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The Effects of Ornamentation on Wolf Spider Foraging

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THE EFFECTS OF ORNAMENTATION
ON WOLF SPIDER FORAGING

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ABSTRACT:

As a secondary sexual trait that can increase reproductive success, ornamentation is believed to be costly for organisms to acquire and possess. This study investigates possible costs of ornamentation on wolf spider foraging by comparing foraging abilities of two male forms that differ in ornamentation upon maturation. The two male forms, found syntopically in a mixed population in Mississippi, USA, resemble two sibling species: *Schizocosa ocreata*, in which males develop large black brushes on their forelegs upon maturation, and *Schizocosa rovneri,* in which males lack ornamentation following maturation. Individuals of both forms participated in foraging trials as penultimates (juveniles) and as matures. Analyses were conducted to compare behaviors and determine changes in foraging abilities between male forms (non-ornamented vs. brush-legged) and between age groups (penultimate vs. mature). Most foraging behaviors of the two male forms during immaturity were similar with the exception that brush-legged males attacked more frequently than non-ornamented males. Brush-legged males attacked less, spent more time moving, and improved capture abilities as matures, while non-ornamented males retained similar trends for these behaviors with age. Additionally, while capture abilities improved with age among brush-legged males, killing abilities remained constant. This disparity was due to increased escapes made by captured prey items, possibly due to hindrances caused by brush presence preventing secure holds onto crickets. In summary, differences in foraging exist between brush-legged and non-ornamented males prior to sexual maturation, and the development of/presence of brushes appears to influence adult male foraging efficiency.

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INTRODUCTION:

Sexual selection is a driving force in the evolution of animal behavior. Intraspecific competitions over mates cause differences in reproductive success among individuals, fueling sexual selection (Darwin 1871). In most species, males compete for choosey females in order to increase their potential fitness by participating in male-male competition (i.e. using morphological weapons against competitors), appealing to female mate choice (i.e. having attractive ornamentation), or executing a combination of these two tactics (Andersson 1994). When selecting mates, females often prefer males who have conspicuous traits, which may increase male competitive ability or influence mate choice (Andersson 1994). These conspicuous traits are termed secondary sexual traits, or physical characteristics that increase the possessor's success in competition for mates, but do not directly aid in fertilization (Darwin 1871).

Ornamentation is a secondary sexual trait occurring in many different forms in both sexes, albeit the majority is found in males. For example, male yellow-knobbed curassow birds have yellow, fleshy knob structures on their maxillary bones while female curassows have none (Buchholz 1991), and female long-tailed dance flies have rows of scales on their legs and inflated abdominal sacs whereas males do not (Newkirk 1970). Females often choose males with more conspicuous ornamentation as mates, suggesting that these traits convey information about the possessor (Zahavi 1975, Andersson 1994). The degree of brightness of blue plumage in male grosbeaks provides information about the male to choosey females, with the bluest males having the largest body sizes, possessing the largest territories, and practicing the greatest amounts of parental care to nestlings (Keyser and Hill 2000). Additionally, offspring of more conspicuously ornamented males could benefit from increased viability and other advantages during

growth due to the level of paternal quality as projected by the degree of ornamentation, such as in stickleback fish in which offspring of brightly colored males benefit from increased disease resistance (Barber *et al.* 2001).

Secondary sexual traits are believed to aid in mate choice and often complement mating behaviors practiced by the possessor of the trait (Andersson 1994). Ornamentation, such as extravagant brushes or feathers, pigmentation, or enlarged appendages, frequently accompanies courtship signals, like vocalizations, vibrations, or physical displays, which together create complex mating displays (Hebets & Papaj 2005). An ornament may increase the overall display's efficacy by making the receiver more likely to detect and understand the display or aid in the signaler's ability to attract mates and increase female receptivity, as seen in *Lycosidae* wolf spiders (Hebets & Uetz 2000). If possessing ornamentation increases an individual's likelihood of mating, investing energy in developing an ornament could increase an individual's fitness.

Despite these benefits described above, ornamentation can be costly to produce and maintain, with energy allocated to ornament development thought to be diverted from energy usually invested in growth and basic maintenance (Badyaev & Ghalambor 1998). The influence of ornamentation on an organism's development has been investigated in studies manipulating stress and diet constrictions during growth. The degree of expression of secondary sexual traits reflects nutritional conditions during development, with less pronounced traits resulting from increased physical or nutritional stress (Ohlsson *et al.* 2001, Uetz *et al.* 2002, Nowicki 2000, Hebets *et al.* 2008, Shamble *et al.* 2009). Internal processes, such as metabolic rates, and performance capabilities, such as endurance and agility, following juvenile development may reflect tradeoffs of

ornamentation as well. In multiple studies, experimental manipulations to ornamentation in both vertebrate and invertebrate species have found energetic and locomotory costs to be related to the degree of expression of an ornament (hummingbirds: Clark *et al.* 2009, fiddler crabs: Allen 2007).

While male sexual ornamentation has been studied in the context of mate choice (Andersson 1994), much less is known about the costs of male ornamentation. For a predatory species such as a species of wolf spider, one possible cost could be in foraging efficiency. Additionally, while studies have investigated the effects of past foraging success on ornament development (Uetz *et al.* 2002, Hebets *et al.* 2008, Shamble *et al.* 2009), few studies have explored the effects of ornament possession on foraging behavior and success.

In order to investigate the effects of ornamentation on foraging behavior, I studied a mixed population of syntopic *Schizocosa* wolf spiders. This particular population, located in Mississippi, contains two male forms differing in ornamental phenotype: brush-legged and non-ornamented, who resemble the species *S. ocreata* and *S. rovneri*, respectively (Hebets & Vink 2007). Brush-legged males acquire large brushes on their forelegs upon maturation whereas non-ornamented males lack ornamentation on their forelegs when mature. The two male forms also differ in their courtship displays; brush-legged males wave their brushed forelegs while stridulating their pedipalps and performing a double "body bounce" along a substrate, and non-ornamented males use a primarily seismic courtship display involving a "body bounce" against a substrate (Hebets & Vink 2007). While males of these two forms differ both phenotypically and behaviorally, females of the two species are indistinguishable from one another, and

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mitochondrial data does not separate the two male forms, suggesting that they may interbreed (Hebets & Vink 2007).

Many studies have investigated the role of leg ornamentation in courtship and reproduction in these species (Stratton & Uetz 1981, Stratton & Uetz 1986, McClintock & Uetz 1996, Scheffer *et al.* 1996, Hebets & Uetz 1999, Hebets & Uetz 2000, Uetz & Roberts 2002, Stratton 2005, Taylor *et al.* 2005, Hebets & Vink 2007,), but studies investigating the costs and influences of ornamentation in the two forms are lacking. This study investigates the effects of ornamentation on wolf spider foraging abilities by comparing behaviors between the two male forms both before and after sexual maturation. I specifically test the hypothesis that ornamentation induces costs in the foraging abilities and efficiencies of ornamented (brush-legged) males.

Two main predictions follow from the hypothesis that ornamentation induces foraging costs on *Schizocosa* male wolf spiders. First, since males resembling *S. ocreata* and *S. rovneri* in the Mississippi mixed population are visually indistinguishable and morphologically identical prior to maturation (Uetz & Dondale 1979, Hebets & Vink 2007), I expected the two forms to demonstrate similar foraging behaviors prior to sexual maturation. Second, due to potential costs of ornament attainment on foraging behavior, I expect to observe differences in foraging efficiency and movement behaviors between immature and mature brush-legged males. I expect this to occur either through prey handling costs and/or through energetic costs. Prey handling costs decrease brush-legged males' prey handling ability, possibly through increased drops and escapes and decreased catches, while energetic costs could be observed in decreased movement and/or decreased attack frequency.

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During the summer of 2008, spiderlings were raised from lab-mated females collected from a mixed population of brush-legged and non-ornamented *Schizocosa* wolf spiders. Parental spiders were collected in the spring of 2007 from near the greenhouse of the University of Mississippi in Oxford, USA. All spiderlings were housed individually with a constant supply of water and were fed either one fruit fly or one pinhead cricket weekly until their third molt. Upon their third molt, spiders were fed one size-matched cricket every other week. Once their metabolic demands required an increase in prey quantity, spiders were fed one size-matched cricket every week from June 2009 until September 2009, after which point all spiders had died. This low quantity diet encouraged active, aggressive foraging while maintaining adequate spider health.

During the spring and summer months of 2009, I observed the foraging behaviors of brush-legged and non-ornamented male spiders. Each tested spider participated in two trials; the first trial was conducted 14-21 days following the spider's penultimate molt (which I will refer to as the 'penultimate trial'), and the second trial was conducted 3-5 days following its mature molt ('mature trial'). The penultimate molt is the molt immediately preceding the maturation molt. I did not feed spiders for 7 days prior to their penultimate trials and for 3-5 days prior to their mature trials. It was impossible to standardize the feeding of the mature trial individuals beyond 3-5 days since we could not predict when spiders would molt. Each spider tested had a unique pair of parents (*i.e.* I had no full or half siblings) and participated in both a penultimate and a mature trial, making this a repeated measures design.

Prior to testing, I weighed each spider, then placed it behind a 6.25x3.0 cm cylindrical acetate barrier within a plastic 13.0x7.5 cm cylindrical arena lined with white

filter paper. Both the acetate barrier and arena were surrounded with opaque white paper. Thus, I had an enclosed space within an acetate barrier (in which the spider was initially placed) held within the larger arena (within which the crickets were initially placed). In the larger arena (outside of the space within the acetate barrier), I placed six freely moving crickets, each ~1/4 of the spider's mass (see *Figure 1* for visual depiction). The spider and crickets acclimated for approximately two minutes before the acetate barrier was lifted, enabling the spider to come in contact and potentially forage on the crickets. Foraging trials lasted 45 minutes.

I recorded all trials onto Sony Mini DV digital videocassettes using a Sony Handycam HDR-HC9 video camera recorder. After 45 minutes, I removed any active crickets from the arena and left the spider in the arena with any subdued crickets until prey consumption ceased and prey remains were discarded. Upon completion of prey consumption, I returned the spider to its container.

I recorded foraging behaviors exhibited by spiders toward the crickets during each 45-minute trial. Recorded behaviors included a spider's latency to attack and each occurrence and stopwatch time of the following behaviors: attacks, catches, misses, drops, escapes, and kills. I categorized these behaviors using the following criteria: 1) attack: spider lunges at or onto cricket, regardless of the outcome; 2) catch: following an attack, spider successfully grasps the cricket for at least 3 seconds; 3) miss: following an attack, spider unsuccessfully attempts to catch a cricket; 4) kill: following a catch, spider kills or fatally injures cricket and begins its consumptive process; and 5) drop: following a kill, spider discards dead or fatally injured cricket. Additionally, I recorded one cricket behavior during trials: escape, occurring after a catch, when a previously caught cricket

escaped from a spider's grasp after withstanding little to no injury. I did not track individual crickets, thus totals of each behavior could apply to any and/or all six crickets in a trial.

Most foraging behaviors were dependent on the number of attacks per trial; with

each additional attack, a spider increased its opportunities to catch, miss, drop, and kill crickets, or to allow caught crickets to escape. Therefore individuals who attacked several times often killed several crickets, whereas individuals who attacked fewer times killed fewer crickets. Due to this relationship, I calculated the ratios of catches, kills, and escapes to the number of attacks before conducting statistical tests comparing these behaviors between ages and forms. Misses and catches are inverse behaviors of each other; therefore, higher proportions of caught crickets reflect lesser proportions of missed

crickets, making statistical tests and graphs including proportions of missed crickets

I also conducted a detailed analysis of the video recordings in order to assess patterns in spider movement behavior during foraging. I determined each spider's movement patterns by measuring its latency to move and its total time spent in forward movement during a 45-minute trial. During trials spiders moved in sporadic bouts, typically lasting between 5 and 20 seconds each, separated by a few seconds to several minutes. I determined the total time spent in forward movement by recording the duration of time for all forward movement bouts in a trial. I quantified latency to move by recording the length of time between the trial start and the spider's first forward movement.

Paired two-sample T-tests and ANOVAs were used to compare behavioral frequencies between male forms, while repeated measures MANOVAs were used to compare changes in behaviors between male forms across age groups (between penultimate and mature trials). I used bivariate fit tests to distinguish relationships between movement durations and foraging behaviors, as well as relationships between male form and movement durations between age groups. All tests were performed with

JMP software (Version 6.0.0 Statistical Discovery™ from SAS 2005), and graphs were

I tested a total of 43 individuals from unique eggsacs in both penultimate and mature foraging trials. Due to limb (i.e. pedipalp or leg) loss upon their final molts, I excluded four individuals from analyses, as wolf spiders often utilize their legs and pedipalps during prey capture. Due to this subtraction, I included a total of 39 individuals in data analyses, comprised of 12 brush-legged males and 27 non-ornamented males. Since a greater number of females mated with non-ornamented males than brush-legged

males during our spring 2008 mate choice trials and produced a greater number of eggsacs possessing the non-ornamented phenotype, there was a greater number of non-ornamented males available for experimentation than brush-legged males.

Most trials shared a similar sequence of events. For a summary of the possible sequences of foraging behaviors, see *Figure 2*. Within the first few minutes, a spider attacked and caught its first cricket. The spider often followed with additional attacks, either catching or missing additional crickets, during the first 5-10 minutes of the trial. In the time between attacks, the spider restrained and continued to injure captured crickets. Crickets escaped from a spider's grasp if they were not sufficiently injured or restrained, or if the spider attempted to carry too many prey items at once. Frequency of attacks and catches tapered off after about 15 minutes, when spiders were more likely to drop dead or fatally injured crickets or further handle and injure caught prey items.

Individuals demonstrated highly variable foraging and movement behaviors across 78 trials. In both penultimate and mature trials, both brush-legged and non-ornamented individuals attacked crickets between 1 and 21 times and killed between 0 and 6 crickets per trial. Spiders caught, missed, and dropped crickets between 1-8, 0-16, and 0-20 times per trial, respectively. Spiders experienced between 0-4 escapes per trial. Latencies to first forward movement ranged between 0.00 and 3.99 minutes after trial start, while latencies to attack ranged between 0.03 and 4.02 minutes after trial start. Total lengths of time spent in forward movement spanned between 0.967 and 10.367 minutes per trial. Spiders remained with subdued prey items in the arena between 5-18 hours post-trial.

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Penultimate Trial Foraging Patterns - Penultimate brush-legged males tended to attack crickets more than penultimate non-ornamented males (*Table 1*). No other differences were found in foraging efficiency (*i.e.* proportion of crickets caught, proportion of crickets escaped, proportion of crickets killed) between penultimate brush-legged and non-ornamented males (*Table 1*). Similarly, no differences were found in the time spent in forward movement between penultimate brush-legged and penultimate non-ornamented males (*Table 1*).

Foraging Patterns of Penultimate vs. Mature Males - Using a repeated measures ANOVA looking at the number of attacks between penultimate versus mature foraging trials for brush-legged and non-ornamented males, I found a significant interaction between age (penultimate vs. mature) and male form (brush-legged vs. non-ornamented) (*Figure 3*). Brush-legged males decreased their number of attacks after maturation while non-ornamented males tended to increase their number of attacks. When comparing the number of attacks only between mature male forms, there was no difference between brush-legged and non-ornamented males (*Table 1*).

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The proportion of crickets caught ($^{\text{# of catches}}/_{\text{# of attacks}}$) across age groups did not differ between brush-legged and non-ornamented males (*Figure 4*), but there was a trend for brush-legged males to increase the proportion of caught crickets after maturation (*Figure 4*). Both brush-legged and non-ornamented males also exhibited a similar pattern in the proportion of crickets killed across age groups (*Figure 5*). Brush-legged males tended to have higher proportions of escaped crickets as matures than as penultimates, while non-ornamented males experienced no changes in proportion escaped (*Figure 6*).

Movement Patterns **-** The pattern of forward movement across age groups did not differ for brush-legged versus non-ornamented males (*Figure 7*), although brush-legged males tended to move more after maturation than non-ornamented males. Additionally, brush-legged males spent more time moving as matures than as penultimates (*Figure 7*). Pooling all data across age groups and male form, I found that individuals who attacked more often per trial spent less time in forward movement (*Figure 8*).

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DISCUSSION:

This study provides support for the hypothesis that ornamentation induces costs on the foraging efficiency of brush-legged males in a species of *Schizocosa* wolf spider. Despite differences in attack frequencies between male forms, penultimate individuals had similar foraging behaviors and capabilities. Additionally brush-legged males

decreased their attack frequency and foraging efficiency following maturation and ornament attainment, suggesting interference from brushes during prey handling. Furthermore, a lack of behavioral differences between penultimate and mature non-ornamented males provides support for ornamentation exclusively affecting foraging behaviors of brush-legged males.

Due to morphological similarities during immaturity, I expected brush-legged and non-ornamented males to demonstrate similar foraging behaviors as penultimates. This prediction was partially supported. Most foraging behaviors were similar between forms during penultimate trials (*Table 1*). Non-ornamented and brush-legged penultimate males had similar proportions of caught, escaped, and killed attacked crickets, reflecting similar foraging efficiencies between the two male forms. However, on average, penultimate brush-legged males attacked a greater average number of times per trial (*Table 1* & *Figure 3*). This finding suggests that either behavioral or motivational differences may exist between the two forms prior to maturation and ornamentation. This disparity could be due to pre-existing genetic or form-specific differences between male forms, possibly reducing the validity of comparisons made between non-ornamented and brush-legged males.

Given the results of previous studies (Badyaev & Ghalambor 1998, Allen 2007, Hasselquist 2008), I predicted brush-legged males to decrease in foraging abilities with age as a result of energetic costs of ornamentation. As expected, brush-legged males attacked at lower frequencies with age (*Figure 3*), but contradictorily spent significantly more time in forward movement as matures than as penultimates (*Figure 7*). While fewer attacks are consistent with the hypothesis of energetic costliness of newly attained

ornamentation, increased time spent moving is not. Past studies conducted on other species have found ornamentation to be influential on internal energetic rates (Allen 2007, Hasselquist 2008), but ornament influence on metabolic rates in spiders is currently unknown and was not examined in this study. This lack of information presents future opportunities for research investigating the effects of ornamentation on metabolic rates among spiders.

Ornament development may induce changes in foraging and movement behavior by requiring tradeoffs between energetically costly behaviors. Brush-legged males may compensate for increased mobility (and the possible increase in energy allocation to this behavior) by decreasing the number of times they attack (and energy allocated to this behavior) while foraging. In contrast, non-ornamented males generally increased both their attacks (*Figure 3*) and movement (*Figure 7*) with age. This suggests that non-ornamented males are able to allocate more energy as matures than as penultimates to both of these behaviors, as opposed to brush-legged males who experience increased mobility but decreased attack capabilities with age. These disparities between the two male forms could be due to differences in ornament possession and development, although further studies investigating energy allocation are needed to support this hypothesis.

Aside from energetic costs, changes in attack frequencies and increased time spent in movement may be due to motivational changes with age. Young male spiders, who are not yet sexually mature, spend most of their efforts foraging, while mature males are searching for mates, which consumes time and energy previously spent foraging. Instead of devoting time and energy toward catching prey, reproductively mature males

may attack less and spend more time searching for mates in order to locate females and reproduce. Hence, decreased foraging with age may result from motivational changes rather than energetic costs from ornamentation.

If increased movement following maturation reflects increased mate search efforts, I expect to observe this change in all mature males. Contrary to this prediction, non-ornamented males did not increase their movement following maturation, whereas brush-legged males did. This contrast suggests a motivational difference between the male forms post-maturation. Previous studies have found differences between matures males of the two forms, such as Hebets and Vink (2007), which found that brush-legged males are more aggressive toward females during courtship than non-ornamented males, as demonstrated through more attempted mounts on unreceptive or juvenile females. This past work provides support for motivational differences between the two male forms, and presents the possibility that motivational differences could be present between brush-legged and non-ornamented males following reproductive maturity, including differences in movement.

As an alternative to causing energetic costs, I predicted that ornamentation would impede prey catching and killing abilities by hindering prey handling. Increases in proportions of caught crickets were observed between penultimate and mature brush-legged males, indicating increased catching ability with age within this form. Despite this increase in catching efficiency, mature brush-legged males killed similar proportions of crickets as they had as penultimates (*Figures 4 & 5*). These findings suggest that some factor affecting mature brush-legged males is hindering males from killing prey items after catching them, otherwise higher proportions of caught prey would correlate with a

higher proportions of killed prey. These behaviors did not differ among non-ornamented males with age (*Table 1*), suggesting that a decrease in prey handling ability exists exclusively in brush-legged males.

The attainment of the ornament, brushes on the legs used to capture prey, may interfere with a spider's ability to kill a prey item following a catch. Brushes could decrease the spider's ability to continually grasp and sufficiently injure a captured prey item, resulting in a greater probability of escapes made by captured crickets among mature brush-legged males. While not statistically significant, captured crickets were three times more likely to escape from mature than penultimate brush-legged males, whereas I did not observe this pattern among non-ornamented males with age (*Figure 6*). Therefore, while brush-legged males improved their ability to capture attacked crickets with age, a greater proportion of caught prey items were able to escape, possibly due to ornament interference (*Figures 4, 5, & 6*). This hypothesis could be tested by removing the brushes from mature brush-legged males and observing its effect on their probability of successfully killing a prey item.

Improved catching abilities following maturation appear to balance higher proportions of escaped prey items with age, therefore resulting in constant proportions of killed prey items over time. By balancing proportions of caught and escaped prey items, mature brush-legged males can maintain similar proportions of killed prey for consumption as they had as penultimates, therefore maintaining foraging efficiencies over time despite costs of ornamentation.

High margins of error due to small sample sizes and possible influences from genetic differences between male forms could have affected the validity of these results.

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While past studies have suggested that males resembling *S. ocreata* and *S. rovneri* in the Mississippi mixed population are members of one biological species (Hebets & Vink 2007), additional molecular and behavioral studies have not confirmed this categorization (Fowler-Finn & Hebets *in prep*, Sullivan-Beckers & Hebets *in prep*). To complement this experiment and remove any influences from form-specific biases, possible genetic differences, and sample size deficiencies, future experiments are necessary to pinpoint the effects of ornamentation on wolf spider foraging.

Ornamentation has been found to influence foraging behaviors in other animal taxa. By inducing energetic costs (Allen 2007, Hasselquist 2008), augmenting risks of predation (Grether 1997, Moller & Lope 1994), and causing changes in foraging strategies (Moller & Lope 1994), ornamentation shapes the possessor's physical foraging capabilities (i.e. mobility, prey capture, etc.), tactics, and potential foraging success. By investigating the costs of ornamentation in a population of *Schizocosa* wolf spiders, additional support for costs of ornamentation has been found.

Reduced foraging efficiency due to ornamentation has been found in other species, such as in barn swallows, a species in which males with experimentally elongated tails capture smaller, less profitable prey items, while males with shorter tails capture large, more profitable prey items (Moller & de Lope 1994). Ornamentation among these birds is believed to create mobility (i.e. flight) costs, impair mobility capabilities, or cause changes in foraging strategies due to the degree of ornamentation in an individual (Moller & de Lope 1994). Similarly to this experiment, other studies have not been able to identify which foraging aspect—whether energetic, physical, or

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behavioral— ornamentation is affecting, or if it is actually a combination of multiple components influencing foraging behavior and success.

Implications from this study are far-reaching across the animal kingdom. Since ornamentation is subject to sexual and natural selection, costs of ornamentation will influence the evolution of secondary sexual traits across many animal taxa, including other species within the order *Araneae*. Many species within the genus *Schizocosa* have sexually dimorphic ornamentation among mature males, either in the form of brushy setation or dark pigmentation on their foremost pair of legs (Stratton 2005). Some species in other *Lycosidae* genera, such as *Alopecosa*, *Evippomma*, and *Pardosa*, also have ornamental brushes on males' forelegs, although the trait is not as common among species as in *Schizocosa* (reviewed in Framenau & Hebets 2007). Since ornamentation is costly to males resembling *S. ocreata*, secondary sexual traits could be costly to foraging among ornamented males in these and other genera.

TABLES AND FIGURES

Table 1. *Summary of foraging behaviors of all trials. ANOVAs compare each behavior between male forms within one age group.*

Attacks		Brush-legged	Non-ornamented	ANOVA *p-values*

	Penultimate	11.667±1.653	8.370±0.846	0.0567

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	Mature	7.917±1.500	9.889±1.083	0.3081
	Mature	0.392±0.087	0.474±0.046	0.3696

Time Spent in				
Movement	*Mature*	277.583±58.244	176.593±28.033	0.0848

Literature Cited

Allen, Bengt J. and Jeffrey S. Levinton. *Costs of bearing a sexually selected ornamental weapon in a fiddler crab.* Functional Ecology, Vol. 21, No. 1 (2007), pp. 154-161.

Andersson, M. Sexual selection. (1994) Princeton University Press, Princeton.

Badyaev, Alexander V. and Cameron K. Ghalambor. *Does a Trade-Off Exist between Sexual Ornamentation and Ecological Plasticity? Sexual Dichromatism and Occupied Elevational Range in Finches.* Oikos, Vol. 82, No. 2 (Jun., 1998), pp. 319-324.

Barber, Iain, Stephen A. Arnott, Victoria A. Braithwaite, Jennifer Andrew, and

Figure 1: *Top-down view of experimental arena prior to trial start, with spider separated from crickets by cylindrical acetate barrier within large cylindrical arena.*

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Felicity A. Huntingford. *Indirect Fitness Consequences of Mate Choice in Sticklebacks: Offspring of Brighter Males Grow Slowly but Resist Parasitic Infections.* Proceedings: Biological Sciences, Vol. 268, No. 1462 (Jan. 7, 2001), pp. 71-76.

Buchholz, Richard. *Older Males Have Bigger Knobs: Correlates of Ornamentation in Two Species of Curassow*. The Auk, Vol. 108, No. 1 (Jan., 1991), pp. 153-160.

Clark, Christopher J. and Robert Dudley. *Flight costs of long, sexually selected tails in hummingbirds.* Proc. of the Royal Society, Vol. 276, No. 1664 (2009), pp. 2109-2115.

Darwin, Charles. The descent of man and selection in relation to sex, 1st edition (1871). Murray, London.

Framenau, Volker W. and Eileen Hebets. *A Review of Leg Ornamentation in Male Wolf Spiders, with the Description of a New Species from Australia, Artoria schizocoides (Araneae, Lycosidae).* The Journal of Arachnology, Vol. 35 (2007), pp. 89-101.

Grether, Gregory F. *Survival cost of an intrasexually selected ornament in a damselfly.* Proc. of the Royal Society, Vol. 264 (1997), pp. 207-210.

Grether, Gregory F. and Richard M. Grey. *Novel cost of a sexually selected trait in the rubyspot damselfly Hetaerina americana: conspicuousness to prey.* Behavioral Ecology, Vol. 7, No. 4 (1996), pp. 465-473.

Hebets, Eileen A. and Daniel R. Papaj. *Complex Signal Function: Developing a Framework of Testable Hypothesis.* Behavioral Ecology and Sociobiology, Vol. 57 (Jan., 2005), pp. 197-214.

Hebets, Eileen A. and George W. Uetz. *Female responses to isolated signals from*

multi-modal male courtship displays in the wolf spider genus Schizocosa *(Araneae: Lycosidae).* Animal Behavior, Vol. 57 (1999). pp. 865-872.

Hebets, Eileen A. and George W. Uetz. *Leg Ornamentation and the Efficacy of Courtship Display in Four Species of Wolf Spider (Araneae: Lycosidae).* Behavioral Ecology and Sociobiology, 47 (2000), pp. 280-286.

Hebets, Eileen A. and Cor J. Vink. *Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders.* Behavioral Ecology and Sociobiology, Vol. 47, No. 4 (Mar., 2007), pp. 280-286.

McClintock, William J. and George W. Uetz. *Female choice and preexisting bias: visual cues during courtship in two* Schizocosa *wolf spiders (Araneae: Lycosidae).* Animal Behavior, Vol. 52 (1996), pp. 167-181.

Moller, Anders P. and Florentino de Lope. *Differential Costs of a Secondary Sexual Character: An Experimental Test of the Handicap Principle.* Evolution, Vol. 48, No. 5 (1994), pp. 1676-1683.

Morse, Douglas H. *Excretion Behavior of Adult Female Crab Spiders Misumena vatia (*Araneae, Thomisidae*).* Journal of Arachnology, Vol. 36, No. 3 (2008), pp. 612-614.

Newkirk, M.R., *Biology of the longtailed dance fly* Rhamphomyia longicauda *(Diptera: Empididae).* Annals of the Entomological Society of America, Vol. 63 (1970), pp. 1407–1412.

Nowicki, S., D. Hasselquist, S. Bensch, and S. Peters. *Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice.* Proc. of the Royal Society, Vol. 267, No. 1460 (2000), pp.

2419-2424.

Scheffer, Sonja J., George W. Uetz, and Gail E. Stratton. *Sexual Selection, Male Morphology, and the Efficacy of Courtship Signaling in Two Wolf Spiders (Araneae: Lycosidae).* Behavioral Ecology and Sociobiology, Vol. 38, No. 1 (1996), pp. 17-23.

Stratton, Gail E. *Evolution of Ornamentation and Courtship Behavior in Schizocosa: Insights from a Phylogeny Based on Morphology (Araneae, Lycosidae).* Journal of Arachnology, Vol. 33, No. 2 (2005), pp. 347-376.

Stratton, Gail E. and George W. Uetz. *Acoustic Communication and reproductive isolation in two species of wolf spiders (Araneae: Lycosidae).* Science, Vol. 214 (1981), pp. 575-577.

Stratton, Gail E. and George W. Uetz. *The inheritance of courtship behaviors and its role as a reproductive isolating mechanism in two species of* Schizocosa *wolf spiders (Araneae: Lycosidae).* Evolution, Vol. 40 (1986), pp. 129-141.

Taylor, Phillip W., J. Andrew Roberts, and George W. Uetz. *Flexibility in the multi-modal courtship of a wolf spider,* Schizocosa ocreata. Journal of Ethology, Vol. 23 (2005), pp, 71-75.

Uetz, George W. and Charles D. Dondale. *A New Wolf Spider in the Genus* Schizocosa (Araneae: Lycosidae) *from Illinois.* Journal of Arachnology, Vol. 7, No. 1 (1979), pp. 86-88.

Uetz, George W., Randi Papke, and Beril Kilinc. *Influence of Feeding Regime on Body Size, Body Condition and a Male Secondary Sexual Character in Schizocosa ocreata Wolf Spiders (Araneae, Lycosidae): Condition-Dependence in a Visual Signaling Trait.* Journal of Arachnology, Vol. 30, No. 3 (2002), pp. 461-469.

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Uetz, George W. and J. Andrew Roberts. *Multi-sensory cues and multi-modal communication in spiders: insights from video/audio playback studies.* Brain Behavior and Evolution, Vol. 59 (2002), pp. 222-230.

Zahavi, Amotz. *Mate selection - a selection for a handicap.* Journal of Theoretical Biology, 53 (1975), pp. 205-214.

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