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The Effect of Prey Movement on Attack Behavior and Patch Residence Decision Rules of Wolf Spiders (Araneae: Lycosidae)

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We used a video imaging technique to test the effects of prey movement on attack behavior and foraging patch residence time decision rules of wolf spiders. Twelve Schizocosa ocreata *(Hentz) (Lycosidae) were tested in an artificial foraging patch stimulus chamber consisting of a microscreen television displaying a computer digitized, animated image of a cricket. Four prey movement treatments were used: (1) a blank screen, (2) a stationary cricket control, (3) a cricket moving for 1 min, and (4) a cricket moving for 10 min. Spiders stayed significantly longer in treatments with higher cricket activity. Spiders also stayed longer when they attacked the stimulus than when they did not. The distribution of patch residence times of spiders indicates a decision rule based on a fixed probability of leaving.*

KEY WORDS: Lycosidae; decision rules; prey movement; prey attack; wolf spiders.

INTRODUCTION

Foraging theorists have attempted to predict the foraging behavior of animals through the use of mathematical models over the last 30 years (for reviews see Shoener, 1971; Pyke *et al.*, 1977; Pyke, 1984). These models assume that fitness may be estimated by some energy or nutrient-related currency (e.g., biomass consumed, prey items taken, rate of caloric intake) and that animals forage in a manner that maximizes one of these currencies. Models for both sit-

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and-wait and actively foraging predators have sought to predict how long animals remain in one foraging patch before moving to another (patch models) so as to maximize their net energy gain/time (Charnov, 1976). Although emphasizing energy as the currency that is maximized has met with some success, less attention has been paid to proximate causes and alternative explanations of observed foraging behaviors (Bell, 1991). Many animals do not forage in a manner that maximizes energy gain (Heinrich, 1983) and this behavior has been traditionally explained by constraints on the animal. Presampling information such as prior patch experience, prey attack (without consumption), or sensory cues are plausible alternatives to energy as a maximizing currency (Valone, 1991).

We examine how the presence of simple sensory cues, without any prey consumption, may be sufficient to modify foraging behavior and patch residence time in a manner similar to what may be predicted by using energy gain as a currency. Perceptual information itself may serve as a predictor of patch residence time if proximal behaviors such as turn rates or locomotory rates are associated with prey perception rather than consumption. Two prefeeding sources of information are tested for residence time decision rules in wolf spiders: (1) prey movement and (2) predator attack behavior.

This study investigates the relationship between visual perception of prey movement and patch residence time decision rules in wolf spiders in order to determine the mechanism of patch assessment. Experiments on wolf spider visual systems strongly suggest that movement, rather than shape of prey, elicits the highest responses (Rovner, 1991, 1993). Here, two "rules of thumb" based on prey movement were tested: (1) a threshold time rule (spiders leave a foraging patch a fixed amount of time after the last prey item was detected) and (2) a fixed probability decision rule (leave a patch based on a constant probability of leaving). In several previous studies of patch-type models of foraging theory with wolf spiders, we have shown considerable within-individual variation in residence time (Persons and Uetz, 1996a, b). High variation in an individual wolf spider's residence times persists even without feeding and in the presence of the same number of cricket prey (Persons and Uetz, 1996a). It is unclear whether this variation is due to a stochastic decision rule or if it is due to variable random movements of prey. Since live crickets move in an unpredictable way, it has previously been difficult to determine the proximate mechanism which the spiders use to evaluate patch quality and the decision rules used based on that patch assessment. However, research using a video imaging technique shows that *S. ocreata* as well as other spiders respond to video images as if real (McClintock and Uetz, 1996; Rovner, 1993; Clark and Uetz, 1990, 1992, 1994). Using a digitally recorded image of a cricket played back on a microscreen television, spider decision rules can be discriminated by experimentally manipulating the length of time a cricket moves in a patch and monitoring the subsequent behavior of the spider.

Hypotheses

Wolf spiders (Lycosidae) are non-web-building, sit-and-wait predators with frequent changes in foraging sites (Ford, 1978). *Schizocosa ocreata*, the spider used in this study, is a medium-size wolf spider commonly found in deciduous forest leaf litter in the eastern United States. These spiders are believed to be food limited (Wise, 1993); consequently, the decision-making process used to determine if a spider stays or leaves a foraging patch may have significant effects on individual fitness. Although foraging theory predicts that spiders, like other animals, should forage in a manner that will maximize energy gain, few studies have found that spiders forage optimally (Morse, 1993; Kareiva *et al.*, 1989; Uetz, 1992). This may be due to stochastic processes in the environment, incomplete knowledge of patch quality, or limited cognitive abilities on the part of the forager. Nishimura (1994) predicts that for a sit-and-wait predator with no memory of previous patch visits, and random movement between patches, the experience of finding prey without attacking it does not contribute to increased foraging efficiency. Consequently, a forager should treat all patches the same. *Schizocosa ocreata* wolf spiders fulfill these requirements but do not treat all patches the same when the amount or type of sensory information varies (Persons and Uetz, 1996a). This fact suggests that visual information from prey may be a suitable currency to use in determining patch residence.

Three hypotheses were tested to determine the influence of cricket movement as an underlying mechanism determining patch residence time.

H_0: Spiders leave patches independent of the presence or movement of cricket prey.

H_1: Spiders increase patch residence time in the presence of a cricket, but independent of prey movement.

H_2: Spiders increase patch residence time with increasing duration of cricket movement.

If the decision to stay or leave a patch follows a Poisson distribution whereby the probability of leaving or staying in a patch is set at the point of cessation of prey movement, or if the probability of leaving a patch is lowered or increased based on prey movement, significant differences in residence time should result even if prey capture is absent.

Three additional hypotheses were tested to determine spider decision rules using predictions of specific graphic models (Fig. 1). Most theoretical treatments of decision rules have used prey encounter (Stephens and Krebs, 1986). Here, cricket movement is used as the decision variable.

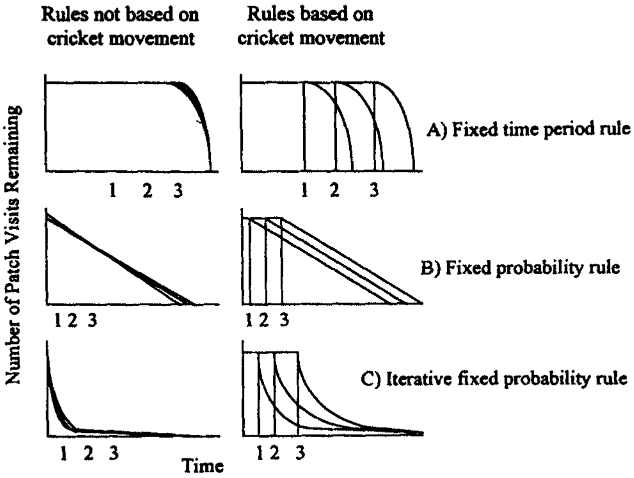

Fig. 1. Hypothetical curves representing six decision rules. The distribution of remaining patch visits is plotted on the ordinate against residence time (abscissa). The shape of the curve indicates which of the decision rules was likely to be used: (A) a step function = (fixed time period rule), H_a in the text; (B) linear decay = (fixed probability rule), H_b; and (C) logarithmic decay = fixed probability (iterative decision-making rule), H_c. The three curves in each graph represent different prey movement durations. The points in time indicated as 1–3 represent cessation of prey movement. The three graphs on the left represent rules that are not based on cricket movement, since there are no differences in the curves at points 1, 2, and 3, whereas the three graphs on the right show increasing patch residence time with duration of prey movement. The 25 patch visits from each of 12 spiders (12 curves) were plotted on the ordinate against residence time and compared with these graphic models. The shape of the curves suggested the decision rule used. See text for further explanation.

H_a: Spiders leave a patch at some preset fixed time period (leave after *n* seconds in patch).

H_b: Spiders leave based on a fixed probability (spider has a constant probability of leaving, analogous to rolling dice and moving when a given number comes up).

H_c: The spider leaves using an iterated decision-making process based on fixed probability [spider repeats the decision-making process (as in H_b) at set time intervals for as long as it remains in the patch].

If energy intake or prey capture is the fitness currency used, then all movement treatments should result in identical distributions of residence time (Fig. 1, graphs on the left). If prey movement is important, deviations in residence time distributions should result and correspond to increases in prey movement (Fig. 1, graphs on the right).

METHODS

Spider Maintenance

Twelve subadult female *S. ocreata* wolf spiders were caught in April 1995 in deciduous forest litter at the Cincinnati Nature Center, Clermont Co., Ohio. Each spider was housed in its own, opaque container, provided water ad libitum, and fed three 1-week old cricket nymphs (*Acheta domestica*) 4 days prior to testing. All spiders were kept under identical conditions at room temperature (22–25°C) in an environment with stable humidity (60–70% RH) on a 12:12 L:D light cycle. The wolf spiders were allowed to mature and assigned to each of the four cricket movement treatments in random order. Each spider was subjected to all four treatments and allowed 25 sequential visits. Spiders were not used until 3 weeks after the final molt and were tested between 0800 and 2000, which corresponds to the natural, diurnal foraging period of this species.

Apparatus and Experimental Protocol

The effects of cricket movement on spider attack behavior and patch residence time were studied experimentally using playback of a computer digitized image of a cricket. This allowed precise control of cricket movement and allowed the determination of the mechanism by which spiders decided to leave a particular foraging patch with respect to prey presence.

Video Playback

The video stimulus represented a computer animation of a cricket but was precisely matched to the movement patterns of an actual cricket. This was accomplished by videotaping a live cricket using a JVC Model GX-N8U video camera and a Panasonic VHS videotape recorder and digitizing the image frame-by-frame using a Frame Grabber-Real Time Video Image Digitizer and a Commodore-Amiga 2000 computer. Then the paint and animation software Deluxe Paint III; Electronic Arts was used to modify the image in a continuously looped animation sequence. A black cricket on a light gray background was used and broadcast on the microscreen television via the computer directly. The playback from the animation was 16 frames/second. The cricket was life-size, representing approximately 85% the size of the spider, and moved from one end of the screen to the other continuously. The cricket movement was controlled manually via the computer and timed for the appropriate duration after the spider entered the chamber with the video cricket image.

The Apparatus

The apparatus consisted of a two-chambered artificial foraging patch (Fig. 2), with one chamber containing a microscreen television (Sony Watchman, Model FDL-310) for display of video images of prey, and the other (antechamber) with no stimuli. The spider was introduced into the antechamber under a clear plastic vial and, after a 2-min acclimation period, allowed freely to enter the second chamber with the moving cricket stimulus on a television screen. A visual barrier across the entrance to the stimulus chamber prevented the spider from observing the televised cricket without entering the stimulus chamber. The duration of time the cricket spent moving after the spider entered the stimulus chamber was standardized at set intervals: blank screen, nonmoving cricket stimulus (control), and 1 min and 10 min of moving cricket stimulus, respectively). The blank screen treatment was used to control for effects of lighting, screen flicker, and heat from the television that may alter the residence time of spiders in the absence of a moving stimulus. The same gray background was used for the blank screen as for the stimulus treatments. For the 1- and 10-min movement treatments, the speed of the cricket was the same. The duration of time the spider remained in the chamber with the cricket stimulus (patch residence time) was measured. Twelve spiders were tested under each stimulus treatment, with 25 sequential patch visits recorded for each spider. The chambers were swabbed with alcohol after 25 visits and allowed to dry before presenting another spider the sitmulus. This was done to remove silk and minimize the effects of any silk draglines produced while in the apparatus. All 25 visits for each of the 12 spiders were then arranged from shortest to longest duration (number of visits remaining) and were plotted against residence time. The shape of the resultant curve was then compared to those predicted from specific decision rules: a step function = (fixed time period rule), H_a; linear decay = (fixed

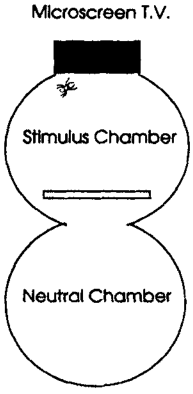

Fig. 2. Artificial foraging patch used to test spider residence time in response to a moving cricket stimulus. The spider is introduced into the antechamber, where it is allowed to acclimate for 2 min. It is then allowed to move freely between the antechamber and the stimulus chamber until it has visited the stimulus chamber 25 times. Patch residence duration is measured from the time the spider passes around the visual barrier in the stimulus chamber until it passes around it again, moving to the antechamber. The cricket image is shown for some interval (blank screen, nonmoving cricket, 1-min moving, 3-min moving, or 12-min moving) and then the stimulus is removed until the next time the spider enters the chamber.

probability rule), H_b; and logarithmic decay = fixed probability (iterative decision-making rule) H_c. (Fig. 1). As an example of a fixed time period rule (step function), a spider may remain in a patch 10 min after entering the patch or, alternatively, remain in a patch 10 min after the last prey item was perceived moving.

Prey attack behavior (i.e., lunges at the screen) was recorded for each spider visit into the stimulus chamber. Behavior was scored as a lunge if the following two behaviors were observed: (1) orientation toward the stimulus and (2) jumping at the screen in the location of the prey stimulus and touching the screen. This behavior was usually followed by the spider tracking the prey item or making a grasping motion with the first and second pairs of legs. Although these behaviors were frequently observed, only the first two criteria were necessary to be scored as a lunge. If the spider lunged multiple times within a single visit, only the first lunge was recorded.

Statistical analysis

The duration of patch visits was subjected to a two-way mixed-model ANOVA to analyze variation in patch residence time. Residence time was natural log (ln) transformed to conform to ANOVA assumptions of normality. The dependent variable, residence time, was tested using individual (random effect) and prey movement treatment (fixed effect) as factors. The F ratio for prey movement treatment was constructed with the interaction term mean squares in the denominator (Zar, 1984) for the appropriate F-ratio for a mixed model. ANOVA analysis was performed with mainframe SAS Version 6.07. Repeated visits of individual spiders were used as replicates for the individual factors. Previous studies have demonstrated that repeated visits by individual spiders are independent (Persons and Uetz, 1996a). Each individual spider was also subjected to a one-way ANOVA with prey movement treatment as a factor and subjected to Tukey post hoc analysis of the means tests. This was done to examine more closely individual spider responses to the different stimulus treatments.

A one-way ANOVA was performed to determine variation in lunges between stimuli treatments with number of visits in which lunges occurred (of 25) per stimulus as the dependent variable and individual spiders serving as replicates.

RESULTS

Prey Attack Behavior

There was some evidence that the spiders recognized the video image as a prey item since lunging behavior was observed only 6 times of 300 visits in the blank screen treatment. This compares to 53, 144, and 196 lunges for the stationary control, 1-min moving, and 10-min moving stimulus treatments, respectively. The lunges at a blank screen could be attributed to the spider responding to its reflection since an acetate surface was used. However, the acetate provided greatly distorted reflected images that the spider could have perceived as prey. Spiders were found to lunge significantly more often in prey stimulus treatments with longer cricket movement ($F_{3,44} = 43.95$, $P < 0.0000$) (Fig. 3). Lunging behavior was often observed even on the 25th patch visit in the moving cricket treatments, which indicates a failure of the spider to learn that the stimulus was not real over the span of 25 visits. Spiders lunged significantly more often at the stationary cricket stimulus than at the blank screen. This suggests that some spiders can recognize even a nonmoving cricket image as prey. It cannot be ruled out, however, that the spider perceived the stimulus as another spider or some other object since we did not test for stimulus shape effects on spider lunging responses. Irrespective of the stimulus, spiders stayed longer in patches where the spider was observed to lunge at the prey image than in those patch visits where lunge behavior was not observed ($F_{1,1198} = 169.85$, $P < 0.00001$).

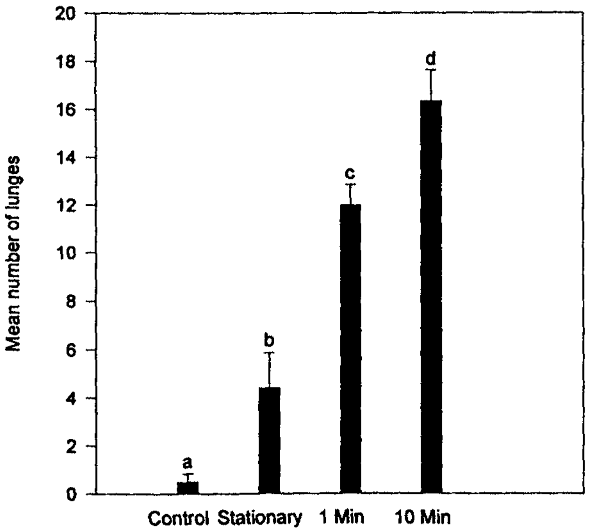

Fig. 3. Mean number of lunges per individual spider by treatment. Letters above bars indicate significant differences based on a Tukey post hoc comparison of means test. Identical letters indicate no significant difference between those treatments.

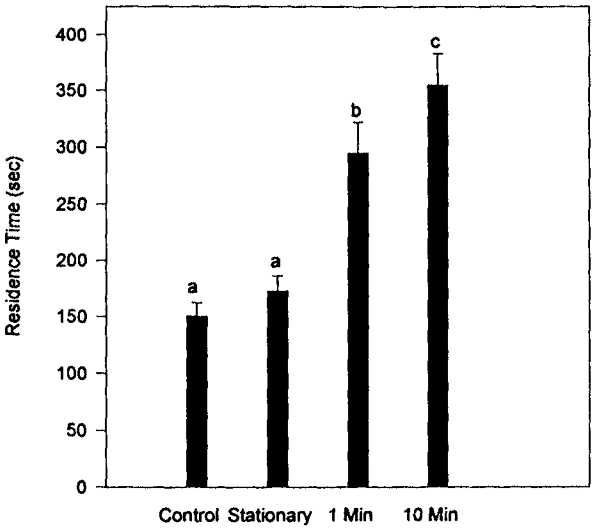

Fig. 4. Mean residence time for each movement treatment. Letters indicate significant differences between treatments based on Tukey post hoc comparison of means. Identical letters indicate no significant difference between groups.

Residence Time

Spiders showed a significantly longer patch residence time with increasing cricket movement (two-way ANOVA; $F_{3,1196} = 36.65$, $P < 0.00001$). Residence time was not proportional to the duration of prey movement, i.e., the mean residence time for the 1-min moving treatment was considerably longer than 1 min, but, the mean for the 10-min moving treatment mean was much shorter than 10 min. This result indicates that (a) prey movement is probably not the only parameter determining residence time (Fig. 4) and (b) a threshold rule is not used by these spiders. When individual variation was collapsed, a Tukey post hoc comparison of the means found that spider residence time did not vary between the blank screen stimulus and the stationary control but did show a significantly higher patch residence with moving stimuli. There were also significant differences in residence time between the 1-min and the 10-min moving stimuli.

Individual Residence Times and Decision Rules

There was significant individual variation in residence time. Ten of 12 spiders showed significant differences in residence time by treatment (Table I).

Table I. Summary (Mean ± SE) of Individual Responses to Prey Movement Treatment[a]

Individual	Blank screen	Stationary	1-min	10-min	*F* value	*P* value
1	53.1 ± 12.7	90.7 ± 20.1	144.6 ± 26.3	181.5 ± 28.1	11.90	0.0000
2	150.2 ± 28.1	134.0 ± 36.9	231.3 ± 48.1	566.8 ± 97.6	8.94	0.0000
3	83.0 ± 36.8	105.4 ± 20.8	302.9 ± 121.2	236.0 ± 76.7	8.37	0.0001
4	184.9 ± 24.5	86.6 ± 18.62	619.0 ± 169.1	516.8 ± 145.7	7.71	0.0001
5	133.6 ± 50.9	168.4 ± 54.6	184.1 ± 38.34	511.0 ± 153.3	7.79	0.0001
6	119.7 ± 26.9	329.3 ± 69.9	310.2 ± 103.1	437.4 ± 100.6	5.50	0.0017
7	154.3 ± 33.7	205.2 ± 47.1	224.0 ± 66.1	480.2 ± 117.1	5.31	0.0021
8	208.9 ± 63.6	155.1 ± 35.7	259.8 ± 43.8	247.5 ± 69.4	4.70	0.0043
9	86.8 ± 12.8	98.7 ± 25.8	349.4 ± 130.8	230.5 ± 53.3	3.94	0.0108
10	140.4 ± 31.2	188.8 ± 31.1	166.5 ± 31.9	397.1 ± 107.3	3.27	0.0244
11	222.6 ± 40.6	313.6 ± 56.7	579.6 ± 121.4	353.6 ± 73.27	2.49	0.0642
12	267.3 ± 76.2	197.5 ± 73.9	166.5 ± 39.1	100.5 ± 18.7	0.69	0.5624

[a] *P* values based on ANOVA test of significant difference between treatments for individual spiders. Boldfaced numbers are those individuals that showed a consistent increase in residence time with treatment.

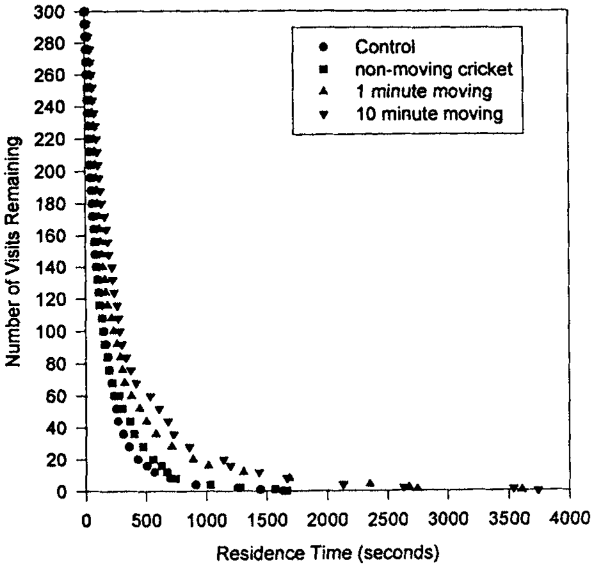

Fig. 5. Combined distribution of residence times for all 12 spiders.

Three of these spiders increased their residence time with increasing cricket movement. Distributions of individual spider residence times showed a negative exponential distribution typical for random events, indicating a fixed probability of moving that was modified by cricket movement but not determined by it. All residence times for all spiders showed a similar distribution (Fig. 5).

DISCUSSION

Lunging Behavior

Results presented here support previous studies that have found that wandering spiders, particularly wolf spiders (Land, 1971, 1972; Seyfarth *et al.*, 1982; Giulio, 1979; Rovner, 1991, 1993), respond principally to prey movement with orientation and attack behaviors. Spiders were observed lunging at the stationary cricket more often than the blank screen (53 times, compared to 6 total for the blank screen). The fact that some spiders attacked prey with no movement suggests that some prey recognition based on shape alone is also possible but not relevant to residence time decision rules. However, based on the experimental design, the possibility that the spiders were perceiving the cricket as a conspecific or other spider cannot be ruled out. Lunging behavior by spiders demonstrates that components of sensory stimuli (e.g., movement and shape), although perceived by the spider, may not necessarily be used equally in a cognitive algorithm for determining residence time. Previous studies with *S. ocreata* have found that vibration information from prey, although used to orient and attack, also has no effect on predicting residence time (Persons and Uetz, 1996a). Laboratory observations of feeding behavior found that not all spiders have the same attack strategies. Most exhibit typical orientation, approach, and attack behavior, but some will wait until the prey moves within lunging range and then attack. These different predatory strategies may be reflected in the results since a lack of an obvious response does not necessarily indicate a lack of prey recognition.

Lunging Behavior and Habituation to the Stimulus

It was apparent that some habituation to the stimulus occurred, since spiders would frequently lunge at the cricket image only within the first 10 s of entering the stimulus chamber. Spiders would then frequently sit in front of the screen for variable periods of time, often reorienting away from the screen. On 31 occasions spiders were observed turning and moving away from the stimulus, almost leaving the chamber and then abruptly turning and attacking the screen again. Spiders were also frequently observed attacking the screen on the next visit when it had stayed only for a few seconds in the antechamber. For the 1- and 10-min moving stimulus, spiders would lunge at the screen during most visits, often lunging on the 24th and 25th visits to the chamber. The prevalence of attacks during the early portion of a patch visit is suggestive of habituation, but the fact that there was no pattern of diminished attacks with subsequent visits indicates that spiders responded to the televised images of prey as if they were real. Removal of the stimulus, even for a very short time, was sufficient to extinguish habituation and resensitize the spider to the stimulus.

Residence Time Rules

Evidence presented here supports a "fixed probability" leaving rule for spiders. Spiders leave patches using an internal rule that does not relate directly to the movement patterns of the prey. All patch residence time distributions for individual spiders, as well as collective distributions of all spiders, were generally of a negatively exponential distribution. These occurred in all prey movement treatments, despite significant differences in residence time based on movement. The variance in residence time did increase with increasing cricket movement treatments, as did the mean residence time. Variation in cricket movement cannot be rejected as a causative factor of residence time variability; however, it is likely that most within-individual differences in patch residence are due to stochasticity inherent in the decision rule. Suter and Walberer (1989) found similar residence times for male–female cohabitations in web-building bowl-and-doily spiders, *Frontinella pyramitela*. They also discovered extreme variability in residence time and found only recent feeding experience and presence of particular females to be of any value in predicting residence time. Such stochastic decision rules are likely to be evolutionarily stable (Suter and Sanchez, 1991). Differences in residence time for web-building spiders have been detected based on feeding history (Hodge, 1987; Vollrath, 1985; Olive, 1982). Hodge (1987) found stochastic residence times for *Micrathena gracilis* with respect to foraging site tenure, but contributed it largely to some undetected environmental or physiological factor. Kareiva *et al.* (1989) found a fixed probability rule used by crab spiders in determining residence time at flower umbels. Although such a rule would result in suboptimal foraging, Kareiva *et al.* suggested that this foraging strategy resulted from an unclear optima. Variation in energy yields were sufficiently high such that the optimal strategy did not deviate greatly from the strategy used by the spider. Other studies have also examined rules-of-thumb of foraging site tenure with orb-weaving spiders (Janetos and Cole, 1981; Janetos 1982a, b), but these too are based primarily on prey capture and energy acquisition. None of these studies tested if it was the perception of prey, the capture process, or ingestion that was contributing the most to observed increases in site tenure. It is likely that prefeeding sensory cues from prey are an important determinant of residence time since there is evidence that foraging sites are chosen based on such cues among web-building and non-web-building spiders (Riechert, 1985; Pasquet *et al.*, 1994; Morse, 1993).

A simple relationship between energy intake rate and residence time may not exist for spiders. If other spider species base residence time on prefeeding factors such as prey capture attempts (lunging) or perceptual cues, as have been demonstrated here, this may account for some discrepancies between predictions of optimal foraging and empirical results (Stephens and Krebs, 1986). Spider residence time was not proportional to cricket movement. One minute of cricket movement had a much larger influence on residence time than 10 min of a moving stimulus. Studies of residence time responses to different densities of crickets found a similar phenomenon, in that spider residence time was not proportional to cricket number (Persons and Uetz, unpublished data). Relative to higher density patches, low prey densities had disproportionately longer patch visits for spiders. Other examples of undermatching of resources have been found where disproportionately more individuals visit patches with fewer resources (Abrahams, 1986; Kennedy and Gray, 1993). In these cases, it is apparent that sensory or cognitive biases are the likely source of this suboptimal behavior rather than external environmental variability. This may explain the fact that 10 of the 12 spiders showed significant differences in residence time due to treatment, but only 3 showed consistent increases in residence time with increased cricket movement (Table I). There is a nonlinear residence time response to cricket movement. This may be caused by a combination of habituation to the stimulus and the fact that initial movement is weighed more heavily than sustained movement. There may also be significant cognitive constraints that prevent spiders from foraging optimally. Previous research with *S. ocreata* has found that these spiders do not appear to have any memory of prior sensory experience in choosing foraging patches (Persons and Uetz, 1996a); nor do they vary their residence time based on prior feeding experience in a patch (Persons and Uetz, 1997). Although most foraging studies emphasize the importance of feeding over perception of prey, some research indicates that perceiving prey results in longer residence times than feeding (Persons and Uetz, 1997).

These results confirm the conventional wisdom that hunting spiders forage longer in patches of higher quality but suggest that prefeeding sources of information may serve as a currency used in decision rules. These data also suggest that simply measuring residence time as a function of prey intake does not fully explain the foraging behavior of these hunting spiders and that other factors may be better predictors of residence time.

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