The effects of prey chemical cues on patch residence time in the wolf spider *Trochosa parthenus* (Chamberlin) (Lycosidae) and the lynx spider *Oxyopes salticus* Hentz (Oxyopidae)

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Summary

Studies were conducted to assess the effects of previous exposure to prey chemical cues on patch residence time in the wolf spider *Trochosa parthenus* and the lynx spider *Oxyopes salticus*, using a four-patch choice test apparatus. Adult female spiders were placed in a central start chamber and then allowed to choose any of four adjacent patch compartments. Odours of prey insects were randomly assigned to each patch compartment. These spiders spent significantly more time in patches containing odours associated with prey insects that are found at the sites where the spiders were collected as compared with control patches containing no insect odour cues, or patches containing odours associated with insects that are not a natural prey item for these spiders. Field-collected lynx spiders exhibited a preference for patches associated with the grasshopper *Schistocerca obscura*, an insect frequently found on shrubs and tall grasses. Field-collected wolf spiders exhibited a preference for patches associated with the odour of the ground-dwelling cricket *Gryllus assimilis*. As compared with spiders collected in the field, spiders reared in the laboratory that had no previous experience with *G. assimilis* or *S. obscura*, showed no preference for either prey species. This suggests that these spiders utilise chemical cues associated with prey to make decisions concerning patch residence time based on previous experience (learning).

Introduction

A number of different proximal cues and other factors are known to affect patch choice and patch residence time in spiders. Factors such as type and structure of vegetation (Morse & Fritz, 1982), moisture (Cady, 1984), ambient temperature (Riechert, 1985; Punzo, 1989), hunger level (Gardner, 1964; Anderson, 1974; Punzo, 1989), and prey abundance (Turnbull, 1964; Roach, 1987), have all been shown to play a role in determining patch choice and the length of time a spider remains at a particular location. It has been suggested that patch choice and patch residence time contribute directly to overall fitness by maximising foraging efficiency (Krebs, 1978; Punzo, 1994).

It is well known that spiders utilise chemical cues to locate potential mates (Tietjen & Rovner, 1980; Foelix, 1982; Chapman *et al.*, 1987; Rovner, 1991). However, there is little evidence that spiders use chemical cues to make foraging decisions. Persons & Uetz (1996) reported that immature female wolf spiders (*Schizocosa ocreata* (Hentz)) may use substrate chemical cues associated with potential prey to modify the amount of time spent in a particular foraging patch. In the present study, we examine the effects of substrate chemical cues associated with the odours of natural prey

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species on patch residence time in the wolf spider *Trochosa parthenus* (Chamberlin) and the lynx spider *Oxyopes salticus* Hentz. Lynx spiders prefer to search for prey in low bushes or herbaceous vegetation, whereas wolf spiders most frequently forage on the surface of the ground (Dondale & Redner, 1990).

Methods

All adult spiders used in these experiments were collected from Dixie County, Florida (2 km west of Governor Hill Lake) during the spring and early summer months of 1994. Spiders were either collected as adults or reared in the laboratory from egg sacs collected from females of each species. Spiders were maintained at 20°C, 70% RH, under a 12L:12D photoperiod regime as described by Punzo (1996). Spiders and spiderlings were provided with water ad libitum and fed on a mixed diet consisting of flies (*Drosophila virilis*, *Musca* spp., *Sarcophaga* spp.) and cockroach nymphs (*Periplaneta americana*). Only adult females without egg sacs were used in these experiments. The body lengths ranged from 5.7–6.7 mm (*O. salticus*) and 6.6–7.5 mm (*T. parthenus*).

On numerous occasions we have collected spiders in the field carrying prey items in their chelicerae. Two common prey species captured by *T. parthenus* and *O. salticus* (unpublished data) are nymphs of the grasshopper (GH) *Schistocerca obscura* (Orthoptera: Acrididae), and the field cricket (CR), *Gryllus assimilis* (Orthoptera: Gryllidae). Owing to differences in habitat preference, grasshoppers are captured more frequently by *O. salticus*, whereas crickets are more commonly associated with the diet of *T. parthenus*. In addition to these two orthopterans, larvae of the dark mealworm, *Tenebrio obscurus* (Coleoptera: Tenebrionidae), a species not associated with the habitats in which these spiders are found (non-prey species, NP), were also used in these experiments. These mealworms were obtained from a laboratory stock culture; grasshopper and cricket nymphs (2–4 mm) were collected in the field using sweep nets. During laboratory rearing or maintenance procedures, the spiders were never exposed to *T. obscurus*, *G. assimilis* or *S. obscura*.

Adult spiders reared in the laboratory from egg sacs collected in the field comprised the laboratory-reared groups (LWS and LLS — lab. wolf spiders and lynx spiders, respectively). These naive spiders had no previous experience with prey species associated with their natural habitats. Spiders collected as adults in the field comprised the field-collected groups (FWS and FLS — field collected wolf spiders and lynx spiders, respectively). Ten different spiders were randomly assigned to each of these experimental groups (FWS, FLS, LWS, LLS) before testing.

In order to assess the effects of olfactory cues associated with prey (if any) on patch residence time in *T. parthenus* and *O. salticus*, we used the apparatus shown in Fig. 1. The test apparatus was constructed of opaque plexiglass and consisted of a central chamber (2 × 2 × 2 cm) in which a spider was placed before the

start of a trial. The spider was prevented from moving into any one of four adjacent patch compartments (A, B, C and D) by a sliding dorsal partition. Each patch compartment measured 2 cm at its junction with the central chamber, with 6 cm-long diagonal sides, a width of 10 cm along the back wall, and a height of 2 cm. Thirty seconds after the spider was placed in the central chamber, a trial was initiated by lifting the partition and allowing the spider to move into one of the four compartments. The duration of each trial was 60 min. The floor of three of the patch chambers was covered with a piece of copy paper that contained odours associated with either *G. assimilis* (CR), *S. obscura* (GH), or *T. obscurus* (NP). This was accomplished by placing paper in the holding cages of each insect species and allowing the insects to walk over the paper for a period of 72 h before testing in the apparatus. For the control group (CO), a clean sheet of paper was used that contained no insect odours. Thus, at the start of each trial, a spider could move freely into and among the four patch compartments. The floor (substrate) of each compartment contained one of the odours associated with the two naturally-occurring prey species (GH or CR), the non-prey species (NP), or the control (CO). The copy papers containing the various insect odours and the control were randomly assigned to each compartment at the start of each trial using a table of random numbers. For each spider, we recorded the total amount of time (out of each 60 min trial) spent in each compartment. Data were expressed as the mean amount of time (in min) as well as the percentage of total time spent on each substrate (percent choice). Each spider was tested only once in order to minimise accumulative effects due to experience. This experiment comprised a $2 \times 2 \times 4$ factorial design (2 spider species; field-collected vs. laboratory-reared; 4 treatments (odours): GH, CR, NP, CO), and data were analysed with a three-way factorial ANOVA (Sokal & Rohlf, 1981).

This protocol allowed us to determine whether or not olfactory cues affect patch residence time as well as to
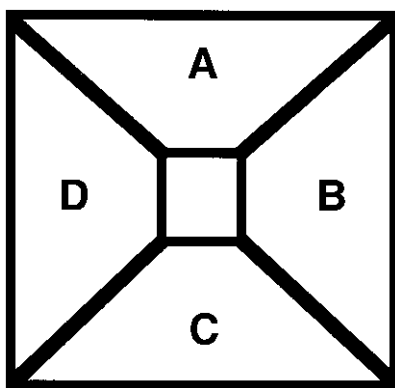

Fig. 1: Diagrammatic representation of the apparatus used to assess the effects of prey odours on patch residence time in *Trochosa parthenus* and *Oxyopes salticus*. Each spider was placed in the central chamber and allowed to choose and move freely among four adjacent patch chambers (A, B, C, and D). The floor of each patch chamber was provided with paper containing the odours of various insects as well as a control chamber containing no odour cues. See text for details.

Spider group	Prey odours			
	CO	GH	CR	NP
FWS	8.3 (1.1)	16.8 (4.2)	24.3 (7.3)	9.6 (2.5)
FLS	11.3 (3.8)	24.1 (6.1)	15.7 (4.4)	8.7 (3.7)
LWS	13.8 (4.1)	16.4 (3.9)	15.7 (2.9)	14.1 (5.5)
LLS	12.7 (4.7)	15.1 (5.2)	14.8 (4.9)	18.2 (4.8)

Table 1: The amount of time (in min) spent on each odour-containing substrate by adult females of *Trochosa parthenus* (Lycosidae) and *Oxyopes salticus* (Oxyopidae). Values represent means ($\pm$ S.D.) for 10 spiders per group, for ten 60-min trials. Spider groups: FWS and FLS (field-collected wolf and lynx spiders, respectively); LWS and LLS (laboratory-reared wolf and lynx spiders). Prey odours: CO (controls); GH (grasshopper); CR (cricket); NP (non-prey species). See text for details.

assess the effects of early experience with prey on future foraging decisions in these spiders. The laboratory-reared spiders (LWS and LLS) had no previous experience with the prey species (GH and CR) normally found in their habitats. Spiders collected as adults in the field (FWS and FLS) however, had ample opportunity to have encountered these prey species during the course of normal hunting activities.

Results

An ANOVA showed a significant effect of treatment (prey odours) ($F_{1,36}=87.506$, $p<0.001$) and rearing condition (field-collected vs. laboratory-reared) $F_{1,36}=26.671$, $p<0.001$) on patch residence time. These two species of hunting spiders spent significantly more time in patches containing odours associated with prey that are found at the sites where the spiders were collected (Table 1). Both species of spiders spent more time on substrates containing the odours of GH and CR than that of a non-prey species (NP) or controls (CO) ($p<0.01$, Duncan Multiple Range Test).

Field-collected lynx spiders, which are known to spend more time off the ground by climbing up into shrubs and tall grasses (Dondale & Redner, 1990), exhibited a preference for patches associated with the odour of *S. obscura* (GH), an insect which is usually found on shrubs and grasses (Table 1, Fig. 2). Field-collected wolf spiders, on the other hand, showed a preference for patches associated with the odour of *G. assimilis* (CR), an insect usually found on the ground where these spiders conduct their hunting activities. The data also indicate that laboratory-reared spiders do not show a preference for any particular prey odour (Table 1, Fig. 2).

Discussion

Lynx spiders of the genus *Oxyopes* Latreille are non-web-spinning spiders characterised by long, spinose legs (Whitcomb *et al.*, 1966; Dondale & Redner, 1990). Such oxyopids are typically found on low bushes, herbaceous vegetation and tall grasses where they hunt for their prey. Wolf spiders of the genus *Trochosa* C. L. Koch do not climb up into vegetation but rather search
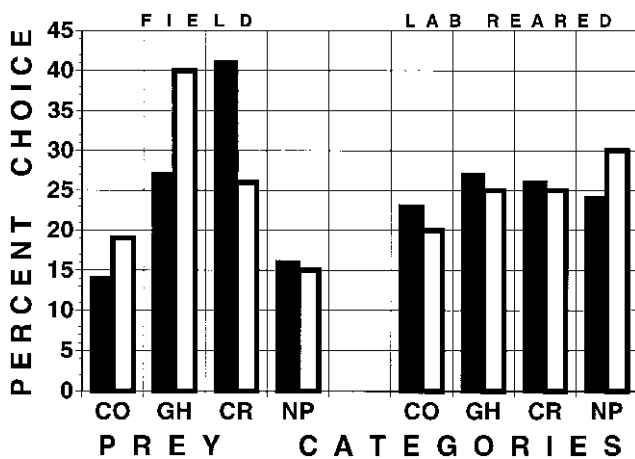
Fig. 2: The frequency (percent choice) at which field-collected and laboratory-reared wolf spiders (shaded bars) (*Trochosa parthenus*) and lynx spiders (clear bars) (*Oxyopes salticus*) were found on various odour-containing substrates. Values represent the percentage of time (out of 60 min) that a spider spent on a particular substrate containing one of four odour treatments: CO (controls; no insect odour); GH (grasshopper odour — *Schistocerca obscura*); CR (cricket odour — *Gryllus assimilis*); NP (non-prey odour — *Tenebrio obscurus*).

for potential prey on the surface of the ground (Dondale & Redner, 1990).

The results from this study indicate that *T. parthenus* and *O. salticus* have the ability to detect chemical cues associated with prey insects. In addition, they use this information to make decisions that determine patch residence time. Adult spiders collected in the field exhibit strong preferences for patches containing odours associated with their natural prey. Laboratory-reared spiders, on the other hand, do not exhibit such preferences. This suggests that these spiders do not possess innate behavioural programs which enable them to respond to odours emanating from specific prey species, but rather learn to associate prey chemical cues with the presence of potential prey as the result of a previous experience of contact with the prey or with a chemical left on the surface of the substrate by the prey. This is either a form of associative learning or an example of olfactory imprinting (Punzo, 1985). For olfactory imprinting, the association between an olfactory stimulus and a particular response must occur during some early critical period of postembryonic development in a relatively short period of time. Although the design of these experiments does not allow us to resolve the issue as to whether olfactory conditioning or imprinting is the mechanism responsible for the observed behaviours, it is clear that previous experience with prey or with a chemical left by potential prey can affect subsequent foraging decisions in spiders.

Although the use of chemical cues in foraging decisions had not hitherto been conclusively established for spiders, it is well known that many insects can modify feeding preferences based on previous olfactory and gustatory experiences. For example, some adult parasitoid insects show a preference for the host species on which they fed as larvae, and deposit their eggs on the same host species (Thorpe, 1939; Vet & Dickie,

1992). Other parasitoids exhibit a more closed behavioural program and show an innate preference for a particular host species regardless of the host they experienced as a developing larva (Vinson, 1976; Punzo, 1995). Numerous orthopteran and lepidopteran insects learn to respond to specific chemical cues associated with certain plants, and then utilise these cues to assess patch quality and make decisions concerning the duration of time spent in a patch before switching to another feeding area (Bernays, 1993). Predatory insects such as mantids and vespid wasps can learn to avoid insect prey that contain chemical defences (Berenbaum & Militczky, 1984; Bernays, 1988). Spiders can also use olfactory and gustatory cues to avoid unpalatable prey (Givens, 1978; Foelix, 1982).

The wolf spider *Schizocosa ocreata* has the ability to perceive chemical cues associated with potential prey (crickets) and spends significantly more time on a substrate containing odours associated with crickets as compared with a control substrate (Persons & Uetz, 1996). However, these experiments utilised a two-substrate choice test apparatus and the species of cricket used as prey was not identified. The authors also did not specify whether or not these crickets represent prey normally encountered by *S. ocreata*. The results of the present study provide further evidence for the ability of some species of hunting spiders to utilise chemical cues in determining patch residence time, and also suggest that some type of learning is involved. Thus, these spiders rely on chemical cues not only to determine the palatability of potential prey, but also to assess patch quality (higher prey density will result in higher concentrations of odoriferous molecules) and to make decisions regarding the length of time spent in a given foraging area.

Acknowledgements

References

ANDERSON, J. F. 1974: Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology* **55**: 576–583.

BERENBAUM, M. R. & MILITCZKY, E. 1984: Mantids and milkweed bugs: efficacy of aposematic coloration against vertebrate predators. *Am. Midl. Nat.* **111**: 64–68.

BERNAYS, E. A. 1988: Host specificity in phytophagous insects: selection pressure from generalist predators. *Entomologia exp. appl.* **49**: 131–140.

BERNAYS, E. A. 1993: Aversion learning and feeding. *In* D. R. Papaj & A. C. Lewis (eds.), *Insect learning: ecological and evolutionary perspectives*: 1–18. Chapman & Hall, London.

CADY, A. B. 1984: Microhabitat selection and locomotor activity of *Schizocosa ocreata* (Walckenaer) (Araneae: Lycosidae). *J. Arachnol.* **11**: 297–307.

CHAPMAN, R. F., BERNAYS, E. A. & STOFFALAND, J. G. 1987: *Perspectives in chemoreception and behavior*. Springer-Verlag, New York.

DONDALE, C. D. & REDNER, J. H. 1990: The insects and arachnids of Canada. Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. Araneae: Lycosidae, Pisauridae, and Oxyopidae. *Research Branch, Agriculture Canada, Publ.* **1856**: 1–383.

FOELIX, R. F. 1982: *Biology of spiders*. 1-306. Harvard Univ. Press, Cambridge, Mass.

GARDNER, T. B. 1964: Hunger and sequential responses in the hunting behavior of salticid spiders. *J. comp. Physiol. Psychol.* **58**: 167–173.

GIVENS, R. 1978: Dimorphic feeding strategies of a salticid spider (*Phidippus audax*). *Ecology* **59**: 309–321.

KREBS, J. R. 1978: Optimal foraging: decision rules for predators. *In* J. R. Krebs & N. B. Davies (eds.), *Behavioral ecology: an evolutionary approach*: 23–63. Blackwell, London.

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.

PERSONS, M. H. & UETZ, G. W. 1996: Wolf spiders vary patch residence time in the presence of chemical cues from prey (Araneae, Lycosidae). *J. Arachnol.* **24**: 76–79.

PUNZO, F. 1985: Recent advances in behavioral plasticity in insects and decapod crustaceans. *Fla Ent.* **68**: 89–104.

PUNZO, F. 1989: Effects of hunger on prey capture and ingestion in *Dugesiella echina* Chamberlin (Orthognatha, Theraphosidae). *Bull. Br. arachnol. Soc.* **8**: 72–79.

PUNZO, F. 1994: An analysis of feeding and optimal foraging behaviour in the solpugid *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae). *Bull. Br. arachnol. Soc.* **9**: 293–298.

PUNZO, F. 1995: The biology of the spider wasp, *Pepsis thisbe* (Hymenoptera: Pompilidae) from Trans Pecos Texas. I. Adult morphometrics, larval development and the ontogeny of larval feeding. *Psyche, Camb.* **101**: 229–241.

PUNZO, F. 1996: Effects of azadirachtin on mortality, growth and immunological function in the wolf spider, *Schizocosa episina* (Araneae: Lycosidae). *Bull. envir. Contam. Toxicol.* (in press).

RIECHERT, S. E. 1985: Decisions in multiple goal contexts: habitat selection of the spider, *Agelenopsis aperta* (Gertsch). *Z. Tierpsychol.* **70**: 53–69.

ROACH, S. H. 1987: Observations on feeding and prey selection by *Phidippus audax* (Hentz) (Araneae: Salticidae). *Envir. Ent.* **17**: 1098–1102.

ROVNER, J. S. 1991: Turning behavior during pheromone-stimulated courtship in wolf spiders. *Anim. Behav.* **42**: 1015–1016.

SOKAL, R. F. & ROHLF, F. J. 1981: *Biometry* (2nd ed.). W. H. Freeman, New York.

THORPE, W. H. 1939: Further studies on pre-imaginal olfactory conditioning in insects. *Proc. R. Soc.* (B) **127**: 424–433.

TIETJEN, W. J. & ROVNER, J. S. 1980: Physico-chemical trail-following behavior in two species of wolf spiders: sensory and etho-ecological concomitants. *Anim. Behav.* **28**: 735–741.

TURNBULL, A. L. 1964: The search for prey by a web-building spider, *Achaearanea tepidariorum* (C. L. Koch) (Araneae: Theridiidae). *Can. Ent.* **96**: 568–579.

VET, L. E. M. & DICKIE, M. 1992: Ecology of infochemical use by natural enemies in a tritrophic context. *A. Rev. Ent.* **37**: 141–172.

VINSON, S. B. 1976: Host selection by insect parasitoids. *A. Rev. Ent.* **21**: 109–133.

WHITCOMB, W. H., HITE, M. & EASON, R. 1966: Life history of the green lynx spider, *Peucetia viridans* (Araneida: Oxyopidae). *J. Kans. ent. Soc.* **39**: 259–267.