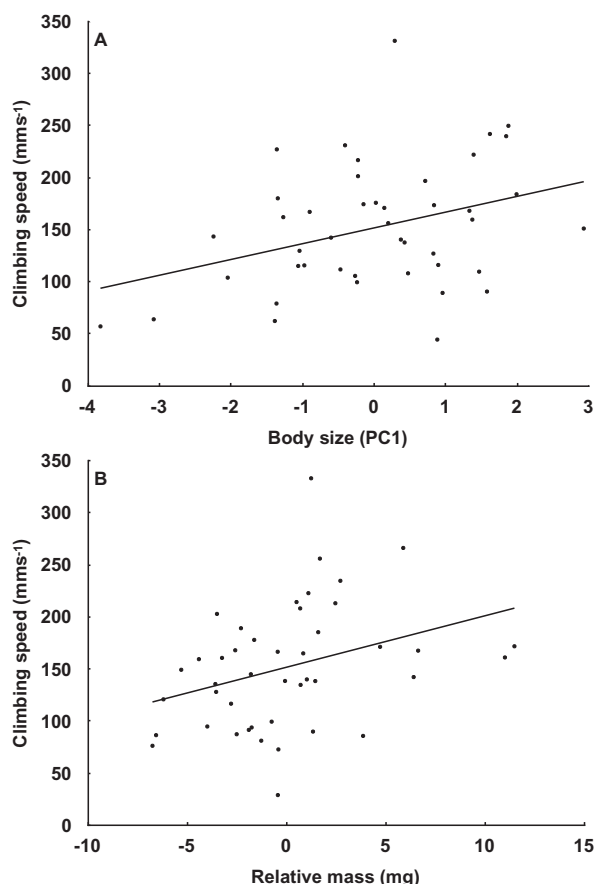


Figure 3. Partial regression plots showing the morphological predictors of vertical climbing speed. Climbing speed increased with both (A) body size (PC1) and (B) relative mass, after controlling for size and relative leg length, in male *Servaea incana*.

perhaps the spiders that ran fastest in the short trials could have already been tired for the exhaustion trials. However, each spider took part in 12 of these trials, over a 10-day period, and there was no evidence that the earlier trials had an influence on performance in later trials (Table 2). Thus, we expect that these trials will have had a minimal effect upon endurance capacity, if any at all.

LINKS BETWEEN MORPHOLOGY AND WHOLE-ORGANISM PERFORMANCE

The present study suggests performance advantages for large size, relatively long legs, and high relative mass in male *S. incana* jumping spiders. Larger spiders were faster on both the horizontal and vertical surfaces and also had greater pulling force than smaller spiders. The positive relationship between body size and running speed in *S. incana* males

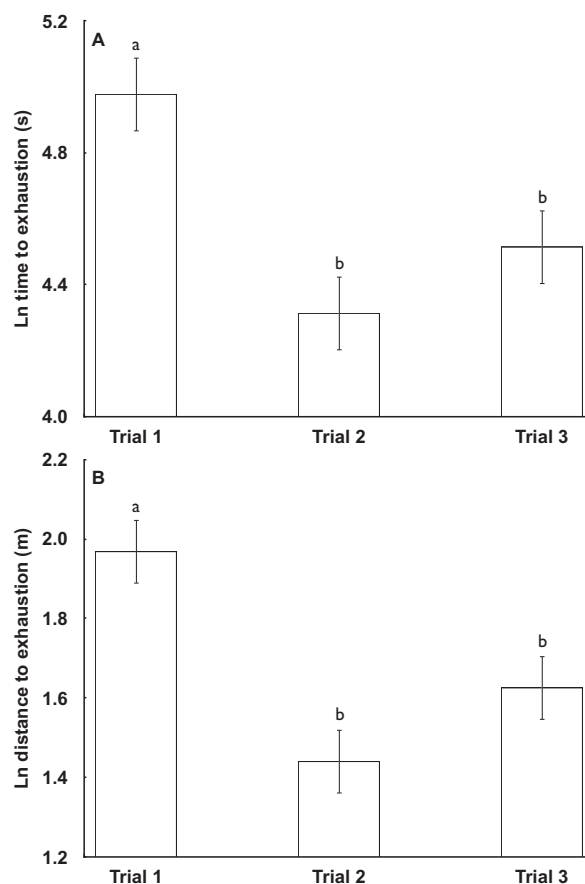


Figure 4. Male *Servaea incana* spiders exposed to exhaustion showed long-lasting reductions in endurance capacity. Performance, measured as (A) time and (B) distance travelled before exhaustion, decreased after the first endurance trials (trials that did not differ are marked by the same letter; Tukey's honestly significant difference).

(Fig. 2) is consistent with those identified in several other spiders that live on the ground or in low foliage, including other jumping spiders (Brandt & Andrade, 2007; Prenter *et al.*, 2010b). Running speed has also been related to body size in the jumping spider, *Jacksonoides queenslandica*. However, unlike *S. incana*, *J. queenslandica* males showed a positive relationship between relative leg length and climbing speed; no relationship between relative mass and maximum running speed; and no relationship between running and climbing speed (Prenter *et al.*, 2010a, b). Species differences in relationships between performance and morphology may reflect adaptations to specific habitats, as in *Anolis* lizards (Calsbeek & Irschick, 2007). *Servaea incana* are rarely found away from tree trunks, whereas *J. queenslandica* often inhabit large boulders and ledges (Jackson, 1988) and these differences in

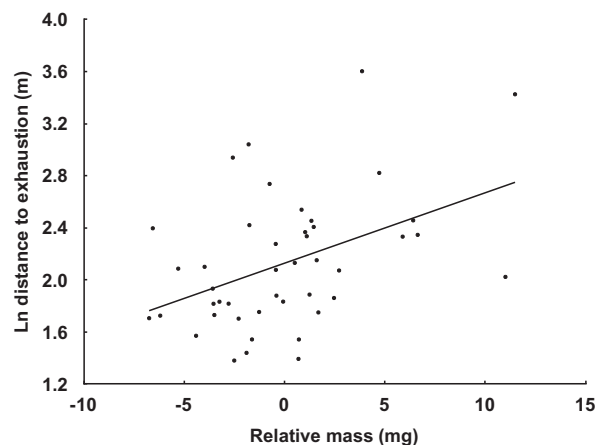


Figure 5. Partial regression plot for the effect of relative mass on the distance run before exhaustion. Individuals that were heavy for their size ran further before becoming exhausted, suggesting that endurance capacity varies with body condition in male *Servaea incana*.

habitat may have evolutionary implications for performance. Although *S. incana* is a quite stout and short-legged spider, *J. queenslandica* is comparatively gracile, and these overall species differences in shape may have implications for how each dimension of size and shape influences performance.

We can expect that there are fitness benefits for being large because large size is associated with superior performance. Assays of running and climbing speed as performed in the present study are assumed to assess the ability to flee from predators and other hazards (Prenter *et al.*, 2010b) or chase down prey. Most jumping spiders are cursorial hunters (Forster, 1977) and strength is particularly relevant for restraint of prey (Clarke, 1986). Owing to their greater speed and strength, we may expect large spiders to be more adept at prey capture. Whole-organism performance is correlated with success in intrasexual contests in some animal groups (Huyghe *et al.*, 2005; Lailvaux & Irschick, 2007; Mowles *et al.*, 2010). In the dung beetle, *Euoniticellus intermedius*, horn length is a strong predictor of both pulling force and fighting ability (Lailvaux *et al.*, 2005). Jumping spiders also commonly engage in apparent 'trials of strength' during escalated contests, pushing against one another (Taylor & Jackson, 1999; Taylor *et al.*, 2001); therefore, the ability to grasp onto a surface and resist being pushed or pulled off may influence contest outcomes. Both size and relative leg length predict pulling force in *S. incana* males, and are also common predictors of fighting ability in jumping spiders (Wells, 1988; Faber & Baylis, 1993; Taylor *et al.*, 2001; Taylor & Jackson, 2003; Elias *et al.*, 2008; Tedore & Johnsen, 2012); therefore, the advantage of

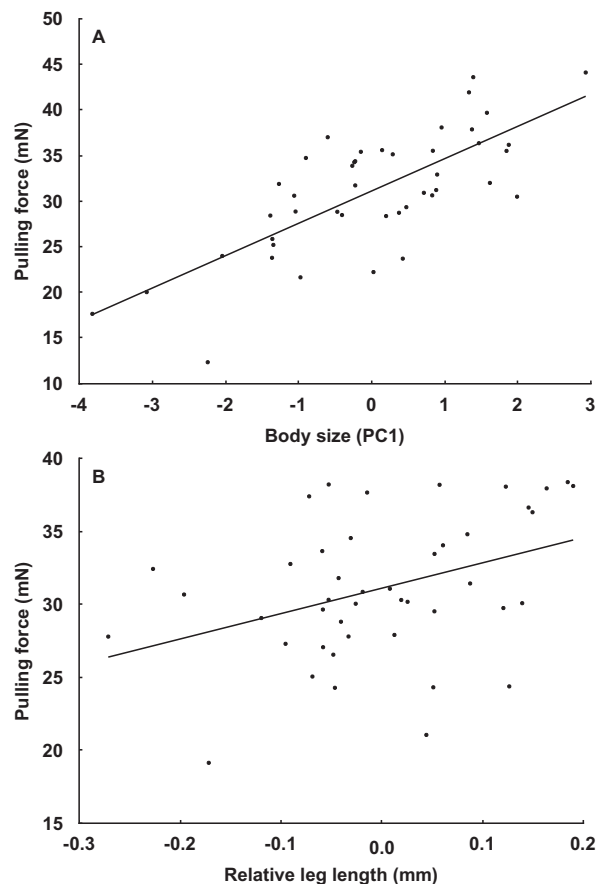


Figure 6. Partial regression plots of the relationship between morphology and pulling force in male *Servaea incana*. Pulling force increased with both (A) body size (PC1) and (B) relative leg length.

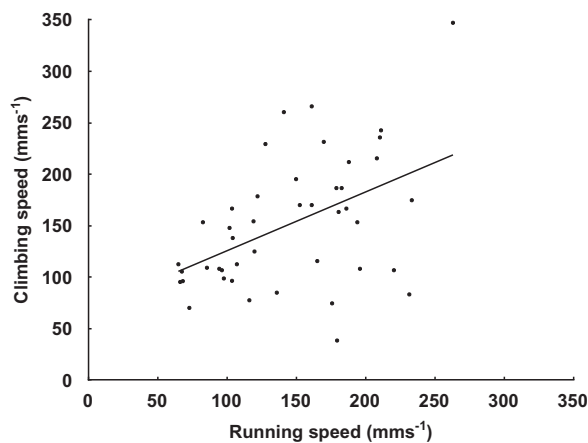
a large body size and long legs evident in jumping spider contests likely arises from the links between these morphological measures and strength (Fig. 6).

Given that small spiders are slower and weaker, and by implication may not be as successful at prey capture, predator escape, and intraspecific contests, what compensating factors might promote the wide range of sizes recorded in *S. incana* (Table 1) and the maintenance of small size? Perhaps large and small spiders are more adept at capturing different types of prey. Large size is sometimes associated with increased viability costs as a result of a longer development time. Female jumping spiders commonly have reduced receptivity after their first mating and are suggested to exhibit first male sperm priority patterns (Jackson, 1980). For species with distinct seasonality, maturing at a particular time of year, males may have a mating advantage if they mature early in the season when virgin females are more abundant than less receptive mated females.

Table 4. Pearson's product moment correlations (r) between pairs of different measures of performance in male *Servaea incana*

	Climbing speed	Ln time to exhaustion	Ln distance to exhaustion	Pulling force
Running speed	0.473	-0.421	-0.250	0.393
Climbing speed		-0.299	-0.046	0.324
Ln time to exhaustion			0.884	-0.098
Ln distance to exhaustion				0.048

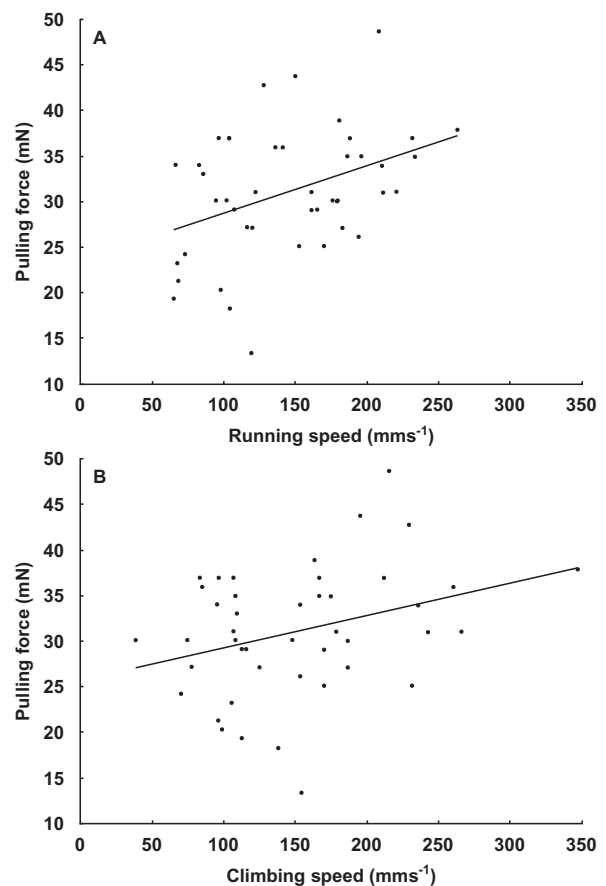
Values in bold indicate statistically significant correlations ($\alpha = 0.05$, two-tailed tests, $N = 44$).

**Figure 7.** Bivariate relationship between running and climbing speed in male *Servaea incana*.

However, to mature early may also mean developing quickly and maturing with a small size (Maklakov, Bilde & Lubin, 2004). Small spiders might also be favoured by reduced conspicuousness to enemies (Vollrath & Parker, 1992; Blanckenhorn, 2000).

A low mass has been hypothesized to be advantageous in spiders when moving against gravity (Moya-Larano *et al.*, 2009; Corcobado *et al.*, 2010). Contradicting the 'gravity hypothesis', larger male *S. incana* and those heavier for their size climbed faster (Prenter *et al.*, 2010b). As we averaged individual mass across trials and feeding experience was standardized, our measure of relative mass is unlikely to represent variation in gut contents or recent feeding history. Differences in relative mass may largely represent variation in overall condition (Jakob, Marshall & Uetz, 1996), reflecting longer-term energy stores and/or muscle mass. Thus, it appears that spiders in better condition were able to pull themselves against gravity more effectively, despite their greater relative mass.

The present study brings the evolutionary trade-offs of jumping spider performance capacity into focus, illustrating the complexity of forces at play

**Figure 8.** Bivariate relationships between pulling force and (A) climbing and (B) running performance. Both measures of speed were positively correlated with pulling force.

with respect to defining the performance capacity of individuals. Performance and morphology are intertwined such that selection for one will commonly lead to evolution of the other. For example, selection for small size may lead to reduced strength and slower running speed in a population. Different dimensions of performance are similarly intertwined; selection for fast running speeds may lead to poor endurance.

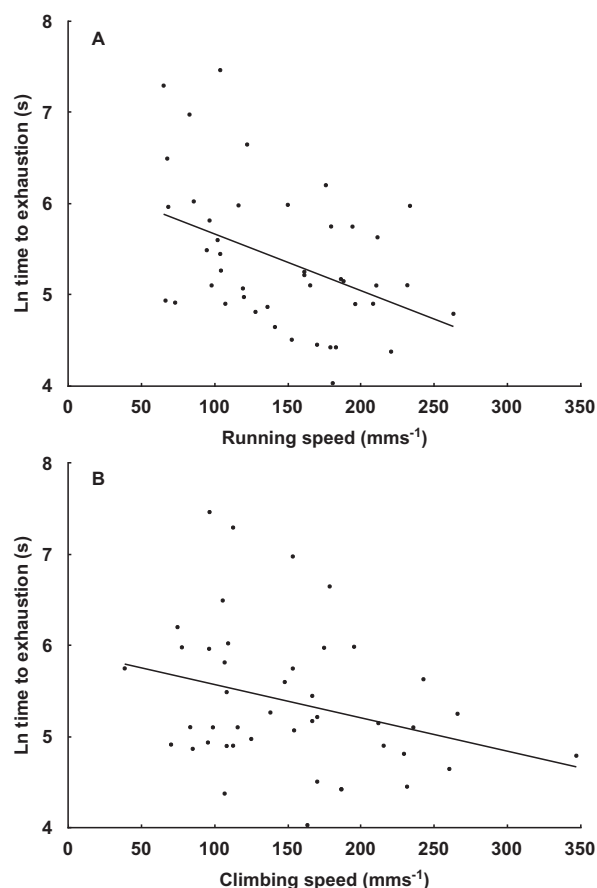


Figure 9. Bivariate relationships between the time until exhaustion and (A) climbing and (B) running performance. Both measures of speed were negatively correlated with this measure of endurance capacity.

Little is known about the mechanisms that underlie relationships between morphology and whole-organism performance in spiders. The investigation of these underlying mechanisms, as well as the selection forces that drive them, is required to understand the evolutionary constraints on morphology and performance.

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