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Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders

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Abstract

Female mate choice decisions are often based on a variety of male characteristics, some of which may reflect male quality via condition-dependent trait expression. Here, we explore the condition dependence of a male secondary sexual trait in a wolf spider and examine its influence on female mate choice. In the wolf spider *Schizocosa uetzi*, mature males possess a multimodal courtship display (visual + seismic) in which they slowly raise and lower their dark colored forelegs. Foreleg color is highly variable among *S. uetzi* males with respect to both total amount and darkness. Using diet manipulations in conjunction with color quantifications, we demonstrate condition-dependent foreleg color. High-nutrient diet males had significantly higher body condition indices and possessed more and darker foreleg color than low-nutrient diet males. However, using multiple mate choice designs, we were unable to demonstrate a female preference for male foreleg color. Using both single and 2-choice mating designs as well as using females from a range of ages, we found that copulation success was consistently independent of male foreleg color. Instead, we found courtship intensity to be the only aspect of male courtship that influenced copulation success—males that copulated displayed more leg raises per second than those that did not copulate.

Keywords: condition dependent, honest indicator, mate choice learning, mate choice, performance, *Schizocosa*, sexual selection

The prevalence and diversity of male secondary sexual characters posited problems for Darwin's theory of natural selection, necessitating the formulation of his theory of sexual selection (Darwin 1871). Although secondary sexual characters can evolve via nonadaptive mechanisms (e.g., pleiotropy), their maintenance and often elaboration are likely due to different selection pressures on the sexes—whether it be natural selection due to ecological differences (e.g., habitats, predators, and foraging) or the result of more commonly studied sexual selection (i.e., male–male competition, female choice; reviewed in Andersson 1994).

A multitude of studies have shown female mating preferences to be an intense source of selection capable of resulting in the evolution and elaboration of male ornaments (e.g., Kodric-Brown 1985; Møller 1990; Hill 1991; Baker 1993; Wilkinson and Reillo 1994; Pryke et al. 2001) and today, a number of hypotheses exist that attempt to explain the evolution of these female preferences (e.g., indirect benefits, Fisherian self-reinforcing selection, indicator mechanisms, direct benefits, and sensory bias; see Andersson 1994). One such hypothesis that has received much attention is the handicap principle (reviewed in Andersson 1994; Johnstone 1995; Cotton et al. 2004a; Andersson and Simmons 2006). The handicap principle suggests that females show a preference for male traits that are costly to produce and that only the highest quality males are capable of fully expressing these traits (Zahavi 1975). Thus, by basing mate choice decisions on these costly traits, females choose males of high quality. Because trait expression is assumed to be costly, one would then expect these traits to be directly correlated with male condition. Indeed, many researchers have found this to be the case (reviewed in Andersson 1994; Johnstone 1995; Cotton et al. 2004a) and have deemed

these male secondary sexual characters honest indicators of male condition and, when this translates into increased reproductive success, honest indicators of male fitness. The term “honest” can be applied in such cases because these costs keep males from falsely advertising their quality.

In order to experimentally explore the relationship between putative honest indicators and male fitness, one must first establish a correlation between condition and the secondary sexual trait(s) of interest. This is often accomplished by manipulating condition directly and measuring the resulting differential trait expression. Although there are a number of ways to influence condition (e.g., stress, parasite load, and hormone level), many studies have used diet manipulations. Diet manipulations are considered good starting points for examining condition dependence because of both the ease with which diet can be controlled and the natural biological relevance of variable food intake (Birkhead et al. 1999; Gray and Eckhardt 2001; Scheuber et al. 2003; Cotton et al. 2004b). Such diet manipulations have been successful in demonstrating condition-dependent secondary sexual trait expression across a variety of animal taxa (e.g., spiders: Uetz et al. 2002; crickets: Holzer et al. 2003; and birds: McGraw et al. 2002). Simply demonstrating condition-dependent trait expression, however, does not necessarily imply active selection via female choice. In order to assert that the condition-dependent trait has an impact on male fitness, variation in secondary sexual trait expression must be correlated with female mate choice. Only then can we begin to understand not only what influences the expression of these traits but also how they are used in a signaling context.

Wolf spiders in the genus *Schizocosa* have proved to be an extremely useful system in which to explore condition-dependent male trait expression and associated female choice due to

their variable and often elaborate secondary sexual characters frequently associated with conspicuous courtship movements (Stratton 2005; Framenau and Hebets 2007). For example, previous work has demonstrated that the male foreleg tufts in *Schizocosa ocreata* are condition-dependent (Uetz et al. 2002) and females are known to choose males based on tuft size and symmetry (McClintock and Uetz 1996; Scheffer et al. 1996; Uetz and Smith 1999; Persons and Uetz 2005; Uetz and Norton 2007). In addition, female choice in *Schizocosa* wolf spiders has recently been shown to be condition dependent, with females raised on high-nutrient diets exhibiting more choosiness than those raised on low-nutrient diets (Hebets et al. 2008).

The species of focus in this study, *Schizocosa uetzi*, is typified by males that possess dark color (likely due to ommochromes; Oxford and Gillespie 1998) on the tibiae of their forelegs. This tibia color varies within a population from medium brown (matching the rest of the leg) to black (see Figure 1 in Hebets et al. 2006). The forelegs that possess this color are involved in the multimodal courtship display of male *S. uetzi*. During courtship, males pair a seismic signal with a less frequent visual signal involving a slow foreleg arch—a raising and lowering of the foreleg while the femur–patella and tibia–metatarsus joints are held at constant angles (Stratton 1997; Hebets et al. 2006). The dark male foreleg color in *S. uetzi* has previously been shown to influence female mate choice only in specific situations. For example, females exposed to males with artificially colored forelegs (black vs. brown) prior to their own sexual maturation were shown to mate more with males of a familiar versus unfamiliar foreleg phenotype as adults (Hebets 2003). Furthermore, although female receptivity was demonstrated to be independent of male foreleg color in the absence of seismic signals (Hebets and Uetz 2000), females were more likely to display receptivity to more ornamented males in the presence of a seismic signal (Hebets 2005). However, the increased receptivity observed in this seismic present experiment was in response to foreleg ornamentation that was elaborated beyond the natural range for *S. uetzi*. Specifically, females in the seismic present experiment were more likely to display receptivity to a video playback of a male with black foreleg brushes versus one with no ornamentation. As stated above, *S. uetzi* males do not possess foreleg brushes and thus, it is unclear how these results could translate into the natural biology of *S. uetzi*. In an attempt to address this, a follow-up study used artificially colored live males mimicking the extremes of the natural range of color in *S. uetzi* (black foreleg tibiae vs. brown foreleg tibiae) to examine female mate choice. This study showed that in the presence of a seismic signal, female mate choice was not dependent on male tibia color (Hebets et al. 2006). Ultimately, although the multiple studies discussed above have certainly increased our knowledge of *S. uetzi* mating behavior, we are still left with fundamental questions regarding the function of male foreleg color, its influence on female mate choice, and its information content.

Here, we used diet manipulations and mate choice trials with males of naturally varying ornamentation in order to determine 1) if foreleg color is condition dependent and 2) whether or not females base their mating decisions on this secondary sexual trait.

Materials and Methods

Spider collection and maintenance

For all experiments, immature *S. uetzi* individuals (both male and female) were collected from a single site in Lafayette County, MS (34°36'N, 89°29'W) from mid-April to late May. In 2005, a total of 199 immature spiders, approximately 2–3

molts away from sexual maturity, were collected for the diet manipulation experiment. For the 3 female mate choice experiments, immature spiders were collected in successive years: 2006 (single-choice trials), 2007 (simultaneous 2-choice trials, old females), and 2008 (simultaneous 2-choice trials, young females). All females and most males were collected as immatures and thus were known virgins.

All spiders were brought back to the laboratory and housed in 6 cm × 6 cm × 8 cm plastic boxes and provided with a constant source of moisture. They were kept on a 12:12 h light:dark cycle and at normal laboratory temperature (ca. 22–24 °C). To monitor development, spiders were checked 2–3 times a week for molts. Molt dates were recorded until their final molt to maturity. All spiders in the female mate choice experiments were fed 2 crickets equal to the spider's body length every week. However, for the diet manipulation experiment, on arrival, all spiders were weighed immediately and then randomly assigned to either a high- or low-diet treatment that varied in both quantity and quality as described below.

Influence of diet on development, size, and secondary sexual traits

In order to determine if diet influences male foreleg color, we manipulated the diet of field-collected immature *S. uetzi* by randomly assigning them to 1 of 2 treatments—high- or low-nutrient diets. All spiders in both diet treatments were fed weekly. Individuals assigned to the high-nutrient diet received twice their body weight in live crickets. The feeder crickets for the high-nutrient diet spiders were fed fish flakes (TetraMin, Blacksburg, VA) and Fluker's Cricket Food (Port Allen, LA) and were given Fluker's Calcium Fortified Cricket Quencher for moisture. Spiders assigned to the low-nutrient diet were fed half their body weight in live crickets. The feeder crickets for the low-nutrient diet spiders were sustained on Fluker's Calcium Fortified Cricket Quencher alone. Cricket shipments arrived weekly and thus low-nutrient diet feeder crickets were without food for less than a week prior to use. To maintain accuracy, every spider and every serving of crickets was weighed immediately prior to each feeding.

After maturity, spiders used in the diet manipulation experiment were preserved as complete specimens in 70% ethyl alcohol. For all specimens in sufficiently good condition, measurements of the width of the cephalothorax at its widest point were recorded using digital calipers. All measurements were taken 3 times by the same individual and the average of the 3 values was used in our analysis. When possible, the male's left foreleg was removed and dehydrated by submersion in increasing concentrations of ethyl alcohol up to 100%. Each leg was treated with methyl salicylate by total submersion for 1 min and 45 s to clear the leg. Immediately after this treatment, the legs were mounted, lateral side up, on a flat glass slide using DPX clear mounting solution and a glass cover slip. These prepared slides were digitally photographed using a Leica DM 4000 B microscope with a Diagnostic Instruments, Inc. Spot Flex digital camera, under 1.25× objective and 1.2× camera coupler magnification. The slides were lit by a stage lamp from below and by dual fiber optic lights (Lumina 150 W) from above to allow for better resolution of surface color. The lighting remained exactly the same across photographs. Unfortunately, the legs of some specimens that perished before being sacrificed were not preserved in good enough condition to be analyzed. In addition, our method for mounting male forelegs resulted in some unusable specimens due to air bubbles entering the legs (see Results).

Color digital images were imported to a computer, where lengths of the femur and tibia leg segments were measured

using Discovery Pro (Version 5.1.0.18 for Windows 2000/XP Professional). These measurements were obtained by recording the linear distance between the most dorsal points at which the target segment met neighboring segments.

The dark color found on the mature *S. uetzi* male's forelegs was quantified for 30 low-nutrient diet males and 22 high-nutrient diet males. The color images were imported into Adobe Photoshop CS2 where they were converted to grayscale. The areas of the tibia and the metatarsus were measured by selecting the segment with the polygonal lasso tool and recording the number of pixels within the selection. Using the same process, values of the mean, median, and standard deviation of the image intensity (a numerical reading where 255 is white and 0 is black) were also recorded for both the tibia and the metatarsus. The darkest area of the tibia was manually identified by measuring the color intensity of the cuticle in the darkest area and recording the corresponding value. The percentage of the tibia covered by color was then calculated by using the threshold command in Photoshop to turn all pixels lighter than a given value white and all pixels darker than that value black, creating a high-contrast, 2-tone image. The threshold was set at one standard deviation darker than the mean tibia color for that year's males. After the black and white high-contrast image was created, the number of black pixels was recorded and the percentage of the tibia covered with dark color was calculated by dividing the number of black pixels by the total number of pixels in the tibia. Contrast between the tibia and metatarsal segments was calculated as the difference in mean color score between the segments. With the exception of the calculation of the percentage of tibia that was pigmented, all measurements were done based on a single image of each slide, but all measurements were independently repeated 3 times. An average of the 3 measurements was used in the final analysis.

Researchers have suggested that studies of condition dependence in which diet is manipulated must have proper controls to ensure that increased trait expression is truly the result of better condition and not simply an artifact of increased size (Cotton et al. 2004a). We compared the change in color with male body size (cephalothorax width) for 2 foreleg segments: the tibia (presumably secondary sexual coloration) and the metatarsus (presumably no secondary sexual coloration). We used the metatarsus as our control because, though slightly variable among males, it appears to be sexually monomorphic and is likely not a sexually selected trait. Slopes of the correlations between body size and leg segment color were compared using a *t*-test statistic as suggested by Zar (1999).

To gauge the effect of our diet treatment on male body condition throughout development, we used the ratio of body mass at maturation to cephalothorax width. We chose not to use residuals here because of the potential for small fluctuations in mass to be exaggerated in residual scores. Because this measure attempts to sum condition across development, we wanted to use a less dynamic measure of body condition.

Female mate choice

Experiment 1: Single choice trials

In order to determine if male foreleg color influences female mate choice, we conducted single-choice mating trials. Once mature, males were separated by visual inspection into 3 foreleg tibia color categories: light ($N = 17$), medium ($N = 18$), or dark ($N = 17$). All individuals were weighed immediately prior to trials. Trials ($N = 52$) took place in a circular plastic arena (20.5 cm diameter \times 7.5 cm height) surrounded by a white visual barrier and with a bottom of white filter paper. Mature females were placed alone in the arena for a minimum of 60 min to acclimate and deposit pheromone-laden silk (exact acclima-

tion times varied across trials). After the acclimation period, one male of a randomly chosen color category was introduced into the arena for 30 min or until copulation. Interactions were scored for the following: latency to initial courtship, courtship intensity (measured by the number of leg raises per second from the first courtship to copulation or the end of the trial), and latency to copulation (measured from the start of the trial). No females or males were used more than once. Females ranged in age from 20 to 33 days postmaturation with a mean \pm standard error, SE, of 29 ± 2.6 days. Males ranged in age from 27 to 38 days postmaturation with a mean \pm SE of 34 ± 2.9 days. When possible, males from these trials were sacrificed and preserved in 100% ethyl alcohol for later quantification of foreleg color as previously described, except that digital images were captured using a Leica MZ 16 stereoscope, lit from above by dual fiber optic lamps (Lumina 150 W).

In order to investigate the influence of body condition on copulation success, we used the residuals of a regression of body mass on cephalothorax width (Jakob et al. 1996). Both body mass and cephalothorax width were natural log transformed in order to standardize residual units across size (see Kotiaho 1999). We chose to use residuals here because we wanted a more dynamic estimation of condition, one which provides an estimate at a specific moment in time (i.e., during the mating encounter). In addition, we wanted a metric by which a female could potentially assess a male's current condition (a dynamic measure) relative to his condition due to development (a static measure). In other words, we wanted a measure of current body condition as compared with expected body condition given degree of coloration—which we now know to be dependent on developmental feeding history (see Results). To examine this, we developed the CRO ratio (condition relative to ornament), which we calculated by dividing the mean tibia darkness (i.e., degree of ornamentation) by the current body condition index (residual + 1). Adding one to the residual eliminated all negative condition indices and distributed the condition residual around 1. Because lower values for tibia color indicate darker leg segments, males with darker legs and in good current condition would result in lower CRO scores than males in poorer current condition or with lighter tibiae.

Experiment 2: Simultaneous 2-choice trials (old females)

In order to determine if females use foreleg color for mating decisions when given the opportunity to compare 2 males, we conducted simultaneous 2-choice trials. Once mature, males were divided into 2 tibia foreleg color groups—light or dark—by visual inspection. Trial pairs (1 dark male and 1 light male) were age matched so that they were never more than 7 days apart. One mature female was placed in a circular plastic arena (20.5-cm diameter \times 7.5-cm height) lined with filter paper and surrounded by a white visual barrier. Leaves were placed in the center to provide both a more natural signaling environment and a refuge for females. Females remained alone in the arena for at least 60 min to acclimate and deposit pheromone-laden silk (exact acclimation times varies across trials). After the acclimation period, one dark male and one light male were simultaneously introduced into the arena equidistant from the female and at opposite ends of the circular arena. Because females were allowed to acclimate without intervention, we were unable to control female orientation on male introduction. Trials lasted for 45 min or until one male copulated. We recorded the latency to courtship for each male, latency to copulation (time from the beginning of the trial) and all male-male interactions (touch and attempt mount) and male-female interactions (touch, attack, copulation, and cannibalism). Again, when possible, males were sacrificed and pre-

served for quantification of color using the same protocol as described above for Experiment 1.

A total of 35 trials were run using this design. Due to limited numbers of males given the 2-choice design, some males were run more than once. However, males were never paired with the same male (i.e., each male-male pairing was unique). A total of 49 different males were used: Thirty were used only once, 17 were used twice, and 2 were used 3 times. All males that were used multiple times were chosen haphazardly and 4 of the 17 males that were used twice mated in their initial trial. We quantified the tibia color from only males used in trials where there was a successful copulation. Female age ranged from 14 to 29 days postmaturation with a mean age (\pm SE) of 20 ± 4.6 days, whereas male age ranged from 9 to 34 with a mean of 19 ± 7.8 days.

Experiment 3: Simultaneous 2-choice trials (young females)

In order to determine if our lack of correlation between female mate choice and male foreleg color from Experiments 1 and 2 (see Results) could be due to using females of an inappropriate age class, we repeated Experiment 2 with younger females. Females from the previously described single-choice and 2-choice mating trials were on average 29 and 20 days postmaturity, respectively. Recent research on a closely related wolf spider, *S. ocreata*, demonstrated that female choosiness varies with age such that young females (2 weeks postmaturation) did appear to make mate choices based on visual ornamentation but older females (≥ 3 weeks) did not (Uetz and Norton 2007). Following from Uetz and Norton (2007), we wanted to be sure that our *S. uetzi* females were tested within a postmaturation window of high choosiness (if such a window exists for this species).

Once mature, males were again separated into 2 color groups—light or dark—by visual inspection. In the first round of trials, females 13–14 days postmaturation were placed in a circular plastic arena (20.5-cm diameter \times 7.5-cm height) lined with filter paper and leaves and allowed to acclimate for at least 60 min. One male of each group was then introduced and the same behaviors outlined in Experiment 2 were again recorded for a 30-min period. Males were never more than 4 days apart in age. Some males were used repeatedly, but again, never with the same male. Eight initial trials were run, each with a different female. A total of 14 different males were used: Twelve were used once (6 dark, 6 light), and 2 were used twice (these males were of an intermediate color and so served once in both color groups depending on the color level of the other trial male). The 2 males that were used twice were not reused in the subsequent trials (see below). Due to an absence of matings by all 8 females in this young age class, we chose to rerun the exact same triads at 26 days postmaturation (a time during which female *S. uetzi* are known to be receptive). Re-running the same 3 individuals in subsequent mate choice tri-

als enabled us to get an idea of whether the lack of mating that we observed initially was due to female age (i.e., females are unlikely to mate if they are 13–14 days old).

Statistical analysis

Statistics were calculated using JMP version 6.0 (SAS Institute; Cary, NC).

All results are reported as mean \pm SE. All *t*-tests are 2-tailed. All data were checked for normality and when necessary, non-parametric statistics were used. Discontinuities between sample sizes (e.g., the presence of larger sample sizes when reporting weights and fewer when discussing color measures) are often due to a loss of quantifiable forelegs during either the course of the experiment, during leg preservation, or during leg mounting.

Results

Influence of diet on male development, size, and secondary sexual traits

Of the 199 immature spiders collected, 115 matured into females and 84 matured into *S. uetzi* males. There was no difference between the initial weights of male spiders assigned to low versus high-diet treatments (low diet: $N = 43$, $\bar{x} = 0.010 \pm 0.0008$ g; high diet: $N = 41$, $\bar{x} = 0.010 \pm 0.0008$ g; Wilcoxon test, $Z = 1.06$, $P = 0.29$). Males subjected to the high-diet treatment molted more times than low-diet individuals before reaching maturation, although this trend was marginally insignificant (low diet: $N = 43$, $\bar{x} = 2.3 \pm 0.1$; high diet: $N = 41$, $\bar{x} = 2.8 \pm 0.2$; Wilcoxon test, $Z = 1.89$, $P = 0.059$). High-diet males matured 2 weeks earlier than low-diet individuals (Julian date, low diet: $N = 43$, $\bar{x} = 168.3 \pm 2.9$; high diet: $N = 41$, $\bar{x} = 154.9 \pm 3.0$; Wilcoxon test, $Z = 3.21$, $P = 0.001$).

Diet manipulations significantly affected the body size and condition of males (Table 1). High-diet males were larger based on tibia length ($t_{53} = 7.1$, $P < 0.001$), cephalothorax width ($t_{53} = 6.94$, $P < 0.001$), and maturation mass (Wilcoxon test, $Z = 5.35$, $P < 0.001$; Table 1). Spider cephalothorax width and maturation mass were highly correlated (Spearman's correlation, $\rho = 0.81$, $P < 0.001$). High-diet males were also in overall better condition as indicated by our index (maturation mass/cephalothorax width; Wilcoxon test, $Z = 4.82$, $P < 0.001$; Table 1). Body measurements are only reported for individuals for which we were able to acquire an adequate set of all relevant measurements ($N = 55$ males of a total of 84; high diet: $N = 28$, low diet: $N = 27$). Similarly, foreleg pigmentation was scored for only those males for which we felt confident in the slide preparation ($N = 52$ males of 84; high diet: $N = 22$, low diet: $N = 30$).

Diet manipulations significantly affected various components of foreleg ornamentation in males (Table 1). High-diet

Table 1. Influence of a diet manipulation on male measures of body condition and foreleg color in the wolf spider *Schizocosa uetzi*

Body measures	High diet (N)	High diet	Low diet (N)	Low diet	P value
Tibia length (mm)	28	2.85 ± 0.06	27	2.19 ± 0.07	< 0.001
Maturation weight (g)	28	0.042 ± 0.002	27	0.022 ± 0.002	< 0.001
Cephalothorax width (mm)	28	2.84 ± 0.06	27	2.25 ± 0.06	< 0.001
Body condition ^a	28	0.015 ± 0.0006	27	0.010 ± 0.0006	< 0.001
Measure of foreleg color					
Mean tibia color (K)	22	46.5 ± 3.8	30	74.1 ± 3.3	< 0.001
% Tibia pigmented	22	46.9 ± 5.8	30	12.3 ± 5.0	< 0.001
Metatarsus-tibia contrast (K)	22	28.0 ± 2.6	30	17.4 ± 2.2	0.002

a. Body condition was calculated as maturation mass/cephalothorax width.

males had darker mean tibia color (Wilcoxon test, $Z = 4.38$, $P < 0.001$), mean percentage of tibia covered by dark color ($t_{50} = 4.49$, $P < 0.001$), and significantly darker mean metatarsal color ($t_{50} = 4.87$, $P < 0.001$; Table 1). Male tibia darkness was negatively correlated (due to darker color indicated by smaller color scores) with male condition (Spearman's correlation, $\rho = -0.50$, $P < 0.001$). There was a significant negative correlation between cephalothorax width, a measure of body size that is set at maturation, and both mean tibia color (Spearman's correlation, $\rho = -0.56$, $P < 0.001$) and mean metatarsal color ($r^2 = 0.13$, $P = 0.01$). However, the change in degree of color per unit cephalothorax width was significantly greater for the tibia when compared with the noncolored metatarsal segment (a leg segment presumed not to be under sexual selection), as indicated by the significantly different slopes in the lines of the 2 correlations between the segments (tibia, metatarsus) and cephalothorax width ($t_{94} = 4.03$; $P < 0.001$; see "Comparing 2 slopes," Zar 1999). Thus, increasing foreleg contrast (metatarsus color - tibia color) is achieved through increases in tibia darkness as indicated by a significant negative correlation (Spearman's correlation, $\rho = -0.78$, $P < 0.001$). Given these correlations, it is not surprising that high-diet males' foreleg contrast was significantly greater than low-diet males (Wilcoxon test, $Z = 3.16$, $P = 0.002$; Table 1).

Female mate choice

Experiment 1: single mate choice

Of 52 pairings, 13 resulted in copulations: 5 with dark males, 6 with light males, and 2 with males of intermediate color. Male mean tibia color differed between the a priori assigned foreleg groups (light, medium, and dark; Kruskal-Wallis test, $\chi^2 = 27.67$, $P < 0.001$; Figure 1a) with all male foreleg groups being different from each other (Wilcoxon test, $P < 0.002$ for all pairwise comparisons; Figure 1a). There was no difference between male foreleg groups in male trial weight (dark: $N = 17$, $\bar{x} = 0.0544 \pm 0.002$ g; medium: $N = 18$, $\bar{x} = 0.0569 \pm 0.002$ g; light: $N = 17$, $\bar{x} = 0.0522 \pm 0.002$ g; Kruskal-Wallis test, $\chi^2 = 2.2$, $P = 0.33$) or male age at the time of the trial (dark: $N = 17$, $\bar{x} = 33.8 \pm 0.7$ days postmaturation; medium: $N = 17$, $\bar{x} = 35.1 \pm 0.7$ days postmaturation; light: $N = 16$, $\bar{x} = 34.2 \pm 0.7$ days postmaturation; Kruskal-Wallis test, $\chi^2 = 2.51$, $P = 0.29$). Two males (1 light, 1 medium) were mature on collection and were not included in the analysis of male age. There was no difference in the latency to courtship between color group males (dark: $N = 17$, $\bar{x} = 163.4 \pm 92.0$ s; medium: $N = 18$, $\bar{x} = 366.6 \pm 89.4$ s; light: $N = 17$, $\bar{x} = 367.6 \pm 92.0$ s; Kruskal-Wallis test, $\chi^2 = 5.34$, $P = 0.07$). Furthermore, latency to courtship did not vary with copulation success (mated: $N = 13$, mean = 278.9 ± 107.6 s; unmated: $N = 39$, $\bar{x} = 307.7 \pm 62.1$ s; Wilcoxon test, $Z = 0.33$, $P = 0.74$).

We found no difference in the likelihood to copulate between males of the different color groups (Likelihood ratio, $\chi^2 = 3.3$, $P = 0.20$; Figure 1b). The above results group our males into our a priori assigned color groups. Similarly, we found no difference in mean tibia color between successful and unsuccessful males (mated: $N = 13$, $\bar{x} = 39.6 \pm 2.8$; unmated: $N = 38$, $\bar{x} = 36.0 \pm 1.6$; Wilcoxon test, $Z = 0.96$, $P = 0.34$). One mated male was not included in these and the following analyses due to incomplete data. We also found no difference in tibia contrast (as measured by the tibia mean color - metatarsus mean color) between successful and unsuccessful males (mated: $N = 13$, $\bar{x} = 30.5 \pm 3.5$, unmated: $N = 37$, $\bar{x} = 33.5 \pm 2.1$; Wilcoxon test, $Z = 0.58$, $P = 0.57$). Again, one unmated male was not included in the above analysis due to incomplete data. A male's current CRO (calculated as tibia darkness/condition residual + 1) also

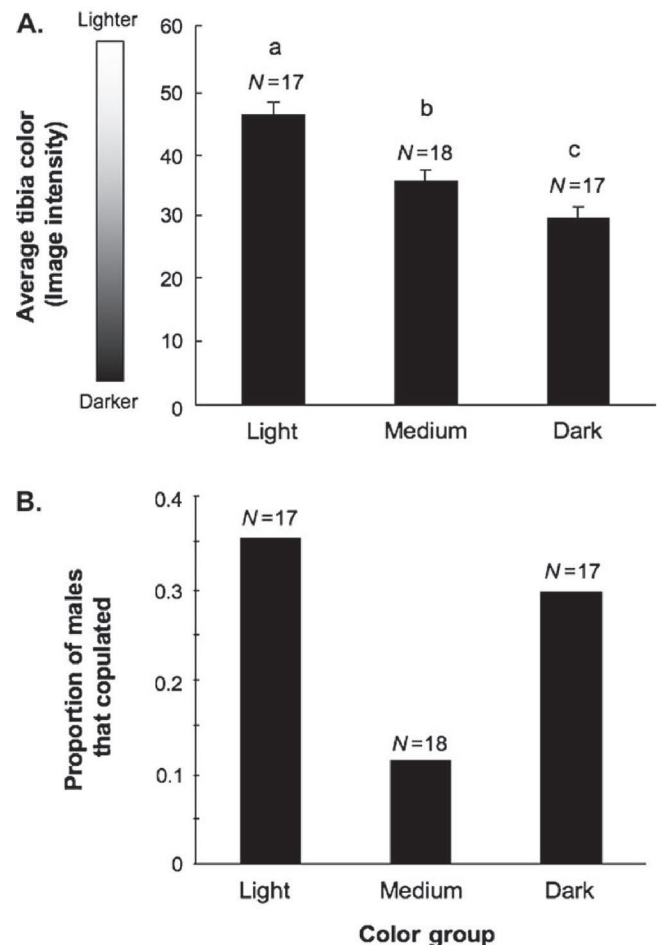


Figure 1. (A) Mean tibia color of each male color group. Lower scores indicate darker color. Mean tibia color differed significantly between the male groups ($P < 0.001$). Letters denote significant differences between groups as indicated by pairwise comparisons using Wilcoxon tests ($P < 0.002$ for all tests). (B) Proportions of males that successfully copulated during a single-choice mate test by color group. There was no difference in likelihood to copulate across males in different color groups ($P = 0.20$).

did not influence copulation success (mated: $N = 13$, $\bar{x} = 40.9 \pm 3.7$; unmated: $N = 38$, $\bar{x} = 36.9 \pm 2.1$, $t_{49} = 0.94$, $P = 0.35$).

Male copulation success was apparently independent of other male physical attributes, including male weight (mated: $N = 13$, $\bar{x} = 0.0527 \pm 0.002$ g; unmated: $N = 39$, $\bar{x} = 0.0552 \pm 0.001$ g; Wilcoxon test, $Z = 0.53$, $P = 0.60$), male body condition (mated: $N = 13$, $\bar{x} = -0.015 \pm 0.035$; unmated: $N = 39$, $\bar{x} = 0.005 \pm 0.02$; $t_{50} = 0.48$, $P = 0.63$), and male age (mated: $N = 13$, $\bar{x} = 34.0 \pm 0.8$ days; unmated: $N = 37$, $\bar{x} = 34.5 \pm 0.5$ days; Wilcoxon test, $Z = 0.70$, $P = 0.48$). Females that mated were not significantly different in age than those that did not (mated: $N = 13$, $\bar{x} = 29.5 \pm 0.7$ days postmaturation; unmated: $N = 39$, $\bar{x} = 29.6 \pm 0.4$ days postmaturation; Wilcoxon test, $Z = 0.97$, $P = 0.33$), but females that copulated weighed significantly less than those that did not (mated: $N = 13$, $\bar{x} = 0.109 \pm 0.007$ g; unmated: $N = 39$, $\bar{x} = 0.126 \pm 0.004$ g; $t_{50} = 2.19$, $P = 0.04$).

Although male color, weight, and age were not useful predictors of copulation success, we did find that copulation success was influenced by variation in male courtship intensity, as measured by the number of leg lifts per second from first courtship to copulation or the end of the trial. Males that copulated

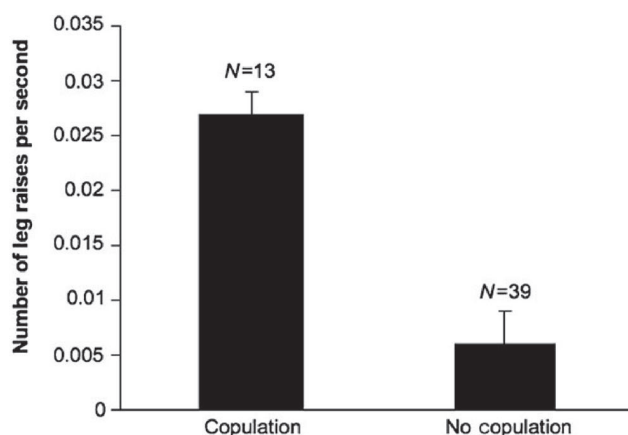


Figure 2. Effect of male courtship effort (leg raises per second) by trial outcome for Experiment 1—single-choice test. Successful males courted significantly more vigorously than unsuccessful males ($P < 0.001$).

courted more vigorously than those that did not copulate (mated: $N = 13$, $\bar{x} = 0.027 \pm 0.003$; unmated: $N = 39$, $\bar{x} = 0.006 \pm 0.001$; Wilcoxon test, $Z = 4.46$, $P < 0.001$; Figure 2). However, leg-waving rate did not influence the latency to copulation (Spearman's correlation, $\rho = -0.27$, $P = 0.37$). Leg-waving rate was also not correlated with male foreleg color (Spearman's correlation, $\rho = 0.09$, $P = 0.53$), male body condition (Spearman's correlation, $\rho = 0.05$, $P = 0.75$), male age (Spearman's correlation, $\rho = -0.04$, $P = 0.76$), male weight (Spearman's correlation, $\rho = -0.01$, $P = 0.94$), female age (Spearman's correlation, $\rho = -0.20$, $P = 0.15$), or female weight ($r^2 = 0.06$, $N = 52$, $P = 0.07$).

Experiment 2: Simultaneous 2-choice trials (old females)

We first confirmed that our a priori color groupings of males (light vs. dark) from trials in which a mating occurred actually corresponded to differences obtained via color quantification. Because some males were used multiple times, the following analysis only includes the first trial for all males. Ultimately, 2 dark males were removed from the following analyses due to reuse and one dark male is missing due to incomplete data. Males in the 2 color groups were significantly different in both tibia color (dark: $N = 11$, $\bar{x} = 36.0 \pm 3.9$; light: $N = 14$, $\bar{x} = 52.3 \pm 3.5$; $t_{23} = 3.11$, $P = 0.005$) and percentage of tibia covered with dark color (dark: $N = 11$, $\bar{x} = 39.9 \pm 7.3$; light: $N = 14$, $\bar{x} = 13.4 \pm 6.5$; $t_{23} = 2.71$, $P = 0.01$). Using all data ($N = 35$), despite the difference in foreleg color, there was an equal number of copulations for the light ($N = 7$ copulations) and dark ($N = 7$ copulations) foreleg groups ($\chi_1^2 = 0.0$, $P = 1.0$). Reanalyzing the data using males only once, we again found no difference in the number of copulations for light ($N = 5$ copulations) versus dark ($N = 5$ copulations) males ($\chi_1^2 = 0.01$, $P = 0.94$). The latency to copulation was also similar across the 2 foreleg groups in this reduced sample (light: $\bar{x} = 525.2 \pm 199.7$ s; dark: $\bar{x} = 967.4 \pm 199.7$ s; $N = 10$, Wilcoxon test, $Z = 1.67$, $P = 0.09$). There was no difference in female age or weight between those that copulated and those that did not (Age—mated: $N = 14$, $\bar{x} = 19.6 \pm 1.2$ days postmaturation; unmated: $N = 21$, $\bar{x} = 20.3 \pm 1.0$ days postmaturation; Wilcoxon test, $Z = 0.07$, $P = 0.95$; Weight—mated: $N = 14$, $\bar{x} = 0.0830 \pm 0.0043$ g; unmated: $N = 21$, $\bar{x} = 0.0907 \pm 0.0035$ g; $t_{33} = 1.57$, $P = 0.18$).

Within those trials that resulted in copulation with a light male, mean dark male tibia color was 29.9 ± 2.2 and mean light male tibia color was 54.3 ± 6.2 (difference: $N = 7$, $\bar{x} = -24.4 \pm 6.0$). We tested the mean of this distribution against a null hy-

pothesis of zero and found the difference to be greater than zero (2-tailed test, $t_6 = -4.1$, $P = 0.006$). In trials where a dark male copulated, mean dark male tibia color was 41.2 ± 1.7 and mean light male tibia color was 49.8 ± 6.2 (difference: $N = 6$, $\bar{x} = -8.5 \pm 6.5$). We tested the mean of this distribution against a null hypothesis of zero and found no significant difference (2-tailed test, $t_5 = -1.3$, $P = 0.26$).

Within each trial, there was no difference between color groups as to which male courted first (light vs. dark tested against a 50–50 distribution: Likelihood ratio, $\chi_1^2 = 2.99$, $P = 0.08$). Courtship order also appeared to have no influence on ultimate copulation success, as we found no difference in copulation success based on which male courted first (Likelihood ratio, $\chi_1^2 = 0.31$, $P = 0.58$).

Experiment 3: Simultaneous 2-choice trials (young females)

None of the 8 young females run through these trials copulated. In order to be sure that this lack of copulation success was a result of female age and not some artifact of the males used, mating design, etc., we reran as many of the exact female–male triads as possible when females were 26 days postmaturation (an age at which females are known to mate readily). Unfortunately, 3 of our males died during that time (2 of which were used twice previously), allowing only 3 full triads to be rerun. Of those 3 triads, one pair copulated (a light male; 33% copulation success), which is similar to the copulation frequencies witnessed in the previous 2 experiments. However, the sample sizes are obviously very small here and should be interpreted with caution.

Discussion

This study examined the condition dependence of foreleg color in mature male *S. uetzi* wolf spiders and tested whether or not this trait influences female mate choice. *Schizocosa uetzi* male foreleg ornamentation is highly variable between individuals (see compiled data from all trials in Figure 3), with tibiae ranging in color from black to medium brown (matching the rest of spider body). Our results demonstrate condition-dependent trait expression: high nutrient diet males had higher body condition indices and possessed both darker color and more color on their foreleg tibiae than low nutrient diet males. This finding differs from Hebets et al. (2006), where they found an inverse relationship between color darkness and percentage cover. This difference is due solely to the analyses used; we calculated the percentage cover on the tibia using a threshold value generated from the population mean color rather than using an individualized threshold based on tibia darkness of each individual. Using a population threshold enabled us to compare color among males raised on different diets using a standard, rather than a shifting threshold. Although male tibiae color appears to be an honest indicator of male condition, we curiously did not find any evidence to suggest that it is currently used in female mate choice decisions. In an attempt to ensure that we would be able to detect female choosiness, if present, our mate choice trials incorporated single-choice and 2-choice mating designs using females across a range of ages. We found male courtship effort (as measured by the number of leg lifts per second) to be the only aspect of males that influenced copulation success.

On a spider's final molt to maturation, their body size and color are fixed. Our results therefore demonstrate that past foraging history can have profound impacts on these adult-fixed traits. Similar results demonstrating an influence of past foraging on adult size and secondary sexual traits have been documented in a closely related brush-legged wolf spider (Uetz et al. 2002; Hebets et al. 2008). In our study, when comparing

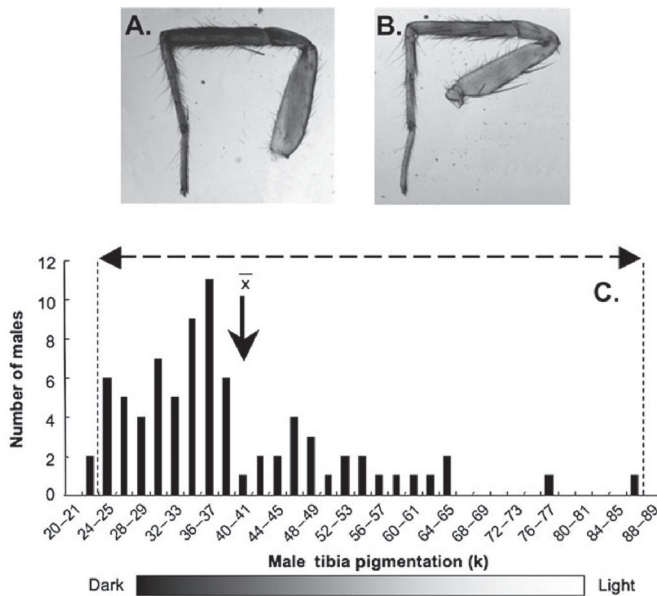


Figure 3. Images of male *Schizocosa uetzi* forelegs with (A) dark ($k = 40$) and (B) light color ($k = 79$). (C) Distribution of *S. uetzi* male tibia color. This distribution includes males from 2 years (2006–2007) that were captured as late juveniles in the field and raised under identical laboratory condition and feeding regimes. The range contained within the dotted lines represents the range of males that copulated in either a single or dichotomous mate choice test. The \bar{x} denotes the average tibia color of males that copulated.

tibia and metatarsus color with cephalothorax width, we found that although both become darker with increased spider size, the slope of the line is significantly different for the 2 leg segments—the tibia slope is significantly steeper than the metatarsus slope. Thus, although all foreleg color increases with improved foraging history, the secondary sexual color of the foreleg tibiae darkens more than background color. This then leads to increased contrast between the colored tibia and the rest of the leg (as seen by our positive correlation between contrast and foreleg color) for males of better condition. Cotton et al. (2004a) propose that because the handicap hypothesis assumes that ornaments are costly, for a given change in condition, ornaments should show a greater degree of change in expression than nonornamented traits. This is precisely what we have found through this comparison of male leg colors. Although our analyses only included a majority subset of our total individuals, our sample sizes are similar for low- and high-diet individuals, and thus, we are confident that our results reflect true differences between the diet treatments.

Based on the condition-dependent nature of foreleg color that we have documented for *S. uetzi* males, one might expect this trait to be important in a female's mating decision. Females would be expected to benefit by paying attention to such a conspicuous trait that is indicative of subadult foraging success. Such female preferences for pigmentation color could be exhibited in a variety of ways. For example, females could exhibit a threshold response (Janetos 1980), where male foreleg color below a certain level would fail to result in copulation. Unless a female *S. uetzi*'s threshold is set extremely low, our first experiment (single choice) should have uncovered such a threshold preference. We would have expected to see more copulations in the mating trials with darker males, but we did not (see Figure 1). However, male foreleg color may be used more as a means of comparing between or among males (Janetos 1980). In the field, densities of *S. uetzi* are certainly

high enough that females could encounter and compare multiple males simultaneously (Hebets EA, personal observation). By using a 2-choice design, our second experiment examined whether females might exert a preference when given the opportunity to simultaneously compare males of varying foreleg color. Again however, we found copulation frequency to be independent of male foreleg color. In fact, it was only in trials in which females chose light colored males that the difference in male coloration between the light and dark males was significantly different than zero, potentially suggesting a preference for light colored males.

Given that *S. uetzi* male foreleg color is condition dependent, it occurs only on mature males, and it occurs only on the legs that are incorporated into male courtship displays (i.e., the forelegs), it is curious that females seem to be ignoring this trait in their mating decisions in the laboratory. One potential explanation for our inability to detect a female preference for male color in our first 2 experiments is that females may not have been tested within their window of peak choosiness but instead in their window of peak receptivity, where choosiness may be minimal. For example, previous work on *Schizocosa ocreata* has found the strength of female preference for brush size, a condition-dependent secondary sexual trait (Uetz et al. 2002), to decline with age (Uetz and Norton 2007). Specifically, female preference for larger brushes is greatest 2 weeks postmaturation, however, by the time females reach peak receptivity at 3 weeks of age they show no preference for brush size (Uetz and Norton 2007). Given these previous results, we were concerned that females from our first 2 experiments may have been too old to show any preference for visual ornamentation. Thus, we included a third experiment in which we used a simultaneous 2-choice design with younger (2 weeks postmaturation) females. Instead of uncovering a female preference, our results from this third experiment suggest that younger females are simply less likely to mate, as none of the females used in this initial experiment mated. Again, although our sample sizes are relatively small for this third experiment, a low likelihood of mating in females less than 3 weeks postmaturation has been observed in several other *Schizocosa* species as well (e.g., *Schizocosa stridulans*, Hebets EA, unpublished data). Thus, we do not believe that our experiments missed a critical age window during which female preferences for male foreleg color may be present. Although our sample size was only 8 due to the limited number of individuals available in 2008, we feel that this should have been sufficient to elicit at least a few copulations. The copulation frequency of *S. uetzi* ranges from ~35% to 50% in laboratory trials (Hebets 2003, 2005), which would translate into 2.8–4 copulations in our third experiment. Instead, we saw zero copulations, suggesting that females are not receptive at this age. Additionally, in compiling female age and copulation results from all 3 of our experiments, we see no pattern emerge with respect to female age and mate choice based on male color (Figure 4). Peak receptivity for *S. uetzi* females appears to be around 3 weeks postmaturation and females across all experiments were completely unreceptive to courtship at 2 weeks postmaturation (Figure 4b), the age at which Uetz and Norton (2007) observed the greatest exertion of preference for *S. ocreata*. We therefore do not feel that female age can adequately explain the seeming lack of female preference for male visual color found in this study.

Another obvious explanation for our lack of evidence of female choice based on male foreleg color is that the foreleg color of *S. uetzi* is used in male–male not male–female interactions. However, we feel that this is unlikely for the following reasons. First, in our experiments, male–male interactions consisted of either 1) males touching and moving away or 2) males attempting to mount each other. We have not observed

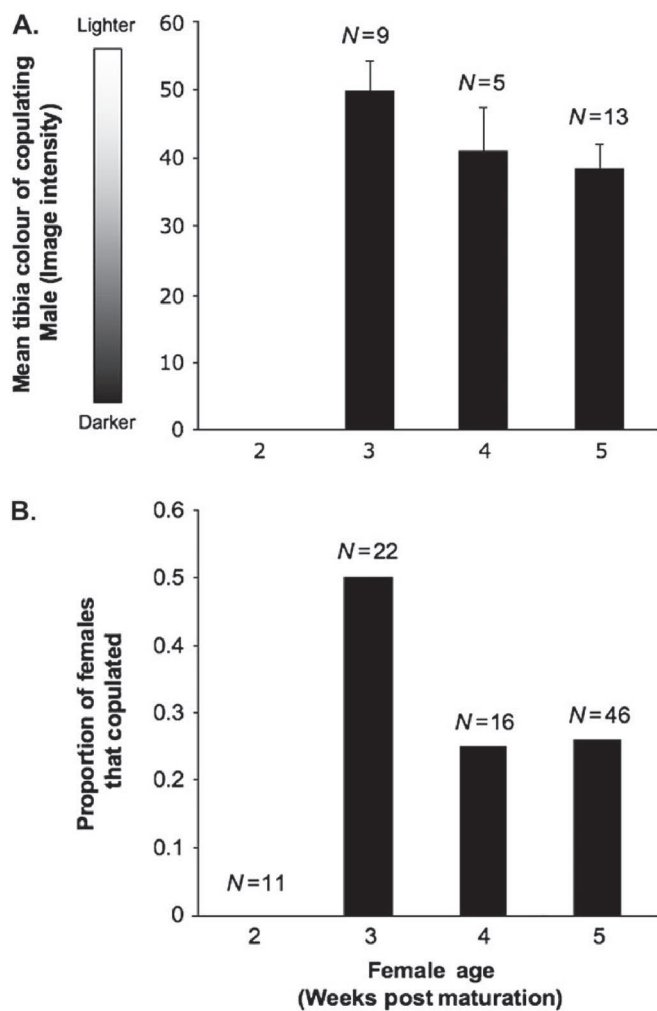


Figure 4. (A) Mean tibia color of copulating males across female age groups. There is no pattern in the degree of color by copulating males based on female age. (B) Proportion of females that copulated by age postmaturation in weeks. Females did not copulate until more than 2 weeks old. Females did not mate in equal proportions across different ages ($P = 0.007$).

any unique signaling behavior associated with male–male interactions in *S. uetzi*—males simply engage in courtship and often direct this courtship to other spiders present (male or female). Second, a study conducted on *S. ocreata*, a closely related species, actually examined male signaling in the presence of females versus conspecific males. Results showed that male signaling occurred more frequently in male–female interactions than in male–male interactions and that the signaling in male–male interactions was not associated with the interaction outcome (Delaney et al. 2007). Results of that study suggested that the main function of male signaling is in male–female interactions. Nonetheless, future work could address this hypothesis explicitly.

Instead of basing their mate choice decisions on male foreleg coloration, *S. uetzi* females in our single-choice experiment seemed to base their mating decisions on male courtship intensity, or leg-waving rate. The rate of male leg waving (number of leg raises per second) was significantly higher for males that copulated versus those that did not copulate. Similar measures of courtship intensity have been shown to be important for male mating success in other wolf spider species including the European drumming spider *Hygrolycosa rubrofasciata*

(Kotiaho et al. 1998) and *S. ocreata* (Delaney et al. 2007). Courtship has been found to be energetically costly in many systems (Kotiaho 2000; Hunt et al. 2004) and thus effort may be indicative of immediate male condition or energy reserves. Previous work with both the drumming wolf spider *H. rubrofasciata* (Kotiaho 2000) and the field cricket *Gryllus lineaticeps* (Wagner and Hoback 1999) has demonstrated that increased postmaturation diet correlates with increased courtship signaling rates. Here, we did not find leg-waving rate to be correlated with male foreleg color (now known to be condition dependent) or male body condition. Nonetheless, leg-waving rate may convey other aspects of male quality (e.g., parasite load: Rantala and Kortet 2003; ejaculate quality: Matthews et al. 1997) or motivation. In the wolf spider *Pardosa milvina*, for example, a recent study has suggested that females might gain an indirect genetic benefit by mating with males that naturally court at a high rate (Hoefler et al. 2009). Females that mated with males with high courtship rates produced more offspring that survived starvation better than those of females that mated with males of low courtship rates (Hoefler et al. 2009). Females of *S. uetzi* may receive a similar indirect benefit, yet this remains to be tested.

Previous studies on other *Schizocosa* wolf spiders have also hinted at the importance of male detectability for female choice. For example, Scheffer et al. (1996) demonstrated that regardless of the presence/absence of male foreleg brushes in *S. ocreata*, females mated with the first male to court. In explaining this pattern, the authors suggested that the male that first captures a female's attention is most likely to copulate, regardless of his phenotype (Scheffer et al. 1996). This female detection argument could similarly be applied to our results discussed above—the observed relationship between leg-waving rate and copulation success. A higher leg-waving rate may increase the likelihood of detection by a female, thus improving a male's chances of successfully mating. In our single-choice design, however, we used a very simple signaling environment and a relatively small space resulting in artificially high male detectability. Thus, it is unclear exactly how an increased leg-waving rate could translate into increased copulation success via increased detection only. Further, we did not find any suggestion that increased leg waving resulted in reduced time to copulation, a pattern that we might predict if increased detection was responsible for the correlation between leg-waving rate and copulation success. Regardless, future studies examining male leg waving are necessary to distinguish between a pure efficacy-based versus content-based explanation for why females mate more with males with a higher leg-waving rate.

Curiously, the one male attribute that appears to correlate with copulation success involves visual signaling—male leg-waving rate—yet our results suggest that the visual ornamentation on this leg is not important. However, because the leg waving occurs simultaneously with courtship stridulation, we cannot be sure that it is the visual component per se that makes the difference. Previous studies have demonstrated that the seismic signal is critical for copulation in *S. uetzi* but that females distinguish among male phenotypes in the presence of a seismic signal (Hebets 2005). In all of our experiments, the seismic signal was present along with the visual signal, and thus, we are unable to tease apart their respective effects. Repeating Experiment 1 using a signal ablation design would enable us to determine if the connection between leg-waving rate and copulation success was driven by the visual signal, the seismic signal, or the combination of the 2. Given results from prior experiments on this species, we predict that females only pay attention to leg-waving rate in the presence of the seismic courtship signal. Furthermore, we propose that the visual color may indeed play a role in female mate choice but only in

circumstances where leg-waving rates are identical. For example, in the one study that demonstrated a preference for more ornamented males in *S. uetzi*, females were choosing between video playbacks with identical male behaviors (e.g., identical leg-waving rates). It may be that the female preference for ornamentation only surfaced there because courtship effort or leg-waving rate was standardized.

Although we have demonstrated male foreleg ornamentation to be a good predictor of a male's developmental condition given our rearing environment, we know nothing about how this trait may develop across environments. An abundance of recent work has highlighted the importance of the environment in phenotype development (see West-Eberhard 2003) and strong genotype by environment interactions (GEIs) with respect to signaling characters have been found in waxmoths (Jia et al. 2000) and voles (Mills et al. 2007), among others. When signal expression varies due to environmental variation or GEIs, these signals may not be the most reliable indicators of male quality or the future success of offspring (Greenfield and Rodriguez 2004). For example, in *S. uetzi*, one could imagine GEIs leading to good quality males expressing dark forelegs under some environmental conditions but light colored forelegs under others. A fixed preference then by females for darker males would be maladaptive under certain environmental conditions, and we would expect the correlation between signal and preference to disassociate. Instead, if female preferences were more plastic and based on successful male phenotypes observed in the current environment, female mate choice decisions could vary based on degree of ornamentation and still remain adaptive. We suggest that this could be facilitated by the type of mate choice learning already demonstrated in *S. uetzi*. In this phenotype learning scenario, males in better condition are expected to mature earlier in the season (as seen in our data). In addition, prior to sexual maturation, females exposed to a particular male phenotype are expected to learn that phenotype and prefer those males in their subsequent adult mate choice (again, previously demonstrated in *S. uetzi*; Hebets 2003). Ultimately then, subadult females would be exposed to males in the best condition, thus enabling them to learn the phenotype of the highest quality males for that particular season. This is an exciting possibility and one that certainly warrants future research.

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