

# Individual- and condition-dependent effects on habitat choice and choosiness

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**Abstract** Research on consistent individual differences in behavior, or “behavioral syndromes”, continues to grow rapidly, and yet, the aspects of behavior under consideration have remained remarkably limited. Here, we consider individual variation in consistency of choice (termed here “choosiness”), as expressed during habitat choice. We repeatedly tested the responses of female Western Black Widows, *Latrodectus hesperus*, to two cues of habitat quality: prey chemical cues and variation in web site illuminance. We estimated females’ response by the distance they positioned themselves from (1) the source of prey chemical cues and (2) the darkest edge of our test arena. Individuals with low variance in their responses are deemed more “choosy”, whereas individuals with high variance are deemed less “choosy”. Generally, most females

initiated web construction near the source of the prey chemical cues and tended to place themselves in low-light conditions. However, we detected strong, repeatable differences in females’ intensity of response, and within-individual variance of response (i.e., choosiness) was correlated across situations: females with highly consistent responses towards cricket chemical cues also exhibited highly consistent responses towards variation in light conditions. When deprived of food for extended periods, females were indistinguishable in their responses towards prey chemical cues, but tended to initiate web construction in brighter lighting conditions. Food-deprived females universally exhibited higher variance and diminished consistency in their responses (i.e., they were less choosy). Additionally, higher choosiness was associated with greater

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mass loss during choice trials, suggesting choosiness is energetically costly. Our results demonstrate that consistency of response to environmental cues is yet another element of behavior that varies among individuals and variation in choosiness could beget speed/quality trade-offs during animal decision making.

**Keywords** Aggression · Choice experiment · Habitat selection · Rapid environmental change · Theridiidae

## Introduction

Consistent individual differences in behavior across time, situation, and ecological context (or “behavioral syndromes”) have received a surge of attention in recent years (see reviews in Dall et al. 2004; Sih et al. 2004, 2010; Bell 2007). Although once commonly considered independently, a growing body of literature indicates various functional categories of behavior are, in fact, interrelated (e.g., boldness, aggressiveness, activity level), owing either to correlated selection (Bell and Sih 2007; Dingemanse et al. 2007) and/or perhaps shared proximate mechanisms (Riechert and Maynard Smith 1989; Carere et al. 2003; Sih et al. 2004, 2010; van Oers et al. 2005; Koolhaas et al. 2010; Kralj-Fiser et al. 2010). Remarkably, despite the increasing number of publications on behavioral syndromes, the trait types under consideration remain quite limited. That is, some trait types (e.g., activity level, boldness, fear, aggressiveness) dominate the syndromes literature (Reale et al. 2007), while other traits (e.g., learning, choosiness, courtship, performance) are underrepresented (Sih and Bell 2008; Pruitt and Husak 2010). Thus, the extent to which these underrepresented trait types exhibit among-individual variation, and the role they play within broader trait complexes remain shortcomings to our understanding of animal personality.

Studies of animal preference and/or choice represent a unique application for behavioral syndromes because variation in individual preference or choosiness has important implications for trait evolution (e.g., the maintenance of trait variation) and experimental design. Typically, choice studies test for nonrandom associations between animal responses and some cue/signal. For instance, one might consider whether females prefer to associate with males possessing brighter coloration relative to other males (Kodric-Brown 1985), or if recruiting pelagic larvae select vacant over densely populated substrates (Grosberg 1981). However, it is almost universally the case that some individuals are unresponsive in choice assays, and these instances are commonly attributed to experimental error; the possibility that responsiveness and/or consistency of response might vary among individuals is largely ignored

(Jaenike and Holt 1991; Jennions and Petrie 1997; Brooks and Endler 2001, but see Riebel et al. 2002 and Campbell and Hauber 2009).

In the present study, we test for among-individual variation in (1) habitat preferences and (2) consistency of response (termed here “choosiness”) towards two cues of habitat quality. Conceivably, individuals with different behavioral tendencies might weigh aspects of habitat quality differently (Pinter-Wollman 2009; Evans et al. 2010); aggressive/bold individuals might select sites with higher prey encounter rates, while passive/fearful individuals might prefer well-protected sites. Alternatively, individuals might vary in their consistency of responses either (1) because individuals detect stimuli and fail to respond or (2) because they fail to detect the stimuli altogether. By testing individuals multiple times, we develop an index of individuals’ consistency of response (i.e., “choosiness”) to various habitat cues, and test whether choosiness is correlated across cue types. Individuals with highly variable responses relative to the average for the population are deemed *less* choosy, whereas individuals with low variability in their responses are deemed *more* choosy. Doubtlessly, choosiness holds a number of energetic costs (e.g., time spent deciding, costs of travel) and benefits (e.g., fewer errors, long-term benefits of superior habitat choice) for individuals, and these likely depend on the environment in which the behavior is expressed (e.g., temporal heterogeneity in habitat quality).

Female Western Black Widows (*Latrodectus hesperus*) construct webs that they occupy for the majority of the lives. Constructing such semi-permanent webs is an energetically costly endeavor (Peakall and Witt 1976; Tanaka 1989; Lubin et al. 1993; Opell 1998), and thus, spiders are often sensitive to cues of web site quality. For example, they commonly select microhabitats with high prey encounter rates (Olive 1980; Gillespie 1981; McKay 1982; Uetz 1986; Gillespie and Caraco 1987; Spiller 1992), favorable microclimates (Almquist 1970, 1973; Riechert 1976), or sites with low pre-existing population densities (Smallwood 1993). Although habitat choice is imposed on all individuals as juveniles, forced web abandonment is not uncommon in adults as the result of intra- and interspecific antagonism (Riechert 1978), ontogenetic shifts in behavior (Hill and Christenson 1981; Kuntner et al. 2010), web damage (Biere and Uetz 1981), repeated encounters with predators (Tolbert 1977), hunger (Wise 1975; McKay 1982), and spatial or structural limitations (Lubin and Robinson 1982).

In this study, we ask the following questions: (1) Do female *L. hesperus* exhibit consistent individual differences in choosiness towards cues of habitat quality? (2) Are individual differences in choosiness correlated across cue types? (3) How is choosiness altered during periods of food

deprivation? (4) Is choosiness associated with mass loss during habitat selection? Identifying individual differences in choosiness and its correlates/costs is valuable for characterizing how animals make decisions, and variation in habitat choice could have important implications for animal dispersion and dispersal across dynamic landscapes.

## Methods

### Study system

The Western Black Widow, *L. hesperus* (Araneae, Theridiidae), is a common tangle web spider throughout the western USA. *L. hesperus* is noteworthy both because of its potent vertebrate-effective venom and because it reaches extremely high population densities in irrigated, urban environments ( $\approx 0.28 \text{ ♀/m}^2$ ) (Trubl and Johnson, unpublished data). *Latrodectus* disperse from their natal webs as early instar juveniles to construct semipermanent solitary webs (Zevenbergen et al. 2008). *Latrodectus* are active at night and spend the majority of daylight hours within web retreats (Pruitt et al. 2009).

### Collection and laboratory maintenance

Adult female *L. hesperus* were collected from a dense urban population at St. James Middle School in Davis, CA, USA in August 2010. Webs occurred in dense patches ( $\approx 2 \text{ ♀/m}^2$ ), and web retreats extended into concrete seating benches. Females ( $N=61$ ) were collected at dusk by disturbing their retreats and chasing them off their webs and into plastic vials. Females were transported to the laboratory at University of California, Davis and housed in 490-ml plastic cups at an ambient photoperiod. Females were fed an ad libitum (one to four individuals) diet of 6-week-old domestic crickets (*Acheta domesticus*) once weekly, and maintained in a laboratory pool for 2 weeks prior to initiating our trial sequence. To track females' body condition, we weighed females daily by chasing them off their webs and into weighing vials. Females were weighed using an A&D GR-202 Semi Micro Balance (readability: 0.0001 g). At the end of our trials, we sacrificed females and measured the tibia of their leg (L4) using digital calipers. We calculated spider condition as the residuals of a linear regression of body mass on tibia length (after Jakob et al. 1996).

Recent feeding history affects many aspects of behavior in *L. hesperus* (Zevenbergen et al. 2008; Trubl et al. 2011), and therefore, we applied two feeding treatments to test for possible condition-dependent effects on habitat choice. Assays were performed in sets of three; one trial per day for three consecutive days. Sated assays

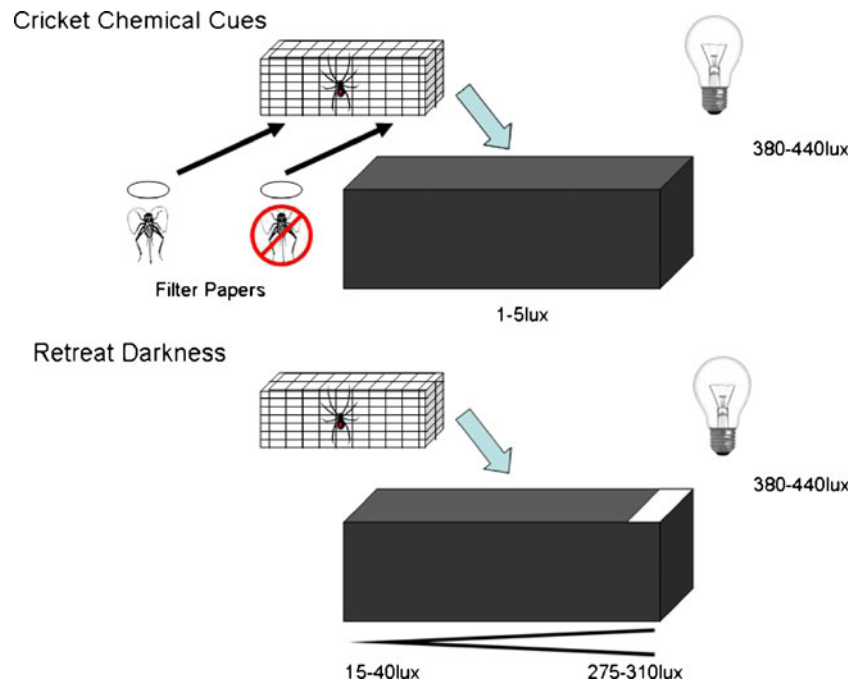
were conducted from 1 to 3 days after a routine feeding and food-deprived trials took place from 9 to 11 days after a routine feeding. The sequence of "sated" and "food deprived" treatments and "cricket chemical cues" and "retreat darkness" assays were interspersed and randomized among individuals, and we allotted one feeding cycle of rest between trial sets. Each female was tested six times with each cue type and feeding regime combination for a total of 24 choice trials. At the end of each set of three trials, females were provided an ad libitum meal of domestic crickets.

### Cricket chemical cues

*L. hesperus* were first demonstrated to respond to prey chemical cues in experimental mesocosms by Johnson et al. (Johnson JC, unpublished data). Our trials occurred within rectangular ( $34 \times 22 \times 9$  cm) arenas made with  $0.5 \times 0.5$  cm Nalgene mesh. We used mesh to construct our arenas because it provided suitable traction for the widows to climb, crawl, and construct webs on all aspects of the enclosure without difficulty. These arenas were then placed within larger black enclosures ( $58 \times 41 \times 15$  cm) which diminished variation in light intensity and air flow within the test arenas (Fig. 1). All of our measurements of light intensity were taken using a handheld photometer (Spectra Cine Candela C-205). Illuminance within closed black enclosures was diminished to 1.0–5.0 lx. Cricket chemical cues were obtained by placing a sheet of filter paper (5 cm radius, Grainger PK 500) within 490-ml plastic enclosures each containing a field cricket (*Gryllus integer*); crickets were also collected from St. James Middle School in Davis, CA, USA. After 2 days, the filter paper was removed and placed at one end of the Nalgene arena and an untreated filter paper control was placed at the opposite end. Our control papers were kept for 2 days in 490-ml plastic enclosures, but without a cricket.

At the start of our trials, test females were placed centrally within the Nalgene mesh arena, which was then placed within a larger light diminishing enclosure, and the top was closed. Females were given 24 h to explore, settle, and initiate web construction. After this time, we noted females' positions within the arena and measured their distance from the filter paper containing prey chemical cues in millimeters using digital calipers. Measurements were taken from females' chelicerae. At the end of our trials, we misted the test arenas with spray bottle to confirm females had initiated web construction. In 100% of our trials, females had initiated web construction within a 24-h test period. To avoid potential confounds of non-experimental stimuli, the orientation of test enclosures was alternated among trials. Enclosures were cleaned between trials with 70% ethanol to remove chemical cues from previous

**Fig. 1** Pictorial summary of the experimental design for our cricket chemical cues and retreat darkness choice assays



assays. Each female was tested 12 times using this procedure (six sated, six food deprived).

#### Retreat darkness

*L. hesperus* strongly prefer to place their retreats within dark protected microhabitats (e.g., wood piles, leaf litter), and extend their capture silk lines towards light (Pruitt JN, personal observation). To test females' response towards light intensity, we placed them within Nalgene arenas and placed these arenas within larger light diminishing enclosures. However, in these trials, we constructed an  $8 \times 18$  cm transparent, plastic window into the lids of each of the enclosures. These windows established a light gradient within the arenas, where one side of the arena experienced high illuminance (275–301 lx) and the opposite side experienced low illuminance (i.e., the “darkest edge”; 25–40 lx; Fig. 1). For reference, the light intensity during a typical sunrise/sunset is  $\approx 400$  lx, and the light intensity during a clear night is  $\approx 1$  lx (Bunning and Moser 1969). Our enclosures were left in laboratory under standard overhead fluorescent lights (380–440 lx) for 24 h; lights were positioned 1.98 m above the enclosures. To avoid potential confounds of non-experimental stimuli, the orientation of test enclosures was alternated among trials. Individuals' response was measured as their distance from the darkest edge of the Nalgene enclosure after a 24-h settlement period. Enclosures were cleaned with 70% ethanol between trials to diminish chemical cues from previous assays. Each female was tested 12 times using this procedure (six sated, six food deprived). To assess potential confounds of temperature versus light

intensity, we placed temperature loggers at either end of our test enclosures in 20 enclosures and recorded the temperature every 6 h for 24 h.

#### Statistical analyses

We estimated the repeatability of females' responses towards cue types using analysis of variance (ANOVA) and partitioning of variances to obtain the intraclass correlation coefficient (after Boake 1989, Iqic et al. 2010). We used nonparametric Spearman's correlations to test for correlations in female choosiness among habitat cues and feeding treatments, and mixed models to test for associations between females' responses and trial order with individual as a random effect. Female choosiness was estimated as the ratio between the average variance of responses exhibited by all test females and the variance of responses exhibited by the focal individual (i.e., average variance of responses for population/variance of focal individual's response). Thus, females with lower than average variance are deemed more “choosy”, while females with higher than average variance are termed less “choosy”. Individuals' choosiness was calculated independently for each cue type and feeding treatment.

To test whether food deprivation reduced females' body condition we used as an ANOVA with each feeding regime and cue type combination as classes, and females' body condition (mass/L4 tibia length) as our response variable. To assess the effects of food deprivation on females' consistency of response, we compared the variance of females' responses during sated and food-deprived conditions using a Kruskal–Wallis test. To

estimate whether choosiness might be energetically costly, we used a mixed model to test for an association between mass loss and choosiness during (1) sets of three choices trials and (2) 3-day periods of rest before and after individuals' trial sequence. If choosiness is costly, or if choosy individuals invest more energy into initial web construction, we anticipate a positive association between choosiness and mass loss during choice trials, but not during periods of rest. To assess whether the cost of choosiness differed among different choice scenarios, we included the interaction terms choosiness  $\times$  trial type in our analysis. We include individual as a random effect in our model, and individuals' starting mass as a covariate. We used paired *t* tests to test for differences in temperature across test arenas during our "retreat darkness" trials (four time checks: 0000, 0600, 1200, 1800). Full test statistics from our post hoc tests are available in our online supplementary materials (Online Resource 1)

## Results

Irrespective of food treatment, females tended to position themselves on the same side of the arena as the source of the cricket chemical cues (sated: 96% of females,  $\chi_{1, 54}^2=14.63$ ,  $P<0.001$ ; food deprived: 92% of females,  $\chi_{1, 54}^2=20.00$ ,  $P<0.0001$ ), and initiated web construction in the darker side of the enclosure (sated: 98% of females,  $\chi_{1, 54}^2=27.00$ ,  $P<0.0001$ ; food deprived: 96% of females,  $\chi_{1, 54}^2=16.55$ ,  $P<0.0001$ ). However, we also detected repeatable differences in female responses towards cricket chemical cues (sated:  $F_{51, 301}=5.00$ ,  $P<0.0001$ ,  $r=0.63$ ; food deprived:  $F_{39, 237}=1.58$ ,  $P=0.022$ ,  $r=0.30$ ) and retreat darkness (sated:  $F_{51, 301}=2.92$ ,  $P<0.0001$ ,  $r=0.47$ ; food deprived:  $F_{38, 233}=1.70$ ,  $P=0.011$ ,  $r=0.32$ ). Repeatabilities were always lower when females were deprived of food. We failed to detect an effect of trial order on females' responses towards either cue type: cricket chemical cue (sated:  $F_{1, 63.85}=0.20$ ,  $P=0.66$ ; food deprived:  $F_{1, 242.8}=1.30$ ,  $P=0.25$ ), retreat darkness (sated:  $F_{1, 122.3}=0.02$ ,  $P=0.87$ ; food deprived:  $F_{1, 48.5}=0.82$ ,  $P=0.37$ ). Additionally, we failed to detect a significant difference in temperature across arenas during our retreat darkness assays: 0000 ( $T_{20}=0.45$ ,  $P=0.66$ ), 0600 ( $T_{20}=1.33$ ,  $P=0.21$ ), 1200 ( $T_{20}=-0.60$ ,  $P=0.16$ ), 1800 ( $T_{20}=-0.09$ ,  $P=0.42$ ).

We detected a significant positive correlation in individual choosiness among cue types for sated individuals; however, this syndrome was nonsignificant in our food-deprivation treatment (Table 1). Choosiness towards cricket chemical cues was significantly correlated across food treatments, but we failed to detect a correlation in choosiness towards illuminance across food treatments. We also detected significant correlations in individuals'

**Table 1** Spearman's correlations across females' choosiness expressed for each cue type and feeding treatment combination: sated (S), food deprived (FD)

	Choosiness for cricket chemical cues (FD)	Choosiness for darkness (S)	Choosiness for darkness (FD)
Choosiness for cricket chemical cues (S)	0.491 <sup>a</sup> $P=0.001$ $N=44$	0.56 <sup>a</sup> $P<0.0001$ $N=52$	0.193 $P=0.245$ $N=45$
Choosiness for cricket chemical cues (FD)		0.139 0.388 $N=47$	0.192 0.245 $N=45$
Choosiness for darkness (S)			-0.0966 0.562 $N=45$

Female choosiness was estimated as the ratio between the average variance of responses exhibited by all test individuals and the variance exhibited by the focal female (average variance of response for all females/variance of focal individual responses)

<sup>a</sup> Denoted significance of  $\alpha=0.008$ , after Bonferroni correction;  $N=51$

average responses across cue types (Table 2): individuals' responses towards cricket chemical cues were positively correlated across feeding treatments ( $r=0.65$ ,  $P<0.0001$ ) and, when sated, we detected a positive correlation between individuals' responses towards cricket chemical cues and their responses to light variation ( $r=0.39$ ,  $P=0.004$ ).

Food deprivation significantly influenced females' responses (i.e., their relative positioning) to cues of habitat quality (Kruskal–Wallis test,  $H_{3,48}=46.22$ ,  $P<0.0001$ ), and

**Table 2** Spearman's correlations between females' average responses towards each cue type and feeding treatment: sated (S), food deprived (FD)

	Responses to cricket chemical cues (FD)	Responses to darkness (S)	Responses to darkness (FD)
Responses to cricket chemical cues (S)	0.653 <sup>a</sup> $P<0.0001$ $N=44$	0.393 <sup>a</sup> $P=0.004$ $N=52$	0.181 $P=0.268$ $N=45$
Responses to cricket chemical cues (FD)		0.382 $P=0.015$ $N=47$	0.180 $P=0.272$ $N=45$
Responses to darkness (S)			0.270 $P=0.095$ $N=45$

Females' responses were estimated as their settlement distance (cm) from the source of prey chemical cues and their distance from the darkest edge of the test arena

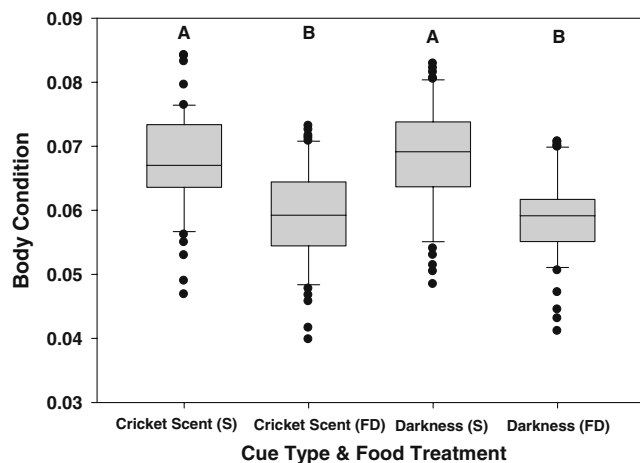
<sup>a</sup> Denoted significance of  $\alpha=0.008$ , after Bonferroni correction;  $N=51$

was associated with depressed body condition ( $F_{3, 207}=24.47$ ,  $P<0.001$ ; Fig. 2). We failed to detect an effect of food deprivation on females' response towards cricket chemical cues, but food-deprived females tended to position themselves farther from the darkest edge of the test arena (i.e., in higher lighting conditions; Fig. 3). Irrespective of cue type, food-deprived females tended to exhibit greater variation in their responses (i.e., they were less choosy; Kruskal–Wallis test,  $H_{3,48}=57.99$ ,  $P<0.0001$ , Fig. 4). However, within each trial type, we failed to detect an association between females' body condition and their choosiness: cricket chemical cue (sated:  $F_{1, 51}=0.43$ ,  $P=0.51$ ; food deprived:  $F_{1, 51}=0.10$ ,  $P=0.75$ ), retreat darkness (sated:  $F_{1, 51}=0.45$ ,  $P=0.50$ ; food deprived:  $F_{1, 51}=0.01$ ,  $P=0.98$ )

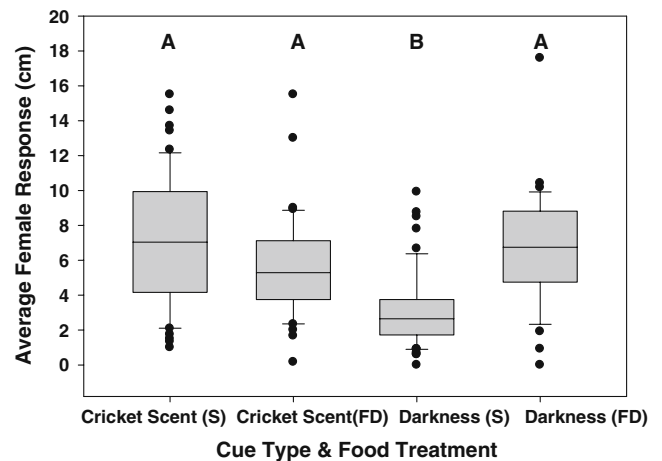
Interestingly, choosiness was associated with greater mass loss during all choice trials ( $F_{5, 212.6}=19.36$ ,  $P<0.0001$ , Table 3, Fig. 5). Furthermore, as evidenced by the interaction term trial type  $\times$  choosiness ( $F_{5, 210.5}=5.14$ ,  $P=0.0002$ ), the relationship between choosiness and mass loss differed significantly among scenarios. However, this result was driven by the nonsignificant association between choosiness and mass loss during resting periods, and when removed, the relationship is diminished ( $F_{3, 210.5}=2.11$ ,  $P=0.10$ ).

## Discussion

The majority of preference studies test for nonrandom associations between animal responses and various cue types; the possibility that individuals might consistently vary in their choosiness is commonly overlooked. Here, we

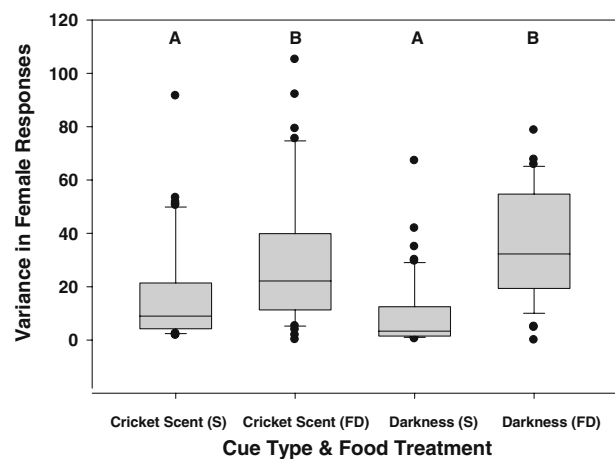


**Fig. 2** Box plots of females' body condition for each cue type (cricket chemical cues, retreat darkness) and feeding treatment (sated (S), food deprived (FD)). Body condition was estimated as the regression of females' body mass (g) on their tibia length of their fourth leg (mm). Vertical shaded bars represent interquartile ranges and vertical lines represent the 90th and 10th percentiles. Bars not sharing a letter differ significantly at  $\alpha=0.05$  using a post hoc Tukey test



**Fig. 3** Box plots of females' response for each cue type (cricket chemical cues, retreat darkness) and feeding treatment (sated (S), food deprived (FD)). Response was measured as females' distance from either the source of cricket chemical cues or the darkest edge within the arena. Vertical shaded bars represent interquartile ranges and vertical lines represent the 90th and 10th percentiles. Bars not sharing a letter differ significantly at  $\alpha=0.05$  using a post hoc Tukey test

demonstrate a behavioral syndrome of choosiness in the Western Black Widow, *Latrodectus hesperus*; when responding to two cues of microhabitat quality, females either exhibited strongly biased and consistent responses towards both cues types or weak/inconsistent responses towards both cues types. Thus, not all *L. hesperus* respond to cues equally and the settlement of some females appears somewhat haphazard (i.e., their responses were highly variable within and across cue types). However, all females exhibited diminished choosiness when deprived of food.



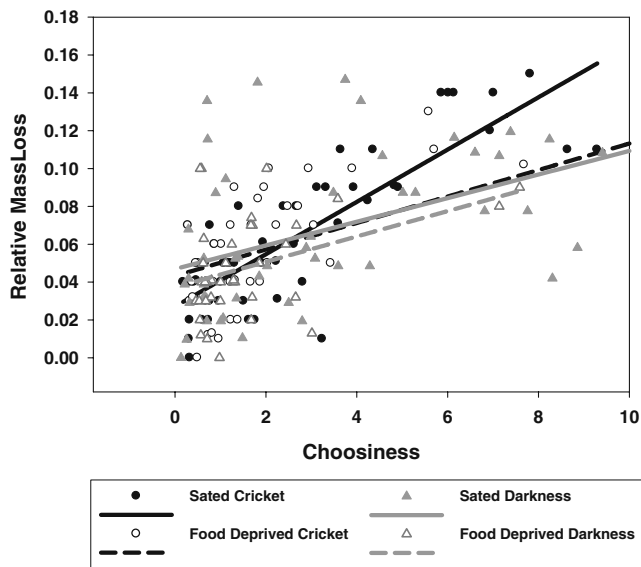
**Fig. 4** Box plots of variance in females' responses for each cue type (cricket chemical cues, retreat darkness) and feeding treatment (sated (S), food deprived (FD)). Food-deprived females exhibited higher variance in their responses. Vertical shaded bars represent interquartile ranges and vertical lines represent the 90th and 10th percentiles. Bars not sharing a letter differ significantly at  $\alpha=0.05$  using a post hoc Tukey test

**Table 3** Summary of effect tests estimating females' mass loss over 3-day period

Source	df	F ratio	P value
Trial type	5, 195.4	2.35	0.04
Choosiness	1, 212.6	19.36	<0.0001
Mass	1, 60.62	6.36	0.01
Trial type × choosiness	5, 210.6	5.14	0.0002
Mass × choosiness	1, 151.5	0.37	0.54
Trial type × mass	5, 190.8	1.67	0.14
Mass × choosiness × trial type	5, 200.2	0.38	0.86

Interestingly, choosiness was associated with greater mass loss during choice trials (Fig. 5), and this finding suggests either (1) choosiness is energetically costly or (2) choosy individuals invest more heavily in initial web construction (i.e., their choices are more decisive). Taken together, our data indicate standard protocols of assaying animal preference could overlook important axes of trait variation and we propose choosiness itself could be an important factor in behavioral evolution.

Food deprivation had a significant effect on the web placement of female *L. hesperus*. Food-deprived females did not significantly differ in their responses towards cricket chemical cues but tended to settle farther from the darkest region of the test arena. These findings are consistent with the hypothesis that hungry, food-deprived females are less responsive to variation in illuminance



**Fig. 5** Interaction plot showing the relationship between individuals' choosiness and relative mass loss (change in mass/individuals' starting mass) over 3 days of choice trials for each trial type. All slopes were statistically distinguishable from zero at  $\alpha=0.001$ . The interaction term trial type × choosiness was not significant ( $F_{3, 210.5}=2.11, P=0.10$ )

(Fig. 3). Alternatively, hungry females could prefer brighter web sites, perhaps because light indicates higher prey encounter rates (i.e., flying insects might be attracted to artificial lighting). However, this latter hypothesis is at odds with our finding that starved females were no more responsive to cricket chemical cues, which seems the more direct indicator of prey encounter rates.

Females universally exhibited more erratic, variable, and less choosy behavior following prolonged periods of food deprivation: (1) repeatabilities were always higher for sated females, (2) we detected cross-contextual correlations in average responses and choosiness for sated females only (Tables 1 and 2), and (3) food-deprived females exhibited higher variance in their responses to habitat cues (Fig. 4). First, these findings suggest individual differences in behavior are more clearly defined when individuals are well fed. Second, and conversely, these data suggest food deprivation generates more erratic/variable behavior in individuals (i.e., it in some sense masks individuals' central behavioral tendencies, or, their "personality"). We propose these findings indicate a relationship between behavioral consistency and body condition. Food deprivation is associated with decreased body condition and diminished energy availability in spiders, including *L. hesperus* (Trubl et al. 2011; Fig. 3). We propose individuals with poor body condition merely have less energy to exert searching for the "best" possible web sites; in contrast, individuals possessing superior body condition might have more energy to explore their surroundings before making their decision (Kasumovic et al. 2009). Thus, it could be suggested that choosiness (Table 1), and/or consistent individual differences habitat preferences (Table 2), are condition-dependent traits of energetic luxury in *L. hesperus*, similar to the exhibition of strong mating (reviewed in Cotton et al. 2006; Hunt et al. 2005; Hebets et al. 2008) and natal habitat (Marshall and Keough 2003; Stamps 2006) preferences in other taxa. Alternatively, food-deprived females might be less able to sense their environment owing to physiological stress, and this could generate more erratic/variable behavior. However, by our interpretation, whether females detect habitat cues and fail to respond, or do not detect them altogether is not vital to our study, because arguably, the phenotypic and ecological outcomes of inconsistent choice would be similar.

Although choosiness was influenced by recent feeding history, individual differences in choosiness were correlated across contexts even when satiation level was held constant (i.e., they are not fully explained by body condition). Given this inter-individual variation, the question then arises of whether it has any adaptive significance in wild populations. Intuitively, choosy individuals might have the benefit of making fewer errors when assessing habitat quality. However, how

selection could benefit nonchoosy individuals is less intuitive. We propose that reduced choosiness might allow individuals a timing advantage, whereby they establish territories early in the season and exploit resources before choosier individuals become established (Chittka et al. 2009). Alternatively, if the environment is highly variable, cues of habitat quality might not adequately forecast future conditions, and thus, choosiness could mean time and energy wasted. Furthermore, as with any behavioral syndrome, correlated behavioral traits could result in performance trade-offs resulting from conflicting selection pressures (Sih et al. 2004), i.e., it might, at times, be advantageous to exhibit choosiness towards some habitat cues but ignore others. Strong trait correlations, however, could preclude individuals' ability to optimally adjust their habitat selection criteria. For example, if there were positive correlations in choosiness among cue types (as detected here), high sensitivity to a *suite* of cue types could result in excessively high standards for settlement.

Finally, our data emphasize a common oversight of the literature of animal choice (e.g., habitat choice, mate choice, and diet selectivity). As mentioned above, choice studies most commonly test for nonrandom associations between animal choice and some suite of options (e.g., Grosberg 1981; Kodric-Brown 1985). Another more recent body of literature has emphasized condition-dependent expression of choosiness (Hunt et al. 2005; reviewed in Cotton et al. 2006; Hebets et al. 2008). However, these investigations could easily overlook individual differences in general choosiness that operate independently of recent feeding history and contemporary body condition, and we argue that this variation could change the expected outcomes of selection. In sexual selection, nonchoosy individuals are thought to weaken selection on ornamentation/courtship and thereby aid in maintaining trait variation (reviewed in Cotton et al. 2006). In diet selection, nonchoosy individuals are perhaps more likely to discover and utilize new food items, and allow for evolutionary expansion of diet breadth. Similarly, in habitat choice, nonchoosy individuals might be more likely to select and utilize novel habitat types, and this could prove valuable during periods of rapid environmental change (e.g., during urbanization) (Pinter-Wollman 2009; Evans et al. 2010; Møller 2010). Furthermore, as evidenced here, there exists the potential for choosiness to be correlated across decision types (mating, habitat, diet), and “discovery” prone individuals are one conceivable outcome. Granted, the data herein were taken under controlled, experimental conditions, and thus, the degree to which individual differences in choosiness manifest in the field is unknown: food availability is highly variable in the field, which could mask individual differences (Tables 1 and 2, Fig. 4);

however, (1) even starved females exhibited repeatable behavioral tendencies (i.e.,  $r=0.30\text{--}0.34$ ), (2) field observations of prey capture indicate *Latrodectus* tend to capture prey at least nightly (i.e., they are usually well fed; Pruitt et al. 2009), and (3) recent meta-analyses have suggested that the signal of individual differences are actually greater in the field (Bell et al. 2009). We suggest further work is needed to address the fitness consequences of individual variation in choosiness, and whether there are predictable, adaptive differences in choosiness and/or selection criteria among populations (e.g., diminished choosiness in urban environments).

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