



# Hunger effects on foraging responses to perceptual cues in immature and adult wolf spiders (Lycosidae)

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The wolf spider, *Schizocosa ocreata* (Hentz), varies foraging patch residence time in the presence of different sensory cues from prey, even without food rewards. This study examines the influence and interaction of hunger state, age and sex on the use of different types of sensory information to determine foraging patch sampling duration. In a series of two-chambered artificial foraging patches, I tested 26 *S. ocreata* once as immatures, and again as adults, under two hunger states (satiated and 7 days without food). Patches varied in the type of sensory information provided by live prey (crickets) as follows: visual cues alone; vibratory cues alone; combined visual/vibratory cues; and control (no prey). Without feeding in patches, the type of sensory stimuli available from prey strongly affected patch residence time, with spiders using primarily visual rather than vibratory cues. Hunger level as a main effect had no influence on residence time, but hunger state did mediate the importance of visual or vibratory information. Significant age- and sex-related differences in patch residence time in the presence of different sensory cues were found. These data suggest that ontogenetic and sex-specific foraging strategies are influenced by use of prefeeding perceptual cues rather than hunger state in wolf spiders.

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Animals forage differently when hungry than when satiated (Caraco et al. 1980; Caraco 1981, 1982; Godin & Crossman 1994). Changes in locomotory patterns (Carter & Dixon 1982; Bell et al. 1985), selectivity to food type (Elner & Hughes 1978; Demott 1993), predator avoidance (Lima et al. 1985; Godin & Crossman 1994; Horat et al. 1994), patch choice (Caraco 1983), and patch residence time (Gardner 1964), are all known to be affected by hunger level. Most studies of hunger effects on foraging decisions measure how animals balance energy gain with various foraging costs such as predation risk, search time, handling time, or other factors. Equally important however is identifying whether changes in hunger state alter the proximate perceptual cues from prey that are relevant to foraging decisions. The physiological state of an animal may mediate changes in threshold responses to proximate food cues or the type of sensory information most important to an animal while foraging, but such relationships have not been well studied (Haskell et al. 1962; Bell 1991). It is likely that for many animals, the threshold level of response towards prey stimuli drops with increasing hunger level and that the number of sensory channels used to detect prey increases.

Krafft (1982) states that among spiders, perception of sensory signals varies with the spider's age, life experience and physiological state. This supposition has been supported with respect to courtship communication (Krafft 1982). However, few studies have examined the effects of hunger on the importance of different prey cues and foraging decisions. Berestynska-Wilczek (1962) found that hungry wolf spiders show predatory behaviour to a wider range of water-borne vibration frequencies than well-fed spiders, suggesting that the importance of vibratory information from prey may vary with the physiological state of the forager. Such changes in reactions to proximate prey stimuli are rarely explicitly addressed with respect to broader foraging decisions such as patch residence time despite a body of evidence that shows sensory cues from prey profoundly affect patch choice and residence time decisions even in the absence of energy gain (Riechert 1985; Morse 1993; Pasquet et al. 1994; Persons & Uetz 1996a, b, 1997a, b).

*Schizocosa ocreata* (Hentz) is a common ground-dwelling arthropod found in complex deciduous forest leaf litter in the eastern United States, and like most wolf spiders, does not build webs, but uses a 'sit-and-wait' foraging strategy with frequent site changes (Ford 1978; Cady 1984). *Schizocosa ocreata* use visual and vibratory cues in their courtship displays (Stratton & Uetz 1981),

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and to locate and attack prey (Persons & Uetz 1996a). They are also capable of perceiving and orienting towards prey with vibratory information only, but appear to use visual information rather than substratum-coupled vibrations to assess patch residence time (Persons & Uetz 1996a). The aim of this study was to: (1) test the influence of hunger state on the use of visual and vibratory information from prey in regulating residence time decisions in foraging patches; and (2) determine whether the use of perceptual cues from prey and changes in hunger level interact differently due to the age and sex of the spider.

## METHODS

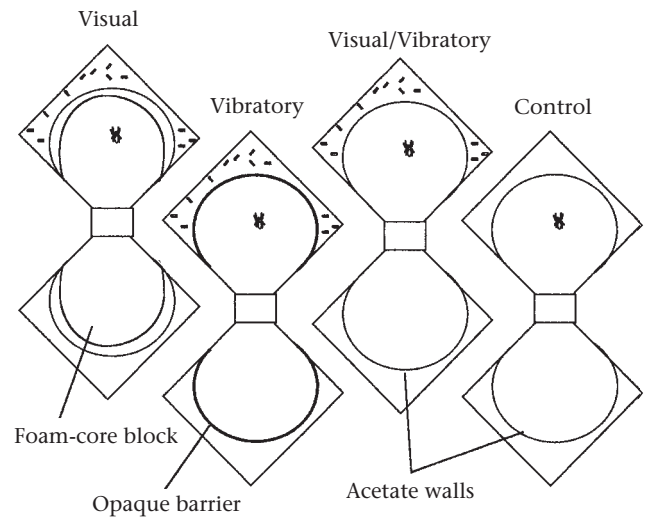
### Spider Collection and Maintenance

I caught 80 immature *S. ocreata* of unknown sex during 14–18 April 1995 at the Cincinnati Nature Center, Clermont County, Ohio. Each spider was housed in its own opaque container, provided water ad libitum, and maintained on a diet of three 1-week-old cricket nymphs every 4 days. I subjected each spider to a series of experimental trials under two hunger treatments. Prior to the experiment, I allowed the spiders to feed to satiation, and then tested only those spiders that had not consumed all of the live crickets available immediately before testing. I then withheld food for 7 days and retested the spiders. After the second testing, I fed the spiders three crickets each. As an assay for hunger state, I used only those spiders that had captured and consumed a cricket within 1 min of presentation. I then returned the spiders to their pretesting feeding schedule (three crickets every 4 days) until maturity. The experiment was repeated again with mature spiders using the same feeding procedure for satiated and hungry treatments. All spiders were kept under identical controlled conditions at room temperature (23–25°C) in an environment with stable humidity and a 13:11 h light:dark cycle.

### Experimental Protocol

I exposed the spiders to a series of artificial foraging patches that controlled for sensory stimuli from prey. I presented each spider with four sensory treatments using crickets as stimuli: (1) visual information alone; (2) vibratory alone; (3) combined visual/vibratory information; and (4) a control (no crickets present). All spiders experienced every sensory treatment under two hunger levels (in the sequence of satiated and 7 days without food). Each spider was presented every combination of these treatments twice, once as immatures and again as adults. Spiders were not allowed to feed on crickets at any time during a trial. All spiders were presented sensory treatments in random order with at least 30 min between treatments.

The artificial foraging patches used for testing patch residence time consisted of four containers made of white foam-core board, each of which differed in the sensory stimuli available to the spider being tested (Fig. 1). Each container housed two round chambers, 20 cm in diam-



**Figure 1.** The artificial foraging environment used for spider testing. Spiders were placed in the 'neutral' chamber prior to each experiment (spider shown in sensory stimulus chamber) and allowed to move freely between the two chambers after a 5-min acclimation period. Using cricket nymphs as stimuli (indicated by specks in stimulus chambers), each pair of chambers differed in the sensory stimuli presented to the spider.

eter, made of transparent 0.08-mm acetate. One chamber served as a neutral chamber into which the spider was introduced, and the other chamber contained 12 crickets that served as stimuli (sensory chamber). I introduced the crickets from behind the acetate wall of each sensory chamber. Each spider was randomly assigned and tested under all four sensory levels. For the visual-only treatment, I placed the cricket on a separate foam-core block from that of the spider so that vibrations could not be transmitted to the substratum that the spider occupied. For the vibratory-only treatment, I covered the acetate wall separating the spider and crickets with an opaque paper barrier. For the combined visual/vibratory treatment, I used only a single transparent acetate wall without a visual or vibratory barrier. The control treatment was identical to that of the combined visual/vibratory treatment, but lacked crickets. The vibration levels in each sensory treatment of the apparatus were tested and found to be significantly different (Persons & Uetz 1996a, 1998). Vibration levels in the visual-only treatment were not significantly different from the control.

An experimental trial consisted of a single spider introduced into the neutral (no cricket stimuli) chamber under a clear plastic vial. After a 5-min acclimation period, I removed the vial and allowed the spider to enter and exit the single sensory chamber freely for 30 min. I videotaped every trial from above, and determined the duration and number of chamber visits by videotape analysis. I placed clean white paper on the floor of each chamber of the apparatus prior to each trial, and swabbed the chambers with clean dry cotton between trials. This was done to remove any silk draglines that might affect subsequent foraging behaviour. I tested 80 spiders under each sensory treatment four times, for a total of 8 h/spider (twice as

immatures and twice as adults, once each under the satiated and the hungry condition). I determined the sex of immature spiders by assigning each juvenile spider an identification number and then sexing each upon maturation.

### Statistical Methods

The statistics used for this study were similar to those described elsewhere (Persons & Uetz 1996a). We performed a complete five-way ANOVA with hunger level, sex, age, individual and sensory stimuli as categorical variables. Individual was treated as a random effect nested within sex. All other variables were fixed and crossed. To analyse the effect of each individual spider across the different treatments, I used four three-way mixed model ANOVAs to analyse the variation in duration of patch visits (Zar 1984). This was done because the individual effect could be treated as a crossed rather than nested effect. In this case, I tested patch residence time, the dependent variable, using individual (random), sensory chambers (fixed), and hunger (fixed) as categorical variables. I performed four ANOVAs separately for adult males, adult females, immature females and immature males, respectively. I also completed four four-way ANOVAs to determine sex and age effects. These ANOVAs were based on data for males, females, adults and immatures, respectively, with individual, sensory stimuli, hunger, and either age or sex as the fourth categorical variable. All data were natural log (ln) transformed to conform to ANOVA assumptions of normality. Only spiders that visited each sensory treatment at least twice under both hunger treatments and age classes were used in the analysis. The last visit into a sensory chamber was omitted from analysis if the spider was in the chamber when the trial time had expired. Only 26 of the 80 spiders tested matched these criteria (females  $N=15$ , males  $N=11$ ).

Because previous studies have demonstrated that spiders choose patches at random and do not vary patch residence time based on previous visits to the patch (Persons & Uetz 1996a, 1997a, b), I regarded all sequential visits into a sensory treatment by a single spider as independent replicates for that individual. Because of the nature of the design, I was also able to compare within-individual variation in sensory bias and patch residence time.

### RESULTS

Although the spiders appeared to increase patch sampling duration slightly when they were hungry compared with when they were satiated, hunger had no statistically significant effect on patch residence time. There was, however, a significant interaction between hunger and sensory treatment, indicating that hunger state affected the use of different sensory cues during foraging decisions. Spiders increased their patch residence time when sensory stimuli were present, indicating that in the absence of prey sampling information, spiders made decisions based on sensory information alone. Furthermore,

**Table 1.** Five-way ANOVA indicating the effects of individual, sensory stimuli, age, sex and hunger level on residence time

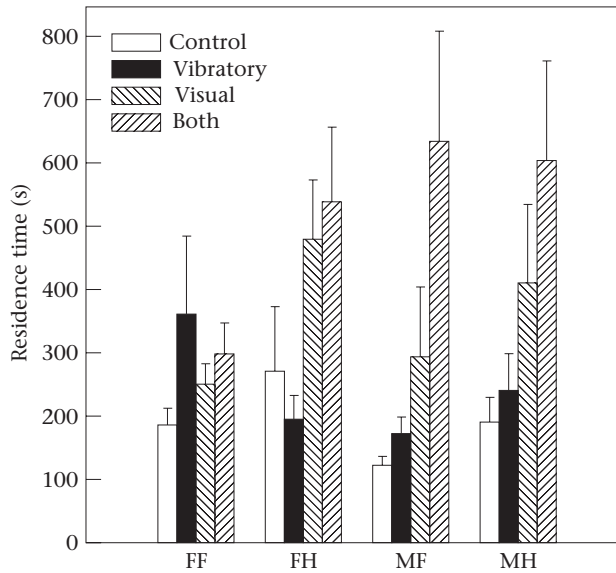
| Source                            | <i>df</i> | <i>F</i> | <i>P</i> |
|-----------------------------------|-----------|----------|----------|
| Individual (sex)                  | 2         | 7.20     | 0.0008*  |
| Sensory stimuli                   | 3         | 83.16    | 0.0001*  |
| Age                               | 1         | 647.98   | 0.0001*  |
| Sex                               | 1         | 6.18     | 0.013*   |
| Hunger                            | 1         | 0.36     | 0.55     |
| Individual*Sensory                | 3         | 0.79     | 0.5      |
| Individual*Hunger                 | 1         | 2.66     | 0.103    |
| Individual*Age                    | 1         | 21.74    | 0.0001*  |
| Age*Sex                           | 1         | 5.88     | 0.015*   |
| Age*Hunger                        | 1         | 3.19     | 0.074    |
| Sensory*Age                       | 3         | 0.47     | 0.704    |
| Sensory*Sex                       | 3         | 0.66     | 0.58     |
| Sensory*Hunger                    | 3         | 3.13     | 0.025*   |
| Individual*Sensory*Age            | 4         | 7.06     | 0.0001*  |
| Individual*Sensory*Sex            | 3         | 0.44     | 0.72     |
| Individual*Sensory*Hunger         | 3         | 0.91     | 0.43     |
| Individual*Age*Hunger             | 1         | 0.67     | 0.68     |
| Sensory*Age*Sex                   | 4         | 4.44     | 0.001*   |
| Sensory*Age*Hunger                | 4         | 2.33     | 0.053    |
| Age*Sex*Hunger                    | 2         | 3.37     | 0.035*   |
| Individual*Sensory*Age*Sex        | 4         | 2.47     | 0.043*   |
| Individual*Sensory*Sex*Hunger     | 4         | 1.26     | 0.28     |
| Individual*Age*Sex*Hunger         | 2         | 0.30     | 0.74     |
| Sensory*Age*Sex*Hunger            | 6         | 1.33     | 0.24     |
| Individual*Sensory*Age*Sex*Hunger | 6         | 1.88     | 0.0797   |

*F* values were calculated based on a mixed model ANOVA. \* $P<0.05$ .

there were also significant differences in residence time attributable to sensory stimuli when spiders were fully satiated. In general, spiders increased patch residence time when visual and vibratory information were presented together relative to when either was presented alone (Table 1).

Spiders of different ages and sexes responded differently to sensory information (Figs 2, 3; Table 1). Visual information affected patch residence for hungry and satiated spiders of both sexes, whereas vibratory information only affected patch residence for satiated, immature female spiders. ANOVA results indicated that male and female spiders differed significantly in residence times, both as immatures and as adults. There were also significant age effects for both sexes (Tables 2, 3), and all age/sex groups showed significantly different patch residence times based on the type of sensory stimuli available. There was a significant interaction of sensory stimuli with age for male spiders, suggesting an ontogenetic shift in perceptual bias, but such an effect was lacking in females (Table 2). Adult spiders had lower patch residence times than immature spiders, and adult males had lower residence times than adult females (Fig. 2). Immature males spent the longest time on average in most patches and responded more strongly to the combined visual/vibratory cues.

All ANOVAs revealed significant individual effects as well as significant interactions between individuals and sensory treatments (Table 4). I calculated mean residence times for spiders in each sensory treatment and used individual spider as a replicate. Results of Tukey post hoc



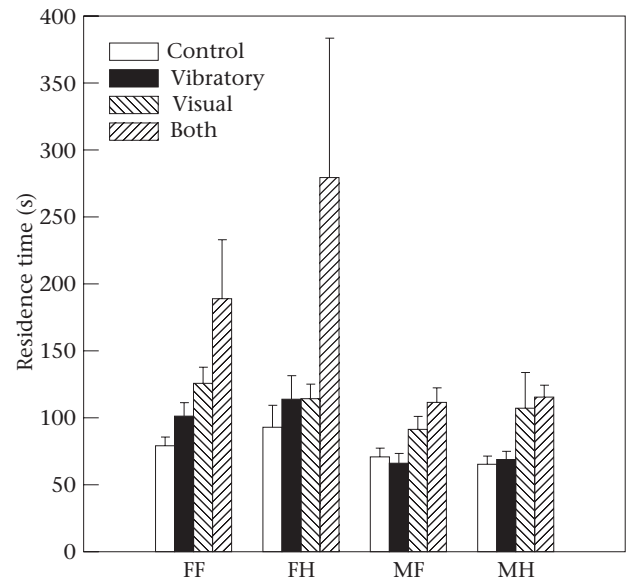
**Figure 2.** Mean residence time (s) for immature spiders in each sensory treatment (males:  $N=11$ , 435 patch visits; females:  $N=15$ , 711 patch visits). Treatments include (1) control, no crickets, (2) vibratory stimuli only, (3) visual stimuli only, and (4) combined visual/vibratory stimuli. Spiders are grouped by sex and hunger treatment (FF: satiated female; FH: hungry female; MF: satiated male; MH: hungry male)

comparison of means tests for adult males and females and immature males and females indicated that the effects of sensory information on residence time between the four groups differed slightly.

## DISCUSSION

Hunger had no direct effect on spider residence time, but did cause significant changes in the use of visual or vibratory information (Table 1). Furthermore, the relative influence of hunger state on the use of different sensory channels was dependent on the sex and age of the spider. There was a significant interaction of hunger and sex among adult spiders but not juveniles (Table 3). Hunger effects on the use of different sensory cues were also significant among females but not males (Table 2). These data combined suggest that the responses of adult females to sensory cues from prey are more sensitive to changes in physiological state than are the responses of males. Studies with carabid beetles found sex-based foraging differences in response to hunger, but hunger was directly related to locomotor patterns of beetles rather than indirectly through variation in the importance of various sensory inputs (Wallin & Ekblom 1994).

The influence of hunger on foraging behaviour among spiders is unclear. Some studies have shown a hunger effect (Gillespie & Caraco 1987; Uetz 1988; Higgins 1990; Higgins & Buskirk 1992; Sherman 1994), while others have not (Vollrath 1985; Provencher & Riechert 1991). Differences in the results of these studies may be largely associated with the duration of food deprivation. Spiders, unlike many other animals, may not alter foraging patterns greatly due to hunger state because they are



**Figure 3.** Mean residence time (s) for mature spiders in each sensory treatment (males:  $N=11$ , 1139 patch visits; females:  $N=15$ , 1195 patch visits). Treatments and groups as designated in Fig. 2.

known to have physiological adaptations to limited feeding opportunities and starvation (Anderson 1974; Greenstone & Bennett 1980; Wise 1993). Consequently, spiders may require very long periods of time without food before behavioural changes are noted. Anderson (1974) found that a larger species of wolf spider, *Lycosa lenta* (Keyserling) had no significant changes in activity patterns after being starved for 30 days. Tanaka & Ito (1982) found that male *Pardosa astrigera* (L. Koch), a wolf spider whose size is comparable to *S. ocreata*, survived over a month when completely deprived of food, with females living over 54 days when starved. Tanaka & Ito noted that a dramatic decrease in respiratory rate occurs with starvation, which presumably corresponds to a drop in metabolic rate without any detectable difference in behaviour. Considering that the food-deprivation period for *S. ocreata* was much less than that for *P. astrigera*, it is likely that extending the hunger treatment to a much longer period of time would increase the likelihood of detecting differences between treatments.

Although the hunger treatment for *S. ocreata* in the present study did not represent starvation conditions, 7 days without food did cause strong differences in the spiders' motivation to feed, but not necessarily their motivation to attack prey. During feeding trials for the satiation treatments, all spiders, and adult females in particular, continued to kill more crickets than they could consume. Such 'wasteful killing' has been documented in other wolf spiders as well (Samu & Bíró 1993). This suggests that the sensory stimuli from prey that initiate predatory behaviour are unrelated to hunger level, and that changes in prey consumption behaviour may precede changes in prey capture behaviour. Previous studies indicate that prey capture and prey feeding are not equally important contributors to determining residence time. Persons & Uetz (1997b) found that spiders that

**Table 2.** Comparison of male and female spiders indicating the effects of individual, sensory stimuli, age and hunger level on residence time

| Source                        | df | F      | P       |
|-------------------------------|----|--------|---------|
| Female spiders                |    |        |         |
| Individual                    | 14 | 10.65  | 0.0001* |
| Sensory stimuli               | 3  | 50.61  | 0.0001* |
| Age                           | 1  | 341.69 | 0.0001* |
| Hunger                        | 1  | 0.43   | 0.51    |
| Individual*Sensory            | 42 | 2.45   | 0.0001* |
| Individual*Age                | 14 | 13.06  | 0.0001* |
| Individual*Hunger             | 14 | 7.23   | 0.0001* |
| Sensory*Age                   | 3  | 1.64   | 0.178   |
| Sensory*Hunger                | 3  | 7.74   | 0.0001* |
| Age*Hunger                    | 1  | 0.22   | 0.64    |
| Individual*Sensory*Age        | 42 | 2.76   | 0.0001* |
| Individual*Age*Hunger         | 13 | 1.17   | 0.292   |
| Sensory*Age*Hunger            | 3  | 0.28   | 0.84    |
| Individual*Sensory*Hunger     | 42 | 1.94   | 0.0003* |
| Individual*Sensory*Age*Hunger | 39 | 3.50   | 0.0001* |
| Male spiders                  |    |        |         |
| Individual                    | 10 | 4.00   | 0.0001* |
| Sensory stimuli               | 3  | 55.40  | 0.0001* |
| Age                           | 1  | 521.61 | 0.0001* |
| Hunger                        | 1  | 7.20   | 0.007*  |
| Individual*Sensory            | 30 | 2.09   | 0.0005* |
| Individual*Age                | 10 | 7.40   | 0.0001* |
| Individual*Hunger             | 10 | 2.43   | 0.007*  |
| Sensory*Age                   | 3  | 3.97   | 0.008*  |
| Sensory*Hunger                | 3  | 0.68   | 0.56    |
| Age*Hunger                    | 1  | 2.08   | 0.149   |
| Individual*Sensory*Age        | 30 | 2.32   | 0.0001* |
| Individual*Age*Hunger         | 9  | 5.14   | 0.0001* |
| Sensory*Age*Hunger            | 3  | 0.53   | 0.66    |
| Individual*Sensory*Hunger     | 30 | 2.24   | 0.0001* |
| Individual*Sensory*Age*Hunger | 27 | 2.45   | 0.0001* |

F values were calculated for a four-way mixed model ANOVA. \* $P < 0.05$ .

attacked without consuming prey significantly increased their patch residence time compared with spiders that were exposed to prey but did not attack. Also, spiders feeding on a single dead prey item in a patch did not result in longer residence times compared with spiders in empty patches (Persons & Uetz 1997a). Collectively, these studies suggest that residence-time decisions are mediated almost entirely by prefeeding sensory cues rather than postingestive feedback mechanisms. This is an important finding considering that the vast majority of foraging studies on residence time decisions strongly emphasize energy gain rather than sensory information as a decision variable (Stephens & Krebs 1986).

Age and sex of a spider contributed more to observed differences in residence time than did hunger level (Table 1). Male and female differences in foraging behaviour have been found in other hunting spiders as well (Givens 1978; Cady 1984). Edgar (1971) found that in another species of wolf spider, adult male *Pardosa lugubris* (Walckenaer) do not increase their weight, but females may double theirs. Givens (1978) found that male jumping spiders use a smaller proportion of each prey item than females. These studies suggest that females have larger energy requirements than males, which would

**Table 3.** Comparison of immature and adult spiders indicating the effects of individual, sensory stimuli, sex and hunger level on residence time

| Source                        | df | F     | P       |
|-------------------------------|----|-------|---------|
| Immature spiders              |    |       |         |
| Individual (sex)              | 2  | 7.31  | 0.0007* |
| Sensory stimuli               | 3  | 24.24 | 0.0001* |
| Sex                           | 1  | 4.98  | 0.033*  |
| Hunger                        | 1  | 1.95  | 0.163   |
| Individual*Sensory            | 3  | 0.93  | 0.43    |
| Individual*Hunger             | 1  | 1.57  | 0.21    |
| Sensory*Sex                   | 3  | 3.62  | 0.013*  |
| Sensory*Hunger                | 3  | 2.24  | 0.082   |
| Sex*Hunger                    | 1  | 0.02  | 0.89    |
| Individual*Sensory*Sex        | 3  | 0.73  | 0.54    |
| Individual*Sex*Hunger         | 1  | 0.00  | 0.99    |
| Sensory*Sex*Hunger            | 3  | 0.36  | 0.78    |
| Individual*Sensory*Hunger     | 3  | 0.99  | 0.4     |
| Individual*Sensory*Sex*Hunger | 3  | 1.27  | 0.282   |
| Adult spiders                 |    |       |         |
| Individual (sex)              | 2  | 9.97  | 0.0001* |
| Sensory stimuli               | 3  | 65.62 | 0.0001* |
| Sex                           | 1  | 3.89  | 0.021*  |
| Hunger                        | 1  | 0.42  | 0.52    |
| Individual*Sensory            | 3  | 2.07  | 0.102   |
| Individual*Hunger             | 1  | 2.34  | 0.126   |
| Sensory*Sex                   | 3  | 0.77  | 0.512   |
| Sensory*Hunger                | 3  | 2.47  | 0.06*   |
| Sex*Hunger                    | 1  | 7.19  | 0.007*  |
| Individual*Sensory*Sex        | 3  | 1.11  | 0.345   |
| Individual*Sex*Hunger         | 1  | 0.32  | 0.57    |
| Sensory*Sex*Hunger            | 3  | 4.04  | 0.007*  |
| Individual*Sensory*Hunger     | 3  | 1.35  | 0.257   |
| Individual*Sensory*Sex*Hunger | 3  | 0.88  | 0.45    |

F values were calculated for a four-way mixed model ANOVA. \* $P < 0.05$ .

explain why females are more likely to change responses to prey cues due to hunger state. In the present study, adult male *S. ocreata* had much shorter residence times than immature or adult female spiders, a common characteristic of many animals with females that are dispersed widely. Previous field studies with *S. ocreata* have found that locomotor rates are higher in adult males than adult females (Cady 1984). The common dictum is that mature male wandering spiders spend most of their time searching for females rather than foraging, although how much time is actually spent on each activity is not known because the two are not mutually exclusive. In this study, I found that adult males showed significant residence-time differences due to different prey stimuli, indicating that male locomotor patterns are at least partially determined by the presence of prey (Table 4).

Although foraging differences between adult male and female spiders are well known, attempts to determine juvenile sex differences have been largely ignored. This study represents the first evidence of foraging differences between prepenultimate immature male and female spiders (Table 3). Previous studies examining sex differences among juvenile spiders have been conducted only on penultimate spiders, in which the genitalia have undergone considerable development, and hormonal

**Table 4.** Comparison of adult and immature male and female spiders indicating the effects of individual, sensory stimuli and hunger level on residence time

| Source                    | df | F     | P       |
|---------------------------|----|-------|---------|
| Immature female spiders   |    |       |         |
| Individual                | 14 | 14.48 | 0.0001* |
| Sensory stimuli           | 3  | 13.17 | 0.001*  |
| Hunger                    | 1  | 0.98  | NS      |
| Individual*Sensory        | 42 | 1.50  | 0.026*  |
| Individual*Hunger         | 14 | 3.93  | 0.0001* |
| Sensory*Hunger            | 3  | 0.94  | NS      |
| Individual*Sensory*Hunger | 32 | 2.99  | 0.0001* |
| Immature male spiders     |    |       |         |
| Individual                | 10 | 4.59  | 0.0001* |
| Sensory stimuli           | 3  | 12.17 | 0.0001* |
| Hunger                    | 1  | 1.31  | NS      |
| Individual*Sensory        | 30 | 1.61  | 0.0247* |
| Individual*Hunger         | 10 | 4.06  | 0.0001* |
| Sensory*Hunger            | 3  | 0.01  | NS      |
| Individual*Sensory*Hunger | 30 | 1.82  | 0.0065* |
| Adult female spiders      |    |       |         |
| Individual                | 14 | 8.97  | 0.0001* |
| Sensory stimuli           | 3  | 9.72  | 0.0001* |
| Hunger                    | 1  | 0.37  | NS      |
| Individual*Sensory        | 42 | 3.82  | 0.0001* |
| Individual*Hunger         | 13 | 4.46  | 0.0001* |
| Sensory*Hunger            | 3  | 1.83  | NS      |
| Individual*Sensory*Hunger | 39 | 2.40  | 0.0001* |
| Adult male spiders        |    |       |         |
| Individual                | 11 | 5.74  | 0.0001* |
| Sensory stimuli           | 3  | 17.84 | 0.001*  |
| Hunger                    | 1  | 1.99  | NS      |
| Individual*Sensory        | 33 | 2.59  | 0.0001* |
| Individual*Hunger         | 9  | 2.46  | 0.0001* |
| Sensory*Hunger            | 3  | 0.58  | NS      |
| Individual*Sensory*Hunger | 27 | 2.65  | 0.0001* |

F values were calculated for a three-way mixed model ANOVA. \* $P < 0.05$ .

influences may have modified the spider's behaviour (Singer & Riechert 1994).

Because adult male and female *S. ocreata* differ in size (Dondale & Redner 1978), and males mature several weeks before females, divergent developmental schedules may explain differential use of sensory information. Developmental differences in sensory systems, the nervous system, and moulting processes may all affect spider sensory structures. Studies with orb-weaving spiders have found profound differences in the central nervous system of immature and adult spiders, as well as males and females (Babu 1975, 1985). Timing of the development of optic neuropiles or the number of vibratory organs may also contribute to measurable ontogenetic shifts in sensory biases (Barth 1985).

A general pattern found in this study across all age and sex categories was a greater reliance on visual than vibratory information in determining residence time in patches (Figs 2, 3). This supports previous findings that vibratory cues are used very little in the residence-time decisions of *Schizocosa* Chamberlin (Persons & Uetz 1996a, b), but significantly alter foraging patterns when combined with visual information from prey. The cause of the differences between groups with respect to their

use of sensory information is unclear. The possibility of sampling error cannot be dismissed, but some variation in the use of sensory information may be partially explained by the habitat structure of *S. ocreata*. It is commonly found inhabiting complex leaf litter associated with the ground layer of deciduous forests of the eastern United States. The amount and level of decomposition of the leaf litter varies with the time of the year. Scheffer et al. (1996) found that this type of leaf litter does not conduct sound vibration well, and they suggested that this may contribute to this species use of a visual mode of communication in their courtship displays relative to other wolf spider species. Such a substratum would favour the use of visual information over vibratory cues in a foraging context because the distance for visual prey perception may be substantially greater than vibratory prey perception, contributing to increased foraging efficiency.

Inter- and intraindividual variation in patch tenure was high and statistically significant (Tables 1–4). Most foraging models, with the exception of some ideal free distribution models (Stephens & Krebs 1986), fail to predict such variation. Extreme stochasticity in prey availability probably contributes to this variability. Spiders may adopt a decision rule that is based on some fixed, or condition-dependent (i.e. hunger state) probability of leaving a foraging patch (Janetos & Cole 1981; Janetos 1982; Kareiva et al. 1989), which would also result in such variation. Alternatively, studies with *S. ocreata* indicate spiders use movement cues from prey to determine patch residence-time, with variability in cricket movement between chamber visits and between individuals contributing most to patch residence-time differences (Persons & Uetz 1997b).

In conclusion, patch-tenure differences between males and females in different stages of development reflect dynamic foraging strategies. Results support a clear ontogenetic shift in foraging from a more 'sit-and-wait' strategy as a juvenile to an 'active-search' mode for adults. Divergent patterns in foraging behaviour are mediated by decision rules based on the importance of different sensory cues from prey. Hunger state plays only a minor role in residence time decisions, to the extent that it mediates the importance of different prey cues. The lack of significant effects of hunger on residence time are probably due to spider resistance to starvation and the importance of sensory rather than postingestive information as a decision currency. Further studies examining the proximate cues governing foraging behaviour and those integrating sensory information into future foraging models should prove fruitful.

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