

Foraging patch residence time decisions in wolf spiders: Is perceiving prey as important as eating prey?¹

Matthew H. PERSONS² & George W. UETZ, Department of Biological Sciences, ML 0006, University of Cincinnati, Cincinnati, Ohio 45221, U.S.A., e-mail: personmh@ucbeh.san.uc.edu

Abstract: Many studies have found that prey capture rates significantly affect how long foraging spiders remain in an area. Perceptual information on prey, even without prey capture, has also been shown to significantly influence spider foraging patch residence time. However, the values of each type of information (e.g., perception, capture, handling and ingestion) in the foraging decision rules have never been compared. This study examines the value of feeding experience *versus* perceiving food in the residence time decisions of wolf spiders. Spiders were exposed to four experimental treatments: 1) a foraging patch with a dead cricket to be consumed; 2) a patch with 12 live crickets behind a transparent screen, but no cricket for consumption; 3) a patch with both live crickets behind a screen and a single dead cricket for consumption; and 4) an empty patch serving as a control. Although feeding resulted in significantly longer patch residence times than the control, the perception of prey was the single most important factor influencing residence time. Results showed no significant difference in residence time between the sensory only treatment and the treatment with both prey consumption and the perception of prey. Analysis of residence times after the spider has fed on a single cricket indicates no significant effect of the experience of feeding in a patch and subsequent visits to that patch. These results suggest that potential energy value weighs more heavily than current or past energy consumed in a patch and that post-ingestive feedback information is less important than pre-ingestive sensory cues.

Keywords: spider, *Schizocosa ocreata*, patch residence time, prey perception.

Résumé: Plusieurs études ont montré que, chez les araignées, les taux de capture des proies ont une influence sur le temps que passent les individus en chasse sur un territoire donné. La perception que les araignées ont de l'abondance des proies dans une parcelle, avant même qu'elles ne procèdent à un certain nombre de captures, a également une influence significative sur le temps de résidence des araignées dans la parcelle. Toutefois, la valeur relative de chaque type d'information (la perception, la capture, la manipulation et l'ingestion des proies) dans les règles de décision concernant la quête de nourriture n'a jamais été comparée. Nous examinons dans cette étude dans quelle mesure l'expérience de chasse (capture et ingestion de proies) et la perception de l'abondance des proies influencent le temps de résidence de l'araignée *Schizocosa ocreata* dans une parcelle donnée. Les araignées furent introduites dans quatre parcelles expérimentales: 1) parcelle avec un criquet mort pouvant être consommé, 2) parcelle avec 12 criquets vivants situés derrière un écran transparent, ces derniers étant inaccessibles aux araignées, 3) parcelle avec des criquets vivants et morts placés derrière un écran et avec un criquet mort accessible et 4) parcelle sans criquet servant de témoin. Bien que les araignées passent significativement beaucoup plus de temps à se nourrir dans les parcelles avec criquets que dans la parcelle témoin, la perception des proies est le seul facteur influençant de façon importante le temps de résidence d'une araignée dans une parcelle donnée. Les résultats ne montrent pas de différence significative au niveau du temps de résidence entre les traitements soumettant les araignées à une expérience uniquement sensorielle et les traitements où les araignées pouvaient non seulement voir des proies, mais aussi les consommer. L'analyse des temps de résidence à la suite de l'ingestion d'un criquet par une araignée dans une parcelle donnée montre que cette ingestion n'a pas d'influence significative sur les visites subséquentes de cette parcelle par d'autres individus. Ces résultats suggèrent que la perception du potentiel énergétique d'une parcelle a plus de poids dans les règles de décision concernant la quête de nourriture que l'information relative aux proies déjà consommées ou en train de l'être.

Mots-clés: araignée, *Schizocosa ocreata*, temps de résidence dans la parcelle, perception de la proie.

Introduction

Because food intake and fitness are related for many animals, energy gain is often used as a proxy for fitness (Pyke, 1984). Rate maximization models of foraging behavior in food patches assume an association between energy intake rates and foraging decisions about patch residence time (Stephens & Krebs, 1986; Pyke, Pulliam & Charnov, 1977). Many studies have implicitly assumed that because animals visit patches and remain in patches in a way that maximizes energy gain, energy provides the information used to determine movement between patches (Charnov,

1976). Usually such studies have focused on intercpatch interval (Cook & Cockrell, 1978), counts of rewards per patch or some other prey capture-related currency to assess patch quality (Formanowicz & Bradley, 1987). However, animals acquire information throughout the predation process which may be used to assess patch quality (Endler, 1991). The type and accuracy of the information used to make foraging decisions about residence time will therefore influence the efficiency of finding food. The mechanism of patch assessment used by a forager will also affect both the quantitative predictions of foraging models as well as the interpretation of such models.

Recently, there has been much interest on the effects of

¹Rec. 1996-03-28; acc. 1996-09-18.

²Author for correspondence.

cognitive (Kacelnik & Todd, 1992; Todd & Kacelnik, 1993; Brunner, Kacelnik & Gibbon, 1992; Real, 1991) and perceptual constraints (Abrahams, 1986; Spencer, Kennedy & Gray, 1995; Gray & Kennedy, 1994) on foraging behavior and the mechanisms of decision-making in many animals. Limitations in memory have been associated with sub-optimal foraging behavior (Bateson & Kacelnik, 1995). Memory constraints may select for animals that use present perceptual information instead of past experience to make foraging decisions. Perceptual information on prey has been shown to significantly influence spider patch residence time (Persons & Uetz, 1996). However, the relative values of perceptual and prey capture information in foraging decision rules have, to our knowledge, never been compared.

We used adult females of the wolf spider *Schizocosa ocreata* (Hentz) (Family: Lycosidae) for this study. These spiders do not build webs, but are common sit-and-wait predators in deciduous forest leaf litter of the eastern United States (Cady, 1984; Wise & Wagner, 1992). Many studies of spiders have implicated foraging site tenure with prey capture (see Richert & Gillespie, 1986 for a review), but most have not tested the effect of sensory cues on residence time (but see Pasquet, Ridwan & LeBorgne, 1994). Previous studies with *S. ocreata* have shown that residence time varies in the presence of different sensory cues and in the absence of prey capture (Persons & Uetz, 1996). There is little empirical evidence for their use of prior experience to determine residence time or choose the next foraging patch (Persons & Uetz, 1996). This study tests the importance of information from prey capture and feeding *versus* information based on prey movement and vibratory cues in influencing patch residence time. We also test if prior feeding experience has any effect on subsequent residence times in a patch.

Methods

We captured twenty-two subadult female spiders on September 28th, 1994 at the Cincinnati Nature Center, Clermont Co., Ohio. Each spider was housed in its own, opaque container. Each round container measured 10 cm in diameter and 6 cm high and was placed in another container with water. A dental wick served as a constant source of water and humidity. Spiders were fed a diet of live one week-old cricket nymphs *ad libitum* twice weekly (*ca* 3 crickets/feeding). We allowed the spiders to mature before conducting experimental trials.

We recorded patch residence time of wolf spiders in an experimental apparatus that allowed detection of prey by visual and vibratory cues. The stimuli for each patch consisted of prey (live cricket nymphs) placed behind clear acetate screens with or without the opportunity for the spider to feed on a single, recently killed cricket (Figure 1). Although wolf spiders are usually considered predators, previous studies have found that they readily accept dead prey and may scavenge for food (Knost & Rovner, 1975). Wolf spiders exhibit stereotypical orientation, approach and lunge responses toward live prey, but these behaviors are generally absent when spiders are presented dead crickets. Laboratory observations indicate that spiders detect and consume dead crickets by chance tactile contact and that

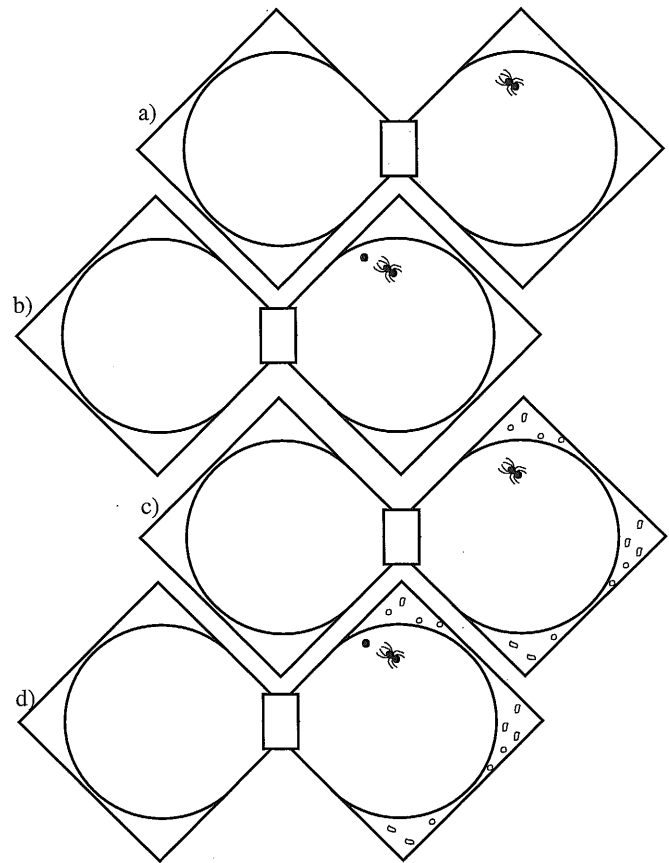


FIGURE 1. Two-chamber experimental apparatus used for spider testing showing four treatments. Spiders are placed in the 'neutral' chamber prior to each experiment (spiders are shown in sensory chamber) and allowed to move freely between the two chambers after a 5-minute acclimation period. Using cricket nymphs as stimuli, each of the four apparatuses differs in the stimuli presented to the spider. The treatments (from top) are: a) control, b) feeding without stimuli, c) sensory stimuli only and d) feeding with sensory stimuli.

olfactory cues or visual cues based on shape are unlikely to be important. Other studies have found that movement cues, rather than shape are the principal component of visual detection of prey in wolf spiders (Rovner, 1993) indicating that a dead cricket would provide little pre-feeding sensory information other than tactile cues. The test apparatus for these experiments consisted of a two-chamber container made of white foam-core board. Each chamber was 20 cm in diameter with transparent acetate walls. One chamber served as a neutral chamber into which the spider was introduced and the other contained crickets serving as visual and vibratory sensory stimuli (sensory chamber). We introduced twelve cricket nymphs behind each acetate wall into the sensory chamber of two of the treatments (sensory stimuli and sensory stimuli with feeding). The other two treatments (control and feeding without sensory stimuli) had identical chambers, but no live crickets present. The feeding treatment was identical to the control except a single dead cricket was provided in the stimulus chamber. Thus, the treatments consisted of the following: 1) sensory perception of prey (visual movement and vibratory cues), without feeding; 2) visual and vibratory cues of prey, with feeding (a single

dead cricket); 3) feeding (single dead cricket) without additional perceptual cues; and 4) a control, no sensory cues from living or dead crickets. Each of the four experimental containers was mounted on its own foam blocks (one foam block under the neutral chamber, the other under the sensory chamber) to prevent the transmission of vibratory information from cricket movement among treatments.

An experimental trial consisted of a single spider introduced into the neutral (no cricket stimuli or food) chamber under a clear 3-cm diameter plastic vial. After a five-minute acclimation period, the vial was removed and the spider was allowed to move freely between the neutral and single sensory chamber for 45 minutes. This allowed sufficient time for replicate visits for every individual under each of the four treatments. Forty-five minutes was also necessary since spiders had difficulty locating dead crickets due to the lack of sensory stimuli and frequently did not find the cricket on the first visit to the sensory chamber. Each trial was videotaped from above and the duration and number of visits to each sensory chamber was determined from videotape analysis. We placed clean white paper on the floor of each chamber of the apparatus prior to every trial. The chambers were also swabbed with clean dry cotton between trials. This removed any silk draglines or residual chemical cues from crickets that might affect subsequent foraging behavior. Each spider was tested once under each of the four treatments. Spiders were fed four live one-week old cricket nymphs once a week for the three weeks prior to testing. All spiders were tested on the seventh day without food. Spiders were randomly subjected to two of the four experimental treatments in a single day; a treatment with feeding was always paired with one without. The treatment without feeding always preceded the one with feeding to control the influence of hunger during the experiment. Spiders were fed an additional three crickets after testing for the day, and were subjected to the remaining two treatments seven days later to return spiders to the pre-testing level of hunger.

Residence time in a patch was natural log (\ln) transformed to conform to ANOVA assumptions of normality. The last visit into a sensory chamber was omitted from analysis if the spider was in the chamber when the trial time had expired. We used one-way and two-way mixed-model ANOVAs to analyze variation in duration of patch visits. The primary parameter, patch residence time, was tested using individual (random effects) and treatment (fixed effects) as categorical variables. The F -ratio for treatment effects was constructed with the interaction term mean squares in the denominator for the appropriate F -ratio for a mixed model (Zar, 1984). All computations were performed with a mainframe SAS (version 6.07; SAS inc.). Repeated visits of individual spiders were used as replicates for the individual factor. Repeated visits by an individual spider have been demonstrated to be independent and used as replicates because sequential visits by individual spiders are independent of previous patch experience (Persons & Uetz, 1996).

Results and discussion

Three separate ANOVA analyses were performed: 1) a test of the effect of treatment on all visits into the stimulus

chamber during the 45-minute trial; (two-way ANOVA with categorical variables = individual and treatment, multiple visits by an individual were used as replicates) 2) a direct comparison of only those visits where feeding occurred *versus* randomly selected visits from sensory and control treatments (one-way ANOVA with treatment as the categorical variable and individual spiders as replicates); and, 3) a comparison of visits immediately following feeding with randomly selected visits from sensory and control treatments. This last analysis was done to examine if spiders had any memory of feeding in a chamber that would affect the next visit into that chamber (one-way ANOVA with treatment as categorical variable and individual spider as replicates). Randomly selected visits for the sensory and control treatments were used as a comparison in the second and third analyses because spiders did not always feed on the dead cricket on the first visit into the test chambers. Randomly selected visits would remove any bias related to the initial chamber visit.

The initial analysis of variance (1 above) was done comparing all patch visits by treatment. Spider residence time varied significantly with feeding and sensory treatment ($F_{3,62} = 12.52, p < 0.0001$). Residence times of individual spiders also varied ($F_{21,763} = 11.78, p < 0.0001$). Based on this two-way mixed-model ANOVA of all patch visits for each individual spider, Tukey post-hoc comparison of means tests showed significant differences between treatments with sensory stimuli and those without (Figure 2a). There were no differences between the sensory treatments with and without feeding, nor between the feeding only treatment and the control (Figure 2a). However, this analysis may not accurately reflect the importance of feeding because only one prey item was consumed in the treatments providing food and the remaining visits to that patch provided a blank chamber or one with sensory information. This may result in a statistical bias for sensory information, because sensory information was presented on every patch visit for the sensory only treatment, whereas the feeding was presented only once. A second analysis was conducted to account for this source of bias.

A one-way ANOVA was performed using information only from visits in which feeding occurred *versus* randomly selected visits for the control and sensory stimuli-only treatments. Results revealed significant differences between treatments (Figure 2b) ($F_{3,86} = 5.35, p = 0.0022; N = 22$). In this case, residence times for the feeding-only treatment were intermediate between sensory-only and control treatments. Again there was no significant difference between the treatment with sensory stimuli and feeding and the treatment with sensory cues only (Figure 2b). The feeding behavior of wolf spiders may partially explain the short residence time during feeding events compared to those in the presence of visual and vibratory cues from live crickets. Wolf spiders are multiple-prey loaders and can capture additional prey while feeding. Even while consuming a cricket, the spiders did not appear to initiate local searching behavior for additional prey but continued to move in a manner similar to that prior to feeding.

If spiders remember a patch as containing food, theory predicts they should stay longer on the second visit to that

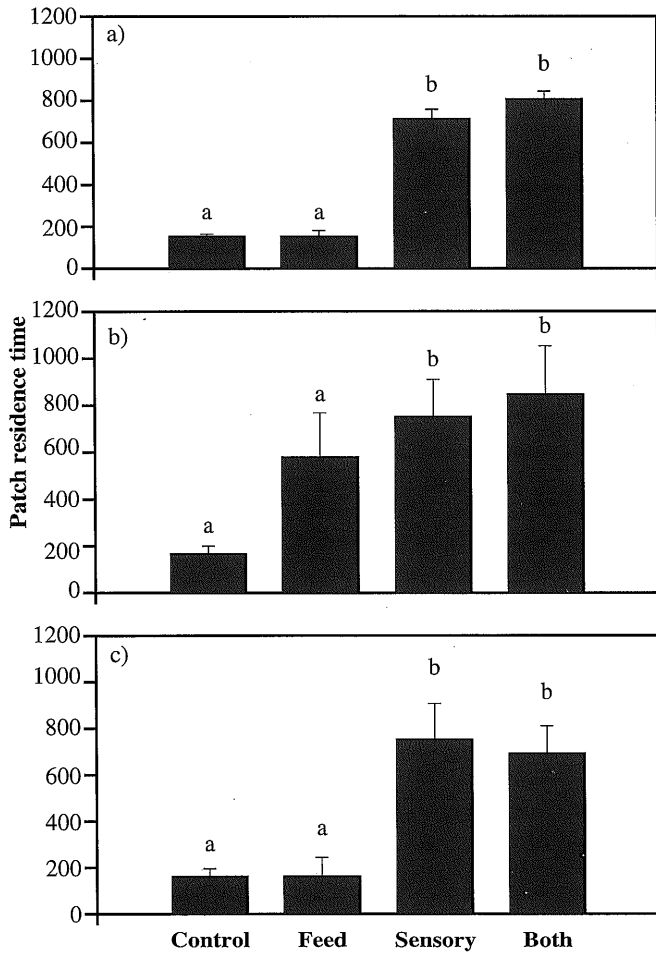


FIGURE 2. a) Mean residence time by treatment (\pm SE; $N = 230$ control; $N = 145$ feed; $N = 148$ sensory; and $N = 241$ both) based on all visits of all spiders to each treatment. Control = no feeding or sensory stimuli; Feed = one dead cricket; Sensory = sensory stimuli only; and Both = sensory stimuli with one dead cricket. b) Mean residence time by treatment (\pm SE; $N = 22$ for each treatment) based on visits where feeding occurred and randomly selected visits to the control and sensory only treatments. c) Mean residence time by treatment (\pm SE; $N = 22$ for each treatment) based on visits immediately following feeding for the feed and both stimuli treatments and randomly selected visits to the control and sensory-only treatments. Lower case letters indicate significant differences between treatments based on Tukey post-hoc comparisons of the means.

patch compared to those patches in which food was not previously provided. To determine if subsequent visits to a patch were longer based on previous feeding experience, we compared the visit immediately following feeding for the two feeding treatments *versus* randomly selected visits for the control and sensory stimuli only treatments. In this case, the treatment with sensory cues alone and sensory cues with feeding were significantly above the control ($F_{3,71} = 9.27, p < 0.0000; N = 20$). This suggests that the experience of a single feeding event does not affect residence times in subsequent patches. These results also indicate that any residual chemical cues from prey were insufficient to modify residence time and there is no additive effect of feeding and sensory experience when combined (Figure 2c).

Simple linear regressions of an individual spider's sequential visits to stimulus chambers and residence time

TABLE I. r, F, P -values* for simple linear regressions of individual spiders' sequential visits to stimulus chambers and residence time. Only spiders that visited a stimulus chamber at least 10 times were used in the analysis. The stimulus represents one of four treatments: control, sensory stimuli only, feeding only and sensory stimuli with feeding. See text for details

Stimulus	r	F	P -value
Control	0.128	0.215	0.651
Control	0.073	0.107	0.747
Control	0.237	0.535	0.480
Control	0.359	4.134	0.516
Control	0.077	0.060	0.811
Control	0.515	3.980	0.071
Control	0.432	3.667	0.074
Control	0.327	0.959	0.356
Sensory only	0.427	2.673	0.128
Sensory only	0.563	4.174	0.070
Sensory only	0.615	4.875	0.058
Sensory only	0.418	2.547	0.136
Sensory only	0.754	10.570	0.012
Sensory only	0.365	2.310	0.150
Sensory only	0.361	1.795	0.210
Feeding	0.025	0.007	0.933
Feeding	0.030	0.016	0.900
Feeding	0.005	0.000	0.985
Feeding	0.397	3.918	0.061
Feeding	0.011	0.003	0.957
Feeding	0.213	0.477	0.510
Feeding	0.064	0.037	0.850
Feeding	0.462	4.621	0.046
Feeding	0.263	0.745	0.408
Feeding	0.476	2.346	0.164
Feeding	0.528	5.411	0.036
Feeding	0.406	2.172	0.169
Sensory & feeding	0.133	0.233	0.637
Sensory & feeding	0.309	1.162	0.304
Sensory & feeding	0.114	0.184	0.675
Sensory & feeding	0.176	0.384	0.547

*Bonferroni corrected α value = 0.0016129.

were performed to determine if spiders increased or decreased their residence time over sequential visits. Only spiders that visited a stimulus chamber at least 10 times were used in the analysis. Spiders should show a decline in residence time with visits if habituation is occurring. Regressions show that none of the slopes were significantly different from zero after a Bonferroni adjustment of the p -value. This suggests that sequential visits to a patch do not increase nor decrease residence time of subsequent visits to the same patch (Table I).

Previous experiments have shown that multiple prior patch visits with sensory experience are not important sources of information for determining residence time but present sensory information is (Persons & Uetz, 1996). Data presented here support these findings and indicate that prior feeding experience is not an important source of information. The apparent lack of use of prior feeding experience as a source of information should be interpreted with caution, since spiders were allowed to feed only once during a feeding treatment. Multiple feedings for a spider during a trial may result in additive effects of feeding experience or serve as a reinforcer, although other studies have found that multiple exposures to sensory stimuli have no effect on increasing or decreasing subsequent residence times to that patch (Persons

& Uetz, 1996). If spiders capture prey in temporally or spatially ephemeral patches, it is unlikely that prior feeding experience would be an important source of information. Nonetheless, perceptual and cognitive constraints may reduce foraging efficiency in these spiders.

These data clearly indicate that the mechanism governing patch residence time in wolf spiders includes both information gained from perceptual cues as well as food intake. However, perceptual information appears to be more important than food intake in predicting patch residence time. It is likely that the current or potential energy value of a patch weighs more heavily in decision-making than previous energy consumed. It also suggests that post-ingestive feedback information (*e.g.*, gut fullness) is less important than pre-ingestive sensory cues.

Acknowledgements

We thank A. DeLay, E. Hebets, K. Delaney and E. Smith for help in collecting and maintaining spiders. Additional thanks go to A. Cady, B. Jayne, J. Shann and D. Wise for various editorial assistance and advice. We thank the anonymous referees of the journal for their valuable comments. This research was supported in part by funds from the National Science Foundation through grant IBN-9414239 (support for G. Uetz), the Department of Biological Sciences and the Arachnological Research Fund of the University of Cincinnati. Additional support was provided by the University of Cincinnati Research Council. Portions of this research were submitted in partial fulfillment of the requirements for the Ph.D. degree in Biological Sciences at the University of Cincinnati.

Literature cited

- Abrahams, M. V., 1986. Patch choice under perceptual constraints: A cause for departures from an ideal free distribution. *Behavioral Ecology & Sociobiology*, 19: 409-415.
- Bateson, M. & A. Kacelnik, 1995. Accuracy of memory for amount in the foraging starling, *Sturnus vulgaris*. *Animal Behaviour*, 50: 431-443.
- Brunner D., A. Kacelnik & J. Gibbon, 1992. Optimal foraging and timing processes in the starling, *Sturnus vulgaris*: Effect of inter-capture interval. *Animal Behaviour*, 44: 597-613.
- Cady, A. B., 1984. Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lycosidae). *Journal of Arachnology*, 11: 297-307.
- Charnov, E. L., 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9: 129-136.
- Cook, R. M. & B. J. Cockrell, 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. *Journal of Animal Ecology*, 47: 529-547.
- Endler, J. A., 1991. Interactions between predators and prey. Pages 169-196 in J. R. Krebs & N. B. Davies (ed.). *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Publications, Oxford.
- Formanowicz, D. R. & P. J. Bradley, 1987. Fluctuations in prey density: Effects on the foraging tactics of scolopendrid centipedes. *Animal Behaviour*, 35: 453-461.
- Gray, R. D. & M. Kennedy, 1994. Perceptual constraints on optimal foraging: A reason for departures from the ideal free distribution. *Animal Behaviour*, 47: 469-471.
- Kacelnik, A. & I. A. Todd, 1992. Psychological mechanisms and the marginal value theorem: Effect of variability in travel time on patch exploitation. *Animal Behaviour*, 43: 313-322.
- Knost, S. J. & J. S. Rovner, 1975. Scavenging by wolf spiders (Araneae: Lycosidae). *American Midland Naturalist*, 93: 239-244.
- Pasquet, A., A. Ridwan & R. LeBorgne, 1994. Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. *Animal Behaviour*, 47: 477-480.
- Persons, M. H. & G. W. Uetz, 1996. The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*, 51: 1285-1293.
- Pyke, H. G., 1984. Optimal foraging theory: A critical review. *Annual Review of Ecology & Systematics*, 15: 523-575.
- Pyke, H. G., H. R. Pulliam & E. L. Charnov, 1977. Optimal foraging theory: A selective review of theory and tests. *Quarterly Review of Biology*, 52: 137-154.
- Real, L., 1991. Animal choice behavior and the evolution of cognitive architecture. *Science*, 253: 980-986.
- Riechert, S. E. & R. G. Gillespie, 1986. Habitat choice and utilization in web-building spiders. Pages 23-48 in W. A. Shear (ed.). *Spiders: Webs, Behavior, and Evolution*. Stanford University Press, Stanford, California.
- Rovner, J. S., 1993. Visually mediated responses in the lycosid spider *Rabidosa rabida*: The roles of different pairs of eyes. *Memoirs of the Queensland Museum*, 33: 635-638.
- Spencer, H. G., M. Kennedy & R. D. Gray, 1995. Patch choice with competitive asymmetries and perceptual limits: The importance of history. *Animal Behaviour*, 50: 497-508.
- Stephens, D. W. & J. R. Krebs, 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Todd, I. A. & A. Kacelnik, 1993. Psychological mechanisms and the marginal value theorem: Dynamics of scalar memory for travel time. *Animal Behaviour*, 46: 765-775.
- Wise, D. H. & J. D. Wagner, 1992. Exploitative competition for prey among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia*, 91: 7-13.
- Zar, J. H., 1984. *Biostatistical Analysis*. 2nd ed., Prentice-Hall, Englewood Cliffs, New Jersey.

