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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

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ABSTRACT. Male *Schizocosa ocreata* (Hentz) wolf spiders (Araneae, Lycosidae) have tufts of elongated, dark bristles on the patella and tibia of the forelegs, which are involved in visual signaling. Previous research has suggested that these tufts are used by females as a criterion in mate choice, raising the question of whether they might serve as indicators of male condition. We tested the hypothesis that tufts are condition-dependent indicator traits with a laboratory rearing study subjecting spiders to lifelong feeding regimens representing successful (high food) and unsuccessful (low food) foraging history, after which males were measured upon reaching adulthood. Mortality varied significantly with experimental treatment, and had a disproportionate impact on some egg sacs assigned to the low food treatment. Age at sexual maturity and several body size measures varied significantly with feeding history. Well-fed spiders survived better, matured earlier, were significantly larger, and were in relatively better condition (measured as a residual body condition index) than deprived spiders. Additionally, well-fed spiders had significantly larger relative tuft size (scaled for body size). These data suggest that male body size, condition and a conspicuous male signaling trait vary with feeding history, and thus have the potential to serve as ‘‘honest indicators’’ of male quality in mate choice.

Keywords: Feeding, condition-dependence, male secondary sex characters, wolf spiders, Lycosidae, *Schizocosa*

Signals used by males during courtship and mating have been studied extensively, and there is general agreement that they function in species recognition (Colgan 1983; Alcock 1998) and also in female mate choice (Andersson 1994; Alcock 1998). There is growing evidence that signals such as elaborate male morphological characters and complex display behaviors convey information to females about male condition or quality, and that females choose mates based on these traits (e.g., ‘‘handicap’’ or ‘‘good genes’’ models; Zahavi 1975; Clutton-Brock & Albon 1979; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984; Zuk 1991; Houde & Torio 1992; Andersson 1994; Kotiaho et al. 1998). Because these elaborate male traits and displays are often costly to produce, and vary in size or expression with the condition of the male, they are deemed ‘‘honest’’ indicators of male quality; only males in the best condition are able to express larger traits (Andersson 1986; Grafen 1990; Johnstone 1995). Additionally, male decorations may serve as ‘‘amplifiers’’ i.e., traits that draw attention to or enhance discrimination of other condition-indicating signaling traits (Hasson 1991; Hebets & Uetz 2000; Taylor et al. 2000).

Several spider families with well-developed visual capabilities (e.g., Salticidae, Lycosidae) utilize visual signaling in courtship communication (Jackson 1982; Richman 1982; Stratton 1985; Uetz 2000). Adult males of these families often exhibit conspicuous visual signaling traits, widely assumed to function in species recognition, driven by selection from potential cannibalism by females (Crane 1949; Jackson 1982; Richman 1982; Uetz & Stratton

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1983; Stratton 1985; Elgar 1991, 1992; Newman & Elgar 1991; Hebets & Uetz 2000; Uetz 2000). Even so, the role of sexual selection via female mate choice has also been considered as a potential force in the evolution of male morphology and decorations (Peckham & Peckham 1889; Jackson 1981; Clark & Uetz 1993; Scheffer et al. 1996; McClintock & Uetz 1996; Elgar 1998; Uetz 2000).

While the question of whether male traits convey information useful to females in evaluating mate quality is central to understanding sexual selection (and the subject of much research with other animal taxa), it is not well understood for spiders. In one extensively-studied species, the wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865), females choose mates based on the percussive ‘‘drumming’’ display of males (Kronstedt 1996; Parri et al. 1997). These displays are energetically expensive and condition-dependent, thereby serving as honest indicators of male quality (Mappes et al., 1996; Kotiaho et al. 1998; Kotiaho 2000). In this study, we examine the influence of feeding history and body condition on a male secondary sexual character (leg tufts) used in visual signaling by the brush-legged wolf spider, *Schizocosa ocreata* (Hentz 1844).

Among the most common spiders in Eastern North America, *S. ocreata* is a well-studied model species whose visual and vibratory signaling behaviors have been demonstrated to serve in species recognition and reproductive isolation (Stratton & Uetz 1981, 1983, 1986; Uetz 2000), as well as mate choice (Scheffer et. al. 1996; McClintock & Uetz 1996; Hebets & Uetz 1999, 2000; Uetz 2000) and male-male aggression (Aspey 1977a, b). These spiders exhibit sexual dimorphism i.e., adult male *S. ocreata* have conspicuous tufts of bristles on the forelegs (used in visual courtship displays) that are absent in females and juveniles. While some previous studies suggest that variation in this conspicuous male visual signaling trait is related to male condition and might influence mate choice (see review in Uetz 2000), the basis of variation in male tufts is currently unknown. In this study, we test the hypothesis that the size of these tufts is condition-dependent, and reflects foraging success, with laboratory rearing studies and measurement of subsequent spiders.

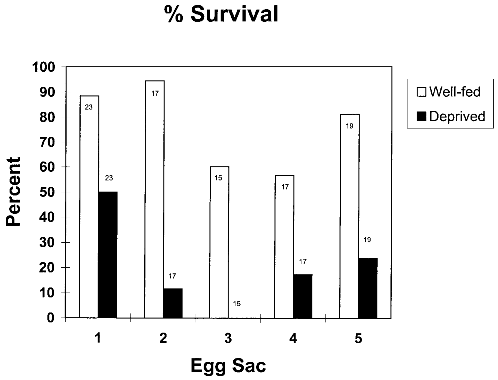

Figure 1.—Percent of *S. ocreata* raised under different feeding regimes (numbers above bars indicate initial N) surviving to adulthood from each of five egg sacs (open bars = well-fed; dark bars = deprived).

METHODS

Wolf spiders used in this study were raised from egg sacs produced by females that were collected from the field as immatures and mated in the lab. Spiders (parents) were collected as penultimate instar juveniles in May and June 1995 from deciduous forest habitat at the Cincinnati Nature Center Rowe Woods facility in Clermont County, Ohio. Representative specimens of this population are located in a number of museum collections, including the Cincinnati Museum of Natural History, the Ohio State University collection, the Museum of Comparative Zoology and the US National Museum of the Smithsonian Institution.

Spiders (parents) were maintained in the lab until maturity under identical controlled conditions at room temperature (23–25 °C) in an environment with stable humidity and a 13:11 L:D photoregimen. Spiders were individually housed in opaque containers (12 cm diam., 5 cm ht.), with clear lids (so spiders are exposed to light cues but are visually isolated from each other). Spiders were provided water ad libitum from a soaked cotton dental wick, and fed 2–3 live domestic crickets (*Acheta domestica* L.) twice weekly.

Female wolf spiders with egg sacs ($n = 5$) were selected at random from a pool of individuals previously mated in the laboratory (each female was paired with a male at random and allowed to mate). Because just-hatched wolf spiders spend a short period of time riding on the mother’s abdomen before dispersing (ca. one week), we waited until spiderlings (offspring of above-mentioned matings) were dispersing to isolate them, then assigned aproximately half of the spiderlings from each egg sac at random to the two feeding regime treatments. Numbers of spiderlings used varied from 30–46 per egg sac, with a total of approximately 90 spiders/experimental treatment. Spiders were then maintained in the laboratory until maturity under the controlled environmental conditions described above. Each spider was given a unique identification number, and spiders were weighed and fed appropriately sized springtails (Collembola) and/or domestic crickets (*Acheta domestica* L.) on a weekly basis. Two feeding regimes were maintained as a 4:1 ratio diet difference based on previous studies (Jakob et al. 1996): 1. well-fed, an amount equal to each spider's body mass twice per week; and 2. deprived, an amount equal to half of each spider's body mass once per week.

Measurements and statistical analyses.—Each male spider was measured at maturity from a digitized image (produced with a JVC GN-8 videocamera with a macro lens, mounted at a fixed distance above the specimen on a 1 mm grid background). Digital measurements were made using NIH Image, a digital measurement program. We measured two frequently used body size measures: body length (BL) and cephalothorax width (CW). Spiders were rotated and placed on their right side to provide a lateral view of legs I, which was used to measure tuft area (TA) as a scribed polygon (area in mm) in NIH Image. Each tuft was measured three times, and a two-way ANOVA was used to determine measurement repeatability (Swaddle et al. 1994). As certain aspects of spider size are more or less fixed at adulthood (e.g., cephalothorax width) while others vary with feeding and water intake (e.g., weight, body length), we also calculated indices of body condition (as in Jakob et al. 1996; Kotiaho 1999; Marshall et al. 1999).

Data were tested for normality and transformed with natural log (ln) or other transformations where appropriate. Data were subjected to statistical analyses using a model with feeding treatment (high food/low food) nested within egg sac. Survival data were analyzed with logistic (log-likelihood) regression analysis, while all other data were analyzed with nested ANOVA. Subsequent comparisons between treatments were made using Tukey post-hoc tests or t-tests, with adjustments for equal or unequal variances. All analyses were conducted using the software package JMP ver. 4.0 (SAS Institute).

RESULTS

Survival to adulthood varied significantly with both treatment and egg sac (Whole model: df = 9, $X^2 = 87.397$, $P < 0.0001$: Treatment effects–egg sac: df = 4; $X^2 = 18.995$, $P = 0.0008$) and feeding treatment (nested within egg sac); df = 5; $X^2 = 74.567$; $P < 0.0001$). Approximately 76% of spiders in the well-fed treatment survived to adulthood, but only 20.5% of the deprived treatment survived (Fig. 1).

Age of male spiders at adulthood varied significantly between treatments (analyzed as nested within egg sacs; $F_{3,4} = 14.85$; $P < 0.001$), but not egg sac ($F_{4,4} = 1.61$; $P = 0.195$). Males from the well-fed treatment matured significantly earlier than those from the deprived treatment across all egg sacs (Fig. 2). For age of females at adulthood, there was also a significant treatment effect (analyzed nested within egg sac; $F_{3,4} = 3.07$; $P < 0.035$), but no effect of egg sac ($F_{4,4} = 0.964$; $P = 0.434$). Females from the well-fed treatment matured significantly earlier than those from the deprived treatment across all egg sacs (Fig. 3). Overall, males matured approximately 10 days prior to females, which is often typical of *S. ocreata* in the field during the Spring breeding season.

Figure 2.—Mean time to maturity (days to adulthood) for male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

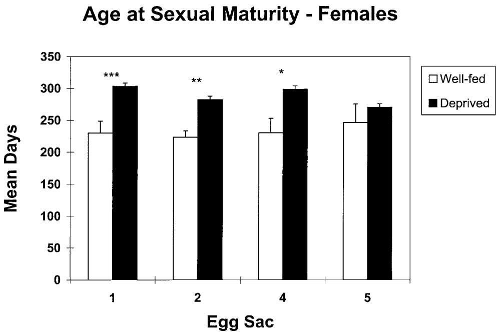

Figure 3.—Mean time to maturity (days to adulthood) for female *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

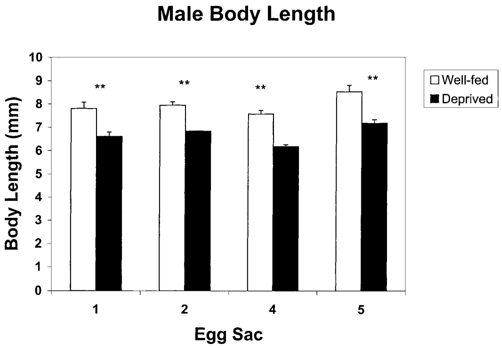

Figure 4.—Body length (mm) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

As one egg sac had no survivors in the deprived treatment, it was dropped from subsequent analysis of adult male measures. Morphological parameters related to overall size (BL, CW) and body condition (residual index) measured for adult males varied significantly with level of feeding, as well as with egg sac in the case of body length (Table 1, Figs. 4–6). Well-fed spiders were significantly larger in size than deprived spiders in most cases, as reflected in data for body length and cephalothorax width (Figs. 4, 5). Body condition varied significantly with treatment, but not egg sac (Table 1); overall, well-fed spiders exhibited higher body condition indices (Fig. 6). Given the low sample sizes for some of the egg sacs, these data must be interpreted with caution.

Repeatability of measurements of tuft area (mm) was determined with two-way ANOVA, as recommended by Swaddle et al. (1994). Between-individual variance was greater than within-individual variance for tuft area ($F_{1,2} = 210.5$, $P < 0.001$), indicating low measurement error (and high repeatability). However, subsequent analyses of tuft area (overall means of three measures for each leg tuft) revealed a consistent measurement bias owing to specimen placement and perspective. To avoid error arising from this bias, we used only the measurement of the (larger) left leg in subsequent analyses. To examine for the influence of overall body size, condition, egg

Table 1.—Nested Analysis of Variance for size male and body condition.

Source	df	MS	F	*P*
Body length (mm)				
Egg sac	3	1.423	4.266	0.012
Treatment (egg sac)	4	3.545	10.62	<0.0001
Error	33	0.333		
Cephalothorax width (mm)				
Egg sac	3	0.253	2.142	0.114
Treatment (egg sac)	4	0.820	6.929	0.0004
Error	33	0.118		
Body Condition Index*				
Egg sac	3	0.042	0.657	0.584
Treatment (egg sac)	4	0.206	3.185	0.026
Error	33	0.065		

* (residual of ln Cube Root Abdomen Volume × ln CW)

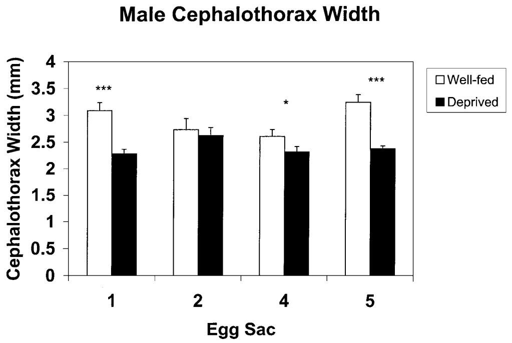

Figure 5.—Cephalothorax width (mm) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

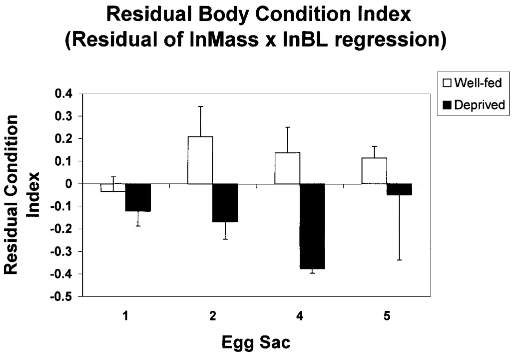

Figure 6.—Body condition index (residual of ln cube root abdomen volume vs. ln CW) for adult male *S. ocreata* raised under different feeding regimes (open bars = well-fed; dark bars = deprived; asterisks denote significant post-hoc Tukey comparisons: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

sac and treatment on tuft area, mean left tuft area was subjected to a stepwise elimination multiple regression analysis with those parameters as independent variables (Table 2). This multiple regression was significant ($F_{5,40}$ = 47.734, $P < 0.001$, $R^2 = 0.715$), but only two variables (treatment and leg length) had significant effects ($P < 0.001$). However, given the potential colinearity of tuft size and leg I length, we tested the hypothesis that feeding regime influences tuft size with an additional analysis. As ANOVA of leg I length revealed a significant effect of CW ($F_{1,37} = 25.303$; $P < 0.0001$), but no treatment effect ($F_{1,37}$ = 0.0076; $P = 0.931$) nor interaction of CW x treatment effect ($F_{1,37} = 3.45$; $P = 0.071$), we felt justified in using a scaled tuft size index (the residual of the regression of tuft area x leg I length). A nested ANOVA of residual tuft area revealed a significant effect of treatment ($F_{4,33} = 3.533$; $P = 0.016$), but not egg sac ($F_{3,33} = 1.39$; $P = 0.262$). Regression of leg tuft area x leg length revealed nearly identical slopes, but significantly different intercepts between experimental feeding treatments ($F_{1,1} = 23.47$, $P < 0.0001$, $R^2 = 0.713$). Tufts were significantly larger across the range of leg length variation for males in the well-fed treatment (Fig. 7).

DISCUSSION

At first, the results of this study might not seem suprising, as a number of other studies have shown that spiders subjected to variation in feeding regime survive differently, mature at different rates and vary in size and activity at adulthood (Anderson 1974; Riechert & Harp 1987; Uetz et al. 1992; Toft & Wise 1999; Walker et. al. 2000). Additionally, as male morphological characters often covary with body size, it might also be expected that they would vary as a consequence of different feeding regimes. However, even with the in-

Table 2.—Stepwise multiple regression analysis of tuft size for male *Schizocosa ocreata* reared under separate food regimes vs. factors of potential influence. Factors are listed in order of stepwise elimination.

Parameter	B (slope)	t	*P*
Body length (mm)	0.136	0.240	0.816
Cephalothorax width (mm)	−0.220	−0.280	0.782
Body Condition Index*	−0.564	−0.420	0.676
Egg sac	−0.201	−1.360	0.481
Treatment	−0.201	−4.70	<0.0001
Leg I length	0.316	4.309	<0.0001

Final Model (Treatment, Leg I length): $R^2 = 0.715$; $F_{5,40} = 47.734$; $P < 0.0001$

* (residual of ln Cube Root Abdomen Volume × ln CW)

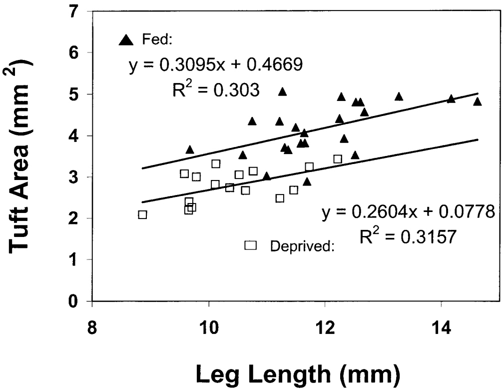

Figure 7.—Linear regression of foreleg tuft size (left tuft area in mm^2) vs. leg I length (mm) for adult male *S. ocreata* raised under different feeding regimes: well-fed (filled triangles) and deprived (open squares).

fluence of body size held constant, the leg tufts of male *S. ocreata* vary significantly with lifelong feeding regime, which demonstrates the potential for this male character to serve as an ‘‘honest’’ indicator of condition based on previous foraging success. Given that previous research has implicated these tufts in female mate choice, findings of this study may have broader implications.

Like a number of other wolf spiders, male *S. ocreata* have elongated, dark bristles on the patella and tibia of the forelegs, creating ‘‘tufts’’ that may function as signals indicating condition, or as signal amplifiers (Uetz 2000; Hebets & Uetz 2000). Several species in the genus *Schizocosa* and the family Lycosidae possess similar decorations (Miller et al. 1998; Hebets & Uetz 2000), and a recent phylogenetic analysis suggests that male tufts are a derived character that has evolved independently several times in this genus (G.E. Stratton, pers. comm.). Scheffer et al. (1996) found that female *S. ocreata* receptivity varied with the presence or absence of these male tufts (manipulated by shaving live males), but only when vibratory cues were absent. They suggested that tufts might increase the efficacy of visual signaling in complex litter habitats, which can constrain vibration transmission. Several other studies with live males as well as manipulated video stimuli indicate that female receptivity to visual courtship signals from males may vary with the size and symmetry of tufts (Uetz 2000). Female receptivity is lower when tufts are absent (McClintock & Uetz 1996; Hebets & Uetz 2000), asymmetric (Uetz et al. 1996; Uetz & Smith 1999), or small in size (McClintock & Uetz 1996; Uetz 2000).

If costly ornaments or displays reflect some heritable characteristic of the male related to viability, both the display and female preference for males based on such display traits would be favored by selection (Andersson 1996). Male traits may reflect quality over different time scales, as ‘‘static’’ morphological traits that are fixed at adulthood may reflect long-term influences (e.g., lifetime foraging success), while body condition indices and ‘‘dynamic’’ behavioral display traits may indicate short-term changes in condition (e.g., energy reserves) (see Gerhardt 1991; Nicoletto 1991, 1993; Moller & Pomiankowski 1993; Hill et al. 1999; Parten & Marler 1999). In the best-studied case of male signaling and female mate choice in spiders, females of the wolf spider *H. rubrofasciata* prefer males with higher drumming rates (Parri et al. 1997). Drumming rates vary with size and condition of males, at least in the short term, and the high cost of this energetically expensive display has a negative impact on male survival during the breeding season (Mappes et al. 1996; Kotiaho et al. 1998; Kotiaho 2000). Results of our study suggest that leg tufts in *S. ocreata* are a static trait that reflects variation in male condition arising from long-term feeding influences. However, even though tuft size in *S. ocreata* is fixed at adulthood, wearing from various sources may damage tufts and diminish their size over the breeding season (P.W. Taylor & G. Uetz, pers. obs.).

The adaptive significance of decorative leg tufts in male courtship behavior and female mate choice, as well as the evolution of these traits, is not fully understood in the genus *Schizocosa*. There is currently no evidence that suggests females of this species gain any direct or indirect benefits by choosing or discriminating among males on the basis of tuft size (or for that matter any other male trait). Ultimately, it may be that these traits serve multiple roles: as species-specific mate recognition cues, as a means of gaining female attention in a complex visual/vibratory environment, as indicator traits or as amplifiers of condition-indicating behaviors. This study demonstrates that in addition to a number of functions previously suggested for these traits, the potential also exists for male leg tufts to serve as visual signals indicating male condition and previous foraging success.

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