

The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae)

MATTHEW H. PERSONS & GEORGE W. UETZ

Department of Biological Sciences, University of Cincinnati, U.S.A.

*(Received 21 April 1995; initial acceptance 30 June 1995;
final acceptance 5 October 1995; MS number: A7310R)*

Abstract. Foraging models emphasize reward and/or prey capture rates as primary determinants of residence time. The influence of sensory information has rarely been examined experimentally, but may also be important in animal foraging decisions. This study examined the influence of sensory cues without food reward on residence time in wolf spiders, as well as the interaction of visual and vibratory information in foraging decisions. It also elucidated the effects of prior sensory experience on foraging decisions in wolf spiders. Sixty mature females of the common wolf spider, *Schizocosa ocreata* (Hentz), were tested in a four-chambered artificial foraging patch. Patches varied in the type of sensory information provided by live prey as follows: visual stimuli alone, vibratory stimuli alone, visual and vibratory stimuli together and control (no stimuli). Spiders were allowed to move freely from chamber to chamber for one hour while the duration, number and sequence of patch visits were recorded. Sensory cues, even without food rewards, are sufficient criteria to influence residence time. Spiders tended to remain longer in patches with visual cues alone or visual and vibratory cues together over those with vibratory information alone. Individuals varied significantly in both residence time and sensory biases between individuals, but none showed evidence of using prior sensory experience to choose patches or modify patch residence duration.

© 1996 The Association for the Study of Animal Behaviour

Many animals forage for resources in spatially or temporally unpredictable patches and assess patch quality in numerous ways. They then use this information to decide how long to forage in a given patch before moving to another (residence time), which serves to maximize energy intake rates (Stephens & Krebs 1986) and may contribute to fitness (Morse & Fritz 1982). Most theoretical models and empirical studies of foraging behaviour have considered prey capture rates as a primary influence on residence time (Charnov 1976; Cook & Cockrell 1978; Sih 1980; McNamara 1982; Morse & Fritz 1982; Cassini et al. 1990), with fewer studies on other types of information (Valone 1991).

Information on foraging patch quality can be gained by (1) sampling, i.e. as a function of prey capture rate per unit time (Stephens & Krebs 1986), or (2) estimating patch quality prior to

exploitation. Pre-sampling information may be in the form of sensory cues, memory of patch quality from previous patch sampling, or knowledge of the relative distribution of resources within patch subtypes (Bayesian foraging; Valone 1991). The use of perceptual information or memory in estimating patch quality in temporally heterogeneous environments has been referred to as prescient foraging (Valone & Brown 1989).

The importance of sensory cues in foraging decisions has often been assumed, but only rarely tested (Rice 1983). Many studies on foraging decisions have stressed the importance of sampling and reward rate to feeding decisions in patch-time allocation, but relatively few have addressed the influence of prescient foraging information (Valone & Brown 1989; Cuthill et al. 1990; Morse 1993; Valone & Giraldeau 1993). Most of the latter have concentrated on learning, memory and Bayesian foraging patterns (Green 1980; Johnson 1991; Kamil et al. 1993) rather than the influence of sensory cues (Young & Getty 1987; Conlon & Bell 1991; Bye et al. 1992). Integration of various forms of information about

Correspondence: M. H. Persons, Department of Biological Sciences, ML 0006, University of Cincinnati, Cincinnati, OH 45221, U.S.A. (email: PERSONMH@UCBEH.SAN.UC.EDU).

patch quality contributes to fitness (Krebs et al. 1974; Lima 1983; Kareiva et al. 1989). The influence of perceptual cues in foraging decisions may, in part, explain some of the disparity between predictions of models of foraging decisions and empirical evidence.

This study tested the influence of the type of information in a patch on residence time in wolf spiders (Araneae: Lycosidae), and assessed their ability to detect and respond to varying sensory cues without access to sampling information. This study concurrently examined the effects of immediately prior sensory experience on residence time.

Study Species

We studied *Schizocosa ocreata*, a common wolf spider found in complex leaf litter of Eastern deciduous forests. This spider's behaviour has been studied extensively with respect to communication (Aspey 1975; Tietjen 1979; Stratton & Uetz 1981, 1983), aggression (Aspey 1977a, b) and behavioural genetics (Stratton 1984; Stratton & Uetz 1986). Its foraging behaviour has been studied as well, although largely with respect to population dynamics rather than individual foraging patterns (Cady 1984; Wise & Wagner 1992; Wise 1993).

Rather than build webs to capture prey, wolf spiders hunt using a 'sit and wait' foraging strategy; i.e. they remain relatively motionless in a given area for a while, and will relocate to a different patch if unsuccessful at capturing prey (Ford 1978; Cady 1984). Wolf spiders are amenable to laboratory study of predatory behaviour (i.e. natural behaviour is well known and can be elicited in the laboratory; Rovner 1980), and protocols for lab-rearing are well established (Stratton 1984; Uetz et al. 1992). Additionally, wolf spiders are ecologically important predators in natural and agricultural ecosystems (for reviews see Riechert 1974; Riechert & Lockley 1984; Wise 1993).

The sensory modes of wolf spiders have been documented with regard to foraging behaviour (Barth 1982, 1985). Lycosids rely primarily on vibratory and visual stimuli in detecting and locating prey (Land 1985; Lizotte & Rovner 1988; Rovner, 1991) but it is not known how various types of sensory stimuli are integrated to mediate foraging decisions. This experiment tested the

relative importance and interaction of visual and vibratory stimuli on an individual spider's decision to leave a foraging patch.

METHODS

Immature *S. ocreata* wolf spiders ($N=217$) were caught 8–15 April, 1992 at the Cincinnati Nature Center, Clermont Co., Ohio and in Wyoming, Hamilton Co., Ohio. Each spider was housed in its own, opaque container, provided water ad libitum, and fed three 1-week-old cricket nymphs every four days to standardize hunger levels for testing. All spiders were kept under identical controlled conditions at room temperature (23–25°C) in an environment with stable humidity and a 12:12 h light:dark photoperiod. The wolf spiders were allowed to mature, and 69 were chosen at random from a pool of 217 spiders.

We studied foraging patterns of wolf spiders in an experimental apparatus that controlled for visual and vibratory cues used in prey detection (Fig. 1). The test apparatus contained four chambers made of white foam-core board. Each sensory chamber consisted of a 20-cm diameter arena with transparent acetate walls. The source of the stimuli was 12 live, immature (1-week-old) crickets, introduced behind each acetate wall except in the control chamber. Chambers differed in the sensory stimulus or stimuli presented to the spider: (1) visual information alone, (2) vibratory alone, (3) both visual and vibratory information and (4) control (no crickets present). The vibration-only treatment consisted of an arena with white paper over the acetate to prevent transmission of visual information. The visual-only treatment had the cricket enclosure mounted on a separate foam-core block from that of the spider. The visual and vibratory treatment lacked either of these modifications. Each chamber was isolated from each other by foam blocks between chambers to eliminate any incidental ambient vibratory and visual stimuli. The box was placed on a 70-cm high table, and sponge foam was placed between the box and table to dampen any ambient vibrations, thus retaining differences in vibration intensity between chambers.

We tested the effectiveness of vibration isolation between chambers using a Bruel and Kjaer accelerometer (Type 4366) high sensitivity vibration pickup loaded to a Bruel and Kjaer sound level meter (Type 2203). Vibration level was measured

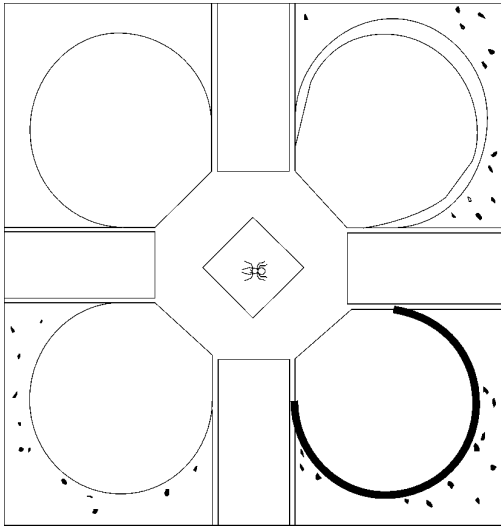


Figure 1. The artificial foraging environment used for spider testing. Spiders were placed in the center of the apparatus prior to each experiment (spider shown in centre) and allowed to move freely between four patches after a 15-min acclimation period. Using 12 immature crickets as stimuli, each patch differed in the sensory treatment presented to the spider. Shown clockwise from upper left, the sensory treatments were (1) control: no crickets behind an acetate screen; (2) visual stimuli only: the crickets and spider were mounted on separate substrata, and the crickets were visible behind an acetate screen; (3) vibratory stimuli only: an opaque barrier was between the crickets and spider; (4) visual and vibratory stimuli together.

in decibels above background noise. A one-way ANOVA showed significant differences in vibration level between the four sensory treatments ($F_{3,119} = 106.38$; $P < 0.0000$). A Tukey post-hoc comparison of means test showed that the visual-only chamber had sound levels indistinguishable from background noise; this was also true for the control chamber. The vibratory-and-visual, and the vibratory-alone chambers were both significantly higher than background noise, and the vibratory-only chamber had significantly higher vibration levels than the visual and vibratory stimuli combined treatment. The statistical difference between vibratory only and visual and vibratory combined may have been attributable to differences in cricket activity in the vibratory-only chamber.

The spider was allowed free access to all four arenas during a trial. We laid down clean white

filter paper in each chamber for each trial and swept the apparatus between trials with a clean, dry cotton swab to remove silk draglines that might contain pheromones and affect subsequent foraging behaviour. The visual range of *S. ocreata* is approximately 30–40 cm, so spiders must leave one foraging chamber to visually perceive crickets in another (G. Uetz, J. Renneker, T. Valerius, unpublished data).

An experimental trial consisted of a single spider introduced into the centre of the apparatus, where it was allowed to move freely for 1 h after a 15-min acclimation period. During the acclimation period, the spider was confined to a clear plastic vial. We videotaped each trial from above and determined duration and number of arena visits by recording and analysing from each videotape. To eliminate the possibility that spiders may respond to differences in the chambers themselves rather than the crickets behind each chamber, we tested 40 adult female *S. ocreata* in an empty apparatus (without crickets). A one-way ANOVA showed no significant differences in residence time between empty chambers ($P = 0.27$).

RESULTS

We analysed data from 60 spiders (nine spiders were omitted from analysis because of their failure to visit all four chambers). We recorded the sequence of chamber visits for each spider and subjected it to a runs test to determine whether chamber choices were random or based on prior chamber visits. All 60 spiders showed a random movement pattern between chambers based on runs tests ($P < 0.05$). To test whether individual spiders increased or decreased their residence time per patch visit with the number of visits to a chamber, we performed simple linear regressions comparing patch visit duration with number of visits. We tested all spiders that visited a single chamber ten or more times within a trial ($N = 27$), and adjusted α values using a Bonferroni correction for multiple comparisons (Table I). None of the spiders analysed showed a significant relationship between sequential chamber visits and residence time. We subjected each spider that made 25 or more total patch visits in the 1-h trial period to a chi-squared test to test whether the number of visits to any chamber significantly deviated from the expected of 25% of total visits to each

Table I. *r*, *F*, *P*-values* for simple linear regressions of 27 individual spiders' sequential visits to a foraging patch and residence time

| Individual | <i>r</i> | <i>F</i> | <i>P</i> -values |
|------------|----------|----------|------------------|
| 1 | -0.0746 | 0.24 | 0.6374 |
| 2 | -0.0184 | 0.78 | 0.3951 |
| 3 | -0.0592 | 0.44 | 0.5233 |
| 4 | 0.2717 | 6.60 | 0.0223 |
| 5 | 0.0918 | 2.11 | 0.1769 |
| 6 | 0.5975 | 15.84 | 0.0032 |
| 7 | -0.1200 | 0.04 | 0.8554 |
| 8 | -0.0795 | 0.34 | 0.5774 |
| 9 | -0.0371 | 0.54 | 0.4783 |
| 10 | -0.1111 | 0.00 | 0.9999 |
| 11 | -0.0395 | 0.05 | 0.8262 |
| 12 | 0.0744 | 1.80 | 0.2121 |
| 13 | 0.5742 | 15.83 | 0.0026 |
| 14 | 0.0609 | 1.71 | 0.2198 |
| 15 | -0.0803 | 0.11 | 0.7483 |
| 16 | -0.0836 | 0.23 | 0.6443 |
| 17 | 0.1995 | 3.49 | 0.0945 |
| 18 | -0.0079 | 0.91 | 0.3618 |
| 19 | 0.4280 | 9.98 | 0.0091 |
| 20 | -0.0258 | 0.60 | 0.4513 |
| 21 | 0.1271 | 2.89 | 0.1147 |
| 22 | 0.2468 | 5.59 | 0.0343 |
| 23 | -0.0389 | 0.21 | 0.6490 |
| 24 | 0.1425 | 3.83 | 0.0682 |
| 25 | -0.0382 | 0.56 | 0.4707 |
| 26 | -0.0278 | 0.57 | 0.4630 |
| 27 | 0.2329 | 6.46 | 0.0210 |

*Bonferroni adjusted α value=0.00185.

chamber. We subjected 28 individuals to chi-squared tests. Even without a Bonferroni α level correction, only three spiders showed significant deviations from expected. This result indicates that spider silk or prior chamber experience were unlikely to have influenced patch visit duration.

We used a chi-squared test using all 60 spiders for the first, second and third chamber visit (of each spider) to determine whether any of the four chambers was visited initially more than would be expected at random. We compared the frequency of spiders' visits to the random expectation of 25% for each of the four chambers of the apparatus. The first ($\chi^2=8.71$, $df=3$, $P<0.05$), but not the second ($\chi^2=2.13$, $df=3$, $P<0.05$), or third ($\chi^2=1.98$, $df=3$, $P<0.05$) chamber visit showed a significant departure from randomness. This first chamber bias was thought to be due to the spiders' initial orientation when the spider was introduced into the apparatus, because the chamber directly

behind the spider was less likely to be entered. To minimize this bias, the first chamber visit for each trial was omitted from ANOVA analysis and all other statistical analyses. We omitted the final chamber visit for each trial if the spider was within a chamber when the hour trial period had expired. This eliminated any chamber visit bias due to trial time constraints. Taken together, these results also justify the treatment of repeated visits of individual spiders to a chamber as independent events, because immediate prior experience has no effect on patch choice or residence time.

We used a mixed model two-way ANOVA to analyse the variation in duration of patch visits. The primary parameter, patch residence time per visit, was tested using individual (random effects) and sensory chambers (fixed effects) as categorical variables. The two-way ANOVA tested the null hypothesis that patch residence time per visit does not vary with the presence or type of sensory cues. This analysis also tests individual differences in patch residence time between sensory treatments. We adjusted *F*-values for the appropriate two-way mixed-model design (Zar 1984) as reported in other studies (Shaffer & Lauder 1985; Wainwright 1989; Jayne et al. 1990). Per-patch-visit residence time for spiders was not normally distributed, so the data were natural-log-transformed to comply with ANOVA normality assumptions. We used the SAS statistical package (mainframe SAS version 6.07) to transform data and perform the ANOVA. We found significant chamber effects ($F_{3,171}=29.34$, $P<0.001$) as well as significant differences between individual spiders ($F_{57,1294}=10.33$, $P<0.001$) and a significant interaction between chamber and individual effects ($F_{171,1294}=1.51$, $P<0.001$; Table II).

The data indicate that with hunger level, patch size, distance between patches and reward rate held constant, sensory cues were sufficient to mediate residence time between patches. When individual variation was collapsed to mean values and subjected to a one-way ANOVA and Tukey post-hoc comparison of the means test, the vibratory-only and control groups showed no significant difference in residence time, and both were lower than the visual or visual-and-vibratory groups. This result suggests that spiders responded to visual information with longer residence times. Significant differences in patch visit duration were found between visual-only and visual-and-vibratory groups. Residence times

Table II. Effect of sensory stimuli (chamber) and individual on residence time. *F*-values have been adjusted for a mixed model ANOVA

| Source | <i>df</i> | Mean square | <i>F</i> | <i>P</i> |
|----------------------|-----------|-------------|----------|----------|
| Chamber | 3 | 1 392 161 | 9.98 | 0.001 |
| Individual | 58 | 7 050 271 | 5.20 | 0.001 |
| Chamber × Individual | 174 | 8 090 452 | 1.99 | 0.001 |

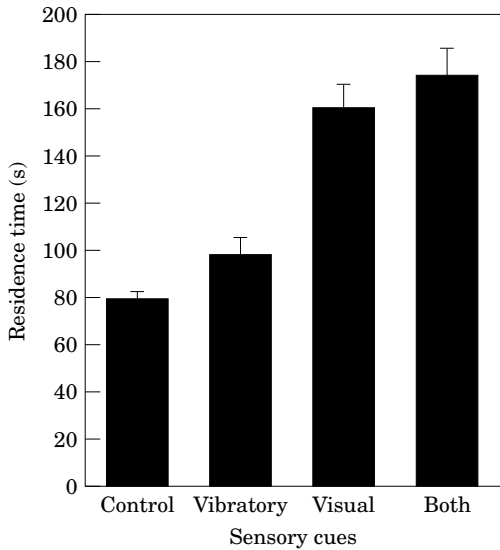


Figure 2. Residence time (s) by sensory treatment (mean +sE) per adult female spider (*N*=60). Treatments included: (1) control (no crickets); (2) vibratory only; (3) visual only; (4) both visual and vibratory stimuli from crickets.

were also significantly higher when visual information was presented alone than when only vibratory information was available. Sources of variation due to individual effects were not subjected to a post-hoc analysis, because significant

differences between individuals may bear little biological relevance for species-level statements about the use of sensory information. Chamber stays varied greatly within and between spiders; however, general biases for specific sensory stimuli were apparent when mean residence times for each sensory stimulus were compared between spiders (Fig 2; Table III).

DISCUSSION

The results demonstrate that *S. ocreata* wolf spiders vary patch residence time on the basis of visual cues, without the use of sampling or prior experience. Because the energy gain from all patches in this artificial environment is zero, simple differences in energy gain cannot explain differences in residence time between patches. Because spiders do not appear to remember previous patches, they are unlikely to base their residence time on previous experience. The relative value of sensory and sampling information may be related to the animal's time budget and differences in the content of the two types of information. Sensory and sampling information are not equivalent in accuracy, because sensory cues lack information on handling time, capture efficiency, palatability and energy value. Perceptually based patch quality assessment may provide a more time-efficient alternative to basing residence

Table III. Number of individuals ranked with respect to mean residence time for each of four sensory treatments (1=shortest residence time, 4=longest residence time; *N*=60)

| Rank | Visual and vibratory | Visual | Vibratory | Control |
|------|----------------------|--------|-----------|---------|
| 1 | 6 | 4 | 26 | 24 |
| 2 | 5 | 6 | 21 | 28 |
| 3 | 16 | 28 | 10 | 6 |
| 4 | 33 | 22 | 3 | 2 |

on sampling information. Spiders must make a trade-off between the time (and energy) spent acquiring information on patch quality and the accuracy of patch quality assessment. Although prey sampling may provide more accurate assessment of patch quality, acquiring that information is often more costly in terms of lost foraging time (Morse 1993). Because *S. ocreata*, like other spiders, may have long time intervals between prey capture (Miyashita 1969; Greenstone 1980), reliance on sampling information (prey capture rates or gut fullness alone) may result in considerable time lost in prey-poor patches. Therefore, it would be advantageous to make decisions regarding duration of patch visits in advance, based on perceived resource value (i.e. perceptual information) rather than actual prey reward rates or prior experience.

The use of sensory information is a simple mechanism for patch foraging decisions, because it requires no memory or learning beyond recognition of prey. Memory of patch quality, although critical to foraging decisions in some vertebrates (Lima 1983; Krebs et al. 1990; Noda et al. 1994) is less likely in some small invertebrates like spiders. Simple mechanistic processes (e.g. responses to detection of movement via visual cues) may control the majority of foraging decisions in animals with limited learning abilities (Giulio 1979). Although the spatial memory and learning abilities of wolf spiders are as yet largely untested, data provided here suggest that spiders do not vary their residence time in a patch based on prior sensory experience in that patch, nor do they appear to choose subsequent patches based on prior sensory patch experience. Perceptual information may be used more in determining residence time, particularly in complex environments where long time periods may exist between prey detection and prey capture. Sensory information may also be of greater value in environments with temporally or spatially unpredictable food resource distribution. In wolf spiders, it is not known whether sampling and perceptual information are combined in foraging decisions. The intensity of ambient vibratory and visual stimuli may provide a reliable indicator of patch quality (prey density) and may be the principal type of pre-harvest information used. Therefore, when hunger level or reward rate are held constant, patch residence time may vary as a function of the intensity and type of sensory stimuli in the environment.

Web-building spiders have longer web residence times in areas of higher prey density (reviewed in Janetos 1986; Riechert & Gillespie 1986; Uetz 1992). Most of these decisions are based on sampling information. Janetos (1982) found differences in residence time between web-building species based on the amount of time and energy expended in building the web; species with greater silk investment had longer residence times. Even so, Riechert (1985) demonstrated that *Agelenopsis aperta*, a funnel-weaving spider, chose web sites based on the perception of vibrations generated from buzzing flies (or artificial vibration sources), but little data suggest that web-building spiders vary their residence time based on perceptual cues. Pasquet et al. (1994) found that the latency to build webs in the presence of prey was shorter than when prey were not present and that the web structure was different between spiders building webs in the presence or absence of prey. Differences in residence time between web-building and hunting spider species may be even more dramatic. Hunting spiders have a significantly smaller investment in a particular foraging patch than web-building spiders and therefore tend to relocate foraging sites more frequently (Ford 1978).

Wolf spiders are likely to use simple decision rules based on sensory input to determine patch residence time in a manner analogous to prey capture-based decisions. A spider deciding when to leave a given foraging patch may use a set period of time after its last prey item was taken (fixed residence time). Hodge (1987) found that in the orb-weaver *Micrathena gracilis*, web site residence times failed to follow a negative exponential distribution. Presumably these spiders change web sites based on a threshold level of hunger or some other fixed interval. These spiders tended to relocate sites 1–2 days after the last feeding, suggesting that prey sampling information is used in assessment. The sensory equivalent of this would be to leave at a fixed time after the last prey item was detected. The number of spiders remaining in a sensory patch plotted over time decays logarithmically (Fig. 3). These data are similar to results found for sheet web-building spiders, *Frontinella pyramitela*, which suggests a stochastic decision-making process described as an iterative dice-rolling strategy (Suter & Walberer 1989). Spiders act as though they roll a die a set period after the last sensory stimulus; if a specific number does not arise, the spider waits in the patch until the

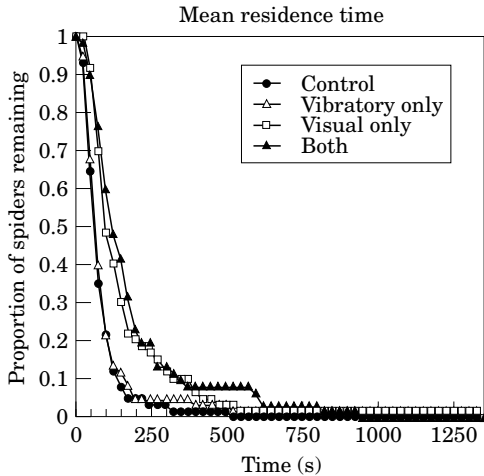


Figure 3. Residence times of all spiders arranged as though spiders entered foraging patches at the same time. Each line represents the four sensory treatments.

next die roll. This process is continued until the predetermined number comes up.

A number of foraging models have attempted to examine patch assessment in sit-and-wait foragers (Nishimura 1991; Beachly et al. 1995). The majority of these studies examine residence time in the context of rate maximization (Caraco & Gillespie 1986; Nishimura 1991) and/or assume linear gain functions for each foraging site (Janetos 1982; Beachly et al. 1995). Other models have incorporated the effects of learning and memory into the decision rules of sit-and-wait foragers (McNamara & Houston 1985, 1987; Nishimura 1994). These models, in their general form, do not account for the special case of decisions made in the absence of prey sampling or prior experience shown by these wolf spiders. Nishimura (1994), however, suggested a simple condition where a forager chooses patches at random and does not base residence time on prior experience. Nishimura noted that to perceive prey without attacking it does not increase foraging efficiency; the forager should thus treat all patches equally. These wolf spiders seem to fit the assumptions of this model, but do not treat all patches equally.

Because *S. ocreata* bear the full complement of sensory organs necessary to perceive both airborne and substratum-borne vibratory information, yet do not use vibratory information to make

foraging decisions regarding patch residence time, vibratory information is likely to be used in other contexts such as courtship communication or orientation to prey. Visual information may serve as a primer for vibratory information, even though vibratory information is not important when presented alone. The reliance on visual cues in the foraging patterns of these spiders, however, may reflect differences in how vibratory and visual information are transmitted through the microhabitat. In the Midwestern United States, *S. ocreata* is commonly found in complex, loose leaf litter associated with upland forests. Vibrations attenuate rapidly in this environment (Uetz 1991; Sheffer et al. 1996), frequently extending no further than a single leaf. Visual perception of prey may extend beyond this distance (30–40 cm: G. Uetz, J. Renneker & T. Valerius, unpublished data) and provide a larger foraging patch to assess, which would reduce the frequency of movement between patches and result in increased foraging efficiency. Such an advantage for visual information may provide selection pressure for a visual foraging bias. Further, male *S. ocreata* have a distinct visual component in their courtship display. Thus, constraints on signal transmission within this environment may be driving the evolution of sensory biases within several life activities of the animal (Endler 1992).

ACKNOWLEDGMENTS

This research was supported in part by funds from the National Science Foundation through grant IBN-9414239 (to G.U.), the Department of Biological Sciences and the Arachnological Research Fund of the University of Cincinnati. Portions of this research were submitted in partial fulfillment of the requirements for M.S. and Ph.D. degrees in Biological Sciences at the University of Cincinnati (for M.H.P.). We are extremely grateful to B. C. Jayne for technical criticism and statistical advice as well as numerous words of encouragement. We thank D. Wise for his helpful comments on an early draft of the manuscript, A. Cady and J. Shann for various assistance. We thank the anonymous referees of the journal for their valuable comments. Additional thanks go to W. McClintock, A. DeLay, A. McCrate, V. Casebolt, D. Kroeger and K. Cook for their advice and assistance with spider husbandry.

REFERENCES

- Aspey, W. P. 1975. Ontogeny of display in immature *Schizocosa crassipes* (Araneae: Lycosidae). *Psyche*, **82**, 174–180.
- Aspey, W. P. 1977a. Wolf spider sociobiology: I. Agonistic display and dominance-subordinance relations in adult male *Schizocosa crassipes*. *Behaviour*, **62**, 103–141.
- Aspey, W. P. 1977b. Wolf spider sociobiology: II. Density parameters influencing agonistic behavior in *Schizocosa crassipes*. *Behaviour*, **62**, 142–163.
- Barth, F. G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In: *Spider Communication: Mechanisms and Ecological Significance* (Ed. by P. N. Witt & J. S. Rovner), pp. 67–120. Princeton, New Jersey: Princeton University Press.
- Barth, F. G. 1985. *Neurobiology of Arachnids*. Berlin: Springer-Verlag.
- Beachly, W. M., Stephens, D. W. & Toyer, K. B. 1995. On the economics of sit-and-wait foraging: site selection and assessment. *Behav. Ecol.*, **6**, 258–268.
- Bye, F. N., Jacobsen, B. V. & Sonerud, G. A. 1992. Auditory prey location in a pause-travel predator: search height, search time, and attack range of Tengmalm's owls (*Aegolius funereus*). *Behav. Ecol.*, **3**, 266–276.
- Cady, A. B. 1984. Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lycosidae). *J. Arachnol.*, **11**, 297–307.
- Caraco, T. & Gillespie, R. G. 1986. Risk sensitivity: foraging mode in an ambush predator. *Ecology*, **67**, 1180–1185.
- Cassini, M. H., Kacelnik, A. & Segura, E. T. 1990. The tale of the screaming hairy armadillo, the guinea pig and the marginal value theorem. *Anim. Behav.*, **39**, 1030–1050.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.*, **9**, 129–136.
- Conlon, D. & Bell, W. J. 1991. The use of visual information by house-flies, *Musca domestica* (Diptera, Muscidae), foraging in resource patches. *J. comp. Physiol. A.*, **168**, 365–371.
- Cook, R. M. & Cockrell, B. J. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. *J. Anim. Ecol.*, **47**, 529–547.
- Cuthill, I. C., Kacelnik, A., Krebs, J. R., Haccou, P. & Iwasa, Y. 1990. Starlings exploiting patches: the effect of recent experience on foraging decisions. *Anim. Behav.*, **40**, 625–640.
- Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.*, **139**, s125–s153.
- Ford, M. J. 1978. Locomotory activity and the predation strategy of the wolf-spider *Pardosa amentata* (Clerck) (Lycosidae). *Anim. Behav.*, **26**, 31–35.
- Giulio, L. 1979. Optomotor responses of the jumping spider *Heliophanus muscorrum* Walck. (Araneae Salticidae) elicited by turning spiral. *Monitore zool. ital.*, **13**, 143–157.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theor. Pop. Biol.*, **18**, 244–256.
- Greenstone, M. H. 1980. Foraging strategy and metabolic rate in spiders. *Ecology*, **61**, 1255–1259.
- Hodge, M. A. 1987. Factors influencing web site residence time of the orb weaving spider, *Micrathena gracilis*. *Psyche*, **94**, 363–371.
- Janetos, A. C. 1982. Foraging tactics of two guilds of web-spinning spiders. *Behav. Ecol. Sociobiol.*, **10**, 19–27.
- Janetos, A. C. 1986. Web-site selection: are we asking the right questions? In: *Spiders: Webs, Behavior and Evolution* (Ed. by W. Shear), pp. 9–22. Stanford, California: Stanford University Press.
- Jayne, B. C., Bennett, A. F. & Lauder, G. V. 1990. Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. exp. Biol.*, **152**, 101–128.
- Johnson, R. A. 1991. Learning, memory, and foraging efficiency in 2 species of desert seed-harvester ants. *Ecology*, **72**, 852–863.
- Kamil, A. C., Balda, R. P., Olson, D. J. & Good, S. 1993. Returns to emptied cache sites by Clark's nutcrackers, *Nucifraga columbiana*: a puzzle revisited. *Anim. Behav.*, **45**, 241–252.
- Kareiva P., Morse, D. H. & Eccleston, J. 1989. Stochastic prey arrivals and crab spider residence times: simulations of spider performance using two simple 'rules of thumb'. *Oecologia (Berl.)*, **78**, 547–549.
- Krebs, J. R., Ryan, J. C. & Charnov, E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.*, **22**, 953–964.
- Krebs, J. R., Healy, S. D. & Shettleworth, S. J. 1990. Spatial memory of Paridae: comparison of a storing and a non-storing species, the coal tit, *Parus ater*, and the great tit, *P. major*. *Anim. Behav.*, **39**, 1127–1137.
- Land, M. F. 1985. The morphology and optics of spider eyes. In: *Neurobiology of Arachnids* (Ed. by F. G. Barth), pp. 53–78. Berlin: Springer-Verlag.
- Lima, S. L. 1983. Downy woodpecker foraging behavior: foraging by expectation and energy intake rate. *Oecologia (Berl.)*, **58**, 232–237.
- Lizotte, R. S. & Rovner, J. S. 1988. Nocturnal capture of fireflies by lycosid spiders: visual versus vibratory stimuli. *Anim. Behav.*, **36**, 1809–1815.
- McNamara, J. N. 1982. Optimal patch use in a stochastic environment. *Theor. Pop. Biol.*, **21**, 269–288.
- McNamara, J. N. & Houston, I. A. 1985. Optimal foraging and learning. *J. theor. Biol.*, **117**, 231–249.
- McNamara, J. N. & Houston, I. A. 1987. Memory and the efficient use of information. *J. theor. Biol.*, **125**, 385–395.
- Miyashita, K. 1969. Effects of locomotory activity, temperature, and hunger on the respiratory rate of *Lycosa T-insignata* Boes. et Str. (Araneae: Lycosidae). *Appl. Entomol. Zool.*, **4**, 105–113.
- Morse, D. H. 1993. Choosing hunting sites with little information: patch-choice responses of crab spiders to distant cues. *Behav. Ecol.*, **4**, 61–65.
- Morse, D. H. & Fritz, R. S. 1982. Experimental and observational studies of patch-choice at different scales by the crab spider *Misumena vatia*. *Ecology*, **63**, 172–182.
- Nishimura, K. 1991. Optimal patch residence time of a sit-and-wait forager. *Behav. Ecol.*, **2**, 283–294.

- Nishimura, K. 1994. Decision making of a sit-and-wait forager in an uncertain environment: learning and memory load. *Am. Nat.*, **143**, 656–676.
- Noda, M., Gushima, K. & Kakuda, S. 1994. Local prey search based on spatial memory and expectation in the planktivorous reef fish, *Chromis chrysurus* (Pomacentridae). *Anim. Behav.*, **47**, 1413–1422.
- Pasquet, A., Ridwan, A. & LeBorgne, R. 1994. Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. *Anim. Behav.*, **47**, 477–480.
- Rice, W. R. 1983. Sensory modality: an example of its effect on optimal foraging behavior. *Ecology*, **64**, 403–406.
- Riechert, S. E. 1974. Thoughts on the ecological significance of spiders. *BioScience*, **24**, 352–356.
- Riechert, S. E. 1985. Decisions in multiple goal contexts: habitat selection of the spider, *Agelenopsis aperta* (Gertsch). *Z. Tierpsychol.*, **70**, 53–69.
- Riechert, S. E. & Gillespie, R. G. 1986. Habitat choice and utilization in web-building spiders. In: *Spiders: Webs, Behavior and Evolution* (Ed. by W. Shear), pp. 23–48. Stanford, California: Stanford University Press.
- Riechert, S. E. & Lockley, T. 1984. Spiders as biocontrol agents. *A. Rev. Entomol.*, **29**, 299–320.
- Rovner, J. S. 1980. Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). *J. Arachnol.*, **8**, 201–215.
- Rovner, J. S. 1991. Evidence for idiothetically controlled turns and extraocular photoreception in lycosid spiders. *J. Arachnol.*, **19**, 169–173.
- Shaffer, H. B. & Lauder, G. V. 1985. Aquatic prey capture in Ambystomatid salamanders: patterns of variation in muscle activity. *J. Morphol.*, **183**, 273–284.
- Sheffer, S. J., Uetz, G. W. & Stratton, G. E. 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.*, **38**, 17–23.
- Sih, A. 1980. Optimal foraging: partial consumption of prey. *Am. Nat.*, **116**, 281–290.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Stratton, G. E. & Uetz, G. W. 1981. Acoustic communication and reproductive isolation in two species of wolf spiders. *Science*, **214**, 575–577.
- Stratton, G. E. & Uetz, G. W. 1983. Communication via substratum-coupled stridulation and reproductive isolation in the wolf spiders (Araneae: Lycosidae). *Anim. Behav.*, **31**, 164–172.
- Stratton, G. E. 1984. Differences in maturation rates of *Schizocosa ocreata*, *Schizocosa roveri*, their F₁ and F₂ hybrids and backcross progeny (Araneae: Lycosidae). *Bull. Br. Arachnol. Soc.*, **6**, 193–199.
- Stratton, G. E. & Uetz, G. W. 1986. The inheritance of courtship behavior and its role as a reproductive isolating mechanism in two species of *Schizocosa* wolf spiders (Araneae; Lycosidae). *Evolution*, **40**, 129–141.
- Suter, R. B. & Walberer, L. 1989. Enigmatic cohabitation in bowl and doily spiders, *Frontinella pyramitela* (Araneae, linyphiidae). *Anim. Behav.*, **37**, 402–409.
- Tietjen, W. J. 1979. Tests for olfactory communication in the species of wolf spiders (Araneae, Lycosidae). *J. Arachnol.*, **6**, 197–208.
- Uetz, G. W. 1991. Habitat structure and spider foraging. In: *Habitat Structure: The Physical Arrangement of Objects in Space* (Ed. by S. S. Bell & E. D. McCoy), pp. 325–348. London: Chapman and Hall.
- Uetz, G. W. 1992. Foraging strategies of spiders. *Trends Ecol. Evol.*, **7**, 155–159.
- Uetz, G. W., Bischoff, J. & Raver, J. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. *J. Arachnol.*, **20**, 207–211.
- Valone, T. J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. *Anim. Behav.*, **41**, 569–577.
- Valone, T. J. & Brown, J. S. 1989. Measuring patch assessment abilities of desert granivores. *Ecology*, **70**, 1800–1810.
- Valone, T. J. & Giraldeau, L. 1993. Patch estimation by group foragers: what information is used? *Anim. Behav.*, **45**, 721–728.
- Wainwright, P. C. 1989. Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. *J. exp. Biol.*, **141**, 359–375.
- Wise, D. H. 1993. *Spiders in Ecological Webs*. Cambridge, Massachusetts: Cambridge University Press.
- Wise, D. H. & Wagner, J. D. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia (Berl.)*, **91**, 7–13.
- Young, S. & C. Getty. 1987. Visually guided feeding behaviour in the filter feeding cladoceran, *Daphnia magna*. *Anim. Behav.*, **35**, 541–548.
- Zar, J. H. 1984. *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, New Jersey: Prentice-Hall.