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Foreleg Ornaments Do Not Hinder Foraging Success in Brush-Legged Wolf Spiders

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Abstract Secondary sexual traits are often assumed to increase reproductive success but can also carry costs for males bearing them. Here, we investigate potential foraging costs of foreleg ornamentation in wolf spiders in the genus *Schizocosa*. Given that the forelegs are involved in securing prey items and that ornaments may also inhibit general mobility, we hypothesized that the presence of ornamentation inhibits foraging success. To test this, we first took an ontogenetic approach. We conducted an experiment to examine variation in foraging behavior before and after ornament development in a population of *Schizocosa* that exhibits two male phenotypes: (a) brush-legged males that develop large brushes of hairs on their forelegs upon maturation and (b) non-ornamented males that lack ornamentation. When comparing penultimate versus mature foraging behavior between these two phenotypes, we predicted (i) reduced foraging intensity upon maturation for males of both groups (due to increased mate-searching behavior) and (ii) a greater decrease in foraging efficiency in brush-legged versus non-ornamented males (due to costs of ornamentation). As expected, we found that when exposed to prey, all males exhibited greater latencies to attack as matures than as penultimates, but unexpectedly, they differed in their patterns of attack frequency; brush-legged males

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decreased the number of attacks upon maturation while non-ornamented males increased. We found no support for our second prediction: neither male phenotype exhibited a change in foraging success upon maturation. Given that foraging behavior differed between ontogenetic stages, making it difficult to isolate the effects of ornamentation per se, we conducted a second experiment with a pure brush-legged population (*S. ocreata*) to directly test the influence of foreleg brushes on foraging behavior. We compared foraging behavior between mature males with brushes present versus mature males with brushes artificially removed and found no effect of the presence/absence of brushes on foraging success. In summary, using both ontogenetic and ornament manipulation approaches, we found no support for the hypothesis that ornamentation influences foraging success; however, we do document phenotype-dependent foraging behavior.

Keywords Ornamentation costs · foraging success · wolf spider · *Schizocosa* · sexual selection

Introduction

Sexual selection theory predicts the evolution of exaggerated sexual display traits, such as ornamentation, which increase reproductive success by increasing either competitive ability or attractiveness to potential mates (Andersson 1994). While sexual display traits are often beneficial for securing mates, they can also be costly for males that bear them (Zahavi 1975). For example, the presence or exaggeration of ornaments can reduce prey capture success by increasing conspicuousness to prey (Grether and Grey 1996), increasing energy expenditure (Basolo and Alcaraz 2003; Walther and Clayton 2005), reducing locomotor capabilities (Garcia et al. 1994; Barbosa and Moller 1999; Allen and Levinton 2007), or increasing predation risk and decreasing survival (Grether 1997; Zuk and Kolluru 1998). Costs incurred through sources of natural selection may therefore limit the expression of sexual ornamentation.

Despite the recognition that costs of ornamentation are widespread, the influence of ornamentation on foraging behaviors has received little attention (*but see* Matyjasiak et al. 1999; Moller et al. 1995). Ornaments may hinder foraging in multiple ways. First, larger ornaments may decrease the bearer's speed and/or mobility (Swallow et al. 2000; Ribak and Swallow 2007; Clark and Dudley 2009), and thus could reduce foraging rates (Oufiero and Garland 2007). Second, among predatory species, ornaments located on appendages directly involved in prey capture could interfere with securing and handling of prey. This type of physical impedance may limit the efficiency of foraging in terms of, for example, the size and number of prey secured (Moller and Delope 1994; Matyjasiak et al. 1999). Reduced foraging success as a result of either of the above-mentioned effects of ornamentation may represent important sources of selection shaping the evolution of sexual ornaments.

Here, we test for potential costs of ornamentation on foraging behavior in wolf spiders, which are ground-dwelling, sit-and-wait predators that prey on a variety of small arthropods (Toft and Wise 1999). Prey capture typically involves quick movements during which an individual lunges and grabs passing prey with its forelegs and pedipalps. We focus on a group of spiders in the genus *Schizocosa* as they provide an excellent opportunity to test the influence of ornamentation on foraging behavior.

This group is ideal for such a study because: (i) their ornaments are located on appendages which can also be used in foraging and locomotion (ii) ornamentation develops only after the final molt to adulthood and thus should influence foraging only in the adult stage, (iii) males exhibit natural variation in the presence/absence of large and conspicuous sexual ornaments on the forelegs both between species and even within single populations, and (iv) male ornaments can be experimentally manipulated (Bern 2011; Hebets et al. 2011; Scheffer et al. 1996; Stafstrom and Hebets 2013; Wilgers and Hebets 2012a). We take advantage of these unique attributes by combining ontogenetic and manipulative approaches to determining costs of ornamentation on male foraging behavior.

We use two populations of *Schizocosa*. The first exhibits a mix of two naturally-occurring male phenotypes that vary in the presence/absence of ornamentation (Hebets and Vink 2007). Brush-legged males develop conspicuous ornaments on the forelegs after maturation; these ornaments consist of large black brushes extending dorsally and ventrally from the foreleg tibiae, and are involved in visual courtship displays similar to those exhibited by males of the closely-related species *S. ocreata* (Stratton and Uetz 1981; Stratton and Uetz 1986; Stratton 2005). In contrast, non-ornamented males do not develop foreleg ornamentation upon maturation and their courtship is similar to males of the closely-related species *S. rovneri* (Uetz and Dondale 1979). While the precise taxonomic status of this mixed-phenotype population has yet to be determined, it has been established that these brush-legged and non-ornamented males are genetically indistinguishable from each other, forming a genetic group that is distinct from its closest relatives *S. ocreata* and *S. rovneri* (Fowler-Finn 2009, Fowler-Finn et al. unpub, Hebets and Vink 2007). In addition to exhibiting natural variation in the presence/absence of ornamentation, this population is of particular interest because it has been the focus of a series of studies investigating costs of ornamentation, including those related to predation (Fowler-Finn and Hebets 2011a; Fowler-Finn and Hebets 2011b) and locomotion (Fowler-Finn et al., unpub).

Using this mixed population, we compared foraging behavior of brush-legged and non-ornamented males before and after maturation (and thus before and after the development of ornaments). Given the likely changes in motivation between penultimate and mature males (e.g. a shift from foraging to mate-searching) (Hallander 1967; Framenau 2005), we expected a priori that in the presence of prey all males, regardless of phenotype, would increase latency to attack, decrease the number of attacks, and increase movement (i.e. related to mate-searching behavior) following maturation. If ornamentation represents a cost for foraging, we expected to observe a greater reduction in attack success following maturation by brush-legged males as compared to non-ornamented males.

The second population used in our second experiment exhibits purely brush-legged males (*S. ocreata*). We use males from this pure population to compare foraging behavior between mature males with their brushes present versus mature males with brushes experimentally removed (i.e. absent). This is an important comparison that allows us to overcome any potential variation between ontogenetic stages or between brush-legged and non-ornamented males in patterns of foraging (e.g. those due to motivational or other behavioral differences) by isolating the physical effects of the presence/absence of brushes on foraging. We predict that if

the physical presence of brushes is costly for foraging, males with brushes absent should exhibit higher foraging success compared to males with brushes present.

Ultimately, we use two experiments: one taking advantage of ontogenetic changes in male ornamentation within a population of mixed phenotypes, and one taking advantage of the ability to experimentally manipulate the presence/absence of ornamentation in a population of purely ornamented males. These approaches enable us to discern potential costs of ornamentation in wolf spiders and to separate these costs from simultaneous effects of behavioral/motivational changes after maturation.

Materials & Methods

Foraging Trials

We implemented the same experimental design and protocol for foraging trials in both experiments as follows. Prior to testing, we weighed each spider, and then placed it in a 13.0×7.5 cm cylindrical arena lined with white filter paper. We initially restricted the spider to the center of the arena within a 3.0×6.25 cm cylindrical acetate barrier during a two-minute period of acclimatization (Fig. 1). Both the acetate barrier and arena were surrounded with opaque white paper. In the larger arena (outside of the space within the acetate barrier), we placed six freely moving crickets, with each weighing $\sim 1/4$ of the spider's mass. Following the acclimatization period, we lifted the acetate barrier, and the spider was able to make contact with and potentially forage on the crickets. We conducted [Experiment 1](#) trials for 45 min; and, as most

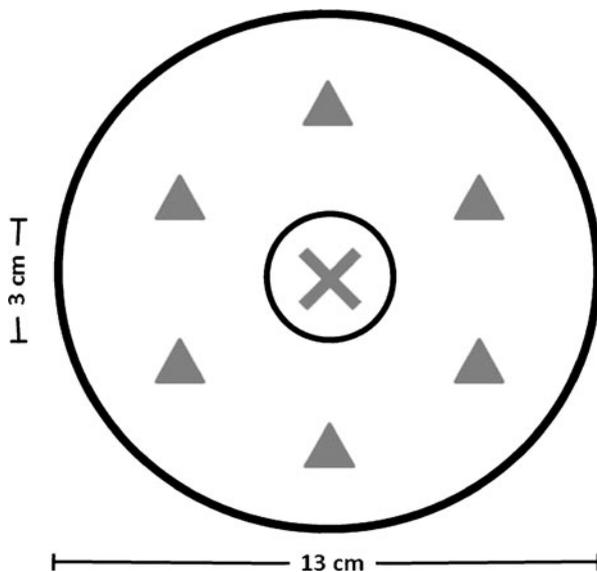


Fig. 1 Experimental design, drawn to scale. Each spider (represented by a gray X) was placed within the central cylindrical acetate barrier in the center of the larger cylindrical arena. Six freely moving crickets (represented by gray triangles) were located within the larger arena, outside the acetate barrier. The arena was lined with white filter paper, and the arena and acetate barrier walls were surrounded by opaque white paper

foraging behaviors occurred within the first 30 min of [Experiment 1](#) trials, we conducted [Experiment 2](#) trials for 30 min. At the end of each trial, we removed any mobile crickets from the arena, and left the spider in the arena with dead crickets until prey consumption ceased and the spider discarded prey remains. In [Experiment 1](#), we scored behaviors related to foraging success during each trial using a scoring rubric that allowed for accurate and efficient recording of behavior real time. We additionally recorded all trials onto Sony Mini DV digital videocassettes using a Sony Handycam HDR-HC9 video camera to assess behavioral differences between the two phenotypes in motivational-related behaviors. In [Experiment 2](#), we solely focused on those behaviors related to foraging success and thus scored behaviors in real time during each trial.

The behavior related to foraging success that we examined in both experiments included all attacks, catches, misses, kills, and escapes that occurred. We categorized the 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 cricket for at least 3 s; 3) *miss*: spider attacks but does not contact cricket; 4) *kill*: following a catch, spider kills or fatally injures cricket and begins its consumptive process; and (5) *escape*: occurring when a previously caught cricket escaped from a spider's grasp after withstanding little to no injury. We did not track individual crickets, thus totals of each behavior could apply to any and/or all six crickets in a trial. We calculated 'attack success' as the proportion of crickets killed out of the total number of crickets attacked during one foraging trial.

For [Experiment 1](#), we also scored videos for behaviors related to potential variation in motivation between male phenotypes. These behaviors included latency to its first attack (i.e. 'latency to attack') as well as each spider's total time spent moving in the forward direction over the entire 45-minute trial (i.e. 'time spent in forward movement').

Experiment 1: Ontogenetic Changes: Brush-legged versus Non-ornamented

In [Experiment 1](#), we compared behaviors of brush-legged ($n=13$) and non-ornamented ($n=18$) males from a population where both phenotypes naturally occur ([Hebets and Vink 2007](#)). We reared spiders from lab-mated females collected near the greenhouse of the University of Mississippi in Oxford, MS, USA in the spring of 2008. We housed spiders individually with a constant supply of water, and maintained them on a life-long low quantity diet. We chose this diet to encourage lifelong active, aggressive foraging while maintaining adequate spider health, in line with a prior study which demonstrated that long-term prey availability limitation increased foraging effort among web-building spiders ([Mayntz et al. 2009](#)). We fed spiderlings either one fruit fly (*Drosophila melanogaster*, raised in L. Harshman's laboratory at Univ. of Nebraska-Lincoln) or one pinhead cricket (*Acheta domesticus*, from Bassett's Cricket Ranch, Inc., Visalia, CA U.S.A.) weekly until their third molt. Upon their third molt, we fed spiders one cricket (*Acheta domesticus*, from Bassett's Cricket Ranch, Inc., Visalia, CA U.S.A.) matched to spider body size every other week. As spiders developed, an increase in prey quantity was required to prevent starvation, thus we increased feeding rate to one size-matched cricket every week. These conditions standardized hunger levels and motivation to feed.

We used a repeated measures design to assess variation in foraging behaviors across stages of maturity (penultimate vs mature) and across phenotypes (brush-legged vs non-ornamented). Each spider participated in two foraging trials: the first during its penultimate instar and the second shortly after maturity. To standardize the timing of trials among individuals, the first trial was conducted 14–21 days following the spider's penultimate molt (the molt immediately preceding the maturation molt) and the second trial was conducted 3–5 days following its mature molt. These trials will be referred to hereafter as the 'penultimate trial' and 'mature trial', respectively. To standardize hunger levels and minimize differences in feeding motivation, we did not feed spiders for 7 days prior to their penultimate trials (i.e. for 7–14 days following the penultimate molt) and for 3–5 days prior to their mature trials (i.e. for 3–5 days following the mature molt). It was not possible to standardize the feeding of the mature trial individuals beyond 3–5 days since we could not be predict when spiders would molt.

All recorded behaviors (number of attacks, time spent in forward movement, latency to attack, and attack success) were entered into the same general linear model (GLM) as separate responses. We included maturity status (penultimate vs. mature), phenotype (brush-legged vs. non-ornamented), and the maturity status \times phenotypes as fixed effects in the model. Because all individuals were tested twice, we included individual ID as a random effect in the models. A significant effect of maturity status indicates a change in foraging behavior with maturation for both phenotypes, and a significant effect of phenotype indicates an overall difference in foraging behavior between brush-legged and non-ornamented males. A significant interaction between maturity status and phenotype indicates a difference in the change in behavior from immature to mature between brush-legged and non-ornamented males. We conducted all GLM analyses and created all figures with plotted error bars representing ± 1 standard error in R 2.15.1 (R Core Team 2012).

Experiment 2: Presence/Absence of Brushes

In [Experiment 2](#), we directly test the physical influence (presence/absence) of brushes on foraging behavior using males from a population of brush-legged *S. ocreata*. We tested mature males only. We collected immature spiders (~3 instars prior to maturity) at Nine-Mile Prairie, near Lincoln, Nebraska, USA, in the spring of 2010. We housed the spiders as for [Experiment 1](#) and fed spiders one size-matched cricket every week. We ensured that brush-legged males from this population and brush-legged males from the mixed population used in [Experiment 1](#) demonstrated similar foraging behaviors by testing foraging behaviors of a subset of these males ($n=18$) according to [Experiment 1](#) protocol and comparing behaviors between the two populations of brush-legged males. We detected no significant differences in any aspects of foraging behavior between brush-legged males of the two populations ($p>0.05$ for all behaviors), allowing us to further explore effects of brushes in *S. ocreata* and complement our results from [Experiment 1](#).

Upon maturation, we randomly assigned each spider to one of two treatments: brushes present or brushes absent. To create these two treatments groups we physically manipulated the presence/absence of brushes. Three days after maturation we placed each spider in a plastic bag and coaxed it into a small hole in one corner of the

bag. We drew the spider's front legs through the hole and placed them upon a piece of styrofoam located under a dissecting scope. Looking through the dissecting scope, we shaved the brushes of the "brushes absent" treatment ($n=42$) using a small syringe needle. As a sham treatment, we manipulated and rubbed the brushes of the "brushes present" ($n=41$) with a pair of soft tweezers to mimic the handling of the "brushes absent" treatment. We allowed spiders to recover for 24 h before participating in a foraging trial.

We did not feed spiders for 3–5 days following maturation, and tested spiders 3–5 days post-maturation using the same procedure used in [Experiment 1](#). We recorded the same behaviors as in [Experiment 1](#) in real time with the exceptions of time spent in forward movement and latency to attack. Additionally we quantified each spider's maximum number of crickets held in its mouth at one time to further explore potential interference of brushes on prey handling.

We conducted two-sample t -tests, with brushes treatment (present vs absent) as a fixed effect and number of attacks, proportion killed, and maximum crickets held in mouth as response variables. All analyses were conducted in R 2.15.1 (R Core Team 2012).

Results

Experiment 1—Ontogenetic Changes: Brush-legged versus Non-ornamented

Our GLM revealed a significant phenotype \times maturity status interaction, indicating a difference between brush-legged and non-ornamented males in change in the number of attacks made as penultimates versus matures. Males of both phenotypes attacked with similar frequencies as penultimates, but brush-legged males decreased the number of attacks made with maturity, whereas non-ornamented males increased attacks with maturity (phenotype \times maturity status: F -ratio=6.115; $p=0.0179$; [Fig. 2a](#), [Table 1](#)). Brush-legged and non-ornamented males both increased latency to attack upon maturation (maturity status effect: F -ratio=7.704; $p=0.0084$), but the non-significant interaction term indicates that the pattern of change from immaturity to maturity did not differ between phenotypes (phenotype \times maturity status: F -ratio=0.000; $p=0.9920$; [Fig. 2b](#), [Table 1](#)). No difference was seen in time in forward movement ([Fig. 2c](#), [Table 1](#)). Finally, brush-legged and non-ornamented males did not differ in rates of attack success with maturity status (phenotype \times maturity status: F -ratio=0.013; $p=0.9090$; [Fig. 2d](#), [Table 1](#)).

Experiment 2—Presence/Absence of Brushes

We found no significant effects of brush presence on number of attacks made, attack success, or maximum crickets held in mouth (all two-sample t -tests: $p>0.05$; refer to [Table 2](#) for individual t -statistics and p -values; [Fig. 3](#)).

Discussion

Using both an ontogenetic approach with a polymorphic population of *Schizocosa* and a manipulative approach using a pure population of brush-legged *S. ocreata*, we

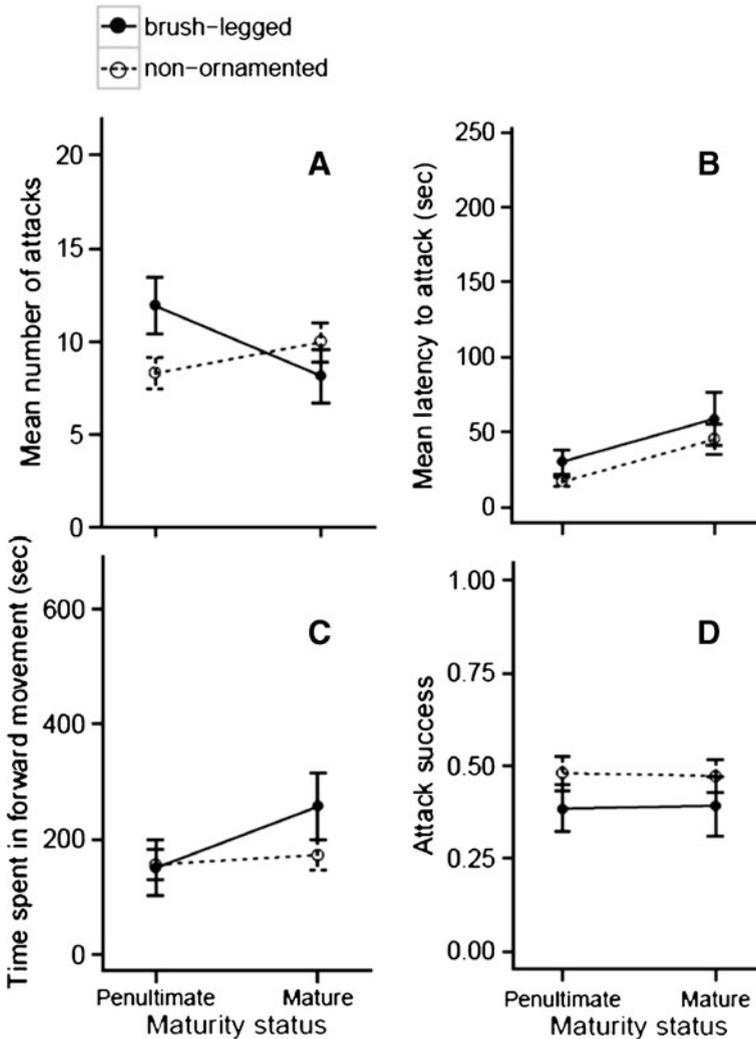


Fig. 2 Summary of each measure of foraging behavior per phenotype across maturity status for [Experiment 1](#). The y-axis ranges are drawn to encompass the minimum and maximum values measured for each behavior. **a** Mean number of attacks per trial, with a significant phenotype \times maturity status interaction ($p=0.0179$). **b** Mean latency to attack per trial, with a significant effect of maturity status ($p=0.0084$). **c** Mean time spent in forward movement per trial, with neither significant effects nor interactions found. **d** Attack success rate, with neither significant effects nor interactions found

found no evidence that ornamentation represents a foraging cost to *Schizocosa* wolf spiders. Data from the mixed population of brush-legged and non-ornamented males revealed similar patterns of foraging success across life stages and removing the brushes of *S. ocreata* males did not influence their foraging success. We also found phenotype-specific changes in behavior across ontogeny: brush-legged males reduced attack rates after maturation while non-ornamented males increased them. Our results are consistent with other phenotype-specific behavioral differences already documented between these

Table 1 General linear model output evaluating variation for each behavioral response with respect to phenotype ('Pheno') and maturity status ('Mat'), including a random term of spider ID ('ID'). * $p < 0.05$; ** $p < 0.01$

Source	d.f.	Attacks		Latency to attack (s)		Forward movement (s)		Attack success	
		MS	F	MS	F	MS	F	MS	F
Pheno	1	14.82	0.481	3294	1.952	26973	0.755	0.1382	2.733
ID(random effect)	39	30.80		1687		35710		0.0506	
Mat	1	0.05	0.002	16694	7.704**	41846	3.102	0.0001	0.002
Pheno × Mat	1	131.74	6.115*	0	0.000	35689	2.646	0.0009	0.013
ID × Mat	39	21.54		2167		13489		0.0696	

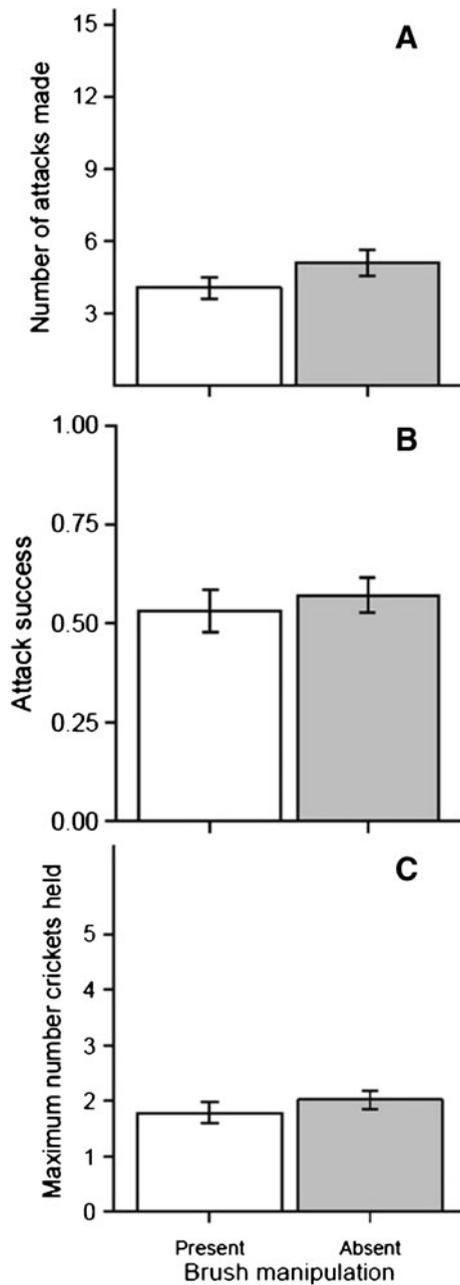
two male forms (Hebets and Vink 2007; Fowler-Finn and Hebets 2011a; Fowler-Finn et al. 2013).

Prior work has demonstrated that ornamentation can increase energetic costs (Allen and Levinton 2007; Hasselquist and Bensch 2008), increase risk of predation (Moller and Delope 1994; Grether 1997; Roberts et al. 2007; Roberts and Uetz 2008; Fowler-Finn and Hebets 2011a), and influence foraging strategies (Moller and Delope 1994; Moller et al. 1995). These wide-ranging costs of ornaments may influence many fitness-related behaviors, including foraging capabilities, foraging tactics, and foraging success. However, we found that ornamentation does not appear to impede the ability to capture and subdue prey in brush-legged *Schizocosa* wolf spiders. We found no differences in attack success between immature versus mature brush-legged males and no differences between mature brush-legged versus mature non-ornamented males. Additionally, experimental manipulation of brushes did not influence attack success, the number of attacks, or the maximum number of crickets a male held at one time. We note here that if our experimental manipulation inadvertently hindered an individual's ability to effectively forage (e.g. by removing critical sensory structures associated with foraging), we would have expected to see differences in foraging behavior between brushes present and absent treatments in the opposite direction of our predictions. As we detected no significant differences in foraging between males with brushes present versus absent, we do not expect that our

Table 2 Summary of two-sample t-tests (brush-legged males with brushes present vs brush-legged males with brushes absent) in Experiment 2. No significant differences were found between treatment groups for all behaviors

Behavior	Treatment	Mean ± 1 SE	t	p-value
Number of attacks	Present	5.12±0.54	1.49	0.14
	Absent	4.07±0.45		
Attack success	Present	0.57±0.04	0.56	0.58
	Absent	0.53±0.05		
Maximum crickets held in mouth	Present	2.02±0.16	0.97	0.34
	Absent	1.79±0.19		

Fig. 3 Summary of each measure of foraging behavior per treatment. The y-axis ranges are drawn to encompass the minimum and maximum values measured for each behavior. **a** Mean number of attacks per trial, with no treatment effect. **b** Mean attack success per trial, with no treatment effect. **c** Mean maximum crickets held in mouth per trial, with no treatment effect



manipulations themselves impacted foraging behavior. Ultimately, data from the two independent experiments suggest that male foreleg brushes in these wolf spiders do

not impose a foraging cost in terms of prey capture success. An additional cost to foraging that could be addressed in future studies includes increased avoidance by prey in response to the conspicuousness of ornamented predators.

Although we did not find ornament-specific foraging differences, we document a pattern of behavioral differences between two male phenotypes (brush-legged and non-ornamented) from a mixed, presumably interbreeding population (Hebets and Vink 2007; Fowler-Finn 2009, Fowler-Finn et al., unpub). Specifically, we observed differences in the number of prey attacked. Observed patterns also hint at a potential difference in movement (see Fig. 2c). Brush-legged males reduced the number of attacks following maturation to a greater extent than non-ornamented males, and the pattern for both species was in the opposite direction. This pattern indicates that brush-legged males may have a lower motivation to forage as adults than non-ornamented males. The trend towards increased movement in brush-legged males may be coincident with this, as these males may spend more time actively searching for females, ultimately reflecting a different courtship strategy than non-ornamented males. These patterns are consistent with previous work that has found differences between these two male phenotypes in relation to other behaviors. Brush-legged males are more sexually aggressive toward females during courtship than non-ornamented males (Hebets and Vink 2007). They also initiate courtship more quickly than non-ornamented males in a predator-free environment (Fowler-Finn and Hebets 2011b). The consistency in behavioral differences between brush-legged and non-ornamented males across contexts may reflect general differences in reproductive strategies between the two male phenotypes that influence a suite of behaviors, including foraging strategy. Such potential differences in courtship and foraging strategies may have significant implications for patterns of reproductive isolation, an intriguing direction for future research.

Observed differences in number of attacks at maturation between the two male phenotypes may also reflect past and present investment in secondary sexual traits such as ornamentation or signaling. Data from multiple *Schizocosa* species have demonstrated the influence of juvenile foraging secondary sexual traits displayed at maturation (Uetz et al. 2002; Shamble et al. 2009; Wilgers et al. 2009; Bern 2011; Rundus et al. 2011; Wilgers and Hebets 2011; Wilgers and Hebets 2012b). For juvenile brush-legged males, foraging may be relatively more important, as these resources can be put into the development of ornaments – which are fixed at maturation. Although brush-legged males rely on both visual and seismic signals for mate attraction, evidence exists for the visual component being more important for mating success (Scheffer et al. 1996). In contrast to brush-legged males, non-ornamented males rely primarily on seismic courtship signaling, which is also known to reflect foraging history in at least two *Schizocosa* species (Rundus et al. 2011; Wilgers and Hebets 2011). In *S. ocreata*, however, seismic signals also vary with male condition and weight (Gibson and Uetz 2008), indicating the high likelihood that adult foraging patterns can also influence sexual signal production and potentially mating success. We propose that the differences we observe in number of prey attacked across life stages between males of these two phenotypes may reflect different strategies for investing in reproductive traits (e.g. the development of foreleg ornamentation and the deployment of courtship signals).

In conclusion, while reduced foraging efficiency due to costs of ornamentation has been found in other taxa (Moller and Delope 1994; Moller et al. 1995; Badyaev and Ghalambor 1998; Allen and Levinton 2007; Hasselquist and Bensch 2008) and other costs of ornamentation have been identified in this species complex (Pruden and Uetz 2004; Fowler-Finn and Hebets 2011b), we found no evidence of costs of ornamentation on wolf spider foraging rates or attack success. However, several behavioral differences between males differing in ornamentation highlight the need for future work to exploring phenotype-specific foraging behavior that is possibly tied to aggression.

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